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Foraging Behavior

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Foraging is the set of processes by which organisms acquire energy and nutrients, whether the food is directly consumed (feeding), stored for later consumption (hoarding), or given to other individuals (provisioning). Foraging behavior plays an important role in evolutionary biology, not only because it is a major determinant of the survival, growth, and reproductive success of foragers but also because of its impact on predator avoidance, pollination, and dispersal adaptations of potential food organisms. From a contemporary perspective, it is surprising how generally the fundamental role of behavior was neglected in early-20th-century studies of evolution and ecology. Following the development of quantitative techniques and field-oriented approaches by European ethologists, however, interest in foraging, along with other aspects of behavior grew rapidly. Most of this research has sought to describe, explain, and predict foraging behavior quantitatively. The development of an a priori predictive approach using optimality theory, in particular, has revealed a richness and complexity in the patterns of foraging that could not have been imagined only a few decades ago. My goal in this chapter is to provide a brief overview of the main issues in foraging behavior and the logical basis of current approaches. I wish to highlight the successes and potential value of these approaches, while recognizing the gaps and challenges for future research.

Historical Context

Contemporary studies of foraging by evolutionary ecologists are based on the synthesis of two research traditions, both emerging during the 1960s. The ethological approach to behavior is illustrated by the research of K. von Frisch and his associates on honeybee foraging and N. Tinbergen and his group on searching behavior of birds. The ethologists' recognition of behavior as an evolved phenotype, their emphasis on its ecological context, and their careful quantitative and experimental fieldwork set the stage for behavioral ecology (Curio 1976). They classified the behavioral components of foraging, an important contribution to much of the ecological work that followed, and identified a number of widespread characteristics such as localized search following the discovery of a prey ("area-restricted search") and enhanced detection following experience of a particular prey type ("search image").

The theoretical approach to population ecology was foreshadowed by the Russian V. S. Ivlev. His earlier research and conceptual framework for the ecological determinants of foraging rate and food selection became widely available with the publication of a book in English in 1961. At about the same time, C. S. Holling, interested in the role of predators in the regulation of prey populations, produced an influential series of papers based on the idea that individual components of foraging behavior could be combined into a model that would predict foraging rates. His papers included both a theoretical framework and experimental studies showing how the relationship between predation rate and prey density (the functional response) would arise from components of predation and influence the persistence of prey populations. A very different theoretical approach was proposed by population ecologists with a more explicitly evolutionary framework (Schoener 1987). In a series of papers starting in 1966, J. M. Emlen, R. H. MacArthur, E. R. Pianka, T. W. Schoener, E. L. Charnov, and others began to develop models predicting the rate of energy gain arising from alternative behavioral rules in different foraging environments. Initially, they focused on food selection, often from the perspective of diet overlap and community ecology. They argued that the diet yielding the highest rate of gain should be the one that occurs in nature because natural selection is an optimizing process. To many students of behavior, this "optimality" approach seemed to demand an unlikely level of sophistication in animals. Most psychologists of the time regarded animals as very simple learning machines, and ethologists were examining the "release" of supposedly fixed sequences of social behavior using crude dummies. Thus, the success of early experimental tests of optimality models was particularly striking, stimulating a rapid increase in theoretical and empirical studies, as this approach quickly dominated the study of foraging.

The 1970s and 1980s witnessed continued growth of the field as behavioral ecologists were emboldened to ask ever more subtle questions and to develop new theoretical tools. In response to the challenges of some articulate criticism from outside the field and new questions within the field, the logical structure and assumptions of optimality models were examined more closely (Stephens and Krebs 1986). The most important development during this period was the incorporation of frequency dependence into the study of foraging using game theory (Giraldeau and Caraco 2000). Harper (1982) successfully applied a large-scale model of habitat selection called the *ideal free distribution* (Fretwell 1972) to local-scale competitive foraging of ducks in a park pond. Barnard and Sibly (1981) recognized the inherent frequency dependence of some individuals' exploitation of the foraging effort of others (kleptoparasitism). These developments stimulated many researchers to recognize that games among foragers were likely to be widespread as well as theoretically and empirically tractable.

At the start of the 21st century, the literature on foraging is growing rapidly, and its concepts are now incorporated into much of ecology and evolution. This is especially true in studies of spatial distribution, predation risk, pollination, and seed dispersal. Foraging theory plays an important though still limited role in fundamental and applied studies of population dynamics and community structure (Fryxell and Lundberg 1997). There are signs of a new appreciation of the importance of understanding the mechanisms underlying foraging behavior. However, the potential for a strong predictive approach to this key ecological interaction is far from realized, and many important questions remain to challenge researchers.

Concepts

Basic Elements of the Foraging Process

Foraging Cycles and Their Components Foraging is a cyclical activity in which a series of behavioral acts leads to the final consumption of each unit of food. To facilitate the development of general theory, the behavior comprising a foraging sequence is divided into functional categories called *components* (table 18.1). For animals that feed on discrete items, whether mobile or not, the "prey cycle" is the basic unit of foraging; this includes search, assessment, pursuit, and handling. When food items are aggregated, multiple prey cycles occur within a patch cycle comprising patch search and/or travel, patch assessment, and patch exploitation. When foragers return to a fixed location to consume or hoard their prey or to provision other individuals and carry multiple prey per trip, prey and patch cycles can be nested within a central place cycle consisting of travel, loading, and unloading components. Multiple prey, patch, and central place cycles are often nested within a meal or foraging bout cycle, which in some species may include travel to and from a foraging site as well as an obligate period of nonforaging while food is digested.

Although useful in the establishment of a general theoretical and empirical framework for foraging, the division of a continuous sequence into

Table 18.1 Components of the foraging process.

1. **The prey cycle**—acquisition of individual food items.
   1.1. **Search**—leads the forager to come into sensory contact with potential prey and terminates when a prey is detected; for cryptic prey, may be divided into phases in which prey are **encountered** (potentially detectable) and **not-encountered** (out of detection distance); may be **active** (involving movement by the forager) or **sit-and-wait** (forager not moving during search).
   1.2. **Assessment**—leads the forager to pursue or abandon detected prey; may also occur during pursuit and handling.
   1.3. **Pursuit**—leads the forager to come into physical contact with detected prey (capture); may include **ambush** (forager not moving during pursuit), **stalking** (approach, often slow, that is difficult for prey to detect), and **overt attack**.
   1.4. **Handling**—leads to consumption of captured prey; may include **food preparation** (e.g., killing, removing shell or spines) and **ingestion** (e.g., grasping, masticating, swallowing).

2. **The patch cycle**—foraging on aggregations of prey.
   2.1. **Search**—leads the forager to detect a patch whose location was previously unknown; when movement is between patches of known location, **interpatch travel** is a more appropriate term.
   2.2. **Assessment**—leads the forager to begin to exploit or to abandon a patch.
   2.3. **Exploitation**—series of prey cycles (sometimes without additional prey search) that leads to consumption of some or all prey in patch.

3. **The central place trip cycle**—foraging that involves movement between a foraging site and a fixed location to which the forager returns with prey.
   3.1. **Outward trip**—movement from the central place to the foraging site.
   3.2. **Loading**—one or more prey or patch cycles leading to accumulation of a prey load.
   3.3. **Return trip**—movement from the foraging site to the central place carrying prey.
   3.4. **Unloading**—deposition of the prey load in the central place (may be replaced by **handling** when prey are consumed rather than stored or provisioned to others at the central place).

4. **The meal/foraging bout cycle**—foraging that occurs in more-or-less discrete periods separated by bouts of other activities.
   4.1. **Travel**—movement to a foraging area from a location at which other activities take place.
   4.2. **Feeding**—sum of activities in prey, patch, and central place cycles.
   4.3. **Processing**—digestion and assimilation of food; although some digestion occurs during feeding and other activities, processing is relevant as a separate category when food consumption is very rapid relative to digestion resulting in a required pause between bouts of feeding; this phase is sometimes called **handling** in ecological (but not behavioral) analyses.
   4.4. **Other activities**—not foraging; may overlap with processing.

separate components is somewhat arbitrary. For example, in some sit-and-wait predators, handling one prey overlaps with search for the next, and wolves may assess the vulnerability of a potential prey by initiating a testing pursuit distinguishable from the all-out effort to capture a prey. Categories may be subdivided, combined, or deleted according to the organism, food type, and question being asked. For example, assessment is often included as part of search, while pursuit can be usefully divided into stalk and attack components.

Measures of Foraging Success Ideally, evolutionary studies of foraging behavior should use measures of foraging success that are correlated as closely as possible with fitness. However, the nutrients and energy obtained by foraging are often allocated simultaneously to survival, growth, and reproduction, making it impossible to examine a single major component of fitness. Furthermore, foraging is so flexible and most studies of it are so brief that it is rarely possible to identify different foraging phenotypes, much less to compare growth or reproductive success among them. (For an exception see Altmann 1998.) Thus, comparisons of foraging behavior are based on estimates of the success in gaining food and the costs of doing so, although the quantitative relationships of these measures to fitness are usually unknown. Any foraging cycle may be terminated before a prey or patch is consumed, as a result of prey escape, abandonment decisions, or nonforaging interruptions. The forager pays costs in time, energy, and sometimes increased risk of mortality as it engages in each component. The benefits in the form of energy and nutrients come only at the end of successful cycles when the food is consumed.

Net rate of energy gain is frequently considered the ideal measure of foraging success. Maximizing this rate provides the most energy for fitness-related activities and permits the animal to minimize its foraging time to allow for other important activities. The estimation of net rate of energy gain requires behavioral measures of foraging time and prey consumption, as well as bioenergetic estimates of the value of the prey and the costs of foraging. Energy costs of foraging are typically obtained from physiological and biomechanical estimates of costs of locomotion under steady-state conditions in the laboratory. When the energy costs of different components of foraging are similar and when costs are very small relative to rates of gain, costs are sometimes ignored and the gross rate of gain is used as a measure of foraging success. On the other hand, net rate of energy gain fails to account for the value of specific nutrients and nonenergy costs such as predation risk and the expenditure of other resources. Thus, appropriate measures of foraging success vary with the species and situation. See Ydenberg et al. (1992) for further discussion of these issues.

Foraging Decisions A key aspect of foraging behavior is its flexibility. Often, an animal has the option of continuing what it is doing, switching to an alternative form (or "mode") of the same component, or switching to another component altogether. For example, when stalking a prey, a lion may at any moment continue the stalk, switch to direct attack, or begin to search for an alternative prey. Furthermore, an animal can switch to alternative aspects of foraging, such as information gathering or aggressive defense of feeding areas, or it can cease foraging altogether. Behavioral ecologists refer to the performance of one of these qualitatively or quantitatively different activities as *decisions,* a term that is meant to reflect the availability of alternatives rather than to define a particular process by which one of the alternatives is selected. *Decision rules* are the relationships between foraging decisions and environmental conditions, such as food density, or organismal states, such as the individual's fat level. They are therefore similar to the concept of *norms of reaction* as applied in studies of phenotypic plasticity (see Pigliucci, this volume), but with the important difference that changes in phenotype (decisions) occur on a smaller time scale. Predicting decision rules is a major goal of evolutionary studies of foraging. Some of the principal foraging decisions are listed in table 18.2.

The degree of flexibility in decision making is potentially highly variable. For example, the decision whether to consume a particular type of potential prey could be fixed for an entire species, could vary among populations exposed to different densities of that prey or alternative prey, or could vary within an individual, according to prey abundance and the individual's current handling skills, physical condition, or nutritional needs and so on. The finer the adjustment of foraging decisions to local conditions, the greater the need for information about those conditions. Such information might come from directly relevant experience (for example, the individual's recent foraging success). Decisions might be based alternatively on simpler rules of thumb that relate to easily measurable environmental characteristics (such as light level or temperature), to the expected abundance of prey, and to the effectiveness or abundance of predators and competitors. The less flexible a decision rule is or the more removed a rule of thumb is from the relevant characteristics, the more one would expect to find discrepancies between observed foraging decisions and the decision offering the highest success. This would be especially true in the case of evolutionarily novel situations. For example, a forager using size as a cue to prey quality might make the wrong choice when presented with a novel food type that is small but nutrient-rich. Conversely, highly flexible decision rules based on an individual's experience of the effects of alternatives should lead to novel forms of foraging behavior and to evolutionary innovation (Lefebvre 2000).

Foraging Constraints and Trade-Offs Some determinants of foraging success are not under the direct control of the organism. In the framework of foraging theory, these are referred to as *constraints.* Constraints are often regarded as being either extrinsic or intrinsic to the organism. The primary extrinsic constraints are the distribution, abundance, and defensive adaptations of potential food items. The animal can select or ignore different food types or forage in different areas but cannot

Table 18.2 Some foraging decisions studied by behavioral ecologists.

1. **Time budget decisions**
    - When to start a foraging bout (e.g., relation to time of day, local conditions, internal state)
    - When to stop a foraging bout
    - When to initiate and terminate controlled interruptions of a foraging bout (e.g., vigilance, grooming)
2. **Spatial distribution decisions**
    - Which specific site to search and the sequence in which to visit multiple sites
    - When to switch to another site
    - How close to other foragers to search (e.g., foraging group size, local density)
3. **Movement decisions**
    - Locomotor mode (e.g., fly versus walk)
    - Speed and gait of movement
    - Duration, timing, and location of pauses during movement (intermittent locomotion)
    - Timing and direction of turns and intervals between them
    - Specific route
4. **Selectivity decisions (choice)**
    - Microhabitat choice (e.g., substrate types, proximity to other foragers)
    - Diet choice
    - Patch choice
    - Behavioral sequence choice: In which order to perform different activities involved in assessment, handling, and patch exploitation
5. **Persistence decisions**
    - Whether to continue assessment, pursuit, handling, patch exploitation, or loading versus returning to search
6. **Food allocation decisions**
    - Whether to consume or hoard a particular item or to provision others
    - Where to hoard
    - Which individual to provision
7. **Defense decisions**
    - Whether to defend
    - What specific area to defend and not defend
    - When to patrol and display
    - Which intruders to respond to and in which order
    - Whether to threaten or attack
    - Attack and display decisions (mode, speed, duration)
    - (*Note:* Intruders will have a parallel set of decisions with regard to defenders.)
8. **Information acquisition decisions**
    - Whether to sample other prey and sites or other foragers
    - When to sample
    - Which sites to sample and in which order
    - How long to sample a particular site

directly control what is actually available. Other extrinsic constraints include the distribution and abundance of other foragers and predators, as well as relevant aspects of the physical structure of the foraging environment (e.g., vegetation density). Intrinsic constraints determine how a particular decision rule, under a particular set of extrinsic constraints, translates into foraging success. Intrinsic constraints include the limited availability of time and energy, bioenergetic limitations (e.g., moving faster often requires a higher rate of energy expenditure per unit distance), sensory capacities (e.g., ability to discriminate colors, to detect immobile prey), and central nervous system capabilities (e.g., ability to remember and integrate recent foraging success, capacity to attend to more than one activity or prey type at the same time). There is also an interaction between extrinsic and intrinsic constraints. Potential food items are a characteristic of the organism, including its ability to recognize, capture, consume, and digest them, and these characteristics can change with experience.

Foraging decisions can affect different aspects of the same foraging component as well as affecting other foraging components and nonforaging components of fitness. For example, a forager switching from sit-and-wait to active search (a movement speed decision) at a given abundance of a particular cryptic prey type (extrinsic constraint) may increase the rate with which prey are encountered but decrease the proportion of those prey that are detected as a result of the forager's sensory physiology (intrinsic constraint). This increase in encounter and decrease in detection rate may either increase or decrease the time cost of search per detected prey. In addition, moving may increase both the rate of energy expenditure as a result of muscle physiology (intrinsic constraint) and the probability of being detected by a predator during search (extrinsic constraints of predator abundance and sensory capabilities). Situations in which decisions that increase one component of fitness decrease other components are called *trade-offs,* and they are ubiquitous (see Roff, this volume). Understanding foraging behavior depends on recognizing the major trade-offs resulting from foraging decisions.

Optimal Foraging

Logical Framework If natural selection has favored the evolution of decision rules that maximize foraging success, or of flexible behavioral systems that can learn which decisions maximize foraging success, the foraging patterns observed in animals should be those that give the greatest foraging success. When we know what alternative decisions are possible and understand the most important trade-offs arising from them under a given set of constraints, we should be able to predict which decision will yield the greatest foraging success under a given set of conditions. In essence, then, the assumption that foraging is a well-designed system allows us to predict its properties using an optimality approach, as in other areas of evolutionary ecology (see Roff, this volume). We use theory to explore the expected properties of foraging systems. Often referred to as an *economic approach,* optimality analyses have been the key to the development of the predictive study of foraging. Differing views concerning how often the basic assumptions underlying the optimality approach are met, or how important deviations from these assumptions are, have led to very different perspectives on the value of this approach. In the resulting controversies, protagonists often ignore its limitations and antagonists ignore its power.

An optimal foraging model is a numerical or graphical hypothesis designed to predict the relationship between foraging decisions and a set of constraints consisting of the environmental conditions and the state of the organism. A model requires the a priori selection of a measure of foraging success to be maximized (the "currency") and a set of mathematical relationships between the decision and the currency for each condition or state. These relationships are a set of constraints that specify the effect of the decision on the costs and benefits of different components of the foraging cycle and the way in which these costs and benefits are combined to determine the currency. Foraging models can predict qualitative trends in decisions with changes in conditions or state or the quantitative value of the decision for specific conditions.

Optimality models are risky enterprises, and there are sound theoretical reasons why they may fail, even if the calculations are correct. As with any adaptive trait, the optimal decision rule may lag behind a fluctuating environment, may not occur at most locations in a spatially variable environment, and may be constrained by the underlying genetics. A model may fail if important contributions to the currency are ignored or if the wrong currency is used. Certain food items, competitors, or mortality risks during foraging may be too recent to have had an effect on the evolution of foraging decisions, and others of historical importance may be absent. Some environmental circumstances may have been too rare or have had too little impact on fitness to lead to the evolution of adaptive responses. Finally, cues relevant to important variables may not be available to the animals' sensory systems.

Pyke (1984), Stephens and Krebs (1986), Mangel and Clark (1988), and Houston and McNamara (1999) and references therein provide detailed discussions of optimal foraging models and their assumptions. The last two references in particular summarize recent advances in the use of dynamic optimization models to integrate the effects of current and future decisions and predict optimal decision trajectories.

Approaches to Testing The primary goal of testing models is not to determine whether or not the model is "correct" (as a simplification of nature, the model is bound to be wrong at some level), but to determine how well it predicts behavior. When a model predicts well, the challenge is to find the range of species and situations in which it continues to predict. When a model predicts poorly, examining the assumptions used in constructing the model may not only improve the model but also generate new discoveries about nature.

Optimal foraging models provide some of the most favorable situations for testing precise, quantitative predictions in the entire field of evolutionary ecology. Foraging is a common activity, often observed and measured with relative ease, and the foraging environment can often be manipulated experimentally. In many areas of evolutionary ecology, only a limited range of decisions is available to be examined, so the consequences of many alternatives are difficult to determine. (If phenotypes are optimal, the strongly suboptimal traits required to demonstrate this should not exist.) In foraging, by contrast, it is often possible to generate foraging situations that permit estimation of the consequences of a full range of decisions. Nevertheless, testing is a more demanding task than is sometimes acknowledged, with its own set of assumptions, and tests can fail (or succeed) for the wrong reasons.

The simplest test of an optimal foraging model is to examine whether the decision rule changes qualitatively with environment or state as predicted by the model. While useful in a preliminary way, such tests are ultimately unsatisfying. It is much more useful to be able to predict the quantitative value of the decision and to be able to measure the discrepancy between prediction and observation. Indeed, this is the only way to determine whether the qualitative prediction is actually valid in a particular case.

All tests make assumptions about the flexibility of the decision rule and the information available to the animal. In some experimental tests, the decision rule predicted by a general model would not be optimal for an animal that actually had perfect knowledge of the test situation and experimental protocols. In other cases, the protocols are appropriate, but the animal may not be aware of the situation. Early tests of foraging models made considerable progress despite ignoring the behavioral mechanisms by which animals gather and use information. However, it is becoming increasingly clear that an integration of the economic approach with these mechanisms will improve both the predictive power of the models and the strength of the tests.

Tests of optimal foraging models typically use observational and experimental methods. Observational tests have a high level of external validity; the data gathered are directly relevant to the ecology of the study population. However, it may be difficult to find a sufficient range of variation in the environmental conditions to test the model, or the variation that occurs may be confounded with other important changes in the environment or the state of the animals. Furthermore, determining the effect of alternative decisions on the currency requires care that individuals with different decisions do not differ in other important ways. Experimental tests can achieve a wider range of environmental conditions or organismal states while controlling for confounding variables, and they facilitate the determination of decision/currency relationships. However, they typically require manipulations involving unnatural food types, food densities, or foraging environments. Poor predictive power of the models is sometimes related to a lack of evolutionary history relevant to the foraging situation under examination.

Comparative tests require evolutionary differentiation of foraging behavior in relation to different environmental conditions. Most tests of optimal foraging models, however, involve short-term responses to variation in environmental conditions, implicitly assuming highly flexible decisions. While comparative study of the evolution of such flexible response systems would be of great interest, I am not aware of any such investigations.

Test Results The most common result of published tests of optimal foraging models is partial support of the predictions. Models often correctly predict qualitative trends but not the quantitative values, or the observations support some but not all predictions. This creates a "half full and half empty glass," in which proponents point to the success (e.g., Stephens and Krebs 1986; Schoener 1987) and critics emphasize the failures (e.g., Gray 1987). In an evaluation of 125 tests, Stephens and Krebs (1986) concluded that predictions were at least partially validated in 71% of tests and clearly not supported in 13% (the rest were ambiguous). Even tests with novel foods and artificial environments have had considerable success. For example, Carlson (1983) obtained a very close fit to the quantitative prediction of a simultaneous choice model when wild red-backed shrikes collecting food for their offspring were offered a choice between mealworm pieces (an unfamiliar food) of different sizes and with different handling times produced by threading the pieces onto wires