

Foraging Behavior

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An animal's survival and reproduction demand that it consume energy and nutrients produced by other organisms. Some animals acquire essential resources in a comparatively simple manner; consider an aquatic filter feeder extracting organic matter from flowing water. Other animals capture resources in a manner requiring a complex series of actions, sometimes involving social relationships; consider a group of lions ambushing, capturing and then competing for a gazelle. The study of foraging behavior spans diverse questions concerning the mechanisms, evolution and ecological consequences of animals' food consumption. Foraging theory, more specifically, assumes that natural selection can shape behaviors that directly govern an animal's energy acquisition. Foraging theory has helped advance understanding of the remarkable diversity observed among different species' feeding behavior. Furthermore, models of individual or social foraging can be linked with models for population dynamics to predict stability and complexity at the level of ecological communities.

I. Numerical and functional responses

A consumer population's birth and death rates, as well as migration rates between populations, may depend on temporal and spatial variation in food availability. Change

in a consumer population's density, driven by change in food abundance, is termed the consumer's numerical response to resource density.

Consumers often affect the population dynamics of the biotic resources they exploit. The rate at which consumers deplete food abundance depends on both consumer density and the amount of the food resource eaten per unit time by each consumer. The latter quantity is termed the consumer's functional response to resource density. Properties of the consumer's foraging behavior can directly impact the functional response. For a discussion of numerical and functional responses, see the entry on Predator-Prey Models.

II. Optimal foraging theory

Optimal foraging theory (OFT) asks how behaviors governing the acquisition and consumption of resources contribute to survival and reproductive success. OFT offers an understanding of prominent behaviors by evaluating their potential adaptive significance. Characterizing foraging as "optimal" follows from the premise that variation in a behavior influencing an individual's survival or reproduction can be subject to optimizing (*i.e.*, stabilizing) selection. Given this premise, foraging theory commonly invokes mathematical optimization as a metaphor for natural selection. OFT has drawn criticism, largely because the models seldom include intrinsic limitations (*e.g.*, genetic constraints) on phenotypes and their evolution. Foraging theorists reply that they seek general principles linking environments to behavior, predictions independent of any particular organism's mechanistic constraints. Furthermore, any OFT model appreciates that constraints on the forager-environment interaction (constraints often defining the

problem) limit the choices or options available to the consumer. OFT has produced quantitative hypotheses about behavior - predictions subject to rejection through experimentation or observation, and the theory has advanced understanding of why certain animals forage as they do.

Behavioral ecologists generally define OFT as the study of solitary, independent foragers, and refer to models of interacting foragers as social foraging theory (SFT). For clarity, this distinction is adopted here; some questions concerning social foragers do not apply to solitaries, and methods ordinarily used to solve the two types of models differ.

A. Model structure

Models in OFT first identify feasible phenotypes. The set may be discrete (*e.g.*, prey types a predator encounters) or continuous (*e.g.*, the length of time an ambush predator remains at one location). Second, the model specifies limitations intrinsic to the organism (*e.g.*, inability to distinguish prey types) or extrinsic (*e.g.*, time available to feed). As indicated above, OFT stresses the latter constraints. Finally, the model's objective function specifies a quantitative relationship between feasible behavioral phenotypes and a "currency of fitness." That is, the model formalizes the hypothesis that lifetime reproductive success (Darwinian fitness) correlates with a measure of foraging performance, the currency. Maximizing the objective function (or minimizing cost) identifies optimal behavior; predictions are deduced from the model's solution. Testing the predictions asks if the behavior of interest has the functional significance proposed in the model. OFT does not suggest that every trait of a forager is an adaptation.

B. Diet breadth

Specialist consumers exploit a narrow range of resources; generalists are less selective. OFT addresses this distinction in a series of models for the prey types (different foods) included in a forager's diet. A basic version, called the contingency model, answers the following question. Given encounter with an item of a recognizable prey type, should the forager consume the item or reject it and search for a more rewarding prey type? The number and identity of the prey types a forager accepts specify its diet breadth.

The contingency model assumes that a forager can search for different prey types simultaneously, since prey are intermingled. But the forager discovers only one item per encounter. When an item is accepted, the forager must stop searching and handle the food to extract energy. Prey types can differ in density (hence encounter rate during search), net energy yield per item, and handling time. The model hypothesizes that a forager's fitness should increase with its average long-term rate of gaining energy. Hence, an optimal diet breadth maximizes the rate of energy gain.

To find the optimal diet, the model evaluates each prey type by the ratio of its net energy yield per item to handling time per item. This ratio is termed the type's profitability. The model's solution requires that the most profitable type be included in the diet. Adding the prey type ranked second implies that the forager will encounter food it accepts more often while searching. But taking the second type will decrease the mean energy yield per item accepted, and/or increase the mean handling time per item. The forager faces a trade-off between faster prey encounter while searching and reduced mean profitability per item eaten. The model's solution yields a simple rule: the forager should expand its diet if its long-term rate of gaining energy when specializing on the most

profitable type is less than the profitability of the second type. If this is true, the expanded diet increases the rate of energy gain. Proceeding from the highest rank in descending order, the profitability of each prey type is compared to the long-term rate of gain for the diet including all types of higher rank, and no others. The first set of prey types where the rate of energy gain exceeds the profitability of the next lower ranked type is the optimal diet. The decision to accept or reject a prey type does not depend on its density, but does depend on the densities of all types of higher profitability. The model predicts that a given prey type is either always accepted or always rejected, and predicts more specialized diets when profitability decreases steeply across ranks, or when densities of the most profitable prey types are increased. Later versions examine diet breadth when prey types are encountered simultaneously, when discriminating prey types imposes a cost, and when profitability of each prey type varies randomly.

Figure 1 about here

C. Herbivory and dietary constraints

The contingency model's assumptions apply to many carnivores, insectivores and granivores, since search and handling ordinarily are exclusive activities. Furthermore, food consumption by these foragers simultaneously yields both energy and other required nutrients. However, understanding the diverse dietary ecologies of herbivores, animals that consume only (or mostly) green plant material, demands modified approaches.

A generalist mammalian herbivore sees palatable food everywhere in its environment; its diet breadth may have no relationship to searching effort. Variation in the availability of different plants may contribute to the complexity of herbivore diets, but foraging theory for generalist herbivores emphasizes that plant species can vary in

digestibility, nutrient profiles, and toxins. Some herbivores include less digestible material in the diet to slow down the rate at which more digestible material passes through the gut. Only digestible material is absorbed and converted to stored energy; too great a rate of passage may reduce the energy extracted from higher quality food. Some herbivores balance their intake of energy and essential nutrients (crude protein or sodium) by consuming combinations of different plants. Other herbivores' mixed diets may expose them to different anti-herbivore compounds, while averting too great a consumption of any single plant toxin.

OFT models generalist herbivore diets by subjecting fitness maximization to constraints assuring that nutritional, physiological or ecological criteria are satisfied simultaneously. Some models identify "strategies" of energy maximization or time minimization. Among feasible diets, one may provide the most energy; another diet may be energetically and nutritionally feasible while minimizing foraging time, and so reducing the herbivore's hazard of predation.

D. Patch residence time

For many animals, foraging consists of repeated cycles of travel between food patches and resource extraction within these patches. One of OFT's most enduring results concerns the length of time a forager should remain in a patch, under the hypothesis that selection favors increases in the long-term rate of energy gain. The solution to the patch-residence problem, called the marginal value theorem, has been applied to a number of seemingly different questions in evolutionary ecology.

The patch-residence model assumes an environment containing one or more patch types. The forager knows the mean travel time between patches, and recognizes each

patch type upon entry. Patch types differ in resource availability; more productive patches yield a greater net energetic gain for fixed residence time. In any type of patch, the forager's energetic gain decelerates as residence time increases. The rate of energy gain is maximal as the forager begins to exploit a patch, and declines continuously with residence time, due to resource depression. That is, depletion of food (or evasive action by the forager's prey) lowers the rate at which the forager gains energy. Given a reduced rate of gain as residence time increases, the marginal value theorem asks when an optimal forager should leave and travel to the next patch.

For an environment with only one patch type, the model predicts that increased travel time between patches increases the optimal residence time. In an environment with many patch types, a forager that maximizes its long-term rate of energy gain will leave each patch at the same rate of increase in its energy gain within the patch, and that rate equals the long-term gain rate. Energy gain and residence time may differ among patch types, but the *derivative* of energy gain within the patch (the "marginal value"), with respect to residence time for that type, is identical across patch types for the optimal forager. This result generated remarkable interest among ecologists, and a number of related models followed. Some relax the assumption of an "omniscient" forager. For example, experience within a patch might help the forager discriminate better from worse patches. Other models compare simpler rules for departure; a forager might leave every patch after a fixed residence time elapses, after capturing a fixed number of prey, or as soon as the time since the forager last found food exceeds a critical "giving up" time.

E. Risk-sensitivity

In winter a forager may have only the daylight hours to consume energy fulfilling its 24-hour metabolic demands. During breeding an individual might have to capture enough prey each day to meet its needs and those of rapidly developing offspring. For these foragers, failure to consume a required amount of energy during a limited period imperils survival or reproduction. If we further assume that energy intake varies randomly among foraging periods, as must often be true, then models for risk-sensitive behavior apply.

Risk-sensitive behavior implies that an individual's preferences respond not only to average benefits, but to the variance in benefits associated with different actions. To demonstrate the idea, consider the "small bird in winter." A forager has T time units available. Total energy intake by time T must exceed the individual's physiological requirement R , or its chance of surviving the non-foraging period is reduced significantly. For simplicity, let the forager choose between two habitats to search for food. Within a habitat the animal discovers food clumps as a random process. When the forager discovers a clump, the amount of energy available within the clump varies randomly.

Foraging ends at time T ; total energy intake is the sum of the amount consumed within each clump discovered. Under reasonable assumptions, the distribution of energy intake follows a bell-shaped curve. The expected total intake is simply the product of the mean number of clumps discovered and the mean energy available per clump. The variance of the total energy intake increases with the variance of the number of clumps discovered and with the variance in the energy available per clump. The animal behaves as if it knows the mean and variance of energy intake for each habitat.

A plausible currency of fitness is the probability that energy intake fails to exceed the requirement. A risk-sensitive forager should choose its habitat to minimize the probability that its intake is less than or equal to R . If the intake variance is equal for the two habitats, the forager should choose the habitat with the greater mean. If the habitats offer the same mean intake but different variances, the choice is not so simple. If the expected intake exceeds the requirement R (food is plentiful) the forager should choose the lower-variance habitat. However, when the mean intake does not exceed R (so that survival is jeopardized) the forager should choose the higher-variance habitat; the animal should “gamble” when losing energy. When both mean intake and its variance differ between habitats, they interactively govern probabilities of energetic failure, and so combine to predict foraging preference.

F. State-variable models

The preceding examples of models in OFT make static predictions. That is, the expression (or choice) of a behavioral phenotype maps directly to a fitness score. More generally, an action may contribute directly to survival and reproduction, or may contribute indirectly by changing the animal’s state. The new state and the advance of time together can affect the animal’s next action. Feedback between behavior and state continue until a final time (*e.g.*, end of the day) is reached, and fitness is scored. State-variable models predict sequences of actions between initial and final times, as a function of state. The models are termed dynamic, rather than static.

Definition of state depends on the question of interest. In foraging theory, state usually refers to the individual’s level of energetic reserves. To demonstrate, recall the diet-choice problem, but in a dynamic context. As the foraging period commences, the

animal might accept or reject a prey type based on its initial energy reserve. As its reserve grows or decays, and as the time remaining to forage declines, the animal might expand or contract its diet. That is, the predicted diet breadth can vary with state, even if prey densities and profitabilities remain constant. At the end of the period, a hypothesized “terminal reward” function maps the final energy-reserve to survival and reproduction. Dynamic state-variable models take the expected value of the terminal reward as currency of fitness; optimal behavior, for given reserve and time remaining to forage, maximizes this expectation.

State-variable models ordinarily require computational solution, so that general predictions are not always apparent. Some interesting applications of state-variable models concern costs of sub-optimal behavior. Suppose a forager makes a prey-choice “error” in the middle of the day, and then follows the optimal policy until the final time. If the error has little effect on the value of the terminal reward, selective pressure is likely weak. However, if the error induces a significant fitness cost, selective pressure on the state-time combination where the sub-optimal choice occurred may be strong.

G. OFT: final comment

The methods used in OFT parallel models in bioeconomics, theory developed to manage ecological resources optimally. Predictions of foraging theory have been applied in anthropology, microeconomics, and psychology. Some ethologists, students of behavioral mechanisms, suggest that OFT offers complex models for simple environments, and that animals may use simpler rules that deal efficiently with complex environments. As knowledge concerning the neural bases of decision-making increases, a combined functional and mechanistic understanding of foraging may emerge.

III. Social foraging theory

Social foraging implies that the functional consequence of an individual's actions depends on both the individual's behavior and the behavior of other foragers, often competitors for the same resource. Social foraging theory (SFT) models generally rely on methods of game theory. Models for dietary choice or patch departure when individuals forage in groups usually make predictions that differ, at least in detail, from the corresponding model in OFT. To emphasize the distinction between solitary and social foraging, this section reviews some issues that concern social foragers only.

A. Group size

Groups ordinarily encounter prey (or food patches) more often than do solitaires, and groups can capture larger prey. Group membership may provide the opportunity to learn locations of food, or to acquire a foraging skill *via* social learning. A group member may be safer from predation than is a solitary forager. But as group size increases, most (or all) group members experience greater competition for food, often leading to aggressive interaction. These benefits and costs, along with mechanisms regulating recruitment/expulsion of group members, govern a foraging group's equilibrium size.

1. Ideal free distribution

Suppose that a population of identical individuals exploits food occurring only in a small number of patches. Suitability of a patch is given by a constant, representing food density; constancy implies that consumption does not reduce food availability. Increasing the number of consumers occupying a patch decreases the feeding rate of each individual in that patch; consumers interact only through scramble competition.

The ideal free distribution (IFD) predicts consumer density in each patch. “Ideal” implies that an individual knows and chooses that patch where its rate of food consumption is maximal. “Free” implies that a consumer can move between patches without energetic cost or behavioral interference. Foragers move until nothing can be gained by moving elsewhere; the sizes of consumer groups equilibrate when each individual has the same resource-consumption rate. The IFD predicts “input-matching,” where the fraction of consumers in a patch equals the fraction of the total resource available in that patch. That is, the distribution of consumers matches the distribution of resources. The IFD is stable in that an individual switching from one patch to another will reduce its resource consumption, as long as all other consumers do not move.

The IFD has prompted a number of further models. Less than “ideal” foragers fail to discriminate resource-consumption rates, or may learn a patch’s suitability only after sampling. Consumers may not be “free;” travel between patches can be costly. Consumers will not be identical if some forage more efficiently, and interference among individuals will affect the impact of local density on resource-consumption rates. Each of these altered assumptions can predict a different patch-occupation pattern.

2. Aggregation economies

In an aggregation economy benefits of group foraging outweigh costs when groups are small. But as groups become large, competitive interactions eventually increase costs beyond any attainable benefits of foraging socially. Therefore, aggregation-economy models assume that the individual’s currency of fitness, as a function of the size of its group, has a single peak. The associated group size is termed, perhaps inappropriately,

the optimal group size. Predicted group size depends on how groups form and dissolve, and can depend on genetic relatedness among group members.

If solitaries can freely enter any group where membership increases their fitness, equilibrium group size will likely exceed the optimal size. However, solitaries may hesitate to enter groups of close relatives, if doing so reduces each relative's fitness. If group members collectively accept or repel a solitary trying to join the group, equilibrium group in the absence of relatedness will be the optimal size. If, however, the solitary is a relative of current group members, the solitary could be admitted.

B. Social Parasitism

Different members of the same group may choose alternate methods to obtain food.

Consider the producer-scrounger distinction, an example of social parasitism. Producers expend effort finding and capturing prey; a producer gets a meal only when it generates a feeding opportunity. Scroungers avoid costs of producing, and attempt to exploit every feeding opportunity provided by the group's producers. If all individuals have chosen to produce, the first individual switching to scrounging will have more chances to feed than any other group member. When the scrounger phenotype is rare, its fitness should exceed a producer's fitness. If all individuals have chosen to scrounge, no food is discovered. As long as a producer can obtain a greater-than-average portion of the food it discovers, the first producer will have a fitness exceeding that of a scrounger. When these conditions hold, the frequency of scrounging will equilibrate where each phenotype has the same fitness. The predicted equilibrium will depend on environmental attributes (*e.g.*, prey density) and the model's fitness currency, but in each case the equilibrium frequency of scrounging will qualify as stable.

Scrounging can appear because individuals seek to increase their own food consumption, or to reduce their foraging costs. For a given group size, more frequent scrounging (*i.e.*, reduction in the number of producers) reduces total food consumption across group members. Each individual's pursuit of its own advantage means that every group member obtains less resource, a consequence of social parasitism.

IV. Foraging behavior to population dynamics

Models of foraging behavior can be written into the growth equations of consumer-resource systems, integrating individual-level processes with the analysis of ecological interactions. Some combined models evaluate consequences of particular foraging preferences or functional responses. Other models assume that foragers respond optimally to varying prey density, to predict effects of adaptive behavior on community stability. The body of results is complex; this section lists only a few prominent lessons.

Suppose that an individual forager's effect on the prey population's growth declines as prey density increases. The consequent decelerating functional response does not tend to reduce density fluctuations in a consumer-resource interaction. However, a sigmoid functional response accelerates at intermediate prey densities, so that the prey mortality imposed by each forager increases with the density of prey. Hence, at some prey densities a sigmoid functional response can stabilize population dynamics. When a consumer population preys on two species, a sigmoid functional response can arise if foragers switch between resources and so concentrate predation on the more common prey. Predator switching can, therefore, stabilize the 3-species interaction. When a

switching predator prevents one prey species from excluding another competitively, the predator's impact is termed a "keystone effect." See discussion of Predator-Prey Models.

Dynamical consequences of foraging preference, and its impact on details of the functional response, have been deduced in analyses of 3-species food chains. A resource is exploited by a consumer which, in turn, is exploited by a third species. The third species might be an omnivore (exploiting both the resource and the consumer) or a top predator specializing on the consumer; omnivory should exert the greater stabilizing influence on density fluctuations.

Parasitoids often exploit a host population with a highly clumped spatial distribution; many patches contain few hosts, and some patches contain many hosts. An inefficient forager fails to respond to host spatial heterogeneity, while an optimal forager searches patches with the greatest host density. In models of this interaction, optimal patch use by the parasitoid tends to stabilize the densities of the two species. Finally, consider a predator with access to two prey species of differing profitabilities. Suppose that the contingency model's average rate of energy gain enters the dynamics as a component of both prey mortality rates and the predator's birth rate. The predator always includes the prey of higher profitability in its diet. It adds or drops the second prey as the density of the preferred prey changes, according to the optimal diet's choice criterion. The resulting pattern of prey consumption does not tend to stabilize the dynamics, and can be destabilizing. In general, adaptive foraging may or may not promote stable ecological interaction; predictions - not surprisingly - depend on model details.

See Also the Following Articles

Behavioral Ecology; Evolutionarily Stable Strategies; Predator-Prey Models

Glossary

granivore an animal that consumes grain

omnivore ordinarily, an animal that consumes both plant and animal material. In models of food chains, an omnivore preys on both a consumer and the resource exploited by that consumer.

optimizing selection natural selection that favors an intermediate phenotype over individuals with either a lesser or greater value of a trait

phenotype observable anatomical, physiological and behavioral traits of an individual. Expression of the individual's genome in the current environment induces the phenotype.

variance a measure of random variation around an average, or expected, value

Further Reading

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Figure legend

Figure 1. The contingency model's optimal diet. Prey types are ranked from highest to lowest profitability, the ratio of net energy yield per item to handling time per item. Profitabilities are indicated by red ✱ symbols. Blue ☆ symbols indicate mean long-term rate of energy gain for a diet composed of the k highest ranked prey types ($k = 1, 2, \dots, 10$). If the profitability of prey type $(k + 1)$ exceeds the rate of gain for a diet composed of the first k prey types, the optimal (rate-maximizing) diet includes prey type $(k + 1)$. If the rate of gain for a diet of k prey types exceeds the profitability of prey type $(k + 1)$, the optimal diet cannot include prey type $(k + 1)$ or any lower ranked prey. (a) Optimal diet includes first three prey types. Profitability of fourth ranked type is less than optimal diet's rate of gain. (b) Same profitabilities as in a, but encounter rates will all prey are increased. Rates of energy gain increase, and optimal diet includes only two highest ranked prey types. (c) Profitabilities decline less rapidly with rank when compared to plot a. Optimal diet includes the six highest ranked prey types.

