

Foraging Theory

DAVID W. STEPHENS
JOHN R. KREBS



MONOGRAPHS IN BEHAVIOR AND ECOLOGY

Foraging Theory

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DAVID W. STEPHENS
and JOHN R. KREBS

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Preface

When we contemplate every complex structure and instinct as the summing up of many contrivances each useful to the possessor, nearly in the same way as when we look at any great invention . . . how far more interesting will the study of natural history become!—Darwin, *On the Origin of Species*

This book analyzes feeding behavior in the way an engineer might study a new piece of machinery. An engineer might ask, among other questions, about the machine's purpose: is it for measuring time, wind speed, or income tax? This is a worthwhile question for the engineer because machines are built with a purpose in mind, and any description of a machine should refer to its purpose. Asking what the machine is for helps the engineer understand how it works. To give a trivial example, we would find it easier to work out how a slide rule operates if we knew it was meant for doing calculations and not for digging holes.

Biologists also ask questions about purpose, about what things are for. For example, Lewontin (1984) says: "It is no accident that fish have fins, aquatic mammals have altered their appendages to form finlike flippers, . . . and even seasnakes, lacking fins, are flattened in cross-section. It is obvious that these traits are adaptations *for* aquatic locomotion" (emphasis ours). In contrast to the engineer, the biologist thinks of design or purpose as the product of natural selection, rather than as the product of a conscious creator. Natural selection chooses traits that are useful in the struggle for survival and reproduction. A lion seems well designed for killing gazelles because traits that make lions good gazelle-killers were useful to the lion's ancestors: they allowed the lion's ancestors to produce more offspring than were produced by lions with other traits.

Design or adaptation is related to fitness (survival and reproductive success) but analyzing design is not the same as measuring fitness. If one attempted to study adaptation simply by measuring survival and reproductive success, one would reach the vacuous conclusion that those that survive and reproduce are those that survive and reproduce (Scriven 1959, Beatty 1980). Even showing that fitness varies between individuals with different traits is not enough to infer adaptation; one must know how the traits influence fitness. In other words, the central question in the study of adaptation is not just whether individuals survive, but how *design* is related to expected survival and reproduction (Mills and Beatty 1979).

Williams (1966) makes this point when he says that measuring reproductive success

focuses attention upon the rather trivial problem of the degree to which an organism actually achieves reproductive survival. The central biological problem is not survival as such, but design for survival. (p. 159)

The study of adaptation, therefore, is an integral part of evolutionary biology, and models of design such as optimality models are not merely shortcut versions of genetic models, as Lewontin (1979) has suggested, nor are they simply a staging post toward the measurement of fitness. They are part of a separate and necessary enterprise: biologists must study the usefulness of traits if the theory of natural selection is to explain adaptation (Beatty 1980).

Optimality modeling, the theme of this book, is one method that raises the study of design from clever “story telling” (Gould and Lewontin 1979) to a position in which “explicit, quantitative and uncompromising” hypotheses allow biologists to “recognize logical implications or to demand that there be a precise congruence between theory and observation” (Williams 1966, p. 273). Other approaches include comparisons between or within species (e.g. Ridley 1984) or between different experimental treatments (Tinbergen et al. 1967). The arguments in favor of and against optimality models are discussed in Chapters 1 and 10 respectively, and we will not repeat them here. Instead, we will briefly sketch a few discoveries that have, in our view, come directly from optimal foraging theory.

First, some examples of phenomena that were already well known, but whose significance was obscured because they lacked a cogent theoretical interpretation. Psychologists knew that animals were sensitive to variance as well as mean reward for at least 20 years before Caraco et al. (1980b) used a foraging model to explain it (Chapter 6). This explanation provided a way of organizing existing evidence, and it made bold and unexpected predictions about which factors should influence animal sensitivity to variance (see below). “Wasteful killing” or “partial consumption of prey” was also well known by students of behavior before foraging theory came to light. But now, instead of viewing it as an oddity or maladaptive peccadillo, behavioral ecologists can make use of economic considerations to account for its occurrence, and they can successfully predict just how wasteful the forager should be (e.g. Cook & Cockrell 1978).

What about phenomena that foraging theory has revealed or highlighted? It is of course impossible to claim that a single approach was the stimulus for any particular discovery, but there seems little doubt that foraging theory played a major role in enabling biologists to discover how pollinator foraging behavior affects the design of plants (Pyke 1978a, Best

and Bierzychudek 1982), and that what are essentially foraging models were important in the discovery of individual variation in mating strategies (Parker 1978).

Furthermore, foraging models have predicted effects and phenomena whose occurrence was not predicted by other theories. The prediction that an animal's energy budget influences its sensitivity to variance in reward is one striking example (Chapter 6), as is the prediction of environmental conditions under which a foraging animal should and should not show exploratory or sampling behavior (Chapter 4). More specifically, optimal foraging models can generate predictions that run counter to currently accepted psychological theory (and that are borne out by observation) about the conditions under which an animal's choice should not minimize the delay until the next reinforcement (Houston 1986). These examples show that foraging theory is more than an elegant technique, that it has provided and will continue to provide insight into why animals behave the way they do.

Lastly, a few words about the contents of this book. Chapter 1 explains the basic rationale of optimality models. We follow this explanation with three chapters on models that maximize the long-term rate of energy intake. Chapter 2 deals with the classical prey and patch models, and Chapter 3 examines modifications of these models: what happens if the forager encounters more than one prey item at a time, for example. In Chapter 4 we consider information, viewing learning from the perspective of gaining and using information economically. This approach differs greatly from the way psychologists usually analyze learning.

In Chapter 5 we examine currencies other than energy gain; economic models of complementary resources offer a potential way to analyze "mixed currencies," but they have seldom been applied in behavioral ecology. Behavioral ecologists might use these models to analyze herbivore diets, although we conclude that for this purpose simpler modeling approaches may be adequate. Chapter 6 discusses the major alternative currency to rate-maximizing in foraging models: minimizing the likelihood of energetic shortfall. Chapter 7 briefly discusses dynamic optimization as a way to model complex extensions of foraging such as daily time budgets and life history tactics. The final three chapters are not directly concerned with theory. In Chapter 8 we introduce the idea that animals may use "rules of thumb" to solve foraging problems. Chapter 9 presents a detailed review of the evidence for and against the basic prey and patch models. The available evidence teaches the empiricist a salutary lesson: one should make sure that the assumptions of the model being tested are actually met. We return to generalities in Chapter 10, in which we try to answer some of the criticisms of the optimality approach. We conclude

that one must compare observed design to an optimality model to find out whether phylogeny, genetics, and ontogeny constrain the design of organisms. So, these criticisms, rather than serving as arguments against the optimality approach, highlight one of its uses.

Our coverage of topics is necessarily uneven. For some topics we attempt a synthesis, for others we simply review the literature. Although we believe this unevenness reflects the state of the art as much as it reflects our own biases, we hope that the reader will be stimulated to develop those parts of the subject that we analyze superficially.

Acknowledgments

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Foraging Theory

1

Foraging Economics: The Logic of Formal Modeling

1.1 Introduction

Some caddisfly larvae spin silken catch-nets. These nets capture small plants, animals, and organic particles that are swept into them by the streams in which the larvae live. The larvae's nets (and often their bodies) are fixed to some immobile object in the stream such as a rock or submerged tree trunk. The nets are not sticky or electrostatically charged: they simply stop particles that are too big to pass through the mesh (Georgian and Wallace 1981). The net-spinning caddisflies have capitalized on their moving medium in an elegant and apparently straightforward way. They have built foraging sieves.

Caddisfly nets are astonishingly diverse. They vary in size, shape, and location in the stream, and, spectacularly, in the structures built to support the net. Wallace and Sherberger (1975) have appropriately described the net and accompanying structure of *Macronema transversum* larvae (Fig. 1.1) as “possibly one of the most complicated feeding structures constructed by non-social insects.” Students of caddisflies (see Wallace and Sherberger 1975) believe that this structure takes advantage of subtle hydrodynamic principles (the law of continuity will slow down the flow across the net in comparison with the flow in the entrance and exit ports; the Bernoulli effect—of water moving across the exit port—will drive water through the structure). Among the simpler net designs are the large-meshed, round, trampoline-shaped nets of most hydropsychid larvae and the long windsock-shaped nets with fine meshes built by philopotamids.

Non-adaptive variation might explain the variety and detail of caddisfly nets, but consider for the moment that net structure reflects the action of natural selection. How then can we interpret the element of its design, for example, its mesh size and shape?

A first step is to find out whether there are systematic trends linking mesh size and shape with environmental factors. A comparative survey shows two trends. First, larger meshes are associated with faster water. Second, size is correlated with shape. Small meshes are usually long and rectangular, and larger ones are roughly square. Both trends can be interpreted in terms of costs and benefits (Wallace et al. 1977). One hypothesis

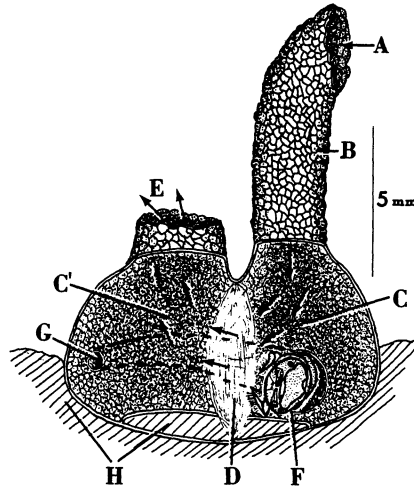


Figure 1.1 Catch-net and feeding structure of *Macronema transversum*. (A) Entrance hole (facing upstream) for in-flowing water. (B) Sand and silk entrance tube. (C) and (C') Anterior and posterior portions of chamber. (D) Capture net. (E) Exit hole for out-flowing water. (F) Anterior opening of larval retreat with larva in place. (G) Exit hole from larval retreat (for faeces and water flowing over gills). (H) Substrate. Arrows represent direction of water flow. Broken lines between (F) and (G) signify approximate position of larval retreat.

is that large meshes can withstand swifter currents because they present less resistance to the flow. A second possibility is that smaller nets are better in slow water because slow streams carry smaller particles. Furthermore, in slow streams fewer liters of water per minute pass through the nets, so the larvae may need to capture a larger proportion of particles to meet their food requirements. Another hypothesis is that the size and shape of the mesh are correlated because of the cost of silk. Caddisfly larvae must use a much greater length of silk to fill a given area with meshes if the meshes are small, but the extra cost can be reduced by making the meshes long and narrow, cutting the cost of cross pieces. This saving may not be possible with larger meshes because the silk stretches when a large particle collides with the net, turning the rectangular mesh into a distorted and ineffective hexagon.

These ideas sound reasonable, but they might be criticized for being no more than plausible stories. They certainly do not meet Williams's (1966) criterion of an "explicit, quantitative, uncompromising" design hypothesis. Formal models may help biologists to evaluate design hypotheses by helping to analyze the problem and by making testable predictions.

To analyze a design problem is to break it into parts and to determine the relationship among the parts. A formal analysis clarifies what the parts of the problem are, and it reveals their full implications and interactions. What relationship between water velocity and mesh size would be expected from the “resistance to breakage” hypothesis? Could the argument about the silk-stretching effects of particle collisions really account for the relationship between size and shape of meshes? Does the “particle size” hypothesis make any predictions that distinguish it from the “resistance to breakage” hypothesis? Formal analysis may help resolve these kinds of questions.

The next step in interpreting design, then, is using models to test the hypotheses. Since both the “resistance” and “particle size” hypotheses might explain the relationship between water velocity and mesh size, a more subtle analysis is needed to distinguish between the following four possibilities: (1) only the “resistance” hypothesis applies, (2) only the “particle size” hypothesis applies, (3) both hypotheses apply, and (4) neither hypothesis applies. A formal analysis might, by generating quantitative predictions from each hypothesis, allow us to distinguish between them. If a model based purely on the “resistance to breakage” hypothesis—incorporating information about silk strength and hydrodynamic forces—accounted for the relationship between current velocity and mesh size, we might tentatively conclude that the essence of the design problem had been captured by these factors alone. We would then have to develop models of the alternative hypotheses to see if they could also account for the data. If more than one model accounted for the data, even in quantitative detail, then even formal modeling would lead to an ambiguous result.

1.2 The Elements of Foraging Models

The foraging models we describe in this book, and optimality models in general, are made up of three components.

1. *Decision Assumptions.* Which of the forager’s problems (or choices) are to be analyzed?
2. *Currency Assumptions.* How are various choices to be evaluated?
3. *Constraint Assumptions.* What limits the animal’s feasible choices, and what limits the pay-off (currency) that may be obtained?

These components may not always represent mutually independent parts of the problem; for example, constraint assumptions clearly depend on what is being constrained. Some authors have broken foraging models into

different components (Schoener 1971, Cheverton et al. 1985, Kacelnik and Cuthill 1986).

Chapter 2 discusses the so-called “conventional models” of foraging theory, and the following chapters discuss changes in the conventional constraint, currency, and decision assumptions in turn (constraints, Chapters 3 and 4; currencies, Chapter 5 and 6; decisions, Chapter 7). The remainder of this chapter presents some general comments about each of these three elements.

1.3 Decision Assumptions

All optimality models consider the “best” way to make a particular decision. How should bones be constructed? What mesh size should a net-spinning caddisfly choose? *Decision* here refers to the type of choice (mesh size or mesh shape?) the animal is assumed to make (or that natural selection has made for it), rather than a specific choice (i.e. deciding that mesh size is to be 10.0 microns by 11.5 microns).

In a formal model the decision studied must be expressed as an algebraic variable (or variables). Mesh size and shape can be represented by a pair of numbers, length and width. Length and width are the *decision variables*. It will not always be possible or reasonable to express the decision as one or two simple variables. A complicated vector (or list) of many decision variables may be more appropriate; for example, in a model of bone structure the *decision vector* might include variables representing bone length, cross-sectional area, alignment of bone fibers, and the locations of muscle attachments.

For some problems even a huge list of decision variables may not suffice. Suppose that a caddisfly larva’s body size affects the structure of its net, and, because net structure partially determines the amount of food captured today, that the structure of today’s net in turn affects the caddisfly larva’s body size tomorrow. A problem like this one is *dynamic*, because today’s decision (net structure) affects tomorrow’s state (body size), which may in turn affect tomorrow’s decision. Dynamic models solve for the optimal path or sequence of decisions. When the decision can be represented by a simple, non-sequential list of decisions, the model is a *static* model. Most of the models we will examine are static, but dynamic models are discussed in Chapter 7.

Foraging models have studied two basic problems: which prey items to consume and when to leave a patch. Modelers have represented the decision variables within each category in different ways. For example, with regard to the first problem, some models of diet have studied the proportions of food of a given type ingested, and others have studied the

probability of pursuing a given prey type upon encounter. These diet models, which make different decision assumptions, are studying different aspects of the problem.

Most models of diet choice solve for the optimal *probability that the forager will pursue a given prey type after encountering it*. Two essential ideas are implicit in this assumption: encountering and recognizing prey types. The notion of “prey type” shows how the three components of a model can be interrelated, because the forager’s ability to categorize its prey into types (a constraint assumption) is implied by this decision assumption.

In most models of patch exploitation the decision variable is *time spent in a particular patch type* or, more simply patch residence time. This decision variable combines mathematical convenience (time is a convenient and continuous variable) and generality. In most examples of animals exploiting patches, whether the patches are clumps of grass, seeds on a tree, or schools of fish, the forager’s decision can be framed in terms of time spent in the patch. However, this assumption can be misleading when there is no strong link between patch residence time and the amount of food acquired from the patch (Chapter 4).

1.4 Currency Assumptions

A model’s currency is the criterion used to compare alternative values of the decision variable. A modeler might compare alternative designs of caddisfly nets using a model that assumes maximization of the number of particles filtered per minute. In general, the modeler supposes that trait *X* will exist instead of other traits if *X* satisfies some existence criterion. Existence criteria have two parts: a *currency* and a *choice principle*. For caddisfly nets the currency is the “number of particles filtered per minute” and the choice principle is “maximization.”

Currencies are as diverse as the adaptations they are used to study, but there are only three common choice principles: maximization, minimization, and stability. Stability is the most general of these, but its generality is not always necessary. If the pay-off (currency) gained by implementing decision *X* depends on the decisions made by other individuals, then stability is the correct choice principle (Maynard Smith 1982). The models in this book all use maximization or minimization, and so they require that a decision’s value is independent of its frequency. (We usually refer only to maximization when speaking in general terms, because any minimization problem can be restated as a maximization problem by maximizing negative currency.) Once the currency and decision variables have been chosen, the modeler must specify the relationship between them.

For example, a modeler might deduce the relationship between the number of particles captured per minute (the currency) and the dimensions of a mesh (the decision variables). This *currency function* must translate the list of decision variables into a single value (in mathematical jargon it must be a real-valued function), because the currency function must rank all possible decisions. (Chapters 5 and 6 discuss ranking alternatives in more detail.)

In most biological optimization problems the modeler chooses a currency *a priori*, largely on the basis of intuition; for instance, a modeler may argue that maximizing the number of particles trapped per minute will make the “fittest” caddisfly, because food limits larval growth. *A priori* currencies usually have physical interpretations: they can be expressed as rates or amounts, for example. Economists and psychologists, on the other hand, often use the observed behavior of a “decision-maker” to specify the currency *a posteriori*. A modeler might suppose that a currency for caddisfly nets has the general form maximize $a\ell^2 + bw^2$, where ℓ and w are the decision variables mesh length and width. An advocate of *a posteriori* modeling would fit the constants a and b so that observed net structure maximized this function. *A posteriori* currencies do not usually have any physical interpretation: they are simply “that which is maximized.” Houston et al. (1982) refer to the distinction between *a priori* and *a posteriori* modeling as the distinction between normative and descriptive optimization modeling, and Maynard Smith (1978) refers to the second approach as “reverse” (or “inverse”—McFarland and Houston 1981) optimization. Most of the models we discuss suppose *a priori* currencies, but Chapters 5 and 6 discuss *a posteriori* currencies.

Conventional foraging models maximize the net rate of energy gain while foraging. More energy is assumed to be better, because a forager with more energy will be more likely to meet its metabolic requirements, and it will be able to spend spare energy on important non-feeding activities such as fighting, fleeing, and reproducing. Energy can be measured both as a cost (the energy expended in performing a particular behavior) and as a benefit (the energy gained by performing a particular behavior). Thus it is possible to talk about the net energy gained from performing a particular foraging behavior. Time is critical because animals may be pressed to meet their daily feeding requirements, and because animals are assumed to fight, flee, and reproduce less well if they are simultaneously foraging.

Schoener (1971) pointed out that there are two simple ways to resolve the dilemma of how to acquire more food while spending less time foraging. The *time minimizer* minimizes the time required to gain a fixed ration of energy. The *energy maximizer* maximizes the amount of energy gained in a fixed time. Both alternatives are plausible currencies, but for many pur-

poses both currencies are equivalent to rate maximization (Pyke et al. 1977). These currencies can differ from each other when food comes in lumps. Suppose you can eat from one of two boxes of food: box A contains many items that yield 8 calories and take 3 seconds to eat; box B contains many items that yield 9 calories and take 4 seconds to eat. Whether the currencies agree or disagree depends on what happens if you do not have time to eat a whole item. If the proportion of total calories you take in is the same as the proportion of the required time you spend eating (e.g. you take in one-half the calories if you spend one-half the time), then all three currencies make the same prediction: choose box A because $\frac{8}{3} > \frac{9}{4}$. However, if you do not take in any calories unless you spend all the required time (e.g. you cannot eat until you crack the nut) the currencies are different. Specifically, if you maximize energy gains in 4 seconds, then box B is the better choice—9 calories instead of 8—but if you minimize the time to take in 5 calories, then box A is better—3 seconds to take in 8 calories is better than 4 seconds to take in 9 calories because any amount above 5 calories is sufficient.

In a stochastic world (a world with random variation) foraging theorists must use averages (or expectations) to characterize rates. However, the value of an average rate calculated over 10 seconds may be different from an average rate calculated over 20 seconds: which average is best? Conventional theory has favored generality and mathematical convenience by maximizing the long-term average rate of energy intake (see Box 2.1).

There are still those (e.g. Tinbergen 1981) who confuse maximizing net rate with maximizing the ratio of benefit to cost, often called “efficiency.” Although there are conditions under which maximizing efficiency makes sense (for example, allocating resources from a fixed total budget—Schmid-Hempel et al. 1985), for most of the foraging problems we discuss it does not. It ignores the time required to harvest resources, and it fails to distinguish between tiny gains made at a small cost and larger gains made at a larger cost: for example, 0.01 calories gained at a cost of 0.001 gives the same benefit/cost ratio as a gain of 10 calories costing 1. The 10-calorie alternative, however, yields 1000 times the net profit of the 0.01 alternative.

1.5 Constraint Assumptions

By *constraints*, we mean all those factors that limit and define the relationship between the currency and the decision variable(s). This is a broad definition that encompasses both the mathematician’s formal use of *constraint* and the everyday use.

A mathematician might define constraints in a purely formal way. Suppose that a currency function relates the number of particles a caddisfly net intercepts per minute (P) to the decision variables length (ℓ) and width (w) and to the stream velocity (v). A modeler might write the function as $P(\ell, w, v)$, and might specify a formal constraint, for example, that the mesh area ℓw must be less than 10 square microns. In the mathematician's purely formal sense the inequality $\ell w < 10$ square microns would be the only constraint in the problem. However, in the everyday sense we would say that the stream velocity constrains the caddisfly's economy.

In the everyday use of "constraint" we imagine some kind of limitation. Limitations are of two biologically different types: those that are intrinsic to the animal and those that are extrinsic. Intrinsic constraints can be further divided into the following categories: (1) limitations in the abilities of animals: honeybees cannot distinguish red from grey, and pigeons cannot distinguish 0.2 milliseconds from 0.5 milliseconds; (2) limitations in the *tolerances* within which animals must live: the forager must acquire 20 milligrams of vitamin A, or it can only tolerate 2 hours of food deprivation. Some biologists have limitations on abilities in mind when they discuss constraints (Janetos and Cole 1981), but others are imagining tolerances (Pulliam 1975).

Extrinsic constraints are placed on the animal by the environment. For example, the stream velocity limits the number of particles that a caddisfly net can filter per hour, and a forager cannot eat more prey than it can find or spend more than 24 hours eating each day. Intrinsic and extrinsic constraints are not mutually exclusive categories. Animal abilities interact with the environment; for instance, both ambient temperature and muscle physiology limit a lizard's running speed. In Chapter 8 we will return to the subject of intrinsic constraints, discussing rules that animals with limited abilities might use to solve their foraging problems.

Conventional foraging models have assumed few constraints on foragers' abilities, and in some important cases they have assumed "no constraints." In our terms even the assumption of "no constraints" is a constraint assumption: it is an assumption about the nature of the limitations on the forager. The advantage of making few constraint assumptions stems from the fact that the limitations on animal abilities vary greatly from species to species: snails and ospreys are not limited in the same ways. Foraging theorists have tried to find general design principles that apply regardless of the mechanisms used to implement them. For example, the elementary principles of a device for getting traffic across a river—that is, a bridge—apply regardless of whether the bridge in question is built of rope, wood, concrete, or steel.

Conventional foraging models make three constraint assumptions: (1)

exclusivity of search and exploitation: the predator cannot exploit (handle) items such as prey or patches while searching for new ones; (2) *sequential Poisson encounters*: items are encountered one at a time, and the probability of encountering each prey or patch type in a short time period is constant; and (3) *complete information*: the forager knows, or behaves as if it knows, the rules of the model. The rules of the model will usually include information about the environment (density of prey) and limitations on the forager's ability. We call this complete information rather than perfect information because it does not imply that the forager is omniscient. A completely informed forager is like a gambler who knows the odds but cannot predict exactly what number will come up on the next spin of the wheel. The assumption of complete information is justifiable for predators in steady-state conditions. Foraging theory has not ignored the question of information gain (see Chapter 4), but the simpler steady-state models are an easier and more useful starting point (Staddon 1983).

1.6 Lost Opportunity

Perhaps the two most important assumptions of the conventional foraging models are long-term average-rate maximization (or "rate maximization" for brevity) and the exclusivity of searching and exploiting. Combining these two assumptions leads to what might be called the *principle of lost opportunity*. In general terms decisions about exploiting items can be assessed by comparing potential gains from exploitation with the potential loss of opportunity to do better. For example, if an item is of the best possible type, then no opportunity can be lost by eating it, since the best outcome that might result from "not eating" it is to happen immediately upon another item of the best sort. By the reverse argument, a forager loses some opportunity when it attacks an inferior item. Many of the results of rate-maximizing theory can be viewed in this way. Gains are assessed in terms of immediate achievements of rate, but losses are assessed in terms of missed opportunities to do better.

1.7 Summary

Formal models of design are valuable because they permit both rigorous analysis and testing. Optimization models consist of three components—decision assumptions, currency assumptions, and constraint assumptions.

The decisions studied by conventional foraging models relate to prey choice and patch exploitation; the currency in these models is long-term average-rate maximization; and the constraints are exclusivity of search and exploitation; sequential, random search; and the assumption of complete information. Many of the results of conventional foraging models are expressions of the principle of lost opportunity.