# OPTIMAL FORAGING: SOME THEORETICAL EXPLORATIONS

by

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# INTRODUCTION

This book had its genesis in a rather disorganized and poorly conceived lecture on optimal foraging theory that one of us (GHO) gave to an advanced ecology class during the winter of 1971. The deficiencies in that treatment, combined with the obvious potential of an improved conceptualization and analysis of the problem, led to the formation of a small seminar on optimal foraging theory attended by Charles Fowler, Nolan Pearson and ourselves. This seminar, which extended over two academic quarters, produced the basic fine-grained foraging models and some hints about wider applications of the results. We both found ourselves independently stimulated to explore the implications of the ideas we had conceived for a wide range of ecological problems and these preliminary explorations, carried out while we were physically widely separated, were sufficiently rewarding that we decided to collaborate to produce the present work.

We have individually brought to this effort very different skills and experiences and much of what there is of value in this book is the result of the mutual interplay of these contrasting abilities. One of us (ELC) has been primarily responsible for the mathematical formulations appearing in the following chapters, while the other (GHO) has provided a larger share of biological insights. Nevertheless we are quite unable to trace the genesis of most of our original ideas and we are both keenly aware that neither of us alone could have produced anything remotely resembling the present work.

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# PART 1. INTRODUCTION AND OBJECTIVES

## Chapter 1. Natural Selection and Foraging Processes

Ideas about predation have played a significant role in biological thought. No such thing as a "predation theory" exists but several theories have been developed around *questions* asked about predators and their activities. They have a key role in concepts of population regulation (Holling 1965, Huffaker 1971), although some have challenged the basic ideas (Errington 1946, 1963). Productivity studies have made use of the notions of predation or trophic efficiencies, and some ecologists have believed that productivity is a major factor to be explained by ecological theory (Warren 1971, Ivlev 1961). Ecological genetics, indeed the development of the concept of natural selection itself, relies heavily on field work related to predation. Frequency dependent selection and mimicry are two outstanding examples (Ford 1964). Theories of learning are based on assumptions and data about the behavior of predators (Krebs 1973), and there is a large literature on the regulation of food intake and the feedback processes involved (*Handbook of Physiology* 1967).

This list is very incomplete and is intended only to point out that predators have been considered in many ways, with the *questions* of interest determining the appropriate type of theory. In this book we explore one type of question about predation, the matter of "prudence" on the part of individual predators, and then examine some of its consequences. This perspective is not new (Elton 1927), but statements in the older literature are often anecdotal and usually lack the conciseness necessary to qualify as testable hypotheses. An example is Elton's view that any predator is restricted to a certain size range of prey because the big prey are difficult to capture, while the small ones are not worth the effort. Foraging behavior should be molded by natural selection because the kinds of choices made by a predator will influence (a) survival during periods of food shortage, if and when they occur, (b) the rate of accumulation of energy reserves for reproduction and, hence, the number of offspring that can be provisioned, (c) and the amount of time that must be allocated to foraging activities. This, in turn, influences the amount of time available for other activities, which also contribute to fitness. In addition, there may be risks associated with foraging, and selection can be expected to mold behavior in the direction of minimizing these risks, whether they are time-related or event-related.

It is significant that these considerations are at least partially independent of any assumption that the predator population is "limited" by the amount of available food. Indeed, we find the concept of limiting factors to be a hindrance rather than a help in understanding the evolution of foraging behavior. Suppose, for example, that a hungry animal takes greater risks while foraging and is therefore captured by a predator. It is pointless to argue whether its death was due to food shortage or predation (MacArthur 1972). A more profitable approach, and the one we have adopted, is to examine the significance of the trade-off between the risks and benefits implied in this hypothetical example, with the objective of developing an understanding of the molding of the behavior in terms of its influence on the fitness of the individual.

Central to many of the arguments about predation have been differing viewpoints about the mode of action of natural selection, that is, what can natural selection be expected to maximize or minimize. One of the earliest attempts at a formalization of the "prudent" predator concept was that of Slobodkin (1961, 1968). His view envisioned the predator population practising a long-term, sustained yield on a prey population. Unless we assume the special conditions necessary for group or interpopulation selection, it is difficult to imagine just how this sustained yield could evolve

(Lewontin 1970). Recently Slobodkin (1972) has revised his earlier notions, but the same requirements for group or interpopulation selection remain. Williams (1966) has discussed the "group selection controversy" in great detail. In this book we will be concerned only with natural selection at the level of the individual and benefits from foraging will be framed in the context of one individual compared to other individuals in the population. There are examples where an individual predator may appear to be acting in a manner not immediately benefitting itself. These "non-optimal actions" may sometimes be shown to benefit kin or to benefit the individual at some latter time (perhaps through information gathered at the present time). In restricting our consideration to individual selection, we do not imply that other types of selection are impossible, but the conditions for the operation of selection at other levels are so restrictive that it is difficult to deal with them analytically.

Development of the "prudent" predator idea at the level of the individual first came with the papers of Emlen (1966), MacArthur and Levins (1964), and MacArthur and Pianka (1966). Similar, more recent work is that of Schoener (1969a, b, 1971), Werner (1972) and Marten (1973). Economic indifference methods have been applied to food preference theory by Rapport (1971) and Covich (1972), and one economist proposed a "careful shopper" model for a study on small birds (Tullock 1971). Royama (1970) and Smith (1971) have applied some of these ideas in the field, and Hamilton and Watt (1970) used geographic central place theory to explain foraging dispersion in birds that roost in large numbers in a single place. A review of some of the early work may be found in the recent books by MacArthur (1972) and Emlen (1973).

A necessary assumption of any model purporting to describe th action of natural selection or one of its outcomes is that the characteristics under consideration are at least partly heritable. The evidence that foraging behavior is influenced by the genetic material of an organism is not as extensive as would be desired, and even among apparently obligatorily monophagous animals, choice of food can be modified by early experiences (c.f. Thorpe 1938). Nevertheless, the capacity to learn new foraging behavior is itself an evolved character which must be provided for genetically.

All our models are phenotypic ones, that is, we identify some characteristic of the foraging process, changes in which can be expected to influence fitness, even though we are ignorant of its mode of inheritance. Such an approach is dictated by the paucity of empirical genetic data, but it probably would be the preferable one even if adequate genetic data did exist. By concentrating our attention on phenotypic traits, the point where selection really acts, we are able to specify more precisely the risks and benefits of an act under various circumstances. From this perspective it is possible to gain insights into the consequences of different forms of genetic programming and to develop hypotheses about them. Since a genotype often does not specify a phenotype, it is more difficult to develop insights by moving in the reverse direction.

# Chapter 2. Optimality Models for Foraging

## 2.1 General Considerations

Building optimality models requires at least two things—first, the choice of a *goal* (what is being optimized?), then the choice of the *game* that the organism will take part in. The game gives the constraints or rules within which the organism must operate. The actual solution to the problem is the actions that an "optimal forager" should be doing—these are hypotheses to be tested.

The theory of natural selection provides a general goal—fitness—perhaps measured by some standard parameter (MacArthur 1962). For all fitness measures, maximization involves the entire life history, which includes reproduction, growth, survival and the timing of life-history events (Gadgil and Bossert 1970, Schaffer 1973, Charnov 1973, Charnov and Krebs 1973).

A phenotypic view of selection generally is concerned with the trade-offs involved in the solution of conflicting problems. Our understanding of trade-offs is most highly developed in the area of life history or reproductive theory, where it is generally assumed (and sometimes known) that the number of progeny produced in a single breeding season is inversely related to adult survival (Williams 1966) or that the number and survival of young in a single clutch are inversely related (Lack 1966, 1968). In this type of theory it is possible to compare directly the conflicting factors because they are included together in a more comprehensive measure of fitness. The most commonly used measure is the Malthusian parameter (Fisher 1958), which is found by implicit solution of the classic stable-age equation (Keyfitz 1969). If the conflicting factors that we wish to compare are not so easily related to some overall measure of fitness, we have a problem of the lack of a common unit to compare the different kinds of benefits. Economists face the same problem and their solution is to invent a common unit such as “utility” and then express the value of all goods in units of utility.

Animal coloration is a good biological example with which to pose the units problem. Hamilton (1973) has shown, by his own work and through a literature review, that black and white are very effective “energy colors,” allowing the animal more control over heat gain than is possible with other colors. However, cryptic (concealment) or social display colors are much more common. It appears that concealment, which aids a predator during the hunt or hides a prey, or social pressure, in terms of opportunities to reproduce, almost always override environmental energy considerations in the evolution of color pattern. These results are qualitative in the sense that we do not compare the “benefits” from a unit of concealment as opposed to a unit of energy color. For many situations we will gain little, if anything, by the more precise trade-off formalism.

However, if we wish to construct a formal (algebraic or geometric) model, we need to specify some common unit for the various factors or relate them to some overall fitness measure. When we do construct a formal model for foraging behavior, we often frame benefits to the organism strictly in terms of food intake, ignoring such factors as predation risk to the forager or the external thermal environment. It is not that these do not act to mold the foraging process, but rather it is that we often wish to consider foraging activity within the constraints that they impose. As an example, suppose that the goal assumed is that “while foraging, a predator acts to maximize the net rate of food intake.” This goal could result from several different kinds of selective pressure. For a fixed amount of time for foraging (regardless of when or where), the organism that acts to realize this goal obtains the most energy. We could build models about the choice of this feeding interval (length, placement in time of day, time between periods, etc.) and once having assumed the interval, we can build models of where and how the forager operates. These are not independent of one another and all interact to produce the foraging behavior that we actually observe. Still, we can ask what the organism should do *given* that certain kinds of decisions have already been made.

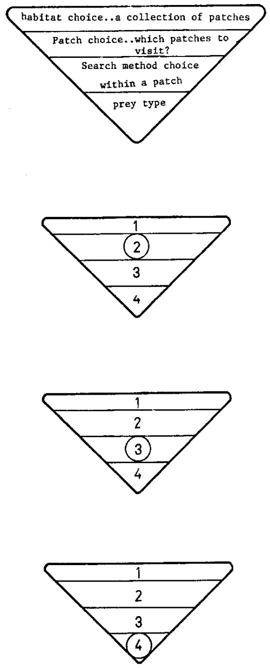
To see how this conceptualization might work consider how predation risk might mold foraging. If the risk is related to the length of time that the forager is exposed, then the minimization of this time exposed seems an appropriate goal (or maximizing the rate of intake while foraging). If the risk is related to certain times (timing), then selection would favor less risky times; if risk is associated with certain places, selection will favor certain foraging patch choice. But *within* these two choices the forager could still operate to be as efficient as possible (max. the rate of intake). Selection might not favor this rate efficiency where the risk is associated with particular components within the feeding sequence that cannot be separated out. For example, the risks associated with attacking dangerous prey cannot be separated from the feeding sequence. After higher level decisions have been made (when to forage, where to forage), they are still present and may dominate the choice as to which prey types to attack.

## 2.2 A Foraging Hierarchy

The arguments in the last section suggest that a first order theory of optimal foraging could focus on the level of action during a feeding interval. Consider the choices or options left open to an animal after it has begun foraging. Certain decisions were made prior to this stage, but certain ones are yet to be made. We may classify these decisions by their place in a *foraging hierarchy*. One characteristic of this hierarchy is the time scale involved in the decision. As an example, consider a bird whose nesting habitat is a certain kind of woods. Once a year the bird makes a decision where to put its nest. This decision yields certain nearby places for foraging and their types may be termed *patches*. Finally, at any point in time the patches contain particular kinds of food items, some of which the bird will attack and some of which it will ignore. The patches visited may change on the scale of hours, while the choice of food items may be on the scale of minutes. Obviously, all of these interact to produce the actual foraging behavior in any time period. In building optimal foraging models, it is often desirable to look at one level at a time, holding the other levels constant or rather considering them to be decisions that the animal has already made. These decisions yield a set of options for control (by the animal) at the level of interest. All of the models in the literature do this, at least implicitly.

Figure 2.1 shows our conception of a typical foraging hierarchy. There are, of course, many other useful hierarchies; some of these will be implicit in the models we investigate. However, the basic concept exemplified by this organization will permeate all of our discussions. A patch (MacArthur 1972) is considered to be a place where a predator, for a specified time interval, encounters particular kinds of prey. Generally a predator can be in only one patch at any one time, although there may be several ways of hunting in any one geographic patch. Classically, the within patch (*fine-grained*) conception is one of predators encountering prey types in proportion to their abundance (MacArthur and Levins 1964). The difficulty with this is that while abundance is generally equated with density, theoretical considerations suggest that it is not possible to separate prey density from other factors in the encounter process such as size of the predator's perceptual field (Paloheimo 1967). Thus, if larger prey are seen further away or if moving prey have a higher recognition probability, these are encountered more frequently than smaller or non-moving prey at the same density (Ware 1971). For this reason, abundance will be replaced with the idea of encounter rate in the fine-grained models developed here.

**Figure 2.1 A typical hierarchical choice during foraging.**



(1) Questions at level 2 relate to which patches are to be visited and how much time is to be spent in any given patch. The habitat is given and levels 3 and 4 are represented by some function f(t), which relates food intake to time spent in the patch.

(2) There may be several methods of hunting within any single patch. Models at this level consider the prey types taken as fixed and look at alternate searching methods.

(3) Choices at the upper 3 levels yield encounter rates with some set of prey types. Questions at this level relate to the rejection or acceptance of the various prey types.

## 2.3 Fitness as a Life History Concept

As previously mentioned, *fitness* is measured over the entire life history. Often our models represent games and goals on a much shorter time scale, and it is usually very difficult, if not impossible, to know just how important these many individual decisions are in overall fitness. Decisions that are made often may be rather unimportant individually, while decisions that commit the animal for the future (where the future is a long time relative to the life cycle) may be individually very important.

For example, nest placement is of much more importance than whether or not a certain prey item (small insect) should be passed over.

Since fitness must be measured over entire life cycles, the possibility exists that the appropriate time intervals for maximizing the benefits of foraging behavior is over a longer period than we usually consider in our models. This long-term maximization requires that benefits foregone at the present time be repaid in greater benefits in the future and that they accrue to the individual phenotype or kinship group. The usual conception in optimal foraging, which ignores these resource management ideas, might best be termed "pure competition" in the sense of economics. Under this view, animals perceive their world as a set of options, from which they pick some optimal set. No single individual or kinship group has enough effect, or control, over the food resources to manage them for increased yield over some longer time interval. The animal is forced "do its best" at any point in time because foraging in a non-optimal way now only increases the feeding time or decreases the catch now, with no future compensations. This is the "open fishery" model of foraging and implies that no single unit can benefit itself by giving up catch today for increased catch tomorrow.

Some examples where long-term maximization may be a useful concept are as follows:

1. If an individual or kinship group can have a drastic effect on the food resources and the effect is "knife edged" in the sense that, after a certain harvest level, a boundary is reached where the food rapidly disappears, then selection for harvest ability beyond this level is absent. This must be so since fitness drops to zero at the boundary and any individual pushing beyond it is not comparatively more fit. If the population is divided into many separate units where the decis-

ions of a single individual can lower the average fitness in a unit, the possibilities for group or kin selection exist.

2. If an individual can exclude other individuals from part of a food resource (close the fishery), the individual possibly can harvest the food over some extended time period. The maximization here might be the total catch over the interval. Huffaker (1970) has suggested something similar to this for animals that use their territories as foraging grounds. Brown (1964) developed the idea of "resource defendability" for those resources where inputs of time and energy in defense increase the net yield of resources to the defender.

A few examples will illustrate these ideas. Suppose that the prey can respond to the presence of the predator through behavioral changes so as to become less available through time. It may be worthwhile for the predator to hunt in such a way as reduce this scarcity effect, even if this reduces the food intake rate in any small time interval. What is necessary is that the action results in increased availability at future times over that which would perhaps result from other hunting methods.

Now suppose, for example, that depletion of resources takes place over a period of time. Defense may be worthwhile against conspecifics and perhaps other species, but still the resource must be undefended relative to some potential exploiters. Birds can hardly keep insects from eating other insects. If the resources are unequally vulnerable to losses from the other exploiters, it may well pay the defender to attack first just those resources that disappear fastest, even if the present capture rates are decreased. Likewise, since prey species grow in individual size during some seasons, it may pay a predator who has *some* "exclusive" rights to a foraging area in these seasons to pass by some prey species, letting them grow. What is needed for these to evolve is that the gain to the predator in the future is sufficiently greater to outweigh the present cost in energy foregone.

3. Food resources change in availability through time and space. Information about probable changes may be important in the foraging strategy. An organism may spend time and energy now to gain knowledge useful at some future time. The "curiosity behavior" may take place during current feeding periods and thus lower the present food intake rate below the possible optimum. This "apparently non-optimal foraging" is worthwhile and favored if the food resources change in availability *and* there are sources of information whose benefits are preferentially available to the finder to outweigh the costs of gaining the information. Holling (1965) has discussed in some detail the fact that many animals investigate or sample new "food" objects placed in their environment. This is especially important for herbivores where jucicious sampling may be necessary to determine the toxic properties of various foods. One ultimate factor in the evolution of colonial nesting in birds is that the colony area is an information center—it allows birds to use their neighbors' foraging success to guide their own efforts (Horn, 1969). In this case, information is not exclusive to the finder because the food must be delivered to the young.

Even though we clearly recognize the possibilities for these long-term strategies, we believe that in many cases organisms are under strong selection pressure to forage "efficiently" over short time spans and it is here that we will concentrate most of our effort.

## 2.4 Some Thoughts on Hypothesis Testing

Suppose that we are comparing the behavior of a predator to the predictions of a formal model. In order to generate the predictions, we assumed a goal and a game. If we tentatively accept that any experimental or observational test does not allow us to reject the *goal*, then the initial rejection, if the data do not support the hypothesis, is appropriately at the level of the *game* under consideration. The first question is, What is wrong with the game that was assumed? Progress in understanding predator behavior under this method comes from refining the games.

However, at least two other kinds of rejection are possible. The first is that the behavior observed, which was at variance with the hypothesis, is related only to the rate of food intake, but that an incorrect goal was assumed. Holling (1974) has suggested that fitness may be "boundary oriented." By this he means that fitness may depend very much on what the animal does when things are unfavorable; when things are good, it is much less important what an animal does. Selection would then favor the ability to handle the "bad times" over the ability to handle the "good times" in a trade-off situation. In terms of energy intake, selection would perhaps maximize the probability that an animal meets some energetic heed, as opposed to maximizing the average intake rate.

The second type of rejection is that the behavior observed is not a result of a rate of food intake decision by the animal. For example, a behavior may be related to predation risk or risk of injury by dangerous prey. The foraging strategy of animals attacking potentially dangerous prey must include behavior to lower the risk. Likewise, if some patches in the habitat have higher risk associated with them (e.g., predation, water loss), the patch choice will reflect the differential risk. Since at present we lack a common unit to compare units of risk and energy, it is very difficult to put them both in the same formal model.

Ideally, tests of optimal foraging ideas should be able to distinguish between alternative games and should allow us to reject some games in favor of others. The tests also should allow us to reject optimal foraging explanations in favor of other ultimate factors (or vice versa). As we shall see, these ideals are met only partially in practice. In addition, the behavior itself may reflect several ultimate factors and several time scales.

## Chapter 3. Characteristics of Predators and their Prey

All organisms require energy and are, in a real sense, predators, even though we do not normally regard, say, green plants as predators on photons and mineral nutrients. The sources of energy are varied and the predators that use them correspondingly are diverse, so that any attempt to develop general hypotheses about predation processes must be sensitive to these variations and utilize rather than ignore them. Conceptually we find it useful to divide these variations into a few categories of key significance for optimal foraging theory.

**Predator–Prey Size Relations.** Some predators exploit prey so small relative to their own size that individual prey are not recognized. At the other extreme, some predators utilize prey so large that the entire life cycle of an individual predator can be carried out on or within a single prey individual or even within or on a specific part of a prey individual. These size relations are important because they are the prime determiners of the frequency with which decisions about prey must be made and, consequently, the importance of an individual decision. In general, the smaller the prey relative to the predator, the greater the frequency of decisions and the less significant is each individual decision. As the size of the prey increases relative to the size of the predator, the frequency of decisions decreases and each decision becomes more important until a single decision may affect the entire life cycle or a number of life cycles of the predator.

**Defenses of the Prey.** With some interesting exceptions, some of which we will explore in detail, most prey have evolved defenses that render them less palatable, more dangerous, more difficult to locate or more difficult to capture. Defenses related primarily to the probabilities of capture make it profitable for the predator to evaluate prey items in terms of their expected energy value, the average being taken relative to the capture probabilities. Other defenses, particularly chemical, cannot readily be expressed in terms of calories and capture probabilities. Rather they may affect the health of the predator over longer time intervals, and their effects may depend upon their frequency in the diet.

With these general characteristics of predator–prey relationships in mind, we consider a classification of types of predators. Our objective is to set the stage for the kinds of foraging models most appropriately developed for each. This classification is not a "real" or "natural" one, but simply a scheme that groups organisms in a way that is useful for the kinds of questions we have posed about the predation process. Other questions would doubtless lead to other classification schemes. We recognize six types of predator:

1. Filter (suspension) feeders,
2. Detritivores (deposit feeders),
3. Parasitoids and parasites,
4. Typical predators,
5. Herbivores,
6. Mutualistic foragers.

We will deal mostly with 4, 5 and 6, but include the others in this general chapter to point out some of the factors that we feel to be important in their foraging strategies.

## 3.1 Filter (Suspension) Feeders

This category of predators includes those whose prey are small enough that they are handled in mass, not one at a time. The prey retained by the filtering device of the predator are a function of mesh diameter and all possible meshes have upper and lower size limits. Small prey pass through the net while larger prey either bounce off it or are large enough to escape the net by active movement. Often these large prey are handled as individual particles and the anatomy for these functions may be different from the filtering device (Jorgenson 1968). This type of predator is most characteristic of aquatic environments and the prey are plankton.

An important characteristic of filter feeding is that most of the energy cost involved in foraging is expended *prior* to the moment the prey come in contact with the mesh. Hence, the decision to accept or reject a prey item cannot save the energy required to bring the prey to the predator. In fact, the rejection of a prey item may require an additional expenditure of energy to remove it from the filter and the process of removal may interfere with the filtering process. Thus, many prey that can be poorly digested and assimilated by the predator are nonetheless ingested.

A key decision for a filter feeding organism is where to locate its filter (this decision may determine, or at least limit, the temporal pattern of feeding). Often movement to a new location carries a high mortality risk or is costly in terms of the time and energy given up in the move. Further, it may be costly to sample new locations, particularly if "getting set up for business" requires the construction of an elaborate filtering device. Finally, the presence of competitors may make finding a new location difficult or the absence of clues as to what is a good place (predictability) may reduce the probability that a move will result in an improvement. However, it is known that some spiders are more prone to move their webs when they experience prolonged low capture rates (Turnbull 1965, Eberhard 1971).

## 3.2 Detritivores (Deposit Feeders)

In most ecosystems the bulk of the energy entering a given trophic level does not pass to higher trophic levels, but instead is lost as heat or enters, on death of the organisms or parts of them, into the world of detritivores. The food of detritivores is non-mobile, but it may be moved from the site of its death to its final resting place. During this movement the prey may be concentrated in particular areas by gravity, stream flow or wind, so that certain locations are much better for a detritivore than others. The spatial and temporal characteristics of detritus distribution depend upon whether it was derived from a plant or an animal. The plant life style is characterized by regular senescence of parts (leaves, bark, flowers, fruit) that tend to be widely dispersed and to appear in the environment on a reasonably predictable basis during the year. Animals, on the other hand, normally die in one piece and provide an unusually rich and concentrated supply of food which is, however, highly unpredictable in space and time. The organisms exploiting these different forms of detritus, not surprisingly, have different life cycles and foraging strategies.

When an organism dies, its defensive mechanisms against predators cease to function. Some defensive mechanisms, such as behavior, immediately become inoperative, while others, such as some chemical defenses, may persist for longer periods of time. However, since most chemical defenses require energy to maintain them within living cells, they are unlikely to remain very long and it is difficult to imagine any selective advantage to an organism from defending its detritus. Therefore, detritus can normally be expected to be an easier source of food to utilize than the living organisms from which it was derived. Subsequent changes in the chemical composition of detritus should reflect primarily changes brought about by the metabolic activities of the earlier organisms that fed on it. Dietary specialization by detritivores might take the form of (1) the nature of the *deposits* exploited and the methods by which they are located, and (2) within a deposit, what chemical processes the animal is specialized to use (i.e., some breakdown by another organism might be necessary before species X can use the resource).

## 3.3 Parasitoids and Parasites

Many parasites spend their entire life cycles within the confines of a single host individual and the choice of prey is an oviposition choice of the adult female. Even for those parasites with complex life cycles involving several host species, a choice of prey need only be made once for each of the major stages in the life cycle, and successful completion of that stage depends upon the correctness of that choice. Therefore, each choice exerts a major influence on the fitness of the organism. Despite the importance of foraging decisions for a parasite, making accurate evaluations of prey is peculiarly difficult for them because the act of predation, i.e. laying an egg on the host or even the completion of the life cycle of the parasite, does not destroy the host. The host continues to survive, at least for a time, and is available to be exploited by other parasites and predators. Nevertheless, the suitability of the host is normally changed if it is already parasitized. The first act of parasitization may mobilize the defenses of the host so that subsequent attacks are less likely to be successful. Conversely, the early attacks may weaken the host and increase the probability of success of subsequent attacks. An already parasitized host may have its behavior and other defenses altered so that it is more susceptible to being captured by one of its "typical" predators. Finally, many parasites and parasitoids are known to be cannibalistic and, in an encounter, the advantage usually goes to the larger of two individuals. Among species that parasitize small prey, such as most Darasitoids, this effect may be so severe that survival probabilities for individuals other than the first are vanishingly small. Thus, parasites face critical problems of estimating host vitality and resistance and the presence of previous parasites within or on the host.

## 3.4 Typical Predators

Included in this category are most organisms normally considered to be predators when predator–prey interactions are discussed in ecology courses and texts. These predators handle their prey individually and many decisions about individual prey items normally must be made during the lifetime of a predator, or even within a single feeding period. This kind of predator has been the object of most of the optimal foraging models previously constructed, but for the most part complications of prey defenses have not been dealt with in these models. One of our objectives in this book is to explore the implications of bringing these complications into foraging theory. We also will deal with problems related to the use of a patchy habitat; this corresponds to level 2 in our hypothetical foraging hierarchy.

## 3.5 Herbivores

In this category we include all animals that chew on, chew up, burrow into or tap into the tissues of living plants, with the exception of those animals that utilize plant tissues that have evolved “to be eaten” by animals (see mutualistic foraging). The prey of these animals are non-motile, but vary enormously in size. In aquatic ecosystems, green plants are among the smallest organisms in the system and the most abundant herbivores are filter feeders. In terrestrial systems, however, green plants often are the largest individuals in the system and their herbivores may be the largest animals living there. For this reason it is difficult to characterize the predator–prey size ratios for this class of predators, but this is a less serious handicap than might be imagined, because the critical importance of the chemical defenses of plants (Whittaker 1970) normally over-rides energetic considerations in prey selection by herbivores. Moreover, since individual plants often are highly subdivided, an herbivore seldom eats all parts of its host plants, and in most cases the concept of the amount of energy per individual prey is not relevant. There is, however, a range of frequencies with which choices of food plants must be made by different kinds of herbivores. Many insects, for example, make a foraging decision only once during their life cycle, at oviposition, while many herbivorous mammals must choose from among many different plants every day. Accordingly, we will divide our consideration of herbivores into size ratio groups and then consider the significance of chemical and physical defenses of the plants for each of these classes of interaction.

## 3.6 Mutualistic Foragers

While most of the prey we have considered enhance their fitness by not being consumed by a predator and have evolved characteristics that negatively influence the probability that they will be consumed, there are food sources that have evolved to be attractive. The prime example of this involves reproduction in terrestrial plants. Green plants are of necessity stationary in a medium offering limited possibilities for the exchange of genetic material among individuals by purely physical means. The physical environment also offers limited possibilities for dispersing the offspring of plants. Nevertheless, there is evidence that survival probabilities of offspring are better away from the parent plant (Janzen 1970). So important are these considerations that the evolution of terrestrial plants is much more a matter of variations and elaborations of methods of dispersing pollen and offspring than of differences in means of capturing energy. The directional and non-storable nature of light dictates that the general form of energy trapping devices will be conservative and explicable by relatively few factors (Horn 1971).

While the total energy exchange involved in mutualistic foraging may be relatively small, its impact on community structure and the evolution of both the predators and the prey is great. The variations in the temporal and spatial characteristics of the resources provided to mutualistic foragers by plants appear to be related to their influence on the foraging itineraries and decisions of individual mutualistic foragers (eaters of pollen, nectar and fruit), but mutualistic foragers are not mutualistic in the sense of adjusting their foraging activities to the "needs" of the plants. The interesting aspects of mutualistic foraging are those dealing with the ways in which foraging behavior of these animals can be "manipulated" by plants to increase pollen transfer and seed dispersal. However, to avoid unwarranted assumptions about the "role" of these animals, we will use terminology that refers to the resource the animals actually use (i.e., pollen, nectar or fruit) and avoid terminology that refers to what we think the animal may contribute to the fitness of the plant.

# PART II. SOME SPECIFIC OPTIMALITY MODELS

The first two chapters in this section deal with two questions. The first is, which kinds of prey should a typical predator attack when the encounter with prey types is fine-grained? The second is, if the prey are separated into clumps or patches (so that a fine-grained model can be assumed only within a clump or patch), which patches should be visited and how much time should be spent in any patch? These are the classic questions of optimal foraging theory. Our formulations are related to the literature in a review in Chapter 6. In Chapter 7 we give a rigorous treatment of the classical questions using a stochastic argument. Chapter 8 considers herbivores where the value of a prey cannot be measured in calories, while Chapter 9 extends some of our earlier notions to mutualistic foragers. Evidence for the various hypotheses is presented in the appropriate chapter.

# Chapter 4. Fine-grained Foraging Models for a Typical Predator

The predator to be modeled has the following characteristics:

1. It encounters individual prey items. The search may be considered only in time or movement, through space may also be modeled.
2. The prey items are handled one at a time and this handling time is unavailable for searching, no new prey may be encountered during the handling of a prey item.
3. When a prey item is encountered, some time may be needed to recognize what type of prey it is. After recognition, the predator has a choice of going after the item or not.
4. The prey are not so large as to be dangerous to the predator.

The models are static and do not specifically include changes in prey abundance. Since all decisions (patch, search mode, etc.) down to the level of the prey types actually attacked are assumed to have been made already, the models will be concerned with the choice of prey types or the parts of prey to consume. For a goal it seems reasonable, at this level, to have the predator maximize the rate of food intake while it actually is foraging. To begin, we must determine the units with which we shall measure the value of a food item. Rapport (1971) simply used "benefits" for *food value* and did not specify the units. Food value often is measured in terms of elementary food types (protein, fat, carbohydrate), specific nutrients, or calories per gram. We have found no literature however, that expresses the costs of foraging activity in any unit other than calories. If foraging models are to express the gain to the predator in terms of *net gain*, the food value for the prey items must be in the same units as the costs of the activity. At present this seems to dictate the calorie as the food value unit. Even if the food value of an item is measured in calories, the cost of the foraging activity is in "physiologically useful calories" (Warren 1971). To be equivalent, this food value also must be measured in these "useful" calories. This means using at least assimilated calories, and eventually we may wish to correct for things such as the internal costs of food processing. The literature on fish energetics suggests that assimilated calories may be the most usable measure at present (Warren and Davis 1967, Warren 1972, Hanson 1972, Kear 1971a,b,c, Paloheimo and Dickie 1965, 1966). For the purpose of this and the following chapter, then, the *goal* for a foraging game is: "The maximization of net assimilated calories per unit time during a hunting period."

## 4.1 Handling Time of a Prey Item

To develop a model for the caloric value of a prey item, first we need to specify the handling times involved with the item. The model is static, but takes into account the time lost in unsuccessful attacks by including the probabilities of such events in the caloric value of the prey. The main parameter of interest is $h_j^*$, defined as the mean handling time for an item of prey type j. The handling time sequence we are assuming is shown graphically in Figure 4.1 for some prey type j. There are, of course, many other possible assumptions, but these will illustrate the basic ideas. We define as follows:

$h_0$ = Time to recognize the prey item as type j after the predator has perceived a prey item

$h_1$ = Time for the predator to get close enough to the item to try to kill it (pursuit)

$h_2$ = Kill or attack time

$h_3$ = Time to eat the item plus any digestive pause

After Holling (1966), we assume the following conditional capture probabilities for type j.

$S_R$ = prob [a prey item is perceived/one is encountered]

$S_P$ = prob [the predator gets close enough to try to kill item/item is recognized and the predator chooses to go after it]

$S_a$ = prob [the predator kills and eats item/predator gets close enough to try to kill (attack)]

Implicit in the model is that any item seen will be recognized in $h_0$ and that the time lost in pursuit or attack of an item not eaten is the same as for an item that is killed and eaten. One more useful parameter is $P_j$:

$P_j$ = prob [predator goes after j after recognition]

This parameter is controlled by the predator.

The possible time events and associated probabilities are as follows:

| Activity | Time for Activity or Event | Probability of Event |
|---|---|---|
| Prey not seen | 0 | $1 - S_R$ |
| Prey recognized, not pursued | $h_0$ | $S_R \cdot (1 - P_j)$ |
| Prey pursued, but no attack | $h_0 + h_1$ | $S_R \cdot P_j \cdot (1 - S_P)$ |
| Prey pursued, attack fails | $h_0 + h_1 + h_2$ | $S_R \cdot P_j \cdot S_P\ (1 - S_a)$ |
| Prey eaten | $h_0 + h_1 + h_2 + h_3$ | $S_R \cdot P_j \cdot S_P \cdot S_a$ |

It follows that:

$$h_j^* = S_R[h_0 + P_j \cdot (h_1 + S_P \cdot h_2 + S_P \cdot S_a \cdot h_3)] \tag{2}$$

Figure 4.1 Handling time sequence for a prey item.

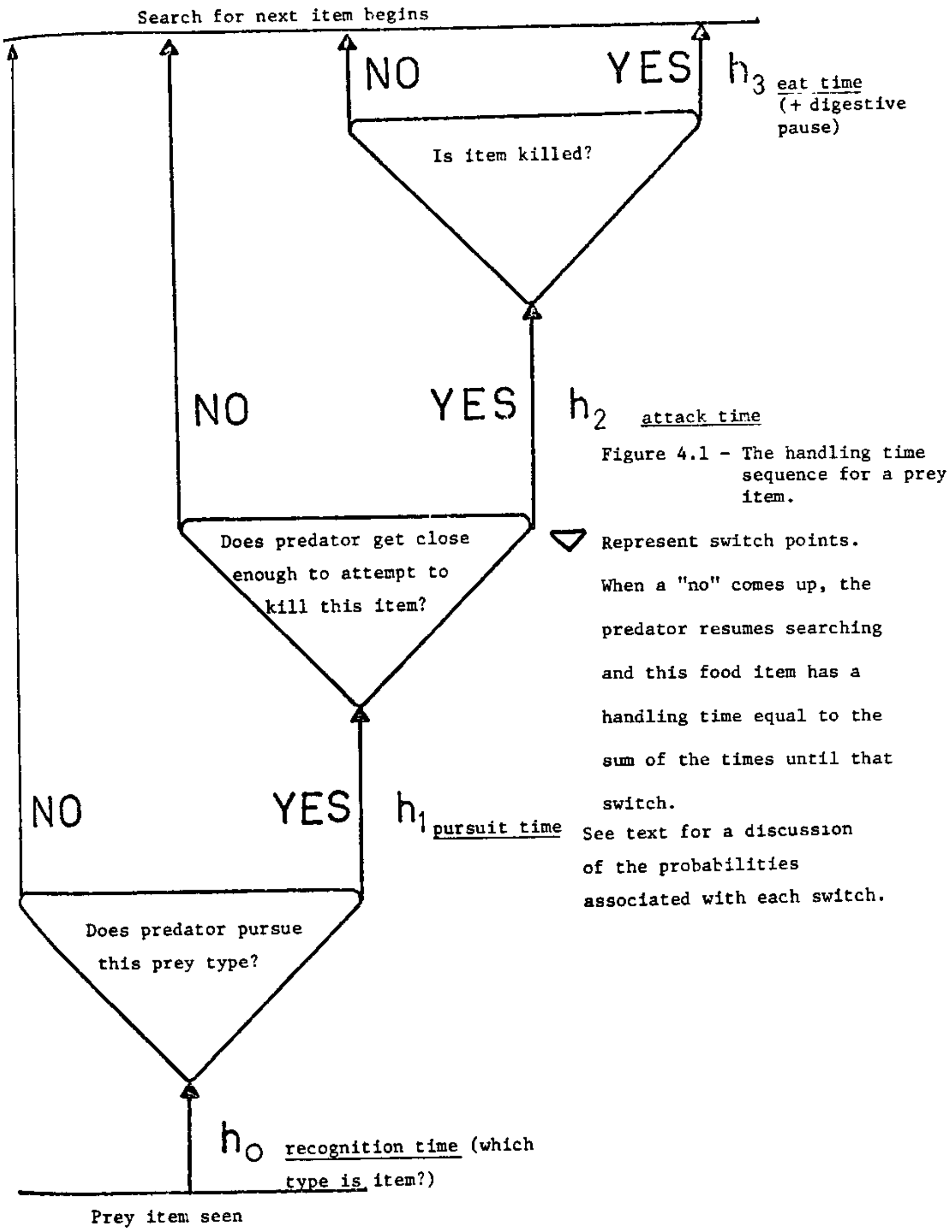


Figure 4.1 - The handling time sequence for a prey item.

▽ Represent switch points. When a "no" comes up, the predator resumes searching and this food item has a handling time equal to the sum of the times until that switch.

See text for a discussion of the probabilities associated with each switch.

## 4.2 Food Value of a Prey Item

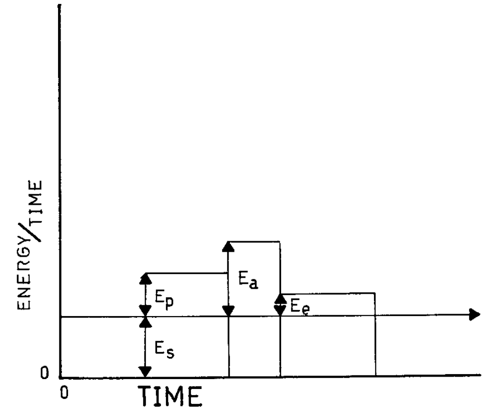
The food value assumption must account for all of the energy during the handling time. The assumption is "knife edged" with one cost applied during pursuit, another during attack, etc. Figure 4.2 shows the assumption for some prey type j. Note that all costs subtract off the cost of searching ($E_s$) from the actual cost of the activity. This parameterization is one of two that are particularly useful, as will be apparent in the development of a renewal theory model of predation.

**Figure 4.2 The energetic costs of handling a prey item.**

$E_S$ is the cost per unit time for searching.

$E_P$ is the cost per unit time during the pursuit time $h_1$, measured above the basic Es search cost.

Ea and Ee are similar costs during the attack time and the eating time, respectively.



Assume as follows:

$E'_R$ = energy expended per unit time during $h_0$ = $E_S$
$E'_P$ = energy expended per unit time during $h_1$ (pursuit)
$E'_a$ = energy expended per unit time during $h_2$ (attack)
$E'_e$ = energy expended per unit time during $h_3$ (eating)
$E_S$ = energy expended per unit time while searching
$E''_j$ = assimilated energy from one item of prey type j

Then let:

$$E_R = 0$$

$$E_P = E'_P - E_S$$

$$E_a = E'_a - E_S$$

$E_e = E_e^{'} - E_S$

$E_k^*$ is defined to be the expected net energy from one item of type j.

The possible events and associated probabilities are given below:

| Event | Probability | Energy Value |
|---|---|---|
| No prey seen | $1 - S_R$ | 0 |
| $h_0$ | $S_R \cdot (1 - P_j)$ | 0 |
| $h_0 + h_1$ | $S_R \cdot P_j \cdot (1 - S_P)$ | $-h_1 \cdot E_P$ |
| $h_0 + h_1 + h_2$ | $S_R \cdot P_j \cdot S_P \cdot (1 - S_a)$ | $-(h_1 \cdot E_P + h_2 \cdot E_a)$ |
| $h_0 + h_1 + h_2 + h_3$ | $S_R \cdot P_j \cdot S_P \cdot S_a$ | $E_j^{''} - (h_1 \cdot E_P + h_2 \cdot E_a + h_3 \cdot E_e)$ |

It follows that:

$$E_j^* = P_J \cdot S_R \cdot [S_P \cdot S_a (E_j^{''} - E_e \cdot h_3) - h_2 \cdot S_P \cdot E_a - h_1 \cdot E_P] \quad (2)$$

One quantity that will be useful is $A_j^*$.

$$A_j^* = E_j^* - S_R \cdot h_j^* \cdot E_S \cdot P_j \quad (3)$$

## 4.3 A Fine-grained Foraging Model

An equation giving the rate of energy intake in a fine-grained situation may be derived as follows.

Let E be the energy taken in during a feeding period of length $\tau$. $\tau$ is made up of $T_s$ (time searching) and $T_h$ (time handling all prey items). A net rate of energy intake ($E_n$) is:

$$E_n = \frac{E}{T_h + T_s} - E_S \quad (4)$$

Let there be k prey types, each type (i) having the following three characteristics:

$\lambda_i$ = number of prey type i encountered in one unit of search time

$E_i^*$ = Equation 2 (expected net energy from one item of type i)

$h_i^*$ = Equation 1 (mean handling time for an item of prey type i)

It follows directly that:

$$E = \sum \lambda_i \cdot E_i^* \cdot T_s$$

$$T_h = \sum \lambda_i \cdot h_i^* \cdot T_s$$

$$E_n = \frac{\sum \lambda_i \cdot E_i^* \cdot T_s}{T_s + \sum \lambda_i \cdot h_i^* \cdot T_s} - E_s$$

or

$$E_n = \frac{\sum \lambda_i \cdot E_i^*}{1 + \sum \lambda_i \cdot h_i^*} - E_s \qquad \textbf{(5)}$$

The first term in Eqn. 5 is a multi-species version of the Holling Disk Equation (Holling 1959). In Eqn. 5, the only things that the predator can control are the values of the $P_i$, whether or not it will go after an item of prey type i. Since $E_S$ is taken to be a constant, Eqn. 5 may be rewritten as follows with a new quantity (Q/R) defined:

$$\frac{Q}{R} = E_n + E_s = \frac{\sum \lambda_i \cdot E_i^*}{1 + \sum \lambda_i \cdot h_i^*} \qquad \textbf{(6)}$$

It will be useful to recognize two cases for Eqn. 6:

a. All $h_0 = 0$,

b. Some $h_0 > 0$.

In a., the recognition of prey types is instantaneous. This situation provides for the proof of a theorem that is basic to the understanding of recent theory in this area. It has a rather interesting history. A special case was proven by MacArthur and Pianka (1966). Pulliam (1972) proved the two prey type case and Werner (1971) proved a still more general case. In 1970–71 at least three people proved it in its most general deterministic form in unpublished work (Charnov 1971, Timmins 1971, Pearson 1971), and Schoener (1969, 1971) derived the basic Eqn. 5 and proved one part of the theorem. The proof given below is that of Charnov (1971, 1973). The theorem is even more general than given here (Charnov 1973), as we shall show after we reformulate the problem as a stochastic process through time (Chapter 6). Finally, a version of the theorem is in MacArthur (1972), although it appears without proof or derivation. MacArthur did, however, stress the most general and important part of the theorem. In Chapter 5, we shall review some of this literature. Because of its central place in recent theory, we will call it a fundamental theorem of optimal foraging.

### 4.3.1 A Fundamental Theorem of Optimal Foraging (FT)

If all $h_0 = 0$, Q/R is maximized when:

1. $P_i = 0$ or 1 ($i = 1, 2 \ldots k$);
2. If the prey types are ranked by the ratio $\frac{E_i^*}{h_i^*}$ , then whether or not a prey type i should be eaten is i) independent of the abundance of type i (independent of $\lambda_i$) and ii) dependent only upon the abundances of those prey types with rank higher than i;
3. The set of prey types to be eaten (the *optimal set*) are those of rank such that:

$$\frac{E_j^*}{h_j^*} > \frac{Q^*}{R} \tag{7}$$

(When Q and R include *only* the optimal set, we will write Q as Q*, thus when Q/R is maximum, it will be written Q*/R.)

These assertions can be proved as follows:

For some prey type *c* assumed not to be in the optimal set, the following inequality must hold:

$$\frac{Q^*}{R} > \frac{Q^* + \lambda_c \cdot E_c^*}{R + \lambda_c \cdot h_c^*}$$

which implies that type *c* has the characteristic that:

$$\frac{Q^*}{R} > \frac{\lambda_c \cdot E_c^*}{\lambda_c \cdot h_c^*} = \frac{E_c^*}{h_c^*} \tag{8}$$

It also is easy to show that the inequality in Eqn. 8 is the condition for $\frac{\partial Q/R}{\partial P_i}$ to be negative, so that *no* prey type in the optimal set makes Eqn. 8 true.

This means that a prey type (j) in the optimal set has the characteristic that:

$$\frac{E_j^*}{h_j^*} > \frac{Q^*}{R}$$

which proves statement 3.

$$\frac{Q^*}{R} > \frac{Q^* + \lambda_c \cdot E_c^*}{R + \lambda_c \cdot h_c^*}$$

Statement 1 is true because Eqn. 7 is either true or false, independent of the value of $P_j$. If true, $P_j$ should = 1; if false it should = 0. Statement 2 is true because $\lambda_c$ cancels out of Eqn. 8. Only those prey types in the optimal set determine Q*/R, so that type c cannot get itself added to the optimal set by being very abundant (e.g., λ large). As the abundance of some type in the optimal set gets large ($\lambda_j \rightarrow \infty$), $Q^*/R \rightarrow E_j^*/h_j^*$, which results in all prey of lower rank being dropped out of the optimal set. Prey type j should be dropped from the optimal set if still higher ranked prey become abundant enough. Figure 4.3 is one useful way of showing these relations. Prey types are accumulated in Q/R in rank order. In Figure 4.3 for some set of $\lambda_i$, the optimal set includes prey types of rank greater than the rank of type 9.

**Figure 4.3 Choice of an optimal set of prey types . . I.**

The prey types are first ranked by the $E_i^*/h_i^*$ ratio and then the cumulative Q/R is calculated by adding prey types to Q/R in rank order.

Q/R is maximized for a set of prey types of rank above the prey type (m), where Q/R first becomes > $E_m^*/h_m^*$ .

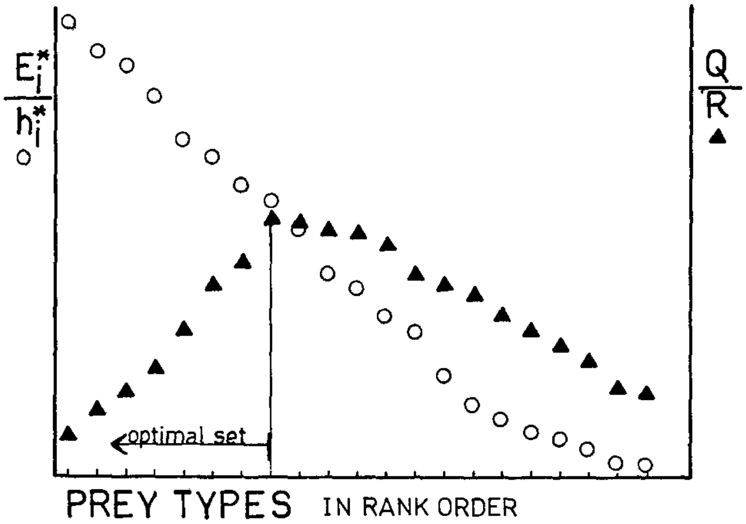


Figure 4.4 is the most general graphical solution for this problem. Individual prey items have associated with them an $E_i^*$ and $h_i^*$ and so may be plotted as points on a graph with coordinates $E_i^*$ and $h_i^*$ . If the ray from the origin with slope Q*/R is plotted, the optimal set includes all prey items above the ray. A–B is meant to represent some prey species. Those individuals close to A are in the optimal set, those close to B are not. A decrease in abundance of a prey above the line causes Q*/R to decrease, an increase in abundance causes Q*/R to increase. If (for example) point *c* in Figure 4.4 has an associated $\lambda_c$ that gets very large ($\lambda_c \rightarrow \infty$), the ray gets steeper $\left(\frac{Q^*}{R}\uparrow\right)$ until it passes through the point *c*. Point *c* also serves to illustrate a useful corollary to the theorem.

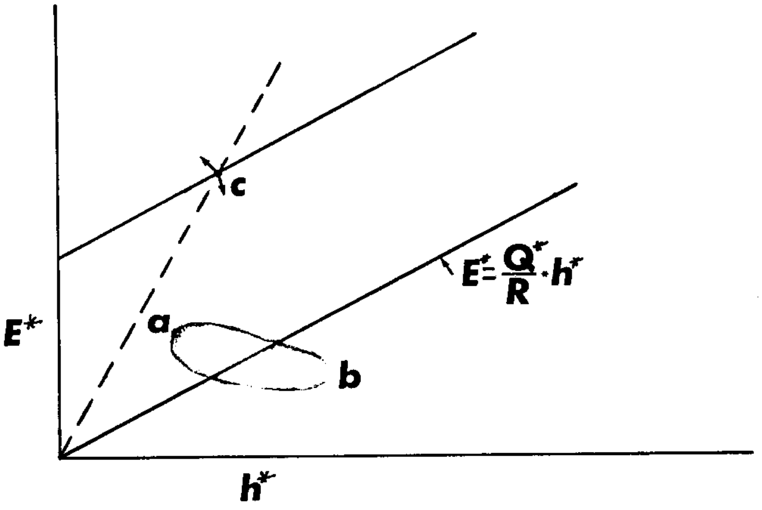


**Figure 4.4 Choice of an optimal set of prey types . . . II.**

Prey types are points on the (h*, E*) plane. The optimal set includes all prey types above the ray from the origin with slope Q*/R.

A single prey species may contain many prey types. a-b represents a single species. Those individuals near *a* are in this optimal set, those near *b* are not.

The point c is a prey type in this optimal set. If we shift c along a line with slope Q*/R, Q*/R does not change in value. If c is moved to above this line, Q*/R increases; if it is moved to below the line, Q*/R decreases.

If $\lambda_i \to \infty$, Q*/R increases until finally it equals $\frac{E_c^*}{h_c^*}$ and can be represented as a ray from the origin passing through c.

**Corollary 1** (referring to Figure 4.4):

If any prey type in the optimal set (e.g. *c*) is shifted in position on the $\left(h_i^*, E_i^*\right)$ plane, the shift has one of three effects.

1. If the shift is along a *line* passing through the point with slope = $\frac{Q^*}{R}$, $\frac{Q^*}{R}$ is unchanged in value.
2. If the shift is to above the line, Q*/R is increased in value.
3. If the shift is to below the line, Q*/R is decreased in value.

Proof: Let $P_c = 1$, and be associated with a Q/R [which we take to be Q*/R, although it need not be assumed that Q/R = Q*/R]. Write the new coordinates of point *c* as follows:

$$E_c^*(\text{new}) = E_c^* + \Delta_c$$
$$h_c^*(\text{new}) = h_c^* + \alpha_c$$

The new Q/R is:

$$\frac{Q}{R}(\text{new}) = \frac{Q - E_c\cdot\lambda_c + [E_c^* + \Delta_c]\cdot\lambda_c}{R - \lambda_c\cdot h_c^* + [h_c^* + \alpha_c]\cdot\lambda_c} = \frac{Q + \Delta_c\cdot\lambda_c}{R + \alpha_c\cdot\lambda_c}$$

If Q/R is not to change in value, $\frac{\Delta_c}{\alpha_c}$ must equal Q/R and so the point *c* is to be shifted along a line with slope equal to Q/R. Results 2 and 3 follow from the appropriate substitutions for $\Delta_c$ and $\alpha_c$.

**Cost of a Mistake**. If a predator goes after a prey type not in the optimal set, it forfeits some energy. This cost of a mistake is calculated as follows. Q*/R is the energy intake rate while feeding on the optimal set. $\frac{E_m^*}{h_m^*}$ is the intake rate while handling an item of type m, not in the optimal set. The rate of energy loss is $\frac{Q^*}{R} - \frac{E_m^*}{h_m^*}$ and the energy forfeited is:

$$E_F = h_m^*\cdot\left[\frac{Q^*}{R} - \frac{E_m^*}{h_m^*}\right]$$

It is clear that the cost of a mistake with prey types of equal rank increases as $h_m^*$ increases.

### 4.3.2 A Second Theorem

In case *b* some of the $h_0 > 0$, that is, it takes time to identify which prey type has been encountered. While the assumption of fixed $h_0$ is unrealistic, it will serve to illustrate the effects of an assumption of this kind. The derived result is discussed in terms of how it differs from the fundamental theorem. First, we rewrite Eqn. 6 as follows:

$$\frac{Q}{R} = \frac{\Sigma\,\lambda_i\cdot E_i^*}{1 + \Sigma\,\lambda_i\cdot S_{Ri}\cdot h_{0i} + \Sigma\,\lambda_i\cdot T_i^*}$$

where $T_i^* = h_i^* - [S_{Ri} \cdot h_{oi}]$.

The $P_i$ appear only in the $E_i^*$ and $T_i^*$ terms. Using the same definition for Q*/R and letting type m be a prey type not in the optimal set, we have an inequality similar to Eqn. 8:

$$\frac{Q^*}{R} > \frac{Q^* + \lambda_m \cdot E_m^*}{R + \lambda_m \cdot T_m^*}$$

which provides the rule that type m has the characteristic that: $\frac{Q^*}{R} > \frac{E_m^*}{T_m^*}$

The converse inequality holds for a prey type in the optimal set. This is similar to the result for case a and Figure 4.4 may be applied, replacing $h_i^*$ with $T_i^*$.

What is different from the previous case is the effects on the optimal set of changes in the $\lambda_i$. There are two cases here.

1. For some prey type m, not in the optimal set:

$$\frac{\partial \frac{Q^*}{R}}{\partial \lambda_m} = -\frac{Q^*}{R}\left[\frac{h_{om} \cdot S_{Rm}}{R}\right]$$

which is negative if $h_{om} > 0$. This prey type will be added to the optimal set if it becomes abundant and lowers Q*/R far enough. At that point it costs the predator too much time to reject the type, so it should be taken.

2. For some prey type j in the optimal set:

$$\frac{\partial Q^* / R}{\partial \lambda_j} = \frac{R \cdot E_j^* - Q^* \cdot h_j^*}{R^2}$$

The above is positive if $\frac{Q*}{R} < \frac{E_j^*}{h_j^*}$ and negative for the converse.

Thus, there are two kinds of optimal prey.

Kind I: $\frac{E_j^*}{T_j^*} > \frac{Q*}{R} > \frac{E_j^*}{h_j^*}$

Q*/R decreases with an increase in abundance ($\lambda_j\uparrow$) of this kind. As $\lambda_j \rightarrow \infty, \frac{Q*}{R} \rightarrow \frac{E_j^*}{h_j^*}$.

Kind II: $\frac{E_j^*}{T_j^*} > \frac{E_j^*}{h_j^*} > \frac{Q*}{R}$

Q*/R increases as $\lambda_j$ increases for this kind.

This double ranking, $\frac{E_i^*}{h_i^*}$ & $\frac{E_i^*}{T_i^*}$, makes the optimization problem a bit more complicated. However, some simple qualitative results follow directly. $h_0$ is a decision time; in situations when it is > 0, the predator has a lower Q*/R and is attacking lower ranked prey. From the prey's point of view, if the prey is of low rank ($\frac{E_i^*}{T_i^*}$ low), it may be advantageous for the prey to let the predator know with little or no time investment ($h_0 = 0$). Any prey of this type does not get itself added to the optimal set by increasing in abundance because $\partial \frac{Q*}{R} \Big/ \partial\lambda = 0$ if $h_0 = 0$. De Ruiter (1967) suggests that many animals have evolved means to interrupt a predator's attack cycle *early*. He mentions "signalling of inedibility" from afar as a well-known example among insect prey.

This second case (b) suggests that a rather important question is the one relating to what a given predator "recognizes" as a prey type. If the estimation by the predator is the E*/h* ratio for an item encountered, there are probably many ways to do this. Selection also will operate at the level of the signals or code used and many interesting questions arise. What are the trade-offs among codes? Are some codes accurate ($E^*/h^*$), but slow (high $h_0$), while others inaccurate but fast ($h_0$ low)? With the arrival of signals, the stage is set for the evolution of cheating.

## 4.4 A Special Case for a Single Prey Type

One other useful graphical result is to consider the prey type model (Eqn. 5) for a single prey type where an individual prey item has the characteristic that it can be fed upon for a variable time period. The predator is assumed to eat the "best parts" (in terms of energy intake per unit feeding time) first, then the next best parts, etc. In this way, the energy from a prey item (E") is a function of the time spent eating on it [e.g., E" = $f(h_3)$].

We further assume that the time and energy involved in an unsuccessful prey encounter are negligible so that Q/R may be written as follows (S is $S_R \cdot S_P \cdot S_a$):

$$\frac{Q}{R} = \frac{\lambda \cdot S \cdot f(h_3)}{1 + \lambda \cdot S \cdot h_3} = \frac{f(h_3)}{1/\lambda \cdot S + h_3}$$

$1/\lambda \cdot S$ is the time between two successful prey encounters (intercatch intervals). In Figure 4.5, two cases are represented for a single assumption for $f(h_3)$.

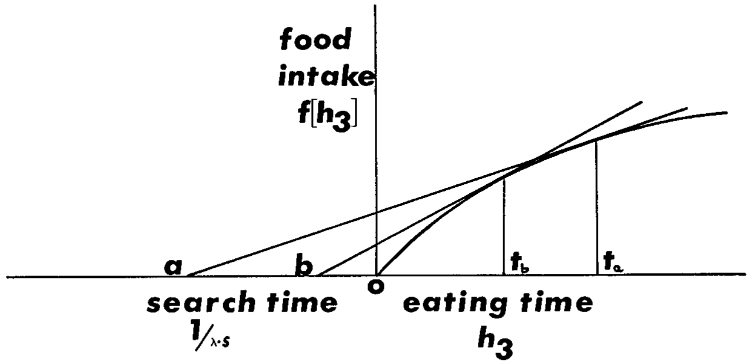


**Figure 4.5 Optimal use of a single prey type.**

$f(h_3)$ is the energy intake function for $h_3$ time units feeding on an individual prey item. $\frac{1}{\lambda \cdot s}$ is the average search time between items. The total rate of energy intake is $f(h_3)/(1/\lambda \cdot s + h_3)$. This is maximized for two cases (a, b), where $f(h_3)$ is held constant while $\frac{1}{\lambda \cdot s}$ is varied. The appropriate $h_3$ is where $\frac{\partial f(h_3)}{\partial (h_3)} = \frac{f(h_3)}{1/\lambda \cdot s + h_3}$ and decreases as $\frac{1}{\lambda \cdot s}$ decreases.

The lines passing through the intercatch time points and tangent to the $f(h_3)$ curve have slopes equal to $\frac{f(h_3^*)}{1/\lambda \cdot S + h_3^*}$, where $h_3^*$ is the $h_3$ at the point of tangency. This is Q*/R. As shown in the figure, the appropriate $h_3^*$ decreases as $1/\lambda \cdot S$ decreases. Where prey items are numerous, the predator should take less from each unit and spend less time doing it.

## 4.5 Tests of Some Hypotheses on the Fine-grained Use of Prey

### The Fundamental Theorem as an Hypothesis

To frame and test the fundamental theorem as an hypothesis, we need to know how the predator ranks prey and how prey are added to or dropped from the diet. If they obey the following two conditions, then at least the *qualitative* behavior of the predator fits the theorem. It will turn out that even at this level of testing, the necessary data are very difficult to come by.

1) Prey types are ranked by the ratio $-E_i^*/h_i^*$ and,
2) Whether or not a prey type is taken depends on Q/R [or some measure of food intake rate] such that low ranked prey are dropped from the diet as Q/R increases.

### 4.5.1 Ivlev's Laboratory Experiments with Fish

Often it is stated that one of the basic predictions from optimal foraging theory is that animals should be more "choosey" in the food they will eat when food is abundant (Schoener 1971). An example of the type of data gathered to demonstrate this is Table 4.1 (Ivlev 1961). Ivlev provided five kinds of food in a tank and calculated what was eaten by small carp (*Cyrinus*) in a one-hour period. He kept the relative densities of the kinds constant, but changed the absolute food density from P to 6P in steps of one. He does not tell us what the P density was and the data are average values (sample size unknown) for the percent occurrence by number in the gut. For this type of fish, the occurrence of some kinds of food went to zero at high food densities. This is consistent with the fundamental theorem, but it also must be consistent with a variety of other models. We have no idea if the prey are dropped out in order of the $E_i^* / h_i^*$ ranks.

Ivlev provides a similar experiment for a zooplankton feeder and this time the results do not show an alteration in the composition of the diet with increasing food abundance [Table 4.1]. He considered this to be a quite separate pattern from the former switching, but the pattern may not be different. Suppose we accept that his prey species are equivalent to prey types. The fundamental theorem says that some types will be dropped from the diet if the average rate of food intake is *high enough*. We have no way of knowing if the rate of food intake was high enough to cause this. Therefore, though the composition of the diet did not change [% occurrence of type Y remained constant], the results still could be consistent with the foraging model. One reason for suggesting this is that predators attacking prey where the $h_i^*$ and $E_i^*$ are small need comparatively high $\lambda_i$ to cause switching.

**Table 4.1:** The effect of increasing total prey density on the proportion eaten in a short term (1–1.5 hrs.) lab experiment with two kinds of fish [from Ivlev 1961].

| Food Type Density of Each Kind | Average % of Numbers in Gut (D) Food density—no absolute density data | | | | | |
|---|---|---|---|---|---|---|
| = $^1/_5$ .D | P | 2P | 3P | 4P | 5P | 6P |
| Midges | | | | | | |
| Tendipedidae | 31.3 | 34.6 | 40.2 | 44.0 | 48.2 | 51.3 |
| Amphipods | 24.0 | 29.8 | 32.4 | 33.7 | 31.3 | 29.5 |
| Non-living food | 19.4 | 20.7 | 18.1 | 19.2 | 19.5 | 20.2 |
| Isopods | 16.2 | 11.0 | 8.5 | 3.1 | 1 | 0 |
| Molluscs | 9.1 | 3.9 | 0.8 | 0 | 0 | 0 |

For Carp [*Cyprinus*] (mean wgt. = 14 gms) feeding on Benthos

| Food Type Density of Each Type | Average % of numbers in gut (D) Food density—no absolute data | | | | |
|---|---|---|---|---|---|
| = ¼ .D | P | 2P | 3P | 4P | 5P |
| *Daphnia* | 35.3 | 35.9 | 38.0 | 39.9 | 40.2 |
| *Bosmina* | 30.2 | 30.9 | 32.1 | 33.5 | 31.4 |
| *Diaptomus* | 26.0 | 26.1 | 24.6 | 24.0 | 25.1 |
| *Cypris* | 8.5 | 7.1 | 5.3 | 3.6 | 3.3 |

For Bleak (*Alburnus*) (mean wgt. = 5.9 gms) feeding on zooplankton

### 4.5.2 Holling's Laboratory Experiments with the Mantid, *Hierodula crassa*

Dr. C.S. Holling kindly has provided us with data from his laboratory experiments of predation by the mantid, *Hierodula crassa*, on houseflies, *Musca domestics*. Since his 1966 monograph is readily available, only certain data will be reproduced here. The work to be described was done under very controlled laboratory conditions with a single prey species. Nevertheless, it is the most complete set of data available. The discussion will take the form of questions.

1. Does the mantid have a measure of the average rate of food intake?

As a measure of hunger, Holling used the amount of food (grams of fly) needed to satiate the animal after a fixed time interval from a previous satiation feeding. Adult female mantids were fed until they would not even accept crushed houseflies presented at the mouth parts, then they were fed again at a specified time interval. If the food eaten at the second feeding reflects the amount of food removed from the gut during the interval, it provides the basis for a model of how fast food is removed from the gut. Holling made 228 such measurements, 12 replicates at 19 time intervals. Figure 4.6 is reproduced from his paper. The data are well described by an exponential decline for the food present in the gut. He estimated the average gut capacity to be one gram. The rate at which food is leaving the gut is AD x G, where G is the amount of food in the gut and AD is a proportionality constant estimated to be 0.05 grams per hour.

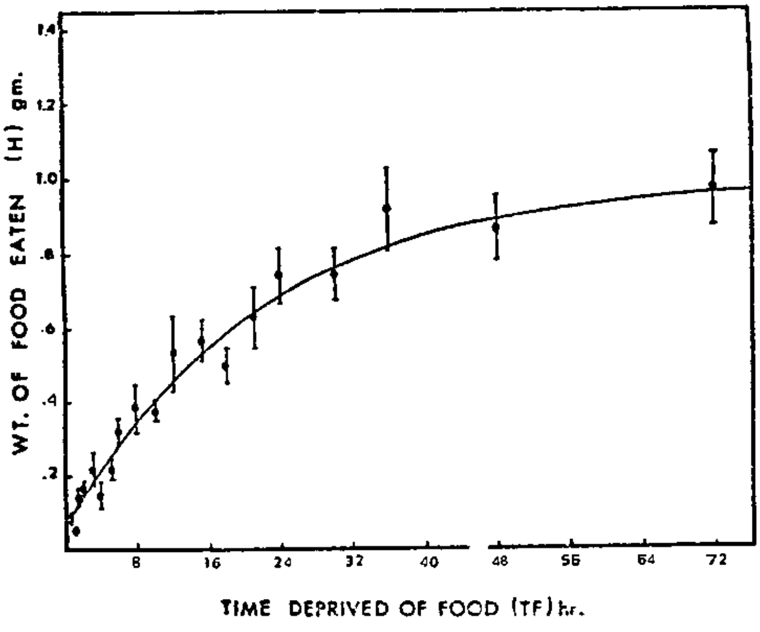


**Figure 4.6 The effect of time of food deprivation on hunger of *H. crassa*.** A: untransformed data (average of 12 replicates ± S.E.). From Hollings, 1966.

If we assume that the mantid is in equilibrium with its food supply, (i.e. during a feeding period), the average amount of food in the gut is constant and the rate of food intake is equal to the rate at which food is leaving the gut. Animals coming into equilibrium with fuller guts thus have a higher rate of food intake than those in equilibrium with more empty guts. Under this model, the mantid can indeed measure the rate of food intake.

2. Is there a prey ranking that may correspond to the $E_i^* / h_i^*$ ranking?

The houseflies were chosen for uniformity of size (0.0245 ± 0.003 gms (1 S.E.), N = 325) and age, so they appear at first to be a single prey type. Since the mantid is a sit-and-wait predator, its choice becomes whether or not it will stalk a fly that has appeared a certain distance away. This allows us to ask, What are the $E_i^*$ and $h_i^*$ associated with a housefly X centimeters from the mantid? The data allow for the calculation of some of the necessary quantities. We will establish that the ratio $E_i^* / h_i^*$ (for houseflies) is decreasing with increasing pursuit distance from the mantid.

$h_i^*$ **Assumption:** we change the original $h_i^*$ assumption by setting the recognition time and the kill time to zero ($h_0 = h_2 = 0$) and splitting the pursuit (here it is a stalk) time into $h_1$ = pursuit time when a kill is made and $h_4$ = pursuit time when no kill is made. We also ignore the recognition probability ($S_R$ ) as it cancels out of the ratio. With these in mind:

$$h_i^* = S_P \cdot S_a \cdot h_3 + S_P \cdot h_1 + \left(1 - S_P\right) \cdot h_4$$

$$\text{Let} \quad h_i^{'} = S_P \cdot S_a \cdot h_3 + S_P \cdot h_1$$

We have the data for the quantities in $h_i^{'}$.

$E_i^*$ **Assumption:** using the new definition for $h_i^*$,

$$E_i^* = S_P \cdot S_a \cdot \left[W - h_3 \cdot E_e\right] - E_P \cdot \left[S_P \cdot h_1 + \left(1 - S_P\right) \cdot h_4\right]$$

where W = weight of one housefly (0.0245 gms).

Let $E_i' = S_P \cdot S_a \cdot W$. We can estimate $E_i'$.

From Holling's experiments come the following relationships:

1. $S_p$ was found to be an exponential decreasing function of the stalking time.
    (a) The mantid stalked at a constant velocity (= 210 cm/hr) and struck at the fly when it got to within 1.5 cm. $S_P = \exp[-a \cdot h_1]$, where $h_1$ is related to stalk distance (P) by the relation $h_1 = [P-1.5]/210$.
2. For non-flying houseflies, $S_a$ was a constant equal to 0.630.
3. $h_3$ was a constant equal to the inverse of the eating rate [0.760 hr/gm] multiplied by the weight of a housefly.

These three relations are adequate to calculate $h_i'$ and $E_i'$ as a function of pursuit distance from the mantid. This is done in Figure 4.7. $h_i'$ is an increasing function of pursuit distance, $E_i'$ is a decreasing function. Thus, the ratio $E_i'/h_i'$ is a decreasing function of pursuit distance.

Since $h_i'$ is increasing with pursuit distance, so is $h_i'$. This follows from the fact that $1-S_P$ and $h_4$ (thus, $h_4 \cdot (1-S_P)$) should both be increasing with pursuit distance. $h_4$ could be considered the mean of an exponential random variable truncated above the associated $h_1$.

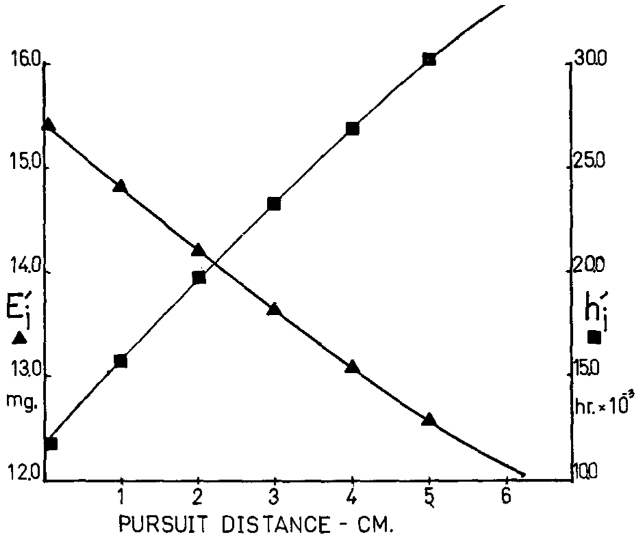


**Figure 4.7 The energy gain ($E_i'$) ▲ and handling time ($h_i'$) ■ values as a function of pursuit distance for the mantid *H. crassa* attacking houseflies, *M. domestica*.** The final result is that the ratio $E_i'/h_i'$ decreases with distance from the mantid. (See text for calculation of $E_i'$ and $h_i'$). Data from Holling, 1966.

Likewise, $E_i^*$ should be a decreasing function because $h_3 \cdot E_c$ is a constant while the pursuit time part $[S_P \cdot h_1 + (1 - S_P) \cdot h_4]$ should be increasing with pursuit distance.

**It follows, then, that $E_i^* / h_i^*$ should be a decreasing function with pursuit distance for the mantid attacking houseflies.**

3. Is the mantid willing to pursue or stalk further for houseflies at low levels of food in the gut?

Experiments to answer this question were carried out with houseflies manipulated directly in front of the mantid. The animals were fed to satiation and then at various time intervals flies were moved towards them until they began a stalk (or a strike if the fly came within 1.5 cm with no stalk). The measurement taken was this maximum pursuit distance for various hunger levels. Figure 4.8 summarizes the results. Only reaction distances above 1.5 cm. represent pursuit distances. The "food in gut" measurement is estimated from the appropriate starvation time. As the food in the gut decreases, the average maximum reaction distance increases. We also have plotted the least squares regression line from the 1966 paper, but newer data suggest that the relationship is non-linear (Holling pers. comm.). Also plotted is the equilibrium food intake rate (= 0.05 x food in gut). One equilibrium position is illustrated. At a food intake rate of 0.01 gms. per hour, the mantid is willing to pursue only flies that appear < 5 cm. away.

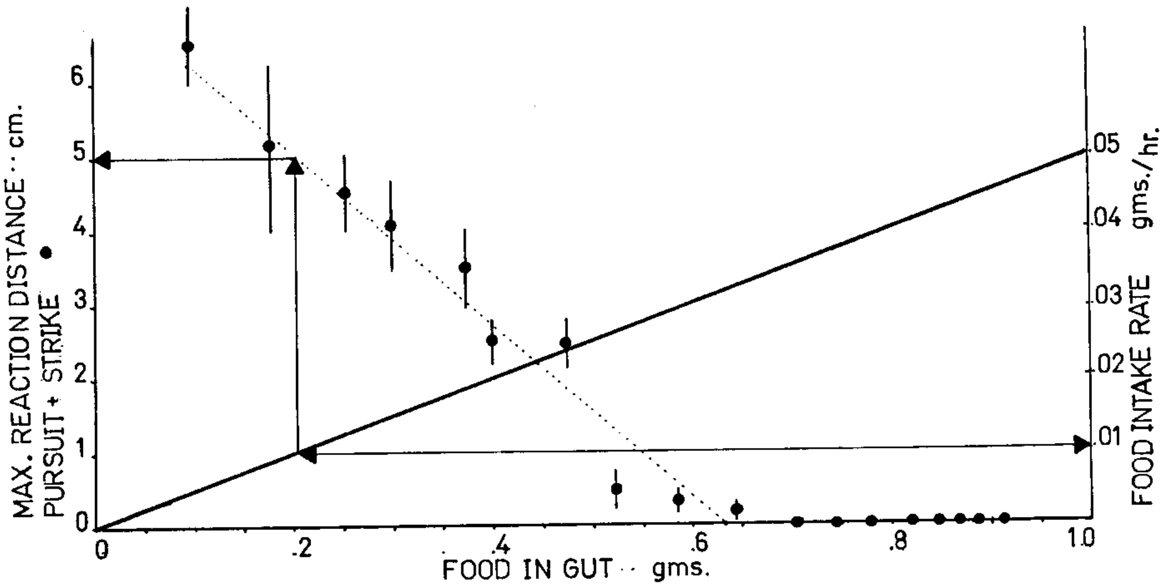


**Figure 4.8 The fundamental theorem applied to the mantid attacking houseflies.**

The rate of food intake is proportional to the amount of food in the gut, so that mantids in equilibrium with fuller guts are maintaining a higher rate of food intake. The circles represent the average, maximum distance that the animal stalked (pursued) or struck at houseflies. Distances up to 1.5 cm are strike distances. The vertical bars are one standard error with 12 replicates. A decrease in *rank* for a prey type is equivalent to a greater pursue distance. As an example, at a rate of food intake of 0.01, the animal is only willing to react to prey that are within 5 cm. Data from Holling, 1966.

From the above calculations, we are led to conclude:

1. The mantid can measure the rate of food intake.
2. Whether or not a prey type (a housefly at a certain distance) is attacked depends on the rate of food intake in the manner suggested by the fundamental theorem.

The qualitative behavior is as predicted.

### Discussion of the Mantid Results

Since the behavior of the mantid is at least qualitatively as predicted by the theorem, this section will discuss where the hypothesis seems to fail and will list certain alternative hypotheses for the behavior observed.

In another set of experiments, Holling presented the animals with moving targets of various size that simulated prey. The animals increased the distance of response to these, just as they did to the houseflies. Some of these targets were large enough so that a similar sized prey would be more than the mantid would eat. With large prey, the mantid fills the gut and then drops what is left of the prey. The reason that the $E_i' / h_i'$ is a decreasing function for the houseflies is that the pursuit time is a significant portion of the total handling time. For these large prey, the eating time is very large when compared to the pursuit time. Under these circumstances, the ratio is not decreasing with pursuit distance, so the theorem does not explain why the distance of awareness is so increased for these prey.

In the test of the hypothesis, an important role was played by the exponential function for food leaving the gut. The evacuation rate has been shown to be greatly influenced by factors such as food type (protein, fat, carbohydrate) and temperature. At least for some cold water fish, the gut evacuation rate is better modeled by a constant than an exponential (Ware 1971). Holling (1966) and Jamieson (1973) have shown that the exponential function appears to fit data from some other insects, but this does not appear to be universally true.

If we forget for a moment the $E_i' / h_i'$ relation with pursuit distance, several alternate hypotheses may be put forth to explain the observed behavior, namely that at low levels of food in the gut, the mantid is willing to move further to get a fly. Is there something associated with the stalk that suggests that hungry mantids should be willing to stalk further? If there is some *mortality risk* associated with stalking, then well-fed mantids simply may be less willing to face this risk. This risk could be related to the distance moved or the change in position of the animal, or to the time spent moving. Possible candidates for this risk factor include: 1) risk of detection by predators—mantids move very little except when stalking and moving prey are much more likely to be detected by predators. Mantids are generally camouflaged with their surroundings and there is some evidence that their characteristic rocking movement during the stalk is an antipredator adaptation. Robinson (1969) found that birds were more likely to respond to objects that moved slowly than when the movement was jerky. Perhaps the birds mistake the rocking for a twig being moved by the wind? 2) Risk of displacement—is a moving mantid more likely to be knocked off the bush? 3) Risk of an inappropriate response—Holling (1973) put forth the idea that the further away a prey item is, the more difficult it is for the mantid to estimate the qualities of the item. The accuracy of the binocular vision for this estimation falls with distance. It could be that a hungry mantid is more willing to accept a mistake than a well-fed mantid, the mistake being perhaps a stalk towards a potential predator. His complete hypothesis is rather complicated and will be developed in a forthcoming paper and book.

### 4.5.3 The Spider *Philodromus rufus* with a Single Prey Type

We earlier developed the fine-grained model where an individual prey item could be treated as a sequence of separate parts to be eaten one at a time. The predator could then eat the "best" parts first, progressing down to the "worse" parts. If these quality considerations relate to the food intake per unit feeding time, then a plot of the total food intake for a feeding time of $h_3$ will be of the same form as $f(h_3)$ in Figure 4.5 if the time and energy costs associated with unsuccessful encounters are relatively small. It is most likely that this idea will apply to a predator such as a free-living spider attacking insect prey. Such a study was carried out by Haynes and Sisojevic (1966) for the crab spider *Philodromus rufus* feeding on a single prey species, *Drosophila melanogaster*. Parts of their data are very difficult to interpret, but the results are still suggestive of some of the ideas discussed above.

The hypothesis to be tested is that marginal intake rate from the prey item ( $\delta f(h_3)/\delta h_3$ should be set equal to the average intake rate (Q*/R)). A qualitative test is that when Q/R is high, less should be eaten from each individual item than when Q/R is low.

The predators are small (3–6 mm in length) ambush hunters with poorly developed eyes. Most encounters with prey are by physical contact. The spider does not destroy the exoskeleton of the prey, but withdraws the body fluids by making a puncture in each body segment. The segments are fed on in a *definite sequence*; eyes first, then head, thorax, abdomen, and finally the legs. The authors were not able to use a hunger measure as precise as Holling's (1966) and could only distinguish two categories (hungry and well-fed). In one set of experiments, immature male spiders were starved for 32 days and then allowed to feed on three flies apiece. The mean feeding time (n = 16) was 181 minutes with a range from 45 to 291. For similar, but well-fed spiders, the mean feeding time was 39 minutes. This result was because well-fed spiders only fed on one or two body segments before they dropped a prey item. The hungry spiders often fed until even the leg segments had been consumed. If we assume that well-fed spiders are maintaining a higher average rate of food intake, then the degree of utilization of a prey item discussed above is as predicted by the model illustrated in Figure 4.5.

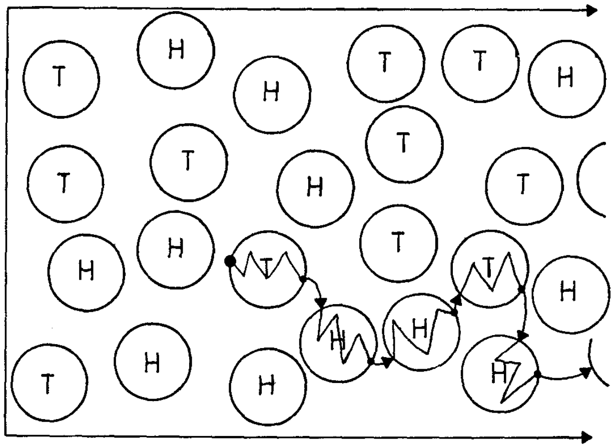
# Chapter 5. Use of a Patchy Habitat by a Typical Predator

## 5.1 A General Model

In this chapter we shall look at the use of a patchy habitat and develop models with reference to a typical predator. The basic idea is that the food items are found in patches separated from one another by areas of no food. This is obviously an idealization, but it seems worthwhile to begin by letting the predator be traveling between patches and hunting for food only within patches. At this level, the concern is not with the prey-type choice, so the energy intake for $T_i$ time units spent in a patch of type i is represented by a function [either $f(T_i)$, $h(T_i)$ or $g(T_i)$], omitting reference to the kinds of prey present. Figure 5.1 shows a hypothetical habitat made up of two patch types (H, T), with the patches distributed at random relative to one another. This means that the probability that a patch is type H [or type T] is independent of the other patches. A predator moves from patch to patch, spending some time in each patch. The animal may or may not know the value of a patch type before it visits a representative patch. A patch may be rejected at any time, with the animal moving on to another patch. Some patch types may not be used. We further specify that the habitat is large enough so that in the time interval under consideration no patches are visited twice. This model originally was conceived for a small bird foraging on pine cones for insect larvae.

**Figure 5.1 A hypothetical habitat of two patch types (H, T).**

Each patch has a probability of half of being an H (they were placed on this figure by flipping a coin). Time is divided into the travel time between patches and the foraging time within patches. Prey can only be encountered inside a patch.



We define as follows:

$D_i$ = density of patch type i in the habitat (i = 1, 2, . . . k)

$D = \Sigma D_i$ = density of all patch types being visited by the predator

$P_i'$ = proportion of patches visited in the habitat that are of type i

= 0 if patch is not being visited by predator

= $D_i/D$ if patch is being visited

$T_i$ = time spent foraging in one patch of type i

$E_T$ = energy cost per unit time in traveling between patches

$E_{si}$ = energy cost per unit time while searching in a patch of type i

$h(T_i)$ = assimilated energy from hunting for $T_i$ time units in a patch of type i minus all energy costs except the cost of searching.

$g(T_i) = h(T_i) - E_{si} \cdot T_i$ = assimilated energy corrected for the cost of searching

$f(T_i) = g(T_i) + T_i \cdot E_T \; [= h(T_i) - (E_{si} - E_T) \cdot T_i]$

$f(T_i)$ corrects for the cost of searching measured above the background travel cost ($E_T$) and is the energy gain for time spent in the patch analogous to $E_i^*$. $g(T_i)$ is thus analogous to $A_i^*$.

As the number of patch types visited increases, the travel time between any two nearest neighbor patches must decrease. The simplest assumption is that this interpatch travel time ($t_s$ ) is proportional to 1/D.

or $$t_s = 1/aD$$

The time for a predator to use a single patch is the travel time ($t_s$) plus the time in the patch. Let $T_\mu$ be the average time to use one patch :

$$T_\mu = t_s + \sum P_i' T_i$$

The average energy from a patch is $E_e$,

$$E_e = \sum P_i' \cdot f(T_i)$$

The average energy intake rate is:

$$E_n = \frac{E_e}{T_\mu} - E_T \tag{9}$$

While this equation is rather intuitive, it can be justified in a rigorous way by modeling predation as a stochastic process. We will consider this in Chapter 7.

Substituting for $T_\mu$ and $E_e$ yields:

$$E_n = \frac{\sum P_i' \cdot f(T_i)}{1/aD + \sum P_i' \cdot T_i} - E_T$$

Let $aD_i = \lambda_i$, then the above may be written in a more familiar form:

$$\frac{Q}{R} = \left[E_n + E_T\right] = \frac{\sum \lambda_i \cdot f(T_i)}{1 + \sum \lambda_i \cdot T_i} \qquad \textbf{(10)}$$

$f(T_i)$ is yet to be dealt with. Our interest is in general relationships, rather than any specific function. All of the arguments relating to $f(T_i)$ can be applied to an expression similar to Eqn. 10, but in terms of $g(T_i)$. This will be discussed at the end of this section.

At least two, distinct assumptions are possible for $f(T_i)$:

(a) $f(T_i)$ does not reflect the presence of the predator,

(b) $f(T_i)$ reflects the presence of the predator. This may be due to the predator "stirring up the prey," making them more available, or due to the prey decreasing in availability, which could be due to a behavioral response by the prey or simply exploitation by the predator.

If the situation is (a), then $f(T_i)$ either reflects a changing prey abundance independent of predator influence or the abundance of prey in i does not change during $\tau$. If the latter holds, the best strategy for the predator is to find one patch of the best type (maximize $f(T_i)/T_i$) and remain in it. This conclusion rests on $\tau$ being long enough so that the time spent searching for this patch is relatively small. This conclusion also was reached by Werner (1972) and MacArthur (1972).

A more realistic situation is that prey abundances change independently of the predator, but it is very difficult to make any general predictions for this case. Factors such as the rate at which the food availability is changing in the patches, the presence or absence of physical or social signals indicating "good patches," and the relative value of searching in patches for information must be important (Royama 1970, Krebs *et al.* 1972). The patch changes may reflect cycles of prey abundance, such as the periodic emergence of some insects (Orians 1966). Under this situation, the predator could “know” in general where it should be at some point in time (e.g., time of day). The predator then could use cues on a much shorter time scale to adjust to the immediate circumstances (e.g., day-to-day variation).

### 5.1.1 The Fundamental Theorem Applied to Patches

Under assumption (b), $f(T_i)$ reflects the presence of the predator in the patch. The predator has control over the patch types it will visit and the length of time it will spend in each patch. The fundamental theorem provides the method to determine the patch choice and the optimal time to be spent in each patch type since Eqn. 10 is identical in form to the basic, fine-grained model. We first assume as follows:

1. The intake rate while in the patch, $\partial h(T_i)/\partial T_i$ goes to zero, causing $\partial f(T_i)/\partial T_i \rightarrow [E_t - E_{si}]$ as $T_i$ becomes large.
2. There is no sampling time necessary to reject a patch type.

Applying the fundamental theorem to Eqn. 10, we see that a patch type j should be visited if:

$$f(T_j)/T_j > \frac{Q^*}{R} \text{ for some } T_j \tag{11}$$

To solve for the optimal $T_j$, we first differentiate Eqn. 10 with respect to $T_j$ and then look for critical points. These points are seen to have the characteristic that:

$$\frac{\partial Q/R}{\partial T_j} = 0 \text{ if } \frac{\partial f(T_j)}{\partial T_j} = Q/R$$

Since this holds for all j in the optimal set, we are led to the somewhat surprising result that the maximization of Q/R for patches implies:

**The marginal energy intake rate [$\partial f(T_j)/\partial T_j$] should be equalized over all patch types (in the choice of $T_j$) and its value should be equal to the average energy intake rate ($Q^*/R$).**

When the intake rate in any patch drops to the average rate for the habitat, the animal should move on to another patch. Thus, the choice is not really one of $T_j$, it is the "moving on threshold" in the intake rate that is important.

There is a much simpler way of arriving at the above results, one which allows $f(T_j)$ to be of very general form. In Figure 5.2, we plot $f(T_i)$ versus $T_i$ for the patch types under consideration. If we then plot the ray from the origin with slope $Q^*/R$, the resulting optimal set of patches includes all those where the $f(T_i)$ curve passes above the ray at some point. In the figure, patches B and C should be visited, A should be passed over. To find the accompanying $T_c$ and $T_b$, we simply construct lines with slope equal to $Q\ /R$ and see where these lines are tangent to the $f(T_B)$ and $f(T_C)$ curves. If there is more than one point of tangency, the appropriate solution is the one where the associated line has the highest intersection on the $f(T_i)$ axis. This result follows from the corollary to the theorem.

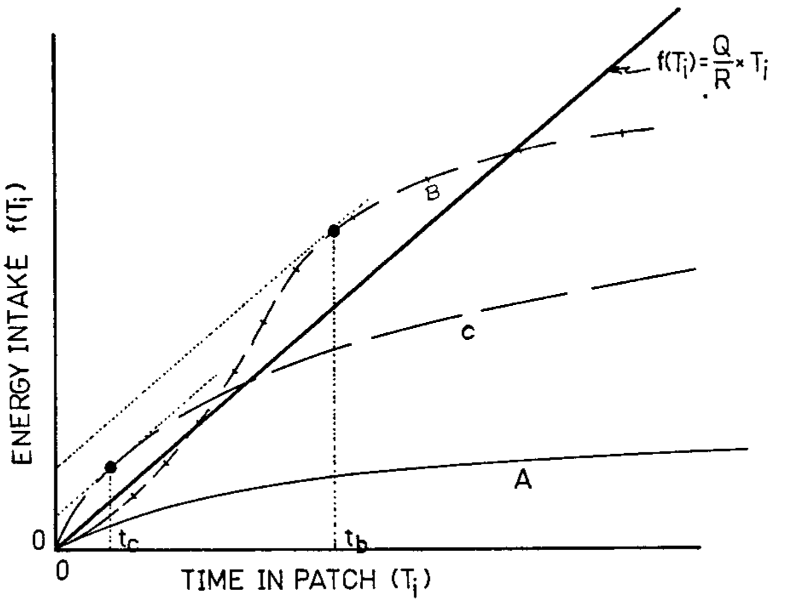


**Figure 5.2 Optimal use of a patchy habitat.**

The energy intake functions $f(T_i)$ are shown for a habitat with three patch types (A, B, C). If the ray from the origin with slope Q*/R is plotted, the patches to be visited are those where the $f(T_i)$ curves pass above this ray. This Q/R is Q*/R. The appropriate time to spend in each patch is found by constructing the highest line tangent to the $f(T_i)$ curve and parallel to Q*/R. Those lines and the resulting times are shown for patch types C and B. Patch type A is not visited with this Q*/R.

### 5.1.2 A Useful Algebraic Identity

Recall that associated with the $E_i^*$ and $f(T_i)$ functions are two new functions, $A_i^*$ and $g(T_i)$. In this section we will derive a useful relation using the pairs. Since Eqns. 10 and 6 are identical in structure (where $h(T_i)$ reflects the predator's presence), the argument will use Eqn. 10.

First note that $E_j^* = A_j^* + S_R \cdot h_j^* \cdot E_S \cdot P_j$ or

$$f(T_i) = g(T_i) + T_i \cdot E_T$$

Eqn. 10 is:

$$E_n = \frac{\Sigma\, \lambda_i \cdot F(T_i)}{1 + \Sigma\, \lambda_i \cdot T_i} - E_T$$

the *summation* being over the patches visited. Substituting for $f(T_i)$:

$$E_n = \frac{\Sigma\left(\lambda_i \cdot g(T_i) + \lambda_i \cdot T_i \cdot E_T\right)}{1 + \Sigma\, \lambda_i \cdot T_i} - E_T$$

$$E_n = \frac{\sum \lambda_i \cdot g(T_i) - E_T}{1 + \sum \lambda_i \cdot T_i} \tag{13}$$

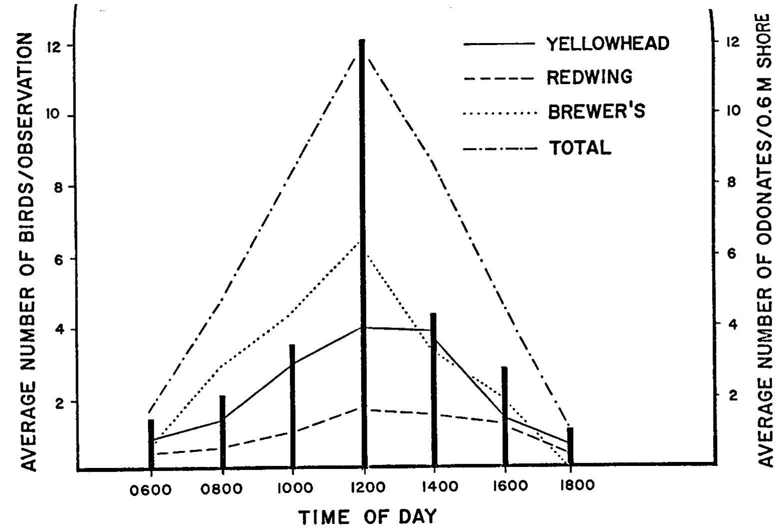
The value of this form is that $g(T_i)$ reflects the net intake while in a patch and $E_T$ only appears once. It should be useful in comparison between habitats or between alternate methods for using a single habitat.

## 5.2 Tests of Patch Use

### 5.2.1 Foraging by Blackbirds

A striking example of changes in prey availability unrelated to the activities of predators is provided by the emergence patterns of aquatic insects in fresh-water marshes. In western North America there are large emergences of damselflies from desert lakes that form the prime foods for several species of blackbirds during the breeding season (Willson 1966, Orians and Horn 1969). During May and June, the peak period of emergence and the breeding season of the birds, the emergence of these insects is concentrated during the latter part of the morning. Relatively few insects are available on the edges of the lakes early in the morning or late in the afternoon. The correspondence between the pattern of emergence of the insects and the intensity of use of the edges of the lakes by foraging blackbirds is striking (Figure 5.3).

**Figure 5.3 Average number of Odonates and the use of the edge of the ponds by foraging blackbirds, Columbia National Wildlife Refuge, Washington.**



The emergence pattern shown in Figure 5.3 is so predictable, except on days of bad weather, that the birds are able to anticipate that the edges of the lakes will constitute the best foraging patches in the environment during the period from mid-morning to early afternoon. The location of best foraging patches at other times of the day is much less predictable and there is evidence from the food delivered to the nestling blackbirds that the adults regularly sample more than one patch type during most hours of foraging (Table 5.1).

**Table 5.1** Percentage of food samples taken from nestling Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), Rush Lake, British Columbia, indicating that the adults foraged in aquatic and upland patches in the environment. A sample constitutes the food delivered to all of the nestlings in a single nest during a one hour time interval. (Data reanalyzed from Orians, 1966.)

| Year | Percentage of samples at different times of day indicating foraging in | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Early morning | | | Mid-day | | | Late afternoon | | |
| | Aquatic only | Upland only | Both | Aquatic only | Upland only | Both | Aquatic only | Upland only | Both |
| 1963 | 20 | 13 | 67 | 86 | 0 | 14 | 31 | 0 | 69 |
| 1964 | 0 | 11 | 89 | 63 | 0 | 37 | 14 | 0 | 86 |

### 5.2.2 Patch Use by Rainbow Trout

In general, the basic result of the patch use game (Figure 5.2) is that the marginal rate of energy intake $\partial F(T_i)/\partial T_i$ should be set equal to the average rate for the habitat (Q*/R) in the decision whether or not to leave a patch. There are several kinds of data that may be brought to bear on this hypothesis. The first kind relates to the foraging decisions of individual predators, most particularly the decisions relating to the leaving of a patch. Ware (1971) found that individual rainbow trout (*Salmo gairdneri*) feeding on amphipods would quit foraging in the benthos and would move into the water column when the capture rate on amphipods dropped below a threshold value. The threshold showed no trend with the quantity of food in the gut and appeared to be a constant, although there is a considerable scatter in the data.

### 5.2.3 The Concept of "Giving-Up Time"

A second type of data at the level of individual decisions is what might be called a "giving-up time." Suppose that the food is of a single type with a small handling time so that the rate of food intake is approximately proportional to the inverse of the average time between food items. In this situation, the predator can use this intercatch time as a measure of the food intake rate. In a habitat with a high average rate of food intake, we would expect the animal to be leaving patches when the intercatch time was still small, relative to a poorer habitat. "Giving-up time" refers to the intercatch intervals the animal uses in deciding when to leave a patch. It seems unreasonable to expect that an animal responds (in a decision to leave a patch) to a *single* intercatch interval above a threshold value. This would always lead to the leaving of a patch while its marginal value was still above the average for the habitat. It is more likely that the animal uses some method of averaging over several catches. However, the time between the last capture and when the animal left the patch is the simplest measure of a giving up time (GUT) and is the one used in the experiments to be discussed.

The hypothesis is qualitative and may be stated as follows:

1. In a good habitat (Q*/R high), the GUT (or average GUT) should be smaller relative to the GUT in a poor habitat (Q*/R low).
2. If an animal is treating several patch types as a single foraging habitat, the GUT should be equal over the several types.

Ryan, Krebs and Charnov (1974), in laboratory experiments with black-capped chickadees (*Parus atricapillus*) foraging in artificial pine cones for parts of meal worms (*Tenebrio*), provide the only test of this hypothesis that we are aware of. The experimental universe consisted of a room with five artificial trees. Pine cones (blocks of wood with holes to hold prey) were arranged in groups of four cones, with three groups to a tree, for a total of 15 groups and 60 cones. Cut-up meal worms were hidden in the cones and white stickers were placed over all the holes, concealing the food and the empty holes. The birds hunted by picking off the stickers. After a set of learning trials, two sets of experiments were carried out. Type I came first and consisted of letting single birds hunt for six 5-minute trials where the density of prey was one item per cone. Between trials the items removed were replaced and the position of the cone groups was changed so that the bird could not learn that a particular place had no food. The variable of interest is the giving-up time for a patch; a patch is taken here to be a cone group. In the next six trials, (type II) three of the trees were made "high-density trees" by increasing the prey density to three items per cone. Data on giving-up time are summarized in Table 5.2. In these data we considered a single sample to be the event of one bird leaving one cone group after having found at least one prey item. In all, six birds were tested. We first tested the hypothesis that the GUT was the same between the high-density trees and the low-density trees within the good habitat. As shown in Table 5.3, we were unable to show any difference. Pooling the data for the good habitat, we then tested that the GUT is smaller in the good habitat; a one-tailed t-test shows a significant difference at the 0.05 level. These results are as predicted by the theory.

**Table 5.2** Giving-up time for Chickadees.

| Habitat | Prey Density | Average GUT | S.E. | Sample Size |
|---|---|---|---|---|
| Good | all trees | 11.38 sec. | 0.956 | 230 |
| Good | 1/cone (low) | 11.66 | 1.18 | 160 |
| Good | 3/cone (high) | 11.26 | 1.60 | 20 |
| Poor | all trees-1/cone | 14.12 | 1.21 | 250 |

**Table 5.3** Comparisons of GUT for Chickadees.

| Comparison | t | Prob. level |
|---|---|---|
| Good (high) – Good (low) | 0.201 | not sig. |
| Good (all) – Poor | 1.78 | $< 0.05$ |

### 5.2.4 Gibb's Data

Another kind of useful data for testing the prediction from Figure 5.2 are those relating to the end result of many similar predators foraging in a single area. The patch use model was built for an individual predator, but this aggregate behavior can be considered as an average over many individuals. The best data of this type are from Gibb (1958). Tits (*Parus*) foraged during the winter for moth larvae embedded in the seeds of pine cones. The birds found the larvae by tapping the cone scales; it is reasonable to suppose that the capture rate was proportional to the intensity of larvae in the cones. When a larva is removed, a characteristic hole is made so that cones sampled in the spring before the emergence of the moth, but after the winter foraging, provide data on the initial and final intensity of larvae. In the fall of 1955, the initial intensity ranged from 10 to 70 larvae per 100 cones in one area. Figure 5.4 shows the spring intensities paired with the initial fall intensities. It appears that the birds foraged so as to equalize the intensity of larvae regardless of the initial intensity. This result also has been noted by Tullock (1971) and Emlen (1973). However, these data do not provide a very strong test of our specific hypothesis. Probably almost any model that had the birds staying where there was lots of food would produce the same pattern over a period of time.

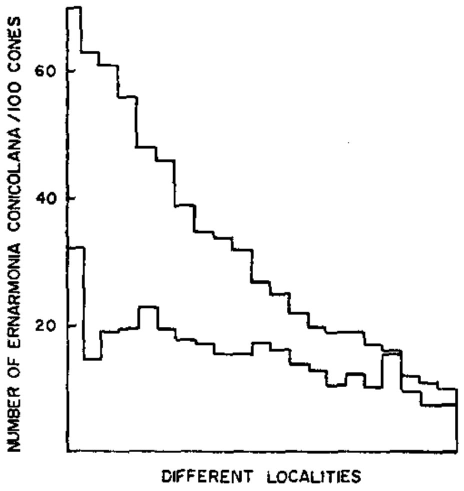


**Figure 5.4 Tits (*Parus*) foraging on pine cones for embedded insect larvae.**

At the beginning of the winter the intensity of larvae was as shown in the upper curve, here arranged in descending order. The lower curve shows the intensity in the spring, after being gleaned by the birds. If the rate of food intake is proportional to the larval intensity, then it appears that the birds equalized the rate of food intake over the several patches. (Modified from Figure 3 in Gibb, 1958.)

## 5.3 Central Place Foraging

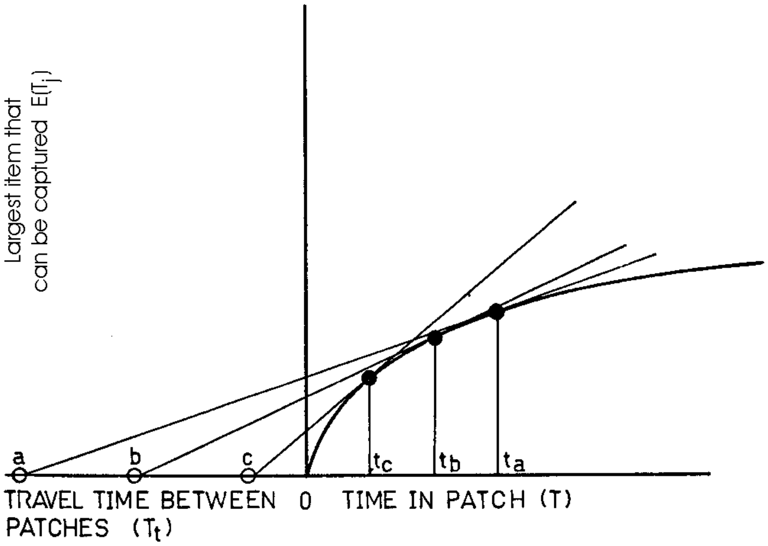
One other aspect of the use of a patchy habitat will be developed in this section. Some organisms feed in one place and rest in another. Since foraging trips often begin at the rest place, the foraging places may be visited in some sequence, giving rise to optimization problems similar to the classical "traveling salesman" problem. The patch use model previously discussed assumes no beginning and no end for the feeding period, so that the only geographic considerations are the interpatch distances. One situation where these other factors must be important is the case of "central place foraging." Hamilton and Watt (1970) have discussed the problem in relation to non-breeding time periods, so that our discussion will be limited to the situation where an animal travels out from a "central place" (e.g. nest, oviposition site) to collect food or other resources which are brought back to the central place. The minimum time unit is a *trip*, consisting of travel and foraging time for the load brought back.

In many situations the food is collected for the young by the parents and here there are strong reasons for believing that it is the amount of food delivered per unit time that should be maximized. This case has been studied most intensively among breeding birds. Assuming that the parents meet their own energetic needs, the growth and subsequent survival of the nestlings is a function of the amount of food delivered by the parents (Lack 1954, 1966, 1968).

Three different types of models will be considered for a hypothetical bird. The first assumes that the adult brings back a *single* prey item per trip. Let $T_T$ be the travel time to and from a patch j. While in the patch, the bird will be presented with opportunities to capture prey items. It seems reasonable to assume that the longer the bird hunts in a patch, the *larger* will be the *largest* food item that it can expect to capture. The capture of a single item will end the trip. In Figure 5.5, $E(T_j)$ is the largest prey item that the bird can expect to capture in $T_j$ time units in patch j. The rate of food delivery is $E(T_j)/(T_j + T_T)$ for any patch j. The bird has the choice of the patch (which j?) and within the patch, the choice of the size of item to accept. As shown in the figure, the larger the $T_T$, the more important is the size of the item chosen.

**Figure 5.5 Central place foraging when a single prey item is brought back on each trip.**

It takes $T_T$ time units to travel to and from patch j. For $T_j$ time units in the patch, the predator can expect to be able to catch a *largest* prey item of size $E(T_j)$; $E(T_j)$ is the largest item that can be captured. This curve is non-decreasing. The energy intake rate per trip is $\frac{E(T_j)}{T_T + T_j}$ and its maximization is shown for three assumptions about $T_T$.



A second model is shown in Figure 5.6. Here the bird brings back some quantity of food with the capture rate a function of time spent in the patch. The capture rate decreases with time spent in the patch because (a) prey respond to the presence of the predator by becoming less available or (b) the feeding rate is decreased as the bird gets more food items in the bill. For some patch a fixed distance ($T_T$) from the nest, the bird should bring back more food, and the average capture rate is higher. The lower curve represents the patch with little food, the upper the patch with more food. Both patches are $T_T$ from the nest. The above prediction holds so long as the curves do not cross. It is also likely that the bird should spend more time in the more productive patch, but this is not a critical prediction because we could easily redraw the upper curve so to make the times be the same. It does seem, however, less likely that the bird should spend less time in the good patch, In fact, one way that the bird could come close to the above strategy would be to spend an equal amount of time in each of the two patches. As shown in Figure 5.6, spending the good-patch time in the poorer patch only slightly decreases the catch rate. Data to test these predictions have been gathered by one of us (GHO) with blackbirds in eastern Washington. Capture rates and total sizes of loads for blackbirds gathering food for nestlings were measured at the edge of a desert lake from a convenient observation cliff situated near the lake. The number of pecks at prey could be counted readily, and if we assume that each peck results in a capture or that the percentage of pecks resulting in a capture is independent of the pecking rate, then the size of the load taken back to the nest increases with increasing capture rate as predicted by the model (Figure 5.7). The scatter of data is least for the male Red-winged Blackbird because all the observations were taken on a single bird that was flying a fixed distance each time from the foraging area to its fledglings. Data for female Redwings and both sexes of the Brewer's Blackbird (*Euphagus cyanocephalus*) were gathered on a number of individuals at varying (and unknown to the observer) distances from their nests. Therefore, each of these individuals was operating under a different central place foraging curve and a higher variance in their load sizes is to be expected.

**Figure 5.6 Central place foraging with capture rate a function of load size.**

The curves show two assumptions for a single patch that is a fixed distance (time) from the nest. The capture rate declines with increasing time in the patch and/or load size. Food is more available in *a*, which increases the optimal load size and increases the average capture rate while in the patch.

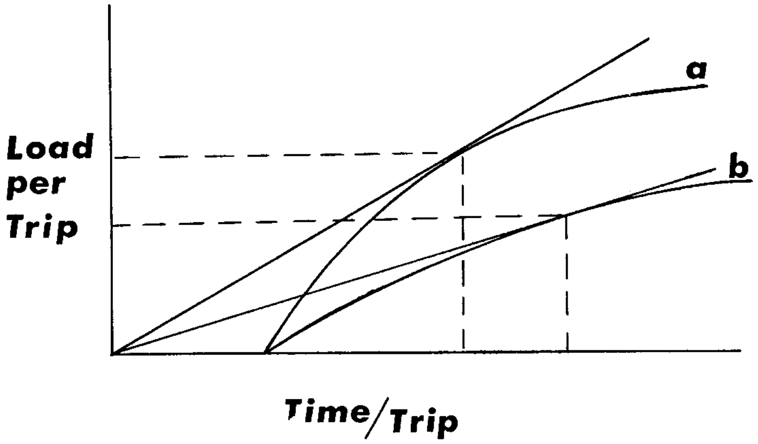
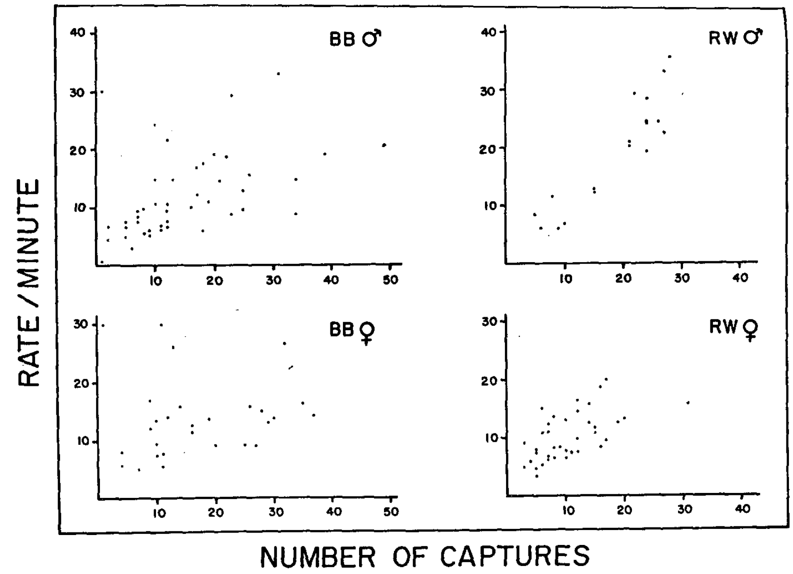


**Figure 5.7 Central place foraging in blackbirds.** Four individuals are represented. All show increasing load size with increasing average capture rates. See text for discussion.



The third model is for a bird returning to the nest with a fixed quantity of prey ($Q_M$). Let:

$q(D_i, Q_i)$ = time to capture $Q_i$ calories of prey at a prey density of $D_i$

$T_T$ = travel time to and from patch visited.

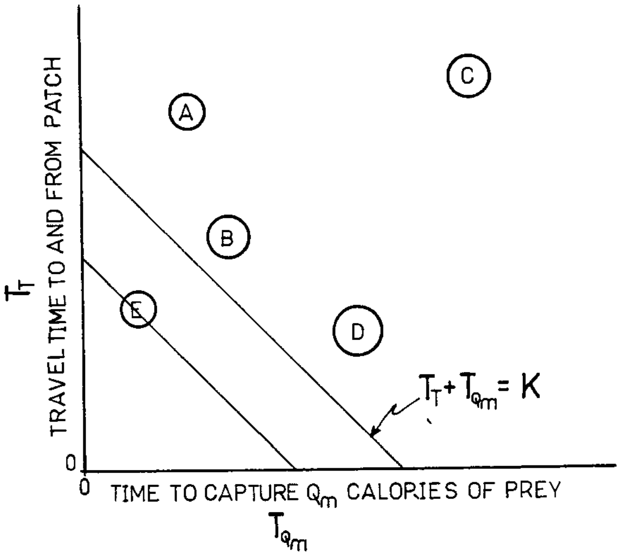
The food delivery rate is $Q_M/(T_T + q(D_i, Q_m)) = D_n$

Figure 5.8 shows a hypothetical situation with five patches. The best patch maximizes $D_n$, or for fixed $Q_M$, minimizes $T_T + q(D_i, Q_M)$.

One interesting thing here is that unless the nutritional needs of the young require specific foods, the items taken should minimize $q(D_i, Q_M)$ within any patch, which is the maximization of Q/R with one slight modification. Since the energy is for the young and not the adult predator, $E_i^*$ should be replaced by $S_R \cdot S_a \cdot S_P \cdot E_i''$.

**Figure 5.8 A simple model for central place foraging.**

The predator visits a patch, captures $Q_M$ calories of prey, and returns to the central place to deliver the food to the young.The goal is to minimize the time for a trip. A–E represent the patches from which to choose. Patch E is the best patch, that which minimizes $T_T + T_{QM}$. The patches are fixed in $T_T$ value, but will change through time in $T_{QM}$ value as prey abundances change.



In the last two chapters we developed a fairly general approach to the use of prey types and patches. We proposed a theorem (a fundamental theorem) and mentioned that at least special cases of it have appeared elsewhere in the literature. This review is meant to relate this earlier literature to our models and results. It does not cover all of the published work and omits unpublished (to our knowledge) manuscripts. It is arranged by paper and should serve as an introduction to the conception of each author. Again, we are concerned primarily only with models relating to prey types and patches.

## 6.1 Emlen, J.M. 1966. The role of time and energy in food preference. *American Naturalist* 100:611-617

This is one of the first papers in the field. Emlen considers only two food types and the optimization is as follows. The predator has just encountered food item $\theta$ (i or j) and has the choice of eating $\theta$ or going onto the next prey item, which, it is assumed, will be eaten regardless of which type it is. The predator maximizes "average energy divided by average time," where average energy is the value of the next item or the value of $\theta$ plus the value of the next item. The average time is the search time plus the time to eat the next item, or that plus the time to eat $\theta$.

He defines as follows:

$C_i$ = net caloric value of an item of i

$T_i$ = time to capture and eat an item of i

$D_{ij}$ = distance moved between an item of i and j

q = inverse of the predator's search velocity

k = energy cost for predator movement (per unit distance)

$P_{is}$ = probability of eating one item of i

$P_{is}^{*}$ = optimal $P_{is}$

$P_i$ = proportion of i in the diet (here he means: Prob (an encounter is with type i))

If the predator does not eat $\theta$, then the average energy/average time is 14 or 15:

$$\text{If } \theta \text{ is type i:} \quad \frac{P_i\left[C_i - K \cdot D_{ii}\right] + \left(1 - P_i\right)\left[C_j - K \cdot D_{ij}\right]}{P_i\left[T_i + g \cdot D_{ii}\right] + \left(1 - P_i\right)\left[T_j + g \cdot D_{ij}\right]} = E_i^{'} = \frac{a_i}{b_i} \tag{14}$$

$$\text{If } \theta \text{ is type j:} \quad \frac{P_i\left[C_i - K \cdot D_{ji}\right] + \left(1 - P_i\right)\left[C_j - K \cdot D_{jj}\right]}{P_i\left[T_i + g \cdot D_{ji}\right] + \left(1 - P_i\right)\left[T_j + g \cdot D_{jj}\right]} = E_j^{'} = \frac{a_j}{b_j} \tag{15}$$

If $\theta$ is eaten, the above become:

$$E_i = \frac{a_i + C_i}{b_i + T_i} \qquad\qquad E_j = \frac{a_j + C_j}{b_j + T_j}$$

The predator should eat $\theta$ if:

$$E_i > E_i^{'} \qquad \text{if } \theta \text{ is i} \tag{16}$$

$$E_j > E_j^{'} \qquad \text{if } \theta \text{ is j} \tag{17}$$

First we note that the inequalities in Eqns. 16 and 17 are *either* true or false. The discussion of the probabilities of them being true or false (which is a large part of his paper) does not seem to fit his deterministic model. $P_{is}^{*}$ or $P_{js}^{*}$ should be either 0 or 1. Emlen then sets out to prove that as prey availability increases, the predator should restrict its diet. We shall use a different method to show this. If i is to increase greatly in abundance, $D_{ji}$ and $D_{ii}$ should go to near zero. The best of all possible worlds is where all of these D → 0. Here both Eqns. 14 and 15 are the same.

$$E' = \frac{P_i \cdot C_i + (1 + P_i)C_j}{P_i \cdot T_i + (1 - P_i)T_j}$$

Now, if $C_j / T_j > C_i / T_i \Rightarrow \frac{C_i}{T_i} < E' < \frac{C_j}{T_j}$, and $P_{is}^{*}$ should be set = $0, P_{js}^{*} = 1$.

It is difficult to let just one type (e.g., i) increase in abundance as both $P_i$ and ($D_{ji}$, $D_{ii}$ ) must change. Criticism of this approach must rest with the restriction to two prey types, the restricted kinds of hypotheses generated (e.g., restricted diet at high prey densities) and the fact that the “next prey item” is to be eaten even if it were passed over at θ. This paper is important primarily for the new question that it asked.

## 6.2 Emlen, J.M. 1973. *Ecology: An Evolutionary Approach*, Addison-Wesley

The only new result here is one related to the use of clumps of food. It is similar to the general patch use model of this book.

Let: C = catch of food

$x'$ = food density in a clump

Assume: 1) $\frac{dC}{dt} = \theta \cdot x'$ $\theta$ is a constant

2) $x'$ decreases with time spent in a patch

Emlen then simply claims (without proof or derivation) that a predator maximizing its average food intake rate should move to the next clump when dC/dT drops to some threshold k. He does not show where k comes from (it should be the average rate of food intake over the clumps),but suggests that it would be lower in poor food areas, and higher in good.

## 6.3 MacArthur, R.H. and E.R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* 100:603-9

These authors state that the basic procedure for determining optimal utilization in time and energy budgets is that an activity should be enlarged as long as the resulting gain in time spent per unit food exceeds the loss. This idea presupposes some sort of ordering of opportunities and this is where they begin. They recognize patch choice and within patch, food choice models.

For the food choice model, the maximization is the capture rate in *numbers* of prey. First, the prey are ranked by increasing handling times.

Let: $T_N^S$ = average search time between prey items when the diet includes N prey types (smallest N handling times).

$T_N^P$ = average handling time per item when the diet includes N prey types.

$$T_N = T_N^P + T_N^S = \text{average time to get one food item} \qquad \textbf{(18)}$$

The object is to choose N so as to minimize $T_N$. The choice of N is very simple using the fundamental theorem.

Our basic equation 6 is:

$$\frac{Q}{R} = \frac{\sum \lambda_i \cdot E_i \cdot P_i}{1 + \sum \lambda_i \cdot h_i \cdot P_i}$$

where $h_0 = 0$ and $E_i \cdot P_i = E_i^*$

$$h_i \cdot P_i = h_i^*$$

Let the $h_i^*$ be constants and let $E_i^* = 1$. Further, define as follows:

$$q_i = \frac{\lambda_i \cdot P_i}{\lambda^*} \quad \text{where } \lambda^* = \sum \lambda_i \cdot P_i$$

By substitution, we have:

$$R/Q = 1/\lambda^* + \sum q_i \cdot h_i$$

But for some N: $T_N^S = 1/\lambda^*$ $\quad$ $P_i = 1$ if type is among N, otherwise $P_i = 0$.

$$T_N^P = \sum q_i \cdot h_i$$

According to the theorem, R/Q should decrease as prey are added to it in rank order (at increasing $h_i$) and reach a single minimum.

Their patch use model is very difficult to understand because certain of the important assumptions are not in the paper. They begin by defining two parameters.

$H_N$ = hunting time within a patch for each item caught by a predator using N patch types.

$T_N$ = travel time between patches for each item caught for a predator using N patch types.

Patches are first ranked in order of productivity, this being defined as the ratio—prey calories caught per unit hunting time in the patch. No mention is made of changes in productivity through time. What is left out of this model is any method of deciding how much time to spend in any patch. $H_N$ and $T_N$ are not only functions of N; they are also functions of the amount of time spent in each of the various patches. If productivity is not changing, the optimal predator does not travel between patches, but remains in the most productive patch.

In talks with E.R. Pianka in December 1972, he indicated that the patch use model was meant to be as follows. Each patch is a *point* on the ($f(T_i)$, $T_i$) plane (Figure 5.2). Since the patches are spatially fixed, the $\lambda_i$ do not change. What changes with changing productivity is the patch positions on the plane. With this knowledge, some of their patch use discussion is simple to understand. Which patches to use can be determined easily by the fundamental theorem. The corollary allows qualitative statements to be made about the effects of changing patch position. Their discussion about large versus small patches refers to the $\lambda_i$ with the $\lambda_i$ increasing for larger patches. For constant $f(T_i)/T_i$, larger patches also have larger $T_i$. Both of these raise Q*/R, resulting in more restricted patch use (as they claim).

## 6.4 MacArthur, R.H. 1972. *Geographical Ecology*, Harper and Row

This is MacArthur's last publication on foraging theory. He begins by stating that food gathering involves (1) the decision where to search (the patch), (2) the search, (3) the food choice decisions, and (4) the pursuit. His answer to (1) is that the predator should go where the expected yield is greatest. For (3) he gives the following:

$$P_j = \frac{\text{pursuit time}}{\text{grams of prey type j captured}}$$

$\overline{P}$ = average pursuit time per captured gram of prey in previous diet.

$\overline{S}$ = average search time per captured gram of prey in the previous diet.

Prey type j should be added to the diet if $P_j \leq \overline{P} + \overline{S}$ **(19)**

There is no claim that the previous diet is optimal, nor is there any discussion of ranking the prey types. From this he concludes that the abundance of j does not affect its inclusion/exclusion from the diet; only the general abundance of food affects this. His terms are similar to some of those in the fine-grained model put forth in this book. By "=" we mean "analogous to" in what follows:

$$1/P_j = E_j^*/b_j^* \qquad \bar{P} = \frac{\sum \lambda_i \cdot b_i^*}{\sum \lambda_i \cdot E_i^*}$$

Summation over the optimal set

$$\bar{S} = \frac{1}{\sum \lambda_i \cdot E_i^*}$$

which makes R/Q* = $\bar{P} + \bar{S}$

Under these assumptions, the models are the same.

### 6.5 Werner, E.E. 1972. *On the Breadth of Diet in Fishes* M.S.

This paper is adapted from Werner's Ph.D. thesis and will be published in 1974. In addition to an optimal foraging model, he gives a very thorough review of size-specific predation in fish. His within-patch model recognizes a prey type as a particle of a certain size, with *b* the largest size present. All prey have the same handling time (k) and all prey attacked are captured. His argument is as follows.

There is some large area that will take $T_S$ units of search time to cover. Any additional time in the area must be in handling prey. Let f(x) be the number of prey in the size interval x, x + dx in the area. If all items (N) in the interval [x, b] are eaten,

$$N = \int_x^b f(x)dx$$

The appropriate handling time ($T_h$) is N · k.

B is the biomass captured:

$$B = \int_{x}^{b} \alpha \cdot f(\alpha) d\alpha$$

An energy intake rate is $\dfrac{B}{T_S + T_h} = \dfrac{\int_{x}^{b} \alpha \cdot f(\alpha) d\alpha}{T_S + k\int_{x}^{b} f(\alpha) d\alpha}$ **(20)**

Letting $\lambda(x) = f(x)/T_S$, the above becomes:

$$= \frac{\int_{x}^{b} \alpha \cdot \lambda(\alpha) d\alpha}{1 + k\int_{x}^{b} \lambda(\alpha) d\alpha} \qquad \textbf{(21)}$$

which is Q/R for the appropriate definition of prey size.

The optimal set here is all prey above some smallest size $(\hat{x})$. Our basic theorem says that $\hat{x}$ must fulfill the condition that $\dfrac{\hat{x}}{k} = \dfrac{Q^*}{R}$, which can also be derived by setting $\dfrac{\partial Q/R}{\partial \hat{x}}$.

His model may be quite useful for zooplankton feeding fish where experiments have shown k to be very near constant over a wide range of prey size (Werner pers. comm.).

## 6.6 Schoener, T.W. 1969. Models of optimal size for solitary predators. *American Naturalist* 103:277-313

## Schoener, T.W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* II:369-404

In these two papers Schoener develops two distinct models for individual predators at a level of within a patch. His 1971 review considers much of the evidence for optimal foraging behavior. Only an overview of his work is included here, with the aim of simplification.

Type I predator: this predator pursues prey that it encounters at various pursuit distances. The energetic cost of activity is a function of predator size, and it is assumed that all prey attacked are captured. The maximization is not like Q*/R because this predator is assumed to be able to do many other activities while searching (i.e., search time is not "lost"). The problem is the *minimization* of the *time spent handling all prey items* to meet some energetic need (N) in the time period $\tau$. A prey type is an insect of length i encountered the distance r from the predator.

Let $E^*(i,r) = C \cdot i^2$ − [pursuit costs] − [eating costs]

$h^*(i,r)$ = [pursuit time] + [eat time]

$X_{i,r}$ = number of prey type (i,r) encountered during $\tau$.

The maximization is as follows:

(1) Prey are ranked by the ratio $E^*_{(i,r)} / h^*_{(i,r)}$, and the summation

$N' = [N + \tau \cdot E_S] = \sum_{high}^{low} X_{[i,r]} \cdot E^*_{[i,r]}$ is made. This summation minimizes the total handling time $\left(\sum X_{[i,r]} \cdot h^*_{[i,r]}\right)$ to meet the total need (N').

One problem here is that $X_{i,r}$ depends upon one another as handling time is unavailable for searching. Schoener also acknowledges this problem. A solution that corrects for this is shown in Figure 6.1. This optimal set is I in the figure and corrects for the missed encounters. The optimal set for this type of predator never contains more prey types than the same animal considered as a Q/R maximizer. The most difficult thing in this analysis is the calculation of the encounter rates.

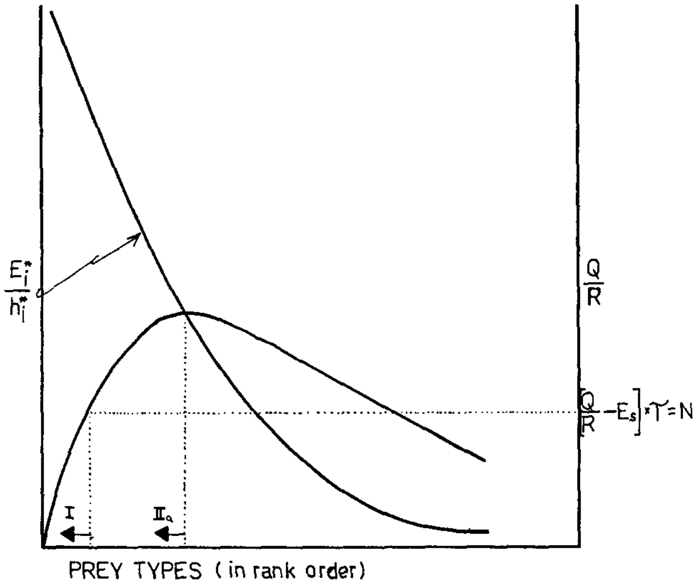


**Figure 6.1 A graphical solution for Schoener's Type I and Type IIa predators.**

A Type IIa predator maximizes Q/R so the optimal set is IIa (all types with rank higher). This solution is identical to that in Figure 4.4.

A Type I predator minimizes the total handling time to meet some energetic need (N) for the time period τ. The method of finding this optimal set (I) is shown in the figure. I depends on N and always includes fewer prey types than IIa (unless I does not exist or is equivalent to IIa).

Type IIa predator: this predator maximizes Q/R, but prey are encountered at zero pursuit distance.

Let: $A_i^* = C \cdot i^2 - [\text{eating costs}]$

$h_i$ = eating time

$p_i$ = proportion of all encounters that are with i

$T_S$ = search time between encounters

$C_S$ = energy cost per unit time in searching

In 1971, the above are combined in the following equation:

$$\frac{\sum_{N_1}^{N_2} P_i \cdot A_i^* - C_S \cdot T_S}{\sum_{N_1}^{N_2} P_i \cdot h_i + T_S} \qquad (22)$$

where $N_1$ and $N_2$ are upper and lower bounds to prey length. Thus the maximization is to eat all prey types between the two size categories. So long as the ranking $A_i^* / h_i$ versus prey length is monotonic or convex, this method will pick an optimal set that is identical to that in Figure 4.4 (see Fig. 6.1). The equation is a special case of (13). To see this, we equate as follows:

$$P_i = \lambda_i \big/ \sum \lambda_i$$

$$T_s = 1 \big/ \sum \lambda_i$$

Substituting these in Eqn. 22 gives:

$$\frac{\sum_{N_1}^{N_2} \lambda_i \cdot A_i^* - T_S}{1 + \sum_{N_1}^{N_2} \lambda_i \cdot h_i} \text{, which is (13).} \qquad \textbf{(23)}$$

He uses the equation to prove that whether or not a prey type *m* is eaten independently of $P_m$, but he does not prove the fundamental theorem.

### 6.7 Rapport, D.J. 1971. An optimization model of food selection. *American Naturalist* 105:575-87

This paper and that of Covich (1972) are very similar. The model assumes very little about predator behavior. In some fixed time interval (τ), a predator is assumed to eat $Q_x$ units of prey species X and $Q_y$ of Y. In Figure 6.2, the *possible* $(Q_X,Q_Y)$ are those enclosed by the convex boundary. Associated with any pair $(Q_X,Q_Y)$ is the value of a function, $A(Q_X,Q_Y)$, assumed to be an increasing function of its arguments. $A(Q_X,Q_Y)$ is the benefit to the predator for eating $Q_X$ of X, $Q_Y$ of Y. The goal of the predator is to maximize *A*. If we plot the curves $A(Q_X,Q_Y) = K$, the problem becomes one of picking from the *possible* $(Q_X,Q_Y)$ the pair that makes K largest.

This is the solution ($Q_{XM}$, $Q_{YM}$) in Figure 6.2. The method is very general and Rapport proceeds to give many examples of possible uses. As an example of the *A* function, the one used for the fine-grained model in this book, is $Q_x \cdot E_x^* + Q_y \cdot E_y^*$. The formulation is restricted to two to three prey types. It appears that most (if not all) optimization models, with two prey types, which depend upon picking quantities of each to eat ($Q_X$,$Q_Y$) to maximize some A($Q_X$,$Q_Y$), can be put in this form.

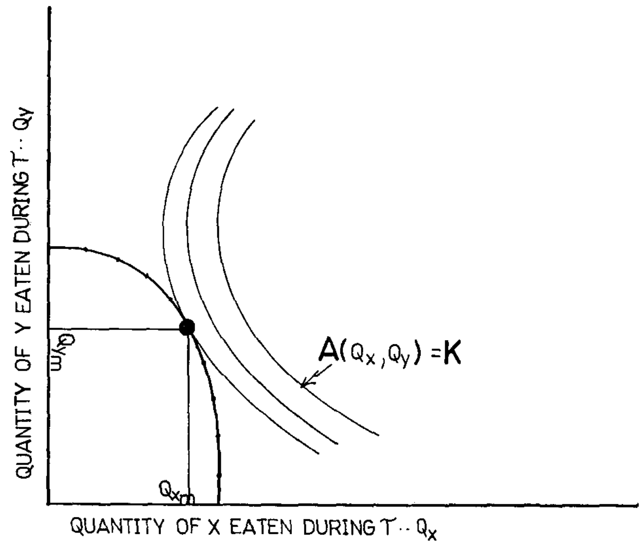


**Figure 6.2 An indifference graph for a predator and two prey types.**

A($Q_X$,$Q_Y$) = benefits for consuming $Q_X$ of x and $Q_Y$ of y during $\tau$. Curves of equal value are *indifference curves*. All of the $Q_X$, $Q_Y$ combinations that are available to the predator are in the region enclosed by the axes and the boundary. $Q_{XM}$, $Q_{YM}$ represents the combination that is possible and maximizes the *A* function. It is the best that the predator can do.

# Chapter 7. Stochastic Models for a "Typical Predator"

In Chapters 4 and 5, we used deterministic arguments to derive equations for the rate of energy intake by a predator attacking individual prey items or traveling between patches or clumps of prey. In this chapter, we shall formulate the problem as a stochastic process through time. The random variable of interest is, of course, the net energy intake in some time interval $(0 \rightarrow \tau)$. As general results, the mean and variance of this variable, at least for $\tau$ large, may be obtained. Since the basic argument is similar for patches or prey types, we shall develop it only for prey types.

Our basic technique is to consider the time between the leaving of a prey item (to begin searching for the next one) as a random event. Suppose that the predator began hunting at time zero and has just finished handling a prey item. Let this be the $R-1^{th}$ item handled. Let $T_R$ be the time elapsed between completing handling of the $R-1$ item and completing handling of the $R^{th}$ item. $T_R$ is the sum of the search time for the $R^{th}$ item and its handling time. $T_R$ can be called the interarrival time, and the beginning of the search for the next item can be termed a renewal point or event. Renewal theory (Cox 1962) is the study of the properties of this type of stochastic process. The $T_R$ are drawn from the same probability distribution and are assumed to be independent of one another. This is a repeating environment assumption (MacArthur 1972).

To make this more precise, we shall use the following definitions:

$h_R$ = handling time for the $R^{th}$ prey item

$T_{SR}$ = time between when the predator resumed searching after the $(R-1)$ item and when it encountered the $R^{th}$ item. (Thus, $T_R = h_R + T_{SR}$)

$E(x)$ = expectation of the random variable x

V(x) = variance of the random variable x

$N\tau$ = number of prey items “left” (renewal points) in a time interval of length $\tau$. A prey item is “left” when the predator resumes searching after handling it.

$E_R$ = a random variable associated with prey item R. The $E_R$ are identically distributed and independent with finite mean and variance. In general, the $E_R$ are not independent of the $T_R$ .

$Z\tau$ = $\sum_{R=1}^{N_\tau} E_R$ , the sum of the $E_R$ for $N_\tau$ prey “left” during $\tau$. We shall not count in $Z_\tau$ any prey the predator has not yet left as this prey is not counted in $N\tau$.

It is easily seen that $Z_\tau$ can be used to represent the energy intake during $\tau$ if the $E_R$ are defined to be the energy reward associated with the R<sup>th</sup> prey item handled.

Because they will be used in several final results, we define the following simplified notation.

$$V(T_R) = \sigma \qquad V(h_R) = \sigma_h^2 \qquad E(h_R) = \mu_h \qquad \operatorname{cov}(T_R, E_R) = \sigma_{r\epsilon}$$

$$V(E_R) = \sigma_\epsilon^2 \qquad E(T_R) = \mu \qquad E(E_R) = \mu_\epsilon$$

$Z_\tau$ can be considered as a cumulative renewal process and Smith’s theorems (Smith 1955) may be used to obtain the asymptotic mean and variance ($\tau \to \infty$). The basic results may be found in Cox (1962, p. 100). We simply quote them here.

$$E(Z_\tau) \simeq \frac{\tau \cdot \mu_\epsilon}{\mu} \tag{24}$$

$$\underset{\tau \to \infty}{V(Z\tau)} \simeq \tau \left[ \frac{\sigma_\epsilon^2}{\mu} + \frac{\sigma_\epsilon^2 \cdot \mu_\epsilon^2}{\mu^3} - 2 \cdot \frac{\mu_\epsilon \cdot \sigma_{r\epsilon}}{\mu^2} \right] \tag{25}$$

Paloheimo (1967, 1971) was the first to use these results to model predator behavior, although he did not consider the accumulated catch ($E(Z_\tau)$) in terms of energy intake. Even though these are derived under the assumption that $\tau$ is large, the approximations may be quite good for "small" intervals depending upon how fast the stochastic process converges to limiting state given by the mean and variance. $Z_\tau$ also can be shown to follow a normal distribution, a result of the central limit theorem. To see how these results may be used to generate energy intake equations, consider the obvious case where the prey items are encountered "at random."

Let there be k prey types, with a type i having associated with it two random variables. The first is the handling time ($h_i$), the second is the energy value ($E_i$) associated with the handling time events. These have been discussed previously. Their means are $h_i^*$ and $E_i^*$. Each type forms an encounter process with the predator. The processes are assumed to be independent Poisson processes through time with parameters $\lambda_i (i = 1, 2, \ldots k)$. During the handling of a prey item, no new items may be encountered.

If we look at the encounter process formed by pooling the k processes (i.e., look at an encounter, regardless of type), the resulting pooled process is still Poisson and the new parameter is $\lambda^* = \sum \lambda_i$. The probability that an encounter is with prey type j is $\lambda_j / \lambda^*$ and is independent of search time ($T_{SR}$) (Cox 1962).

With the above in mind, the search time between encounters ($T_{SR}$) is seen to have a negative exponential distribution with mean and variance as follows:

$$E(T_{SR}) = 1/\lambda^* \quad \textbf{(26)}$$

$$V\left(T_{SR}\right)=1/\lambda^{*2} \qquad \textbf{(27)}$$

We have for the R<sup>th</sup> renewal:

$$E\left(h_R\right)=\mu_h=\sum\frac{\lambda_i}{\lambda^*}\cdot h_i^* \qquad \textbf{(28)}$$

$$E\left(E_R\right)=\mu_e=\sum\frac{\lambda_i}{\lambda^*}\cdot E_i^* \qquad \textbf{(29)}$$

$$V\left(E_R\right)=\sigma_e^2=V\left[E_i^*\right]+E\left[V\left(E_i\right)\right] \qquad \textbf{(30)}$$

$$V\left(h_R\right)=\sigma_h^2=V\left[h_i^*\right]+E\left[V\left(h_i\right)\right] \qquad \textbf{(31)}$$

$$Cov\left(T_R,E_R\right)=\sigma_{re}=Cov\left(h_R+T_{SR},E_R\right)=Cov\left(h_R,E_R\right) \qquad \textbf{(32)}$$

Now: $T_R=T_{SR}+h_R$, so $\mu=E(T_{SR})+\mu_h$

or

$$\mu=1/\lambda^*+\sum\frac{\lambda i}{\lambda^*}\cdot h_i^* \qquad \textbf{(33)}$$

Since $Cov\left(T_{SR},E_R\right)=0$, $\sigma^2=V\left[T_{SR}\right]+\sigma_h^2$

$$\sigma^2=1/\lambda^{*2}+\sigma_h^2 \qquad \textbf{(34)}$$

If we substitute Eqns. (29) and (33) into Eqn. (24), the following results:

$$E\left(\frac{Z_\tau}{\tau}\right)_{\tau\to\infty} \simeq \frac{\sum \lambda_i \cdot E_i^*}{1+\sum \lambda_i \cdot h_i^*} \qquad \textbf{(35)}$$

which is identical to Eqn. (6) (= Q/R).

Substituting Eqns. (29) to (34) into Eqn. (25) gives the variance for $Z\tau$.

$$V(Z_\tau)_{\tau\to\infty} \simeq \left[\frac{\sigma_e^2 \cdot \lambda^*}{1+\sum \lambda_i \cdot h_i^*} + \frac{\mu_e^2\left(1+\sigma_h^2 \cdot \lambda^{*2}\right)\lambda^*}{\left(1+\sum \lambda_i \cdot h_i^*\right)^3} - \frac{\lambda^{*2} \cdot \mu_e \cdot \sigma_{re} \cdot 2}{\left(1+\sum \lambda_i \cdot h_i^*\right)^2}\right] \cdot \tau \qquad \textbf{(36)}$$

For a more general situation, we need not specify the form of the distribution functions for the inter-search times ($T_{SR}$) of the various prey types and need only assume that the process (1) is adequately modeled as a renewal process, and (2) it continues for a long enough period of time for our results to hold. Under this assumption, we can claim that there exists some $q_i$ = Prob (an encounter with type i), which may or may not be the same value as Prob (an encounter with i), conditioned as some fixed $T_{SR}$. Thus Cov($T_{SR}$, $E_R$) may no longer be equal to zero.

In any event, we can argue as follows:

Let $\mu_r = E(T_{SR})$, the average search between items, whether or not the item is handled. It follows from the renewal formulation that:

$$\mu = \mu_r + \sum q_i \cdot h_i^*$$
$$\mu_e = \sum q_i \cdot E_i^*$$

or from Eqn. (24)

$$\frac{Q}{R} = \frac{E(Z_\tau)}{\tau} \simeq \frac{\sum q_i \cdot E_i^*}{\mu_r + \sum q_i \cdot h_i^*} \qquad \textbf{(37)}$$

We let $q_i/\mu_r = \lambda_i^\circ$ where $\lambda_i^\circ$ can be considered as the average encounter rate with type i in the presence of the other k−1 types. The above may be written as:

$$\frac{Q}{R} = \frac{\sum \lambda_i \cdot E_i^*}{1 + \sum \lambda_i \cdot h_i^*} \qquad \textbf{(38)}$$

With the Poisson encounter model, $\lambda_i^\circ = \lambda_i$ and is only a function of type i. In general, this need not be assumed.

If in the proof of the fundamental theorem (Chapter 4) the $\lambda$ are written as $\lambda^\circ$, we see that the theorem also must apply to this general model. Abundance or encounter rate ($\lambda^\circ$) is not such a straightforward quantity now (it may depend on the other prey types present), but it plays the same role as $\lambda_i$ did previously. If in Eqn. (38), $E_i^*$ is replaced with $f(T_i)$ and $h_i^*$ with $T_i$, we see that the marginal value theorem for patches should also hold in this general case.

We close this chapter by noting one last result. Suppose that the predator began searching at time zero and instead of letting the time interval of interest go from $0 \rightarrow \tau$, we let it go from $T \rightarrow T + \tau$, where T is very large. Our interest, then, is in the catch during an interval of length $\tau$, which begins a long way away from the first interval. Under this model (called an equilibrium renewal process) and, with the further assumption that the $E_R$ and $T_R$ form a sequence of mutually independent random variables, $E(Z_\tau)$ is given by:

$$E(Z_\tau) = \frac{\tau \cdot \mu_E}{\mu} \quad \text{(or equation 24 is exact)}$$

For a proof, the reader is referred to Cox (1962), page 94.

It will rarely be the case where the $E_R$ and $T_R$ can be assumed to be independent, so generally we will have to settle for the limiting stochastic results. It would be interesting to know just how the process behaves in small time intervals before the convergence. Of particular interest is whether a diet of more prey types than those in the optimal set or a diet of fewer types leads to greater short-term energy intake. Another question of interest is in the effect of variance. The coefficient of variation goes to zero for large $\tau$, but for any fixed $\tau$, the variance is a function of the prey types eaten. It may well be that some prey type should be eaten for its effect on the variance in intake rate, even if it lowers the mean. In this way, the animal might trade a high average but variable intake rate for a lower but less variable one. We are at present studying some of these ideas, and the results will be published elsewhere (Pearson and Charnov in prep.).

# Chapter 8. Herbivores

Despite their abundance, the tissues of living plants are difficult sources of energy for animals, and their varied physical and chemical characteristics mean that simple caloric considerations of prey quality are not appropriate for defining herbivore choice strategies. Plants as prey have the following general characteristics.

1. An individual prey item containing a specific number of calories is difficult to specify or meaningless. The tissues of a single plant cannot all be consumed by a given herbivore, and determination of the exact quantity of suitable food present is tedious and involves arbitrary decisions. Plants are large and structurally diverse, and subdivided into many individual units, especially leaves. A leaf would be the appropriate unit of food for some herbivores, while for others the unit might be a spray of leaves on a branch. Still other herbivores tunnel through leaves and may complete their life cycle within the confines of a single leaf, without consuming it in its entirety.
2. In most cases, the rate of assimilation of usable energy is limited by the rate at which the food can be processed in the gut and not by the rate at which it can be discovered and ingested by the herbivore. Plants are with rare exceptions not cryptic, they have limited escape behavior, and the size of their organs exceeds the gut capacity of most herbivores.
3. Each individual plant is effectively an island in space and time (Janzen 1968). Herbivores may have difficulty in locating isolated plants, but once the prey has been discovered, there is no additional pursuit time.

4. For most herbivores, the rate of ingestion of food is potentially so rapid that the gut can be filled in a relatively short time. This allows much or most of the food processing to be carried out in a suitable hiding place.
5. There is little variation in the energy content of plant tissues (calories per gram dry weight), with the exception of seeds, which, because they commonly contain large quantities of fat, have many more calories per gram. Slight differences in caloric content of plant tissues may influence the grazing behavior of herbivores (Paine and Vadas 1969), but, in general, other chemical components of plant tissues are much more important in food selection and suitability than purely caloric consideration. These include protein levels (Bell 1970, Klein 1970) and toxic compounds.
6. Most plants are heavily defended physically and chemically (Whittaker 1970) and these defenses are highly species-specific, each plant species producing a unique array of compounds. A few defensive compounds are known from a number of plant species (nicotine, for example, has been detected in over a dozen genera of plants (Hegnaver 1969)), but most are restricted to a single species or to a few closely related species. No two plant species have an identical array of defensive substances, and there is reason to believe that different combinations of chemicals influence the suitability of the plant tissue as food in different ways.
7. There may be many herbivores on a single plant and their survivorship may be a function of that number because of their combined effects on the plant or the probability that predators will be attracted. Therefore, determination of host suitability requires an assessment of density of conspecifics already on the plant.

The size range of plants relative to their herbivores is great and continuous, but for purposes of discussion, it is useful to recognize two extreme size ratios that direct attention to the major types of differences of particular significance for optimal foraging theory. We recognize (a) herbivores so much smaller than the plant that most or all of their foraging can be done on a single plant or part of the plant, and (b) herbivores so large with respect to the size of the plants on which they feed that many different plants must be eaten daily or during the life cycle. These differences influence the kind and number of proximate foraging choices that an herbivore must make and are key factors in the evolution of the diets of herbivores. In the following treatment we exclude herbivores that filter small aquatic plants from an aqueous medium and predators on seeds. Here our argument is static; evolutionary aspects of food choice will be dealt with in a later chapter.

## 8.1 Foraging Patterns Among Small Herbivores

For a small herbivore the choice of a host plant is often an oviposition choice for the female, and fitness may be maximized by depositing the eggs so that larval survival is maximized. If we assume that physical factors, predators and parasites on the eggs and young are random with respect to host plants, we can explore the choice of oviposition site in terms of the suitability of the plant as food for the herbivore. If the egg-laying female knows the relative suitability of all of the host plants in the areas in which she is searching, her oviposition problem is a patch selection problem, but the suitability of the patch is not in terms of her survivorship, but of the survival of her offspring. Nevertheless, the total number of eggs she will be able to lay will be determined, short of the deposition of the entire clutch, by her mortality rate during the search. Thus, the advantages of laying a higher percentage of eggs on more suitable hosts is balanced against the probability that she will die while searching for them. In addition, the number of eggs laid per host should be a function of the advantages or disadvantages of an increased number of larvae in a restricted area on a plant. In general, it appears that unless the larvae are toxic and gain protection from being together and conspicuous, the advantages in overcoming the defenses of the plants are less than the risks of predation on herbivores feeding externally on the leaves of plants. Either the eggs are laid one at a time and the female is physiologically programmed to require a minimum amount of flying between each laying of an egg, or the eggs are laid in clumps, but the larvae immediately disperse.

Among insects that feed in protected positions under the surface of the plants, however, the advantages of numbers in overcoming the resistance of the plants override the risks of predation. In bark beetles, for example, the attacking females release a powerful pheromone that attracts new females to the tree, often in sufficient numbers to weaken the tree sufficiently to increase the survivorship of all the adults and their larvae (Samaniego and Gara 1970, Browne 1968).

A rich literature on host plant selection by phytophagous insects demonstrates the importance of chemical information on the choice process. Chemical clues are probably the most reliable sources of information about the suitability of plants as food because each plant species is chemically unique; these chemicals are the major determinants of palatability of most species of plants, and many of the chemicals are volatile, permitting decisions to be made without having to consume any tissue. However, few of the studies on host plant selection deal with ovipositing females, and there are even fewer data on distance perception, particularly in mixed communities of plants where a complex array of volatile chemicals will interfere with the ability of the female to locate a particular plant. The data of Tahvanainen and Root (1972) suggest that host finding behavior may be impaired severely by a modestly diverse plant community. In fact, once the ovipositing female is in the general vicinity of the host plant, she may depend on visual locating cues. Therefore, ovipositing females may be a selective force favoring leaf mimicry among plants (L. Gilbert pers. comm.). It is even possible that some of the volatile chemicals of plants are convergent among sympatric species, thereby reducing the host finding efficiency of the females, but we know of no data on this point.

Once an egg is deposited on a plant, the newly hatched herbivore need only decide on what parts of the plant to feed and where to hide when it is not feeding, although it may elect to leave the plant at some future time. As indicated previously, caloric differences in tissues are unlikely to be important, but differences in chemical defenses are. Also, for small herbivores, foraging is often a very risky activity. A partially consumed leaf is a conspicuous signal of the past activity of an herbivore, and most small herbivores are conspicuous when they are in feeding position on the leaves. This high risk associated with foraging is offset partially by the usual high rate of ingestion that permits foraging to be confined to a shorter period. Nevertheless, we expect significant departures from a model of optimal foraging in the direction of sacrificing foraging efficiency to reduce exposure to predation.

The concentration of toxic substances in plant tissues strongly affects the probability that an herbivore feeding on those tissues will be taken by a predator. Any detoxification system has a maximum rate at which it can handle and detoxify chemicals. Therefore, an herbivore eating a more highly defended tissue may have to feed at a slower rate, will not be able to grow as rapidly, and will therefore be exposed to predation for a longer period of time. For example, Feeny (1970) found that the insects feeding on the more palatable young oak leaves grew rapidly and completed their feeding stages in a few weeks, while those insects feeding on older and better defended oak leaves grew much more slowly, with many of them actually took more than one year to complete their life cycles. If the probability of being taken by a predator per unit time remains constant, the chances of completing the life cycle are inversely related to development time.

### 8.1.1 Predictions for Small Herbivores

These considerations lead to the following predictions of feeding choice patterns for small herbivores:

**Selection of Host Plant**

1. Since the deposition of the egg is likely to commit the herbivore for a significant fraction of its developmental life, ovipositing females should be highly selective. Unless counter selection, in the form of high death rates during the search period, is very strong, more surviving offspring will result from restricting oviposition to the best host plants. Therefore, we expect a high degree of host plant specificity among small herbivores.
2. If heavier attack by herbivores weakens the defenses of the plant, the ovipositing female should respond positively to signs of previous oviposition on the plant and should tend to lay many eggs per host plant. On the other hand, if there are disadvantages in numbers, i.e., the risk of predation increases with density or if higher densities of prey deplete the food supply, females should lay single or few eggs per plant or single or few eggs per section or part of the plant.
3. Egg-laying should be timed so that the young are foraging when the maximum amount of poorly defensed tissue is present.

**Foraging Patterns**

4. If a herbivore possesses a detoxification system able to handle the best-defended tissues of its host plant at maximum ingestion rates, it should be relatively indiscriminate in its choices of tissues to eat. However, if the rate of detoxification limits the rate of conversion of plant tissues into usable energy, the herbivore should select those host tissues that are least well-defended.
5. Generalized, small herbivores should prefer plant species that are poorly defended and, when feeding on better-defended species, should be restricted to the most vulnerable tissues.

6. The animal should restrict the time spent feeding in exposed positions.
7. Since food can be ingested much faster than it can be processed, actual feeding times should be concentrated to times when risk to predators is lowest.
8. There should be a direct correlation between the conspicuousness of the herbivore on the food tissue (either when feeding or resting) and the extent to which the herbivore sacrifices foraging efficiency to reduce predation.
9. Hiding places should be located sufficiently far from the feeding sites that predators cannot locate the herbivores by first detecting damage to the plant tissues and then searching nearby. For small herbivores with good mobility, such as adult beetles and orthopterans, this may often involve leaving the plant to hide in or on the soil, but for herbivores with poorer mobility, the hiding places should be closer to the feeding sites. This may prevent herbivores with poor locomotory ability, or those for whom movement is risky, from utilizing certain plant species that do not have good hiding places in close enough proximity to the feeding sites.

Available evidence on foraging behavior of small herbivores shows that not all species conform to these predictions. A major reason for this is probably that our models have considered only a single species of herbivore, the plants on which it feeds, and the predators to which it is exposed. Yet the risk from predation will be influenced strongly by the presence of other herbivores and non-herbivorous prey also at risk to the same predators. It is this combined prey availability that will determine the overall density of predators, the profitability to the predator of searching in particular places on the plant, the kind of search modes adopted by the predators, etc. These considerations will be taken up in Chapter 11.

### 8.1.2 Foraging of Small Herbivores

Data are available to test some of our predictions for small herbivores. The best information concerns the general dietary patterns of species since this kind of information can be collected fairly quickly. Even so, most entomological collections record at most the plant on which the insect was found. Unfortunately, presence on a plant does not indicate that the plant is a food source for the insect, even if the insect is known to be an herbivore. Available information on butterflies and moths, the best-known herbivores, have been summarized by Ehrlich and Raven (1965). Many of these species eat a single species of plant or at most a few closely related species. Herbivorous orthopterans also have been studied extensively and a significant, though unknown, proportion of them are oligophagous (Isely 1944, Gangwere 1961, Mulkern 1967).

The hiding places and strategies of herbivorous insects include mimicking leaves, parts of leaves, clumps of leaves, stems, flowers, branches and dangerous insects such as hymenopterans (Wickler 1968). As yet, however, there has been no systematic analysis of the distance of hiding places from feeding sites or any correlations between the vulnerability of the herbivore when it is actually feeding and the distances it moves. The ability of an herbivore to exploit a plant may be determined in part by the suitability of hiding places on the plant and the motility of the herbivore (Schultz and Cates in prep.). Where climate permits, many herbivores feed strictly at night. The range of predators to which they are exposed is reduced then and an important sensory mode for predators, vision, is of limited use. Therefore, total predation pressure at night probably is less than during the day and certain foraging patterns are viable at night that would be too risky during the day when visually hunting predators are active.

The best-studied example of selection by herbivores of poorly defended plant tissues is Feeny's (1969, 1970) work on the insects that exploit the leaves of oak trees (*Quercus robor*). Those species that eat the better tissues grow rapidly, feed in exposed positions, and escape total destruction by satiating their predators. Those species that exploit the better-defended older leaves not only grow more slowly but they also are better hidden from predators. Most of them live within the tissues of the leaves and eat out the softer parenchyma tissues, but some roll up leaves. These rolled leaves can be, and are, ripped open by birds, but the device increases the predator's pursuit and handling time for that prey and thereby expands the range of conditions under which those insects are not included within the optimal set of the birds. There are insufficient data to test the corollary prediction that the proportion of species that roll leaves should be higher among more slowly growing species that live on better-defended tissues than among faster growing species that eat more nutritious plant tissues.

## 8.2 Foraging Patterns Among Large Herbivores

Large herbivores are unlikely to be able to detoxify the diverse array of defenses of the many plants present in their environment, but nevertheless they must ingest many different plants daily or during their life cycle. Among the larger herbivores, mammals, which are the best known, rely on two primary detoxification systems for handling plant defenses, the gut microflora and microsomal enzymes within their cells, particularly the liver (see Freeland and Janzen in press for a general review). Highly adapted grazing mammals, unlike carnivores or omnivores, have alkaline stomachs with active microfloras that detoxify many secondary plant chemicals (Dobson 1967, Langan and Smith 1970, Longhurst *et al.* 1968, Shirley and Schmidt–Nielsen 1967, Williams–Smith 1967). The microsomal enzymes are located on the endoplasmic reticula and appear to be involved primarily with the decomposition of toxic chemicals (Schuster 1964) into an easily excretable form that will not readily pass through cellular membranes. Both of these systems are probably induced ones that improve in their ability to handle toxic chemicals following initial exposure (Conney and Burns 1972, Velles 1967). Thus, a plant that might cause severe illness if ingested in large quantities the first time may be relatively harmless to an experienced herbivore.

If the rate of ingestion of plant tissues is high, but the rate at which materials can be handled and detoxified in the gut is low, then the rate at which food can be consumed and converted into usable energy will be determined by the kinds of chemicals present in different plants and how they interact in the gut of the herbivore. The possibilities for two tissues are diagrammed in Figure 8.2. The results can be extended qualitatively to additional tissues.

The effects of a chemical on an animal may depend upon the other chemicals with which it is mixed in the gut. If the chemicals enhance one another's effects, then an herbivore, by mixing its diet, must actually eat less per day than if it ate only one of the plants (Fig. 8.1A). If the chemicals do not mutually enhance one another's effects, but simply add to the total amount of toxin the animal must handle, the tissues may be treated as if they were substitutable, as we have assumed in previous foraging models (Fig. 8.1B). Alternatively, an herbivore may be able to handle a larger total amount of toxin provided no one of them is present above a certain concentration. If the different tissues have different chemicals, then the herbivore may be able to ingest the maximum amount of both tissues each day (Fig. 8.1C). Finally, the chemicals may mutually inhibit one another's actions so that the herbivore can actually consume more of each if it is able to mix its diet (Fig. 8.1D). For example, deer can eat more Sagebrush (*Artemisia tridentata*) and Juniper (*Juniperus osteosperma*) per day if they are fed together than they can when given only one of the plants. Similarly, if Gambell's Oak (*Quercus gambellii*) is mixed with juniper and sagebrush, the total amount of plant material consumed per day rises even more (Smith 1959). In fact, case D may be very common for generalized herbivores.

**Figure 8.1 Maximum food consumption by a generalized herbivore.**

$Q_1$ max = maximum amount of plant tissue #1 that can be ingested per day

Q2 max = maximum amount of plant tissue #2 that can be ingested per day

Four cases are represented:

A: Chemicals are mutually enhancing so that mixing foods reduces the amount that an herbivore can consume.

B: Prey are perfectly substitutable.

C: Chemicals are non-interacting so that an herbivore can eat the maximum of both.

D: Chemicals are mutually inhibiting so that an herbivore can eat more of both tissues by mixing them in the diet.

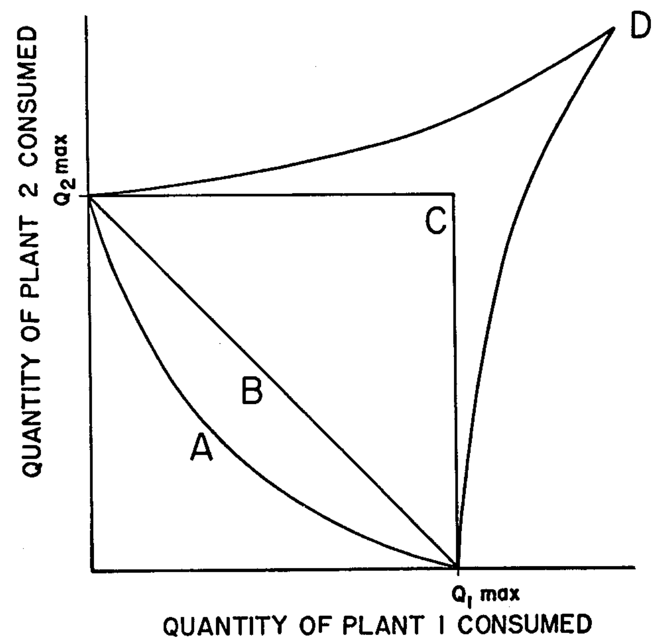
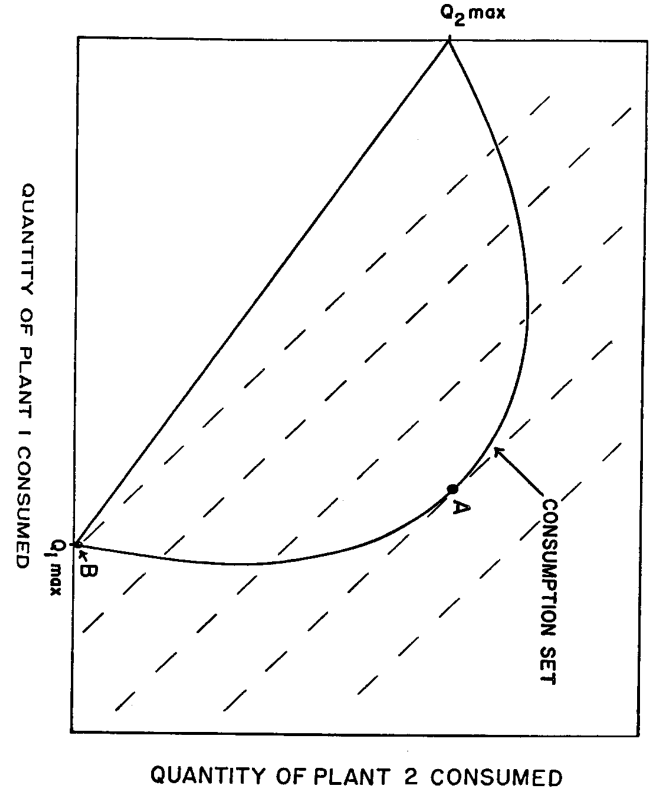


**Figure 8.2 Consumption sets for generalized herbivores.**

Adaptive functions are represented by dashed lines. *A* is the optimal diet when the foods inhibit one another's toxic effects. *B* is the optimal diet when the foods are substitutable or mutually enhancing in their toxic properties.



If by mixing its diet the herbivore can actually eat more per day than it can of any single plant, the total amount that can be eaten of different combinations of plant tissues, the *consumption set*, is convex (Fig. 8.2). To determine the optimal diet, we construct adaptive functions under the assumption that fitness is a direct function of the total amount of energy consumed. That is, the adaptive functions are linear and have slopes determined by the relative abundances of the plants (Fig. 8.2). For convex consumption sets, the optimal diet is always a mixed one, but for concave consumption sets, which result when the toxins are mutually enhancing, the optimal diet is always a single plant species, determined by the relative abundances of the plants and the concentrations of their toxins, i.e., on $P_i$ max.

In general, the risks associated with foraging are very different for large herbivores than for small ones. In the first place, large herbivores are preyed upon primarily by animals with similar life-history characteristics and similar sensory capabilities as they themselves have, i.e., the main predators on herbivorous vertebrates are other vertebrates. These predators find it easier to locate their prey by signals emanating directly from the prey rather than searching first for signs of partially consumed vegetation because the herbivore may have to situate itself in less protected sites while grazing. The larger the herbivore, the less the risk, but also the larger the number of plants that must be consumed per day and, hence, the greater the number at foraging decisions per unit time.

### 8.2.1 Predictions for Large Herbivores

From these considerations we make the following predictions about optimal foraging by large herbivores:

**Selection of Host Plant**

1. Specialized, large herbivores should conform to the general predictions for specialized, small herbivores except that the larger number of choice decisions will require a greater difference in the suitability of available plants to favor dietary specialization than is the case for smaller herbivores.
2. Generalized, large herbivores should prefer those parts of plants that are less well defended and/or that contain unusually high amounts of proteins, vitamins and minerals.

3. Unfamiliar plants should be ingested initially in small quantities and only taken regularly if there are no adverse physiological effects from the previous ingestions.
4. Plant tissues should be mixed in the diet to maximize the amount of food that can be ingested per day if the different plants have mutually inhibitory chemicals or if the herbivore can handle a greater total load of toxins if no one is present in high concentration. This requires sensitivity to the chemicals present in the tissues and the ability to judge the consequences of different mixes of tissues in the gut.
5. If plant toxins are mutually enhancing in their effects on the herbivore, the optimal diet should be the least amount of mixture compatible with obtaining the required vitamins and minerals. Preference should be shown for the plant that can be ingested in the greatest quantity without overloading the detoxification system of the herbivore.
6. Tasting and sampling of a variety of plant species should be carried out regularly by large herbivores. This can lead to the addition of new plants to the diet and the maintenance of the ability to handle the chemicals of plants that may be important in the diet at some future time when relative abundances of plants change.
7. Since detoxification systems are at least partially induced, the previous diet should influence choices such that plants eaten in the recent past are favored over plants not eaten recently.

### Foraging Patterns

8. Production of young should be timed to coincide with maximum availability of poorly defended species of plants and/or maximum availability of poorly defended tissues.
9. The larger the herbivore, the less restricted should be the times and places of foraging.

### 8.2.2 Foraging of Large Herbivores

Most larger herbivores are generalized foragers, though they do exhibit preferences among species. Specialized mammalian grazers are rare, e.g., koalas (*Phascolarctus cinereas*) in species-poor Australian eucalyptus forests, sloths (*Bradypus, Choloepus*) in neotropical forests of high species diversity, and the Red Tree mouse (*Phenacomya longicaudus*) in the coniferous forests of northwestern United States. The more generalized species appear to select food both on the basis of protein content (Bell 1970, Klein 1970) that is highest in young, rapidly growing tissues, and on the basis of concentrations of defensive chemicals (Bell and Janzen 1971, Rodgers 1967, Rodgers *et al.* 1967, Rozin 1967, Rozin and Rodgers 1967, McLean 1970, Coe 1967, Freeland 1973). Terrestrial molluscs also appear to be generalized foragers and do not grow properly if forced to consume single species of plants, even if that species is generally highly preferred as food (Paine and Orians in progress). In particular, early successional annual and biennial plants, which escape from grazing in part by their unpredictability in space and time, are more palatable to slugs than are later successional and climax species that have no such possibilities of escape (Cates and Orians in press).

Some mammals are known to sample extensively among available plants and to be able to associate ingestion of plants with digestive discomfort many hours later (Garcia and Koelling 1966, Smith and Roll 1967). Though detoxification systems are inducible, it is difficult to determine how much a large herbivore deviates from the fine-grained optimal foraging model because selectivity does not reduce the rate at which energy can be processed and only increases the amount of time actually spent in search and ingesting. Therefore it is necessary to estimate risk while foraging in order to determine the cost of not filling up on the first plants to be encountered. Currently, we have no way of making these estimates.

# Chapter 9. Mutualistic Foraging

The production by plants of attractants that result in the transfer by animals of pollen to conspecific stigmas and seeds to places where their probabilities of survival are better than they would be under the parent plant provides some especially interesting and unusual optimal foraging problems. It has long been clear that these plant–pollen, nectar–eater, and plant–fruit–eater interactions represent a complex case of coevolution, but simply recognizing this does not provide any insights into the real nature of the interactions and, in fact, may lead to the erroneous assumption that what is optimal for the plants and the animals are the same. Natural selection presumably has molded pollen, nectar and fruit eaters so that they select plants to visit in a manner that optimizes their own foraging efficiencies, while plants have been molded to maximize their own fitness. This is unlikely to result in the evolution of rewards that will maximize energy intake by animals because the animals would benefit from larger rewards to their efforts, while plants benefit by reducing the reward to the minimum that will still attract the animal.

In this chapter we will view first the rewards of nectar, pollen and fruit as resources to be exploited in an optimal manner by animals. At this stage we take the characteristics and distribution of flower and fruit types and their rewards as given and determine the optimal choice for the animal. Then we examine the production of a food reward by the plant as an optimal energy allocation problem with one of several goals that seem to us to be appropriate under different circumstances. With those insights we will explore the implications of these formulations for the evolution of flowers, fruits, and the animals that eat them.

## 9.1 Exploitation of Nectar and Pollen

Since most flowers produce nectar and pollen for only a short period of time, managing the resource for future use is not usually an option for animals using these resources. Therefore, the itineraries of pollinators can be modeled as a case of "pure competition" in the sense we have used it previously in this book.

The basic fine-grained foraging equation is applicable to a pollinator with the following modifications:

1. $S_P$, $S_S$, the probabilities of capture given a decision to pursue, are normally either equal to 1, since flowers do not evade pollinators, or close to zero if the flower has a morphology that excludes the pollinators from the reward.
2. Handling and pursuit times include the time it takes the pollinator to fly to the flower once it has been perceived, the time required to enter the flower and find the pollen or nectar, and the time required to extract the reward. The time to enter the flower and find the reward may decrease as the pollinator acquires more experience with the flower, and the extraction time is highly variable since the amount of reward in the flower at the time it is visited depends on the time of day and number and time of previous visits by other pollinators.
3. $E_e$ , calories expended per unit time while eating is normally less than $E_S$ because, for most pollinators, eating can be done while perched rather than in flight (even hummingbirds utilize perches when given an opportunity).
4. $E_i''$ , the energy content of one item (flower) is not fixed for a given species, but varies as a function of season and time of day and the number and time of previous visits of pollinators to the flower.

The expected amount of reward in a flower drawn randomly from species *i* can be calculated if we know the timing of reward production and the visitation rate of pollen and nectar eaters. An animal with no further information at its disposal can expect this reward for visiting flower of that species, but, by possessing information about the temporal pattern of reward production by flowers of species *i* and information about the foraging habits of other pollen and nectar eaters, a foraging animal can substantially improve its energy intake.

For a forager the encounter rate with various flowers is a function of overall flower density and the usual contagious distribution of plants and of the flowers on individual plants. For example, if flowers are synchronously in bloom on a plant, then once the animal has reached a plant in flower, the average distance between flowers, and hence $\lambda_i$, is no longer the statistical average for all flowers of that species, but is much higher for subsequent visits to flowers on the same plant. If the forager is able to perceive the other flowers and therefore has information on this aspect of reward distribution, it can improve its harvest of energy by modifying its itinerary and visiting all active flowers on the plant it has discovered before moving on. Thus, an individual plant may be considered to be a patch and our patch model is appropriate.

The suitability of these patches depends on the intra- and inter-individual flowering synchronies within and among species of plants and the physical arrangement of flowers on plants. Some of these are subject to modification by natural selection and are thus part of the strategies of plants. For the moment, however, we simply will assume distributions of rewards and examine the optimal choices of the animals exploiting these rewards.

It is convenient to recognize two cases of the itineraries of pollen and nectar eaters, a “basic” foraging pattern and a central-place foraging pattern. Many pollinators, such as male hummingbirds, female hummingbirds outside the breeding season, and most adult butterflies and moths, are gathering energy for maintenance or for future reproduction and have no need to return with food to a central place. Breeding female hummingbirds, some bats and many social hymenoptera often are gathering reward to be returned to a central place (the hive, cave or nest) and therefore the constraints of central-place foraging are applicable.

If we view choice of plant to visit as a fine-grained problem, the basic predictions from our fine-grained foraging model hold within the constraints listed above. The choice of the optimal set of plants to visit is determined as before and plants are added to or dropped from the list of those visited according to their $E^*/h^*$ ratios. Thus, the higher the rate at which the forager can ingest energy in the general foraging area, the fewer the kinds of plants it should visit. During the day, however, there will be, especially in temperate regions with marked diurnal temperature fluctuations, significant changes in $E_S$ of a foraging animal. The net gain of energy while foraging from flowers will be high when ambient temperatures are high and lower when ambient temperatures are lower. This is especially important for the larger flower visitors, such as bumblebees (*Bombus*), which may maintain temperatures well above ambient (Heinrich and Raven 1972). Therefore, bees can maintain positive net energy balances on flowers of lower $E^*/h^*$ values when it is warm than when it is colder, but this does not mean that the bees should include these lower-reward flowers in their optimal set. In fact, if nothing else has changed, our model predicts the reverse. When temperatures are higher, and $E_S$ is therefore lower, if the availability of pollen and nectar in the area is constant, pollen and nectar exploiters should actually reduce the number of species of flowers they visit. An increase in net energy gain, whether due to an increase in resource availability *or* a decrease in $E_S$, causes a contraction of the optimal set of flowers to visit. The fact that large bees are observed to visit flowers offering a low rate of energy intake primarily during the warmer parts of the day must mean that total nectar and pollen availability is less then. Reduced food supplies during the middle of the day would be expected to result if the rate of depletion of nectar produced during the night by the combined activities of all foragers in the area exceeds the rate of production of new nectar during the day. There is substantial empirical evidence that this is often the case (Heinrich 1972, Heinrich and Raven 1972).

If the flowers on a plant are treated as a patch within which the forager has an expected rate of encounter with new flowers and an expected rate of harvest of energy per flower, the forager should remain on that plant, visiting flowers until the marginal value of that patch is equal to the average value of all patches in the general foraging area. In order to make this evaluation, the forager needs to know its expected rate of energy intake in all available patches and its rate of energy intake in the patch it now finds itself. Normally, the latter can be assessed only by sampling a number of flowers within the patch because their average energy content will depend on factors unknowable in advance. For example, if the plant has just recently been visited, the energy content per flower will be low. A territorial nectar eater can know the interval between its visits to flowers, but a forager who has been absent from the area cannot possess in advance information about visits while it was gone. Little work has been done on patch evaluation by nectar and pollen exploiters, but apparently hummingbirds sample a few flowers in a patch and move on if the reward per flower is low. The length of time birds remain in the patch is expected to be a function of the interval since the last visit of another bird (Orians pers. observ. in Costa Rica).

If the general availability of rewards declines during the day (or season), i.e., the average value of all patch types decreases, then the forager is expected to add patches to its optimal set in the same manner described above, unless there are compensating factors, such as a reduction in $E_S$ by a rise in temperature.

An important component of the marginal value of a patch is the fact that many flowers have inflorescences that are strong enough and sufficiently compact to support the weight of the pollen or nectar eater and allow it to walk rather than fly between individual flowers. The potential energy savings for an insect such as a bumblebee are enormous because the energy expended while walking can be as much as a hundred times less than the energy expended during an equal period of flight (Ludwig 1962). Hummingbirds and bats, however, are unable to walk between flowers, though hummingbirds occasionally are able to reach several flowers from one perch, and their energy savings would be limited to the reduction in flying distances between flowers that are more tightly packed.

For those exploiters of nectar and pollen engaged in central-place foraging, patches further away from the central place must yield energy at a higher rate than closer patches if they are to be included in the optimal set. Also, a central-place forager that discovers a previously unknown good foraging patch on the way to a more distant patch should alter its itinerary to utilize the closer patch. Therefore, the results of the Wenner (1967) and Johnson (1967) experiments with honeybees are exactly what we expect and do not constitute evidence that requires special explanation. However, there do not appear to be any unusual aspects of pollen and nectar as resources that require elaboration of the results discussed in Chapter 5.

## 9.2 Production of Nectar and Pollen

The size of the reward produced per flower, the temporal pattern of reward production and the nutritional characteristics of the reward are all under the "control" of the plant, and will evolve to maximize the fitness of the plant. We find it convenient to recognize two types of plants that represent the extremes of a continuum of flowering strategies. We call these (a) efficiency maximizing plants and (b) rate maximizing plants.

**Efficiency maximizing plants.** For these plants, the goal is the maximization of transfer of pollen to conspecific stigmas per unit of energy expended. We assume time is no constraint for these plants, that flowering extends uniformly throughout the year, that the gross time of production of pollen and nectar is unimportant, and the expected value of an individual pollen grain is high and independent of time. Since the plant is a continuous producer of pollen and nectar, the expectation of reward for a visitor to the plant also is independent of time except for short-term (diurnal) fluctuations! The expectation of reward at a particular flower, however, may change with the age of the flower.

For such plants the penalty of sometimes not being in the optimal set for one or more of its visitors is less than for rate maximizing plants. There is a much higher probability that the flowers of these plants will be morphologically specialized and be visited by specialized animals, because the predictable availability of the flowers over long time periods makes them a reliable energy source over the entire life cycle of the pollen and nectar eaters. For the same reasons these plants should be less involved in short-term competition for visitors.

**Rate-maximizing Plants.** For rate-maximizing plants, the goal is to maximize the rate of visitation to the flowers and, hence, the rate of movement of pollen grains to conspecific stigmas. For these plants the gross timing of reward production is important and the penalty for not being visited for even a short period of time is high. These plants are less likely to have morphologically specialized flowers or to have specialized visitors attending them. They are likely to be involved in short-term competition for visitors, and selection may favor heavy energy commitment to rewards if it enables the plant to attract a large number of visitors rapidly. If the plant does not face any energy limitations, this pattern presumably could be carried out over long periods of time, but any real plants could do so only at the expense of depleting its energy reserves for seed and fruit production and vegetative growth.

Because of the shortness of the time during which flowers of a given species of rate-maximizer are present in the environment, at the time of initiation of blooming most of the visitors to the plant will be unfamiliar with it and will have to learn something about its reward characteristics, i.e., the expected value of the patches it forms. This provides opportunities for the plants to exercise deceit or mimicry by attracting visitors without providing them with a reward. The first visits to the flowers of a rate-maximizing plant are likely to be the most important because (a) the most pollen will be picked up per visit and (b) the probability that the ovum reached by a pollen grain is still unfertilized is greatest. Therefore, even if the visitors learn that the plant is not worth including in their optimal set, some pollen transfer and fertilization should have occurred before their foraging choices will have been significantly altered (Fig. 9.1).

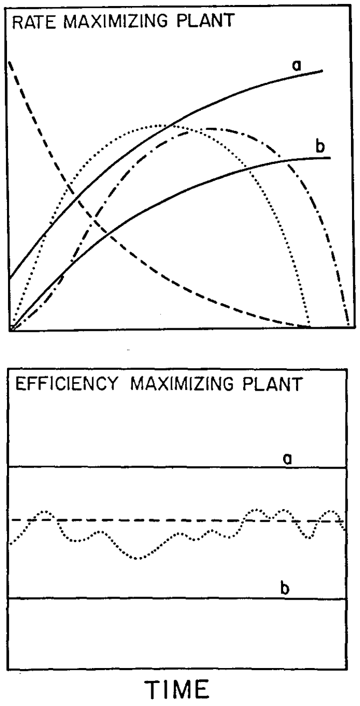


**Figure 9.1 Hypothetical relationships among flowering pattern and rates of visitation by nectar eaters for rate-maximizing ad efficiency-maximizing plants.** Patterns are compared for long-lived and short-lived foragers.

-.-. Number of visits per unit time
---- Useful pollen transferred per visit
____ Percent of visitors knowledgeable about flower
.... Number of flowers in bloom/plant
a = flower visitor long-lived
b = flower visitor short-lived

Evolutionary responses by visitors to the characteristics of a plant will occur slowly because the value to a visitor of "knowing" about a plant at the time of its first visit is low if the plant is present only a short period of time. The loss in energy from being deceived by a plant that is in bloom for only a week is much less than the loss from being deceived by a plant with a four-month blooming season. If we let $C = \frac{\text{length of time pollinator is active}}{\text{length of time plant is in bloom}}$, then high values of C should be associated with weak selection for genetically based recognition of flowers, while low values of C should be associated with strong selection for both learned and genetic responses that reduce the probability that an individual flower visitor will be deceived.

Thus, for rate-maximizing plants, there appear to be two opposite selection pressures. Since failure to be visited for even a short period of time is a serious loss, selection should favor a high energy return to visitors to those plants, as provided by large and conspicuous heads or inflorescences and high reward. On the other hand, the short blooming time of these flowers enhances opportunities for cheating, which could lead to the evolution of conspicuous visual signals and mimicry, but low level of reward. The former outcome should be more likely in places where the most important visitors to flowers are longer lived and with lower recruitment rate because more of those pollinators may “know” about the flower when it first comes into bloom and fewer naive animals will appear during the blooming period. Deceit and mimicry are most likely where visitors are short lived and with high recruitment rates.

**Manipulation of Visitor Itineraries.** For both kinds of flowers, the size and temporal pattern of reward production can influence choice of the optimal set by foraging pollen and nectar eaters. As mentioned previously, it is not sufficient to show that a visitor can achieve a positive energy balance by visiting a flower because that does not assure that the flower will be included in the optimal set. In addition, the value to the plant of a visit depends on the previous itinerary of the visitor, i.e., how many plants of other species it has visited since it last picked up conspecific pollen, and its future itinerary, i.e., how many plants of other species it will visit before it comes to another conspecific. These probabilities can be influenced by features of both flower morphology and reward structure.

It is easy to restrict visitation to small animals simply by reducing the amount of pollen or nectar available per flower, assuming a constant rate of extraction. This causes the flower to be dropped from the optimal set of larger foragers even if the animal can achieve a net energy gain from visiting the plant, unless the rate at which the forager can harvest energy in the environment is so low that the optimal set includes all plants that yield positive net energy balances. Smaller visitors are difficult to exclude by changes in reward size per flower, however, and morphological devices appear to be most important here.

The most effective non-morphological way of increasing the probability of successive visits to conspecific flowers is the temporal pattern of reward production. If a flower produces its nectar at a particular time of the day, as many of them do, this may increase the value of that plant sufficiently to cause the optimal set for the forager to contract to it alone. However, the extent of contraction of the optimal set should be proportional to the energy commitment by the plant. Thus, there is a trade-off between the cost of increasing the probability of subsequent visits to conspecific flowers and the value of reducing intermediate visits to other flowers (Fig. 9.2). The energetically cheapest solution to that problem is a morphological one that precisely places pollen on the visitor such that it is unlikely to be rubbed off by visits to any other kinds of flowers. This strategy is best illustrated by many orchids in which the pollen are compacted into pollinia that are deposited on bees in species-specific locations (Dodson 1965, van der Pijl and Dodson 1966).

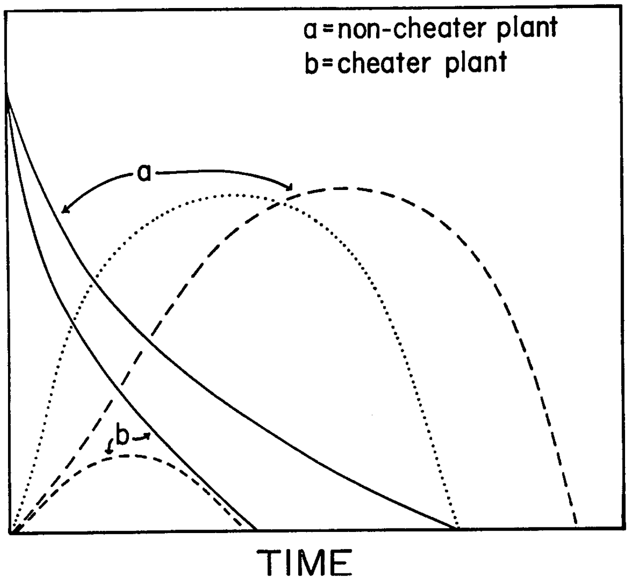


**Figure 9.2 Hypothetical patterns of flowering and visitation to cheater and non-cheater plants.** Symbols as in Figure 9.1.

Opposing selective pressures on plants are generated by the fact that those features that increase the value of the patch formed by the plant, i.e., size and number of the reward units and clumping the units into heads on which the animal can walk, favor extensive exploitation of units on the plant by an animal during a single visit. This increases the probability that pollen from one flower will be deposited on the stigma of another flower on the same plant rather than being moved to a different plant. Even if the male and female reproductive parts mature at different times, most of the pollen will have been lost before the forager leaves the plant. If the nectar production continues during the successive maturation of male and female parts of the flower, self pollination will be avoided but at the cost of a high loss of pollen and a higher energy commitment to reward production.

It is possible that the genetic consequences of self-fertilization *within* flowers on a plant are significantly different than self-fertilization *among* flowers on a plant. Given the open growth systems of plants, flowers on different branches are derived from cell lines separated from one another by many divisions. Therefore, opportunities for somatic mutations to be incorporated into the reproductive structures are much greater than for parts of the same flower. If so, the fitness of seeds derived from ova fertilized by pollen from flowers on a different branch of the same plant may be higher than the fitness of ova fertilized by pollen from the same flower. If this is the case, mass flowering larger woody plants should have less temporal segregation of maturation of male and female reproductive parts and more synchrony of blooming than is the case for small, herbaceous plants with a smaller number of flowers all borne on a single stem. These latter plants should exhibit sequential blooming of flowers, even within the same head or clump, and greater time differences of maturation of male and female parts.

The previous discussion has assumed that the only concern of the visitors to flowers is an energetic one. However, it is known that pollen and nectar may provide special nutritional needs of animals. Some butterflies, for example, gather pollen to obtain amino acids (Gilbert 1972), and recent evidence suggests that many nectars contain amino acids that are vital to the health and reproductive success of animals that utilize them as food (Baker and Baker 1973). If the forager must harvest particular rewards to obtain a specific nutrient, then its optimal set will depart from that predicted from our fine-grained energy model and the patch model. We are unable to evaluate these changes because we do not know how to equate a unit of special nutrient with a quantity of energy sacrificed, because both must be translated into fitness units by as yet unknown transformation rules.

## 9.3 Exploitation of Fruits

Fruits as resources to be exploited are similar to pollen and nectar supplies with the exception that size and characteristics of the available energy are more readily perceived at a distance than is the case with flowers. In fact, most plants signal the ripeness of fruit by bright colors or volatile chemicals, probably because the plant loses fitness if the fruit-eaters cannot distinguish fruit in which the seeds are not yet ready to be dispersed from the parent plant. Also, since most fruit-eaters that can effectively disperse seeds are long-lived vertebrates, the population usually is composed of a larger percentage of knowledgeable individuals than is the case with flower visitors. Therefore, opportunities for deceit and mimicry by fruits are doubtless very poor.

Exploitation of fruit is best considered as a patch choice problem with the individual plant as the patch unit. The patches differ in their characteristics in relation to the flowering strategy of the plant, i.e., whether it is a rate-maximizer or an efficiency-maximizer. In fact, natural selection of the fruits may be the more powerful molder of flowering strategies because the probability of survival of seeds may be more strongly affected by timing of dispersal than success in pollination is affected by timing of flowering. In any case, a rate-maximizer will produce an abundance of fruit over a very short period of time, while an efficiency-maximizer will have a small quantity of fruit present at any time but will be a reliable source of fruit for a long period of time.

When in fruit, a rate-maximizing plant will offer a potentially high harvesting rate to a fruit-eater whose optimal choice should normally be to remain within the tree until the fruit supply begins to wane, i.e., the marginal value of the patch declines. This choice, however, conflicts with the value to the plant of its fruits since the seeds will be defecated directly under the tree in the zone of highest expected mortality of the seeds and seedlings (Janzen 1970). Such a seed distribution could be accomplished equally effectively with no investment in fruit at all and therefore natural selection should favor characteristics of fruits or other aspects of plants that make it desirable for fruit-eaters to expand their optimal sets of plants to visit. This problem will be considered in the next section.

## 9.4 Production of Fruits

The selective pressure for the evolution of fruit presumably is that survival of seeds and seedlings is better at some distance from the parent plant than directly under it. Therefore, the evolution of fruits will be determined by their effectiveness in moving seeds away from the parent. Also, since “away” consists of many different patches, some of which are totally unsuitable for germination and survival of the young plant, fitness can be increased by any devices that increase the probability that the seed lands in a more favorable patch. The first of these two problems appears to be more readily influenced by characteristics of fruits than is the latter.

The size of the seed, which is adoptively determined primarily by the value of the energy reserves to the seedling under different conditions of competition (Salisbury 1942), sets limits on the sizes of fruits and the animals capable of eating them. Large seeds must be surrounded by large fruits and, above a certain size limit, the fruits are too large to be consumed by arboreal animals (Smyth 1971). Terrestrial mammals are likely to move shorter distances than arboreal animals and if they simply consume the fruit on the ground underneath the tree, the plant has derived no benefit from the investment in fruit tissues. If, however, the food is storable, it is to the advantage of the *mammal* to move it away from the parent tree where losses to other seed predators are higher. The problem is that fruit tissues, in general, are not readily storable as they spoil rapidly. Not surprisingly, the fruits of large, seeded plants that are dispersed by scatter hoarding rodents are hard and serve primarily to protect the seed. It is the seed itself and not the fruit that is the object of consumption by these mammals, and survival of the seed is dependent upon either (a) the animal forgetting where the fruit is stored or (b) the animal dying from some cause before it has a chance to retrieve its stores.

An effective way by which a plant can expand the diets of the animals that eat its fruits is through the nutritional characteristics of the fruit. If the fruit of a plant constitutes a complete diet for a fruit eater, its optimal strategy is to remain in the plant until depletion of the fruit supply. Unless a rate maximizing plant can mature its seeds at different rates so that fruits ripen slowly over a long period of time, which would only be possible if survival probabilities for germinating seeds were uniform over time, it will inevitably constitute a patch of high value for a short period of time. However, if the fruit eater must ingest a variety of fruits to balance its diet, then it will have to expand its optimal set even when fruit on the plant is abundant. Fruits are known to be nutritionally diverse and numerous observations of birds at fruiting trees suggest that they seldom remain for very long in a single plant, but move on even though more fruit is available. We suspect that the problem of dealing with optimal foraging decisions by fruit-eaters has been the major selective force in the evolution of the nutritional characteristics of fruit.

Alternatively, it might be profitable for the fruit-eater to move away from the plant if the plant were a poor hiding or resting place. A slight improvement in survival would suffice to favor movement to a safer site, but we don't know if the evolution of plants has been influenced by this. Many tropical plants ripen fruits when they are leafless, but this can be explained in other ways (fruiting during the dry season, enhancing conspicuousness of the fruit).

The problem of influencing the patch distribution of dispersed seeds appears to be largely unsoluble by plants. Certain fruit-eaters do tend to move primarily in specific habitat types and are therefore more likely to drop seeds in some patch types than others, but this is likely to result from the simple fact that the adult plant is growing in that particular patch type. It is difficult to know how further modifications of the fruit could improve the habitat distribution of seeds. It is also difficult to conceive why plants would benefit by restricting the range of species of animals that used their fruits except in those cases where the fruit is purely protective and it is the seed that is the food source of the animal. Corresponding to this, it is a well-known fact that fruiting plants are typically visited by many species of animals, especially in the tropics.

# PART III. THE EVOLUTION OF OPTIMAL FORAGING

In the previous chapters we have dealt almost exclusively with static models of optimal foraging. That is, we have assumed some distribution or density of prey and modeled the optimal responses of the predator to these situations. These models allowed us to predict changes in the behavior of the predator if there is, say, a short-term change in prey abundance, but we have assumed no constraints on the ability of the predator to modify its behavior under different circumstances.

In the following chapters we wish to consider longer-term effects of predators and prey evolving under different average circumstances. For example, what characteristics should predators have if they have evolved in an environment with a low-average encounter rate with prey? How will these evolved characteristics restrict the ability of the predators to change their behavior in response to short-term changes in prey availability? What trade-offs may exist between the optimal solutions to different sub-problems within the foraging process? We consider these kinds of questions from the perspectives of both the predators and the prey.

# Chapter 10. Evolution of the Characteristics of Predators

It is useful to organize a discussion of the evolution of predators from the perspective of the hierarchy of foraging behavior presented in Chapter 2. We choose to begin with higher level decisions and proceed toward lower level ones.

## 10.1 Evolution of Habitat Selection

We define a habitat as a collection of patches to be used by an organism during a breeding cycle. Choice of habitat is a decision that may be made a single time during the life of an organism or, perhaps, as often as each breeding cycle, and each choice is a highly significant one. In habitat selection, time is always a constraint because (a) there is a finite probability of death while searching, (b) habitats may fill up so that expected fitness declines over time, and (c) breeding success is usually reduced by a delay. Therefore, natural selection may favor acceptance of a patch that is less than the average suitability of all available patches at the time the choice is made. This may be one reason why so many organisms have evolved to use familiarity with a site (having bred there before or having been raised there) as a basis for selecting a breeding habitat rather than taking time to engage in a more thorough search.

The theory of habitat selection has been explored in some detail by Fretwell (1972), Fretwell and Lucas (1969) and Orians (1971). The wisdom of choices depends on a complex sum of temporal and spatial suitability of the relevant patches within the habitat over the time dimension of the breeding cycle or other long term time unit. Since a major element of 'anticipation' of resource availability in the future is involved, many of the cues used in selecting habitats are indirect. Some organisms with long breeding cycles are able to perceive resource availability directly and to base habitat selection on it. For example, jaegers that exploit dense populations of lemmings for breeding move over the tundra until they find concentrations of prey and breed there (Pitelka, Tomich and Treichel 1955). Bay-breasted Warblers (*Dendroica castanea*) settle at locations of outbreaks of Spruce Budworms (*Choristoneura fumiferana*) and disappear from otherwise suitable coniferous forests when budworm population are low (MacArthur 1957). Organisms with short breeding cycles are better able to choose habitats on the basis of directly perceived prey availability. Herbivorous insects detect their host plants directly and parasites find single hosts that serve as a habitat for a complete life cycle or several cycles. In these cases the food items are actually the habitat and no new treatment is required here.

Where habitat selection must be made on indirect criteria, the evolution of criteria is more complex. We expect that organisms will evolve to utilize the available clues that are the best predictors of future resource availability. Only birds have been studied intensively from this viewpoint and they appear to rely strongly on the physical structure of the habitat (MacArthur 1961, MacArthur, Recher and Cody 1966, Cody 1968, Karr 1971). The structure of the vegetation is a highly reliable indicator of the ease of use of different searching modes and is probably also as good an indication of future resources as any available to the birds. Pearson (in prep.) has recently shown that at least some tropical birds have lower rates of prey capture when they forage at the upper and lower extremes of their foraging height range than when foraging in the middle where they are found most frequently.

## 10.2 Evolution of Searching Mode

To explore the evolution of searching modes, it is useful to assume a number of static situations, determine the optimal pure competition response to these situations, and then explore the consequences of changes in the relevant prey characteristics. We begin with a consideration of prey distributions and then turn to prey density.

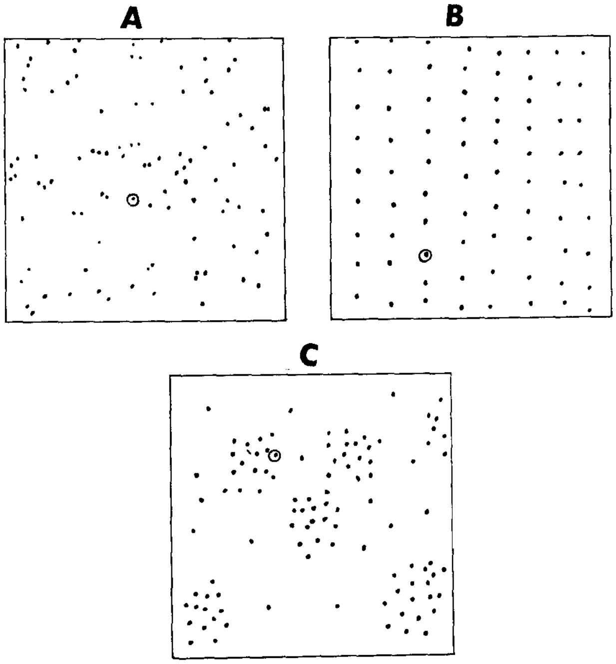
**Area Restricted Searching.** Let us represent prey as non-moving points on a plane that differ in their pattern of distribution (Figure 10.1). Suppose that the predator has just encountered and eaten a prey at ⊙ in A, B and C. The question of interest is, where should the predator concentrate its searching effort after leaving ⊙? In A, the prey are randomly distributed (Poisson), which means that any area not previously searched is equally likely to have prey. In this case, any regular searching pattern (which does not cover any area previously searched) is equally good. In B, the prey have a regular or orchard-like distribution; prey tend not to be found near one another, so here the predator should move out of the area where it just captured a prey item. The best tactic here would be to lock the search pattern into the regularity of the prey distribution. In C, the prey are clumped; the predator should search in the immediate neighborhood of a previously captured prey item. Along with this there should exist a rule telling the predator when a clump is "cleaned out" so that it can move on in search of a new clump. The patch use model discussed earlier can be applied here, even though the clumps themselves are searched for.

**Figure 10.1 Optimal searching in three prey distributions.**

A: prey are points distributed at random. Any area not previously searched is equally likely to have prey.

B: prey are distributed in a regular pattern—the predator should move out of the area where a prey was just encountered.

C: prey are distributed in a clumped pattern—the predator should search in the same area and have some rule for deciding when the clump is "cleaned out"; then it should search a new clump.



Clumped distributions are the most common pattern in nature (Pielou 1969), so searching in the immediate neighborhood of a previously captured prey item should be a common feature among predators, at least those searching for relatively immobile prey. Tinbergen, Impekoven and Franck (1967) called this behavior "area restricted searching" and presented evidence for it in carrion crows (*Corvus corone*) searching for chicken eggs. The effect has been demonstrated for birds, in the field (Smith 1971) and in lab experiments (Krebs, MacRoberts and Cullen 1972), and for at least one fish, the three-spined stickleback (*Gasterosteus aculeatus*) (Beukema 1968). There are also many studies on insects that provide supporting data (Fleschner 1950, Laing 1938, Mitchell 1963, Dixon 1959, 1970, and Banks 1957). Even unicellular predators exhibit increased frequency of turning following an encounter with a prey item, a behavior pattern that results in a more intensive search of the vicinity of the capture (Fraenkel and Gunn 1940, Macnab and Koshland 1972).

Above we introduced the idea of a clump being "cleaned out." In Chapter 5, the f(T) function made use of a similar assumption. As previously suggested, this may be due to actual exploitation by the predator (lowering the density of prey); it also may be due, however, to behavioral responses by the various prey species. Suppose that the presence of the predator or the act of pursuing (and capture) itself causes the prey in the immediate neighborhood to become less available to the predator; then the capture rate is depressed (at least locally), giving rise to something like the f(T) functions. If the prey change in habits or position, it may well be that the transition time is a time of greater vulnerability (so that the capture rate is increased, at least initially). This change in prey behavior (making them more difficult to capture) due to presence of a predator is illustrated by the data of Hyatt (1973), who used mayflies as prey and Kokanee (*Oncorhynchus nerka*) as a predator with an experimental universe consisting of a 50-gallon aquarium with a dark-slate bottom. Since the edges were dark metal, the four corners were dark and earlier experiments demonstrated that the risk of attack was lower for a mayfly in a corner. Figure 10.2 shows the distribution of mayflies in the tank with or without the predator present. The predators were satiated and were not actively hunting (although they would sometimes chase a prey item). In similar experiments with a substrate of gravel, leaves, sticks, etc., the movement was down or under, rather than to a corner, but the effect on availability to the predator was the same. Goss-Custard (1970) also has demonstrated this effect for a wading bird (the redshank, *Tringa totanus*) walking over a mud flat.

If this "depression effect" proves to be important in the field situation, its implication in ecological theory may be far-reaching. Not only is it important for our conception of the use of a patchy environment (the f(T) function), but it may play a basic role in competition theory. A basic effect resulting from competition is exploitation or a decrease in availability of food resources and this is usually taken to mean a decrease in density of the food resources. Looked at from the point of view of a predator, availability could equally well be decreased due to behavioral changes by the prey. Species could compete simply by depressing the resource availability in our sense. We term this *depression competition* to separate it from exploitation competition. It also is possible, however, that species A could cause a behavioral change in the prey so as to make the prey more available to a species B with a different method of hunting. Even if A reduced the resource density, B could benefit if there was a compensatory change so as to increase availability. Actually, the concept of prey density loses usefulness in a complex environment. The predator does not know density, but encounter rates. Any predator hunting a prey species capable of this depression should possess alternative hunting methods so as to lessen the impact of the change by the prey. Some resources clearly can not be depressed in our sense (e.g., seeds) and we might expect predators on these to show fewer alternative hunting methods on the same resource.

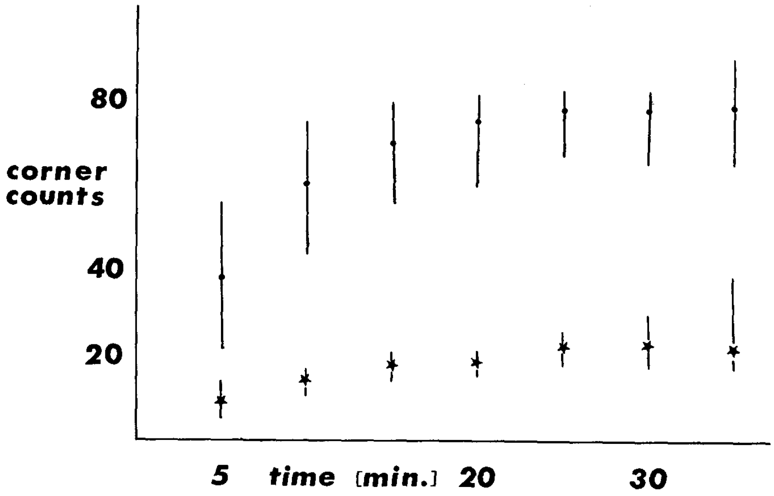
**Figure 10.2 Depression of prey availability by a fish.**

One hundred mayfly nymphs were placed in a 50-gallon aquarium. The corners of the tank were dark and provided a refuge from predation. In the absence of the predator, about 20% of the prey were in the corner. In the presence of a predator (Kokanee, *Oncorhynchus nerka*) about 80% were hidden.

● predator present * predator absent

Vertical bars indicate the range of five replicates.

(From Hyatt, 1974)



This is considered to be a rather short-term effect, so that an important parameter is the recovery time for the prey. If the predator leaves, how long before the prey resume "normal" activities? There is also a longer-term effect, to be discussed shortly, where recovery is equivalent to recruitment.

## 10.3 Changes in Predator Behavior with Changes in Prey Density

We have already shown that a reduction in availability of one or more prey within the optimal set for the predator should result in the expansion of the optimal set. Here we wish to consider the possibility that the predator might wish to change other components of its searching behavior.

It is common in predation models to assume a $\lambda_i$ (average encounter rate) to be proportional to some

$$\lambda_i = a_i \cdot D_i^0$$

density measure for prey type i (Holling 1959, Royama 1971). If $D_i^0$ is the average prey density,

In search models (Paloheimo 1967, 1971), $a_i$ is modeled as a function of predator movement, size of the predator's perceptual field, etc. Suppose that type i is distributed at random on a featureless plane with mean density $D_i$. The prey items are non-moving points. The area (A) that must be covered to find a single point can be considered as a random variable with a negative exponential distribution (with density function $f^0(A) \quad A \geq 0$). If r is the perceptual radius of the predator as it moves over the plane with velocity v, the area covered is related to the search time (T) by the relation:

$$A = 2 \cdot r \cdot v \cdot T, \text{ then } 2 \cdot r \cdot v = a_i \text{ and } a_i \cdot D_i^0 = \lambda_i$$

so:

$$f^0(T) = D_i^0 \cdot a_i \cdot \exp\left[-a_i \cdot D_i^0 \cdot T\right] \; T \geq 0 \tag{37}$$

Paloheimo (1967, 1971) has discussed the fact that Eqn. 37 should be only an approximation for the searching time density function (even if the prey distribution is Poisson). Since prey are seen some distance (r) away, the predator brings new areas into its field of view as it moves toward the prey item seen, but this time is not counted as search time, it is handling time. This actually contradicts our assumption that no new prey may be encountered during the handling of a prey item. However, Eqn. 37 should be a good assumption at low prey-densities, and at high prey-densities, it is the handling time characteristics (not the search) that primarily determine the capture rate.

Even though $\lambda_i = 2 \cdot r \cdot v \cdot D_i^0$ is a very simplistic assumption, it is useful to examine some of its implications more closely. The fine-grained model with a single prey type may be written as follows:

$$E_n = \frac{\lambda \cdot E^*}{1+\lambda \cdot h^*} - E_S \quad \text{(omitting the subscript i)} \qquad \textbf{(38)}$$

Letting $D^0 \rightarrow 0$, we have that:

$$En \simeq 2 \cdot r \cdot v \cdot D^0 \cdot E^* \qquad \textbf{(39)}$$

There are several possibilities for control by the predator to increase $E_n$.

1. If v is a result of predator movement (it can be a result of prey movement with a stationary predator, or movement by both), v and $E_S$ are positively related (Warren 1971) and there may only be some range of $2 \cdot r \cdot D^0$ where the gain with v increasing exceeds the loss.
2. v and E may be negatively related if a faster moving predator scares prey, making them more difficult to capture, or if a faster moving predator is less likely to recognize a prey item it has come upon (i.e., $S_R$ decreases as v increases).

1 and 2 suggest that increasing predator search velocity may not be a good tactic under some conditions. Ivlev (1961) found that hungry fish did not have a higher search velocity than well-fed fish.

3. r and $E_i$ should be negatively related if:
   a. increasing pursuit distance lowers the capture success;
   b. increasing r results in increasing energy costs for handling the item.

   However, they may be positively related if:
   c. increasing pursuit distance raises the capture success. This would be so if the predator made a more careful pursuit or if the prey were less likely to be "spooked" by a predator shifting from searching to pursuit at a distance further from the prey.

For a., the predator may have an inflexible method of pursuit or stalk. In c., the predator can adjust the method. One result is fairly straightforward—more care should be taken in handling each individual prey item. The handling time is unimportant, but capture success is.

Situation a. is likely to hold for predators that pursue their prey by flying out from a perch because the initiation of the pursuit is necessarily conspicuous and the opportunities to vary pursuit flight are minimal. Young (1970) has suggested that the brilliant coloration of large, highly palatable *Morpho* butterflies in neotropical forests may actually be a conspicuous signal that induces early perception and pursuit of the butterfly by birds. If probability of capture is negatively related to distance of pursuit, young birds would soon learn that it was not profitable to pursue the butterflies.

As we can now see, even this simple assumption about the relationship between X and prey density results in many possible optimal behaviors for the predator at low prey-densities. If we allow D to get very large ($D \rightarrow \infty$), Eqn. 38 approaches as follows:

$$E_n \simeq A^{*}/b^{*} \tag{40}$$

For this case, the relations are very complex and difficult to treat analytically because the effects of the predator on the distribution and behavior of the prey become so complex. We will not develop this case further here.

## 10.4 Predator Behavior in a Featured Environment

As we have indicated, the most serious assumption in the previous model was that of a featureless environment. Since all environments are featured, we now relax that assumption and explore some consequences.

Assume that the featured environment contains a number of places where prey may be located and that these places differ with respect to the ease with which the predator can search in them and how well prey match their background. To avoid complications of changes in prey density, we further assume that the rate of recruitment of prey exactly matches the rate of removal of prey by the predator. A predator searching over this environment will locate selectively and consume prey that are more conspicuous to it, either because they are located in places more easily searched by the predator, or because some are better hidden, i.e., they match the background better. Even under our very restricted assumptions of prey recruitment behavior, the effect of the action of the predator is to reduce the fraction of prey that are situated in the more conspicuous places. This should produce a gradual reduction in the rate at which the predator encounters and captures prey, a phenomenon called "losing your marbles" by F.E. Smith (1972). If we allow the prey to selectively recruit into those sites in the environment where their probability of capture is lower, a reasonable possibility since prey in those places should have a higher probability of living until reproductive maturity, the predator will lose its marbles even faster.

A predator faced with a microhabitat shift in its prey distribution has two possible strategies. First, it could adopt an alternative search mode that enabled it to find prey in the other sites more efficiently than was possible with the first mode. Second, it could expand the area over which it hunted so that it foraged less often over the same piece of ground. If the prey recruit and move around, the longer the interval of time between visits by the predator, the greater the probability that more prey will be found in easier-to-locate sites. Both doubtless occur, though we do not know their relative frequencies. In the highland pine forests of Guatemala, Yellow-backed Orioles (*Icterus chrysater*) and Banded Wrens (*Campylorhynchus zonatus*) both forage by searching among the clumps of needles and by searching among epiphytes and in cracks in the bark of small and medium-sized pine branches. During foraging bouts of orioles and of wrens, no individual was found to use both foraging modes within a single bout (Orians, unpubl. observs.), suggesting that it may be difficult to shift rapidly from one search mode to another in a featured environment like a tree.

Given single predator and single prey, the expected evolutionary result is that the prey should evolve to be increasingly more difficult for the predator to locate, while the predator evolved to become increasingly effective in locating the prey with its new characteristics. Evolutionary stability may be introduced into the system by the presence of additional species of predators and prey. Suppose, for example, a second predator was more effective in finding the prey in a different part of the featured environment than the first predator. The prey will stabilize phenotypically when the selective pressure caused by each of the predators is equalized; this is likely to occur with a poorer match to either of the features of the environment than would be the case if there were but a single predator. Similarly, if there are multiple prey, each of which requires a different predator morphology or different searching mode for most efficient capture, the optimal phenotype for the predator is one that is less effective on any prey type than the pure specialist, i.e., the jack of all trades is master of none.

## 10.5 Response of Predators to Changing Rates of Prey Recruitment

Continued existence of a predator in an environment is dependent upon a positive rate of recruitment of its prey, but different prey have highly varied rates of recruitment. For moving predators, the rate of recruitment will determine the average frequency with which a given area can be searched profitably. Recruitment here also could be taken to be the shorter term prey behavior renewal.

Some prey have recruitment rates that are essentially instantaneous or so close to it that availability is uninfluenced by the predator's harvesting rate. This is characteristic, for example, of light and plankton in the waves washing over sessile intertidal organisms. There is no selective advantage to movement if prey recruitment rates are this high, which is presumably why photosynthetic plants and the dominant organisms of the rocky intertidal are sessile. The proximate response of moving predators to low rates of prey recruitment is an increase in the size of the home range. If the prey are economically defensible, this can be expected to lead to the evolution of defense of the foraging area (Brown 1964, Brown and Orians 1971). Viewing territoriality from the perspective of optimal foraging theory shows the inappropriateness of attempting to assess the foraging significance of a territory by measuring, as is usually done, the percent of total prey in the defended area actually consumed by the predator. The advantage accruing from defense of a foraging area is not obviously related to percent of prey eaten, a number unknowable to the predator, but *is* related to its effects on encounter rates with prey, which, as we have just seen, can be complexly related to the frequency of passage of predators through an area.

There are also predators that hunt from stationary positions for prey with slow rates of entry into the search area. Some, such as sea anemones and web-building spiders, are sessile or effectively so during a hunting period, while others, such as trapdoor spiders and *Anolis* lizards, may search out an area around a stationary hunting perch. For the former organisms, a low rate of prey arrival should result in the acceptance of virtually all prey that come into contact with the animal or its trap, and the ability to withstand long periods of starvation. Since movement and its attendant complex morphological and physiological machinery is not necessary, such animals can evolve low metabolic rates and exist on low encounter rates with prey. The extremely slow metabolic rates of sea anemones (Zeuthen 1953) probably represent the extreme of this kind of adaptation.

For predators that pursue prey from a fixed foraging spot, the expected responses of lowering the rate of prey arrival are (a) expansion of the range of prey included in the optimal set by an increase in the radius over which prey are pursued, or (b) change in the fixed spot. An even more interesting case, which may illustrate the evolutionary outcome of these foraging considerations, concerns the trap-door spiders of western Australia. Rainfall in western Australia decreases from the vicinity of Perth on the coast toward the interior deserts. It is reasonable to suspect that prey abundance (number of prey moving per minute into a circle of radius $r$ around the entrance of a trap-door spider) is directly related to rainfall, and Main (1957) found that the species living near Perth would not pursue prey beyond the distance possible while still maintaining contact with the burrow entrance with the hind legs. In successively drier areas, the species of spiders will pursue prey for increasing distances from the entrance to their burrows. This behavioral gradient has evolved probably in response to both the prey abundance gradient and the risk from predation by birds and lizards to a spider away from its burrow. It is not known if the maximum pursuit distance varies with hunger level or size of prey, but clearly there are major, genetically determined differences among the species of spiders studied.

## 10.6 Evolution of Information Gathering Ability

If one kind of predator regularly needs to pursue prey over longer distances than another, then the two should evolve different morphologies and behavior. Since the entire fields of comparative morphology, physiology and behavior deal with these adaptive problems, there is no need for us to review familiar concepts. We do wish to show, however, that the perspective of optimal foraging theory sharpens insights into the evolution of these features. There is a trade-off between the advantage in energy intake deriving from a change and the cost of that change. Consider, for example, the evolution of sensory capacities from the point of view of providing additional information about prey. From our perspective, this additional information could be useful in two distinct ways, First, the predator might be able to perceive the prey at a greater distance, more effectively against a concealing background, etc. This has the effect of increasing $\lambda_i$ for a set of the total array of potential prey. The additional sensory capacity would be favored if the higher encounter rates provided the animal energy to offset the cost of producing and maintaining the sensory system and the neural mechanism for processing the information. Second, the improved sensory capacity might increase the ability of the predator to detect that the prey does or does not fall within the optimal set. This could save the predator valuable pursuit time that would otherwise be wasted on prey not included in the optimal set. It also could function to reduce decision time if the predator could tell at a greater distance or more quickly that the prey was or was not to be pursued.

Suppose that the desired estimation is the $E^*/h^*$ ratio for a prey item encountered. Since the decision is to attack or not attack, the estimation need only establish this fact. As shown in Figure 10.3, accurate estimation is useful only for prey that fall near the choice boundary. If $Q/R$ is known (to be discussed below) some rather inaccurate signals may be used for the prey items that clearly will fall above the boundary. Since the cost of a mistake is less for small prey ($h^*$ small), we also might expect less accurate estimation (little time investment) to be accepted here. For predators attacking prey that can escape once detected, two interesting situations arise. E* may well be a function of the environment of the predator–prey interaction so that the predator may wait for E* to increase. On the other hand, once having detected a prey item, the predator may decrease capture success by waiting. One of us (ELC) has observed that his house cat will attack without hesitation the place where a hand, pencil, etc., has disappeared under a blanket or newspaper. Could the cat be responding to the fact that, in nature, a small animal moving under an object must be vulnerable for at most a split second longer?

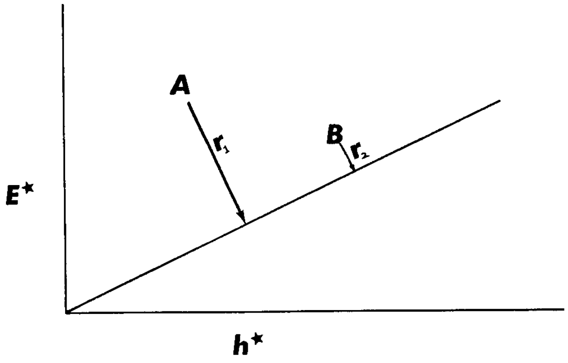


**Figure 10.3 The effects of improved perception by a predator.**

For any prey item encountered, the predator must estimate where it lies on the (h*, E*) plane. An estimate is called precise if it falls near the true value. If the ray from the origin gives the cutoff, then precise estimation of A is unimportant, as A should be taken and any estimate within radius $r_1$ will lead to that decision. B also should be taken but estimates less precise than radius $r_2$ sometimes will lead to a wrong decision. Thus, precise estimation is worth more at B. The value of a correct decision also increases with the distance from the origin.

Consider the example of a trap-door spider in a region with high rates of prey passage in the vicinity of the tunnel entrance, so that foraging away from the tunnel has not been advantageous. Energy invested in visual or other sensory modes that would enable the spider to recognize prey at a distance greater than the usual pursuit distance would confer no benefits to the animal. However, a trap-door spider from the desert might derive considerable benefit from the ability to discriminate prey at greater distances from the burrow.

The second kind of estimation is of Q*/R or of the shorter term marginal capture rate. We noted earlier that the intercatch interval might be a useful measure here. Also useful (as demonstrated with the mantid) is the amount of food in the gut. The basic question the predator is asking is, how well am I doing? By using a combination of remembering capture intervals and knowing the contents of the gut, we believe that most predators may be able to assess their encounter rates with prey during the recent past and to use this as an estimate of expected encounter rates in the future. This capacity does not appear to be unreasonable for even small and simple predators. It yields valid decisions about giving-up time and which prey to include in the set of types to be pursued.

Additional information is particularly valuable when prey distributions are variable in space and time. If the variation is predictable, i.e., prey reliably become abundant at a particular place at a particular time, ability to anticipate this change is valuable. A well-developed sense of time is present in most animals. For example, bees are able to remember that certain flowers produce nectar at specific times of the day and to remember the locations of those flowers. Such capacities are to be expected in all vertebrate predators that have exploited prey where this information would have been useful. The cost of this ability is not known, but the capacity is, in part, a by-product of circadian clocks that serve several purposes.

Another source of information about patchily distributed prey is the foraging activity of other individuals. The capacity to respond to this information is widespread and the price is no more than an occasional glance away from one's own foraging activities. This information is most valuable if the prey is so large that the first individual to arrive cannot entirely consume it, or if prey are patchily distributed and the numbers in each patch exceed the short-term harvesting ability of the first predator to find them.

We have noted that when prey are unpredictable in space and time, it may pay for the organism to depart from short-term optimal foraging patterns in order to gain information that may be useful in the future. We term behavior that functions in this manner *curiosity*, and though it apparently sometimes kills cats, and presumably other organisms as well, it must have its advantages. The fundamental relationship is clear—the greater the uncertainty of food distribution, the greater the potential benefits from curiosity. Whether or not these benefits can be realized depends on other features of the organism's life history. For example, a barnacle could make little use of information about prey availability elsewhere, but even relatively sedentary animals such as sea anemones and web-building spiders may move if capture rates are low in a particular spot.

Like most foraging behavior decisions, curiosity may relate to various time spans of decisions. We have considered already curiosity at the time of habitat selection and pointed out the strong time constraints, particularly for organisms of high latitudes where breeding seasons are short. Curiosity also is important at the level of exploration of different patches with the habitat. Selection should favor curious behavior especially at times when competing demands for the time are weakest, because this minimizes the cost relative to these other activities of the effort devoted to exploratory behavior.

An unpredictable food supply in space or time may result in a lower average expectation of energy intake for the habitat, or it may change the value of different patches without affecting the average value of the habitat. If the former is the case, the organism should stay in patches longer and should expand its diet in the patches in which it is present. If the latter is the case, the marginal value of a patch when it is appropriate to leave is not changed nor is the optimal set of prey items. Therefore, the former is a much more complex problem and the payoff of additional information is higher. There is ample evidence that many organisms are curious, but in no case can this be related to the unpredictability of food resources or the nature of that unpredictability. This is an important area for research at the juncture of ecology and ethology.

# Chapter 11. Evolution of the Characteristics of Prey

## 11.1 Factors Affecting the Fitness Prey

Predation is seldom random with respect to prey phenotype and behavior, and has long been recognized as a major molder of the appearances of prey (Cott 1940, Kettlewell 1961, Cain and Sheppard 1950, Fisher 1929). Assuming a fine-grain model, in an environment with optimally foraging predators, a particular phenotype of prey could be at a relative advantage to others of its species for any of the following reasons:

a. the probability that the predator elects to pursue it ($P_j$) is lower;

b. its probability of being detected by a predator ($S_R$) is less;

c. the probability that the predator captures the prey given that it pursues ($S_a \cdot S_P$) is lower;

d. the handling time for the prey item is increased;

e. its energy content $\left(E_i''\right)$ measured as useful energy to the predator, is less;

f. it takes the predator longer to decide whether or not to pursue it ($h_0 > 0$).

We will discuss first those factors that influence whether or not the prey is within the optimal set, and then turn to the evolution of reduced detection of prey.

Since evolution normally proceeds by small steps, it is unlikely that any change in the prey will move it from always being in the optimal set to never being there. Besides, a prey may be included or excluded because of the abundance of other prey of higher rank. All that is necessary for a trait to be favored is that it increase the range of conditions under which the prey is excluded from the optimal set.

The probability that a predator captures a prey item is a function of the conditions under which the attack occurs and, of interest here, the type of escape response shown by the prey. It is reasonable to suppose that a predator is more successful if it can anticipate the escape pattern of the prey and act accordingly. This is familiar to every experienced field entomologist who learns, by determining the escape response of a species, where to swing his net. If this is so, a relative advantage should accrue to prey individuals that utilize an unusual or unpredictable escape pattern (Fisher 1956). There is some evidence of intraspecific escape polymorphism among insects, but it appears to be rarer than might be expected. This could indicate the existence of even more severe disadvantages with alternative escape behaviors, possibly because of the presence of other kinds of predators. In some cases, it may result from the strong advantage to remaining with the group (Tinbergen 1938).

A variety of prey traits tend to increase handling time for the predator. They include physical protection, anti-swallowing postures, noxious chemicals that must be separated from the remainder of the prey before it is ingested, etc. These traits, though of basic interest, are less important in the present context and will not be dealt with further.

The useful energy content of a prey to a predator is a complex function of total energy content of the prey, the form in which the energy exists (the chitin of insects is an energy-rich molecule, but is sufficiently costly to break down that most predators derive relatively little from it), the presence of toxins that influence the efficiency of extraction of energy from the prey, etc. Also, ingestion of a mildly toxic prey may affect adversely subsequent foraging efficiency of the predator and this loss should properly be ascribed to the toxic prey, thereby decreasing its real value to the predator. Any such characteristic should be effective in reducing the percentage of time a prey item is included in the optimal set of a predator.

Decision time has not received much attention in the theoretical predation literature, and we assumed it to be zero in the first models in this book. It is potentially very important, though, especially for predators that are large in size relative to their prey and hence must take large numbers of prey. Insectivorous birds, for example, regularly have to find an average-sized insect every few seconds to meet energy demand (Gibb 1960); at this rate of capture, a decision time of even a fraction of a second may be sufficient to make it not worthwhile for the predator to bother trying to make the decision. It is perhaps no accident that most cases of mimicry involve responses of insects to insectivorous vertebrates, all of which are high-capture-rate predators. (It also could be due to the fact that biological science is the product of vertebrate and not invertebrate sensory and integrating systems.)

In addition to these factors, predators may elect not to pursue if the prey is dangerous, i.e., it may fight back or sting the predator, or if the prey is perceived to be dangerous, whether or not it really is.

## 11.2 Evolution of Toxic Prey

The value to a predator of capturing a toxic mutant of a prey is less than that of other individuals of the species, and it would be advantageous to the predator to avoid that individual if it could recognize it. However, for such a mutation to spread through the population, the predator must be able to sample without lethal effects on the prey, or else the benefits accrue equally to unprotected individuals. Selective mechanisms for spreading such mutants have been dealt with by Fisher (1958). For the moment, we assume that a prey population has a certain frequency of toxic mutants that are indistinguishable to the predator. The effect of these mutant individuals is to increase the range of conditions under which that prey species as a whole does not lie within the optimal set, because their presence is equivalent to lowering the average energy per unit time from pursuit of that prey. When the prey do fall within the optimal set, the predator should attack indiscriminately and reject the toxic ones on contact. The conditions for rejection of the prey species increase with increasing proportion of toxics in the population, which sets the stage for automimicry (Brower 1972).

Presumably, any toxic chemical produced by a prey can be detoxified by a predator, but whether the predator will evolve that ability depends on its relative costs and benefits. If we assume a fixed metabolic cost for detoxifying a unit of a toxin, or that the cost of detoxification is unrelated to the abundance of the prey producing the chemical, then the value to the predator of evolving a detoxification mechanism should be directly proportional to the abundance of the prey and its ranking if it were made non-toxic. Detoxifying a rare species that could make only a small increment to the diet or a species of low rank that would only occasionally be included in the optimal set would not be profitable. On the other hand, if a particular prey were readily available at an otherwise critical time of the year, the ability to handle that prey could have an influence on fitness out of proportion to its average potential inclusion in the diet. Such a situation might well favor detoxification under the rule that death and the opportunity to reproduce are so important that they readily override energetic considerations (Hamilton 1972).

It is important to remember that a toxic prey is simply a species of organism possessing chemicals that a *particular* predator is unable to handle. It does not follow that other predators find the same prey toxic, nor does it follow that a non-toxic prey was not toxic to the same predator at some time in the past. We predict the incidence of toxicity in nature on the basis of whether or not selection has favored the evolution of detoxification mechanisms on the part of the predators, as follows:

a. large or common prey (in terms of the potential diet of a predator) should seldom be toxic;
b. toxicity should most readily evolve among prey with a highly equable distribution, i.e., no one species predominates in the diet of the predator;
c. toxicity should be more common where the number of prey species is high;

d. sympatric species should have unique toxins because then no predator can detoxify more than one prey species by a single physiological change, i.e., there should be selection for character divergence in toxic defenses.

Evidence in support of these predictions comes from the prevalence of mimicry systems in tropical regions where species have more equable distributions and few species are as common as many of the temperate zone species. Nevertheless, the virtual absence of population studies of tropical insects makes it impossible to provide a survey of relative abundances of mimetic and non-mimetic species or to know the potential increase in the energy intake of predators from a detoxification system.

### 11.3 Evolution of Müllerian Mimicry Systems

It has long been recognized that relative abundances of model and mimic are important in the evolution of Bates mimicry systems (Wickler 1968). For Müllerian mimicry, however, it has been assumed generally that the relative abundances of the species were irrelevant since all members of the complex would derive benefits from learning by the predator. This argument, however, neglects selection for detoxification by predators and provides no explanation why Müllerian mimicry systems in a given locality never have a large number of species in them, which would be expected if the number and/or abundances of member species were not important in the evolution and stability of the system.

If we view the evolution of a Müllerian mimicry system from the viewpoint of a predator, it is likely, since the prey were initially at least somewhat toxic, that the energy losses to the predator would be minor. Nevertheless, as the number of species in a mimicry system increases, the losses in foraging efficiency of the predator also increase, for several reasons. First, the total prey-recognition time of the predator will increase as a higher fraction of total prey-encountered will be members of the complex. Second, Müllerian mimicry complexes often have Batesian mimics associated with them and, as the size of the complex grows, it will pay the predator to be able to make finer discriminations among members of the complex. Third, the protection of the mimicry complex may result in larger populations of the constituent species, possibly at the expense of palatable prey for the predator in the same area. This increases the potential benefit to the predator from an ability to detoxify one or more members of the complex. From the arguments we advanced earlier, the most likely member to be detoxified first will be a large and common one.

A point may well be reached where tolerance and/or detoxification by a predator of the defenses of a member of the complex is favored. When that occurs, selection becomes highly disruptive within the complex because the predators should have difficulty in telling the now-palatable member from the others and will necessarily sample many individuals in the process of learning. All well-adapted members of the complex are likely to be vulnerable at this point since they will have evolved a complex set of behavior patterns based on their seldom being attacked. Therefore, with relatively short pursuit times and a high probability of capture given a decision to pursue, the predator may find it profitable to pursue and capture many individuals and to discard the still unpalatable ones rather than taking a great deal of time in attempting to make finer discriminations among members of the complex.

If this model has any validity, it suggests that the limits in size of Müllerian mimicry complexes are set by a threshold of detoxification by a significant predator, which initiates a rapid disruption of the complex. The implication is that a cycle of Müllerian mimicry complexes may well exist, with a slow build-up, during which time the mimicry is improved, more species are added to the complex, and the combined abundances of the species increase, followed by a rapid break-up, and then another slow reconstruction of the complex with some of the same or perhaps different species. Evidence of such a process might be sought in tropical areas where butterfly collections that span at least a century are available and the present phenotypes can be compared with those taken when European scientists first explored the areas.

## 11.4 Aspect Diversity of Prey

As was first suggested by Rand (1967), predators foraging in a featured environment can be expected to select for divergence of their prey. Rand tied his hypothesis to the existence of search images by the predators, but there appears to be no convincing reason to do so. All that is required is that predators using different searching modes, or images, do not find all prey with equal effectiveness. In the process of losing their marbles (Chapter 10), predators cause their prey to diverge until the changes make them equally vulnerable to other predators using different search modes. This view suggests that prey may compete for hiding places and that the record of the selective action by the predators is preserved in a series of morphological and behavioral attributes readily amenable to measurement. Rand termed this variation 'aspect diversity.'

Ricklefs and O'Rourke (1973) measured aspect diversity of moths captured at lights at night on Barro Colorado Island, Canal Zone, near Tucson, Arizona and near Aspen, Colorado. They measured 12 morphological characteristics on each species and found that the average similarity (coefficient of association) for all species pairs in each locality was lowest in Panama, the sample with four to five times as many species as the temperate samples. Nevertheless, the average similarities of each species to the next most similar species was nearly the same in the three communities. They concluded that total 'aspect space' was greatest in Panama, but that all communities showed strong evidence of mutual accommodation of the species to predation pressures.

Unfortunately, the host plants and normal feeding and resting places of the moths in these samples are unknown, and more adequate tests of the notion that predators maximize the differences among coexisting prey species (i.e., make them coarse-grained) will require this kind of information. An aspect-diversity profile for hot desert communities in Argentina and Arizona is being constructed by Schultz and should provide a valuable contribution to our understanding of this vital evolutionary impact of predators on their prey.

# Chapter 12. Some Concluding Remarks

It is our belief that adaptation is a powerful tool to postulate in ecological studies, and that involvement with trade-offs, which are the heart of the evolution of adaptation, is a useful way of asking questions about ecological problems. This approach is, however, an unusual one in science. Physical systems have been studied for a longer time and physicists are the source of much of the conceptual notions about doing science. They do not study their systems in this manner. Physical systems are not evolving systems in the sense that the properties of the components have not been modified by a process analogous to natural selection. This has made it possible for physicists to make rapid progress in the study of physical systems by isolating the components of the system and then restructuring the system. Biologists have been aware that biological systems were different than physical systems, but emphasis was placed primarily on the greater complexity of biological systems, and the significance of mutual adaptation among the component parts was relegated to secondary importance. As a result, biologists have attempted to mimic the analytical techniques of physics and to study complex systems by analyzing them into components and then attempting to reconstruct the entire system from the properties of these components as determined in isolation. The advent of powerful computers seemed to offer hope for building more powerful models of complex ecosystems, and modern ecosystem studies are in a real sense children of the computer.

We believe in the usefulness of a modeling approach, but cannot agree with many of the questions that are at the heart of modern ecosystem studies. One common component of these studies is the postulation of goals for the system, such as maximization of efficiency, maximization of energy flow, minimization of entropy, maximization of diversity, etc. Natural selection is known to work at the level of individuals, but there is no evidence for it at the level of the ecosystem, nor is there a plausible mechanism for its operation. Since we are unable to conceive that an ecosystem or even a species can have an evolutionary goal or that they are units of selection, we have found these concepts to be distracting rather than helpful in our search for more powerful insights into the evolution of the biological world around us. For practical human-oriented goals, such as maximizing yield from a fishery or wood from a forest, these are useful concepts, but then *we* are assuming the role of the selective agent rather than attempting to understand the selective pressures that produced the organisms in the first place.

We do not believe that this attitude is reductionist because we do not claim that there are not system's level properties (those that are not to be found upon examination of any single component population), only that those properties are a result of individual selection.

As we worked on the theories presented in this book, the concept of information gradually assumed a more important position in our thinking. Achievement of any goal requires appropriate response to signals, but there is always a price on the capacity to respond and the act of responding, but the benefits from it are not always worth the price. In many ways ecology is the science of applied behavior, that is behavior applied to fitness. To solve all of the problems it faces, not just finding food, an organism makes decisions in response to information. The molding of response patterns and capacities by natural selection is an exciting area where fruitful collaboration between ecologists and ethologists would be profitable.

As evolutionary ecologists, our approach to optimal foraging has been purely phenotypic. We have left it to our hypothetical organisms to solve their own genetic problems. It might be suspected that our ignorance of genetics would have been an impediment to the development of foraging theory, but we have not felt so constrained. We know that in the real world organisms exist whose foraging responses are rigidly, genetically preprogrammed and those whose foraging decisions are readily modified by experience. Unless we have reason to believe that limitations of genetic systems prevent organisms from achieving the optimal phenotypic solution we have suggested for them, we believe that genetics need not be a major concern for the pursuit of this kind of theory. We have been equally cavalier about potential constraints imposed by the physical environment and are not more troubled about that than about our lack of concern about genetics. It is quite possible that future developments of foraging theory will encounter conditions of potential genetic constraints; if and when that occurs, it will be appropriate to devote attention to those matters.

As is the case with all abstract models, it is difficult to prove that an organism does or does not fit it. We have presented data that are in agreement with predictions of the theory, but the value of theoretical explorations of this kind is not limited to generating data to test its postulates. This is fortunate because some of the parameters of our models are extraordinarily difficult to measure and probably will never be measured directly. Instead the model can be used, as we have indeed done, to generate many corollaries, some of which yield predictions that are testable with reasonable effort. It was this potential of optimal foraging theory that captured our imaginations and led to the production of this book. We have personally changed our perceptions of a number of ecological processes by working on the models and exploring their implications.

Since reality consists of a set of questions and attempts to answer them, we believe that our models are useful in studying reality. They have led to a number of interesting questions and each new involvement with the theory generates still others. All have the useful characteristic of focusing on the organism actually facing problems of existence in an unpredictable world. We see utilizers of photons and mineral nutrients instead of primary producers; detritivores instead of decomposers; pollen and nectar eaters instead of pollinators, etc. We find these conceptual shifts helpful and non-trivial, but the real test will be the questions that others are induced to ask from reading what we have done.

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# APPENDIX. A Glossary of Terms

This glossary includes those terms appearing on pages in addition to the page of definition. It excludes terms from the literature review chapter as they are defined for each paper separately.

| Term | | Definition | Page of Definition |
|---|---|---|---|
| $A_j^*$ | = | average energy value per encounter with prey type j uncorrected for the basic search cost | 28 |
| $D_i$ | = | density of patch type i in the habitat | 51 |
| $D$ | = | $\sum D_i$ = density of all patch types being visited by a predator | 51 |
| $D_i^0$ | = | average density of a prey type when prey are considered to be non-moving points on a featureless plane | 123 |
| $E_a'$ | = | energy cost per unit time while attacking a prey type (above the basic cost of searching) | 28 |
| $E_e'$ | = | energy cost per unit time while feeding on a prey item (above the basic cost of searching) | 28 |
| $E_F$ | = | energetic cost of a mistake | 34 |
| $E_j^*$ | = | average energy intake per encounter with prey type j, corrected for the basic search cost | 28 |
| $E_j''$ | = | assimilated energy from one item of type j | 28 |
| $E_n$ | = | net energy intake rate | 29 |
| $E_p'$ | = | energy cost per unit time during pursuit (above the basic cost of searching) | 27 |
| $E_R$ | = | energy value associated with the R$^{th}$ prey item encountered in the stochastic models | 81 |
| $E_s$ | = | energy cost per unit time while searching | 27 |

| Term | | Definition | Page of Definition |
|---|---|---|---|
| $E_T$ | = | energy cost per unit time while traveling between patches | 51 |
| $f(T_i)$ | = | assimilated energy for $T_i$ time units in a patch of type i corrected for the interpatch travel cost ($E_T$) | 51 |
| $f(h_3)$ | = | E" as a function of eating time ($h_3$) | 37 |
| $g(T_i)$ | = | assimilated energy for $T_i$ time units in a patch of type i uncorrected for the interpatch travel cost ($E_T$) | 51 |
| $h(T_i)$ | = | assimilated energy for $T_i$ time units in a patch of type i uncorrected for the cost of searching while in the patch | 51 |
| $h_j^*$ | = | average handling time per encounter with prey type j | 25 |
| $h_R$ | = | handling time for the $R^{th}$ prey item encountered (a random variable) in the stochastic models | 80 |
| $h_0$ | = | recognition time | 24 |
| $h_1$ | = | pursuit time | 24 |
| $h_2$ | = | kill time | 24 |
| $h_3$ | = | eat time | 24 |
| $P_j$ | = | predator choice parameter | 25 |
| $P_i'$ | = | proportion of patches being visited by a predator that are of type i | 51 |
| Q/R | = | the gross energy intake rate | 30 |
| Q* | = | when Q and R only include the optimal set Q is written this way | 31 |
| r | = | predator perceptual radius | 124 |

| Term | | Definition | Page of Definition |
|---|---|---|---|
| $S_p$ | = | probability of a successful pursuit | 25 |
| $S_a$ | = | probability of a successful attack | 25 |
| $S_R$ | = | recognition probability in an encounter with a prey type | 24 |
| $T_i$ | = | time spent in a patch of type i | 51 |
| $T_i^*$ | = | average handling time per encounter with a prey of type i corrected for the recognition time | 35 |
| $T_R$ | = | inter-arrival time per prey item in the stochastic models | 80 |
| $V$ | = | predator search velocity | 123 |
| $\underset{\tau\to\infty}{E(Z_\tau)/\tau}$ | = | asymptotic mean for the rate of energy intake | 81 |
| $\underset{\tau\to\infty}{V(Z_\tau)/\tau}$ | = | asymptotic variance for the rate of energy intake | 81 |
| $\lambda_i$ | = | average encounter rate with prey type i or patch type i | 29 |
| $\lambda_i^0$ | = | average encounter rate with an item of type i in the presence of the other k−1 types | 84 |