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**INFORMATIONAL CONSTRAINTS IN OPTIMAL FORAGING: THEORETICAL
DEVELOPMENT AND FIELD EXPERIMENTS WITH HUMMINGBIRDS**

The University of Arizona

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INFORMATIONAL CONSTRAINTS IN OPTIMAL FORAGING:
THEORETICAL DEVELOPMENT AND FIELD
EXPERIMENTS WITH HUMMINGBIRDS

by

William Albert Mitchell

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA
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As members of the Final Examination Committee, we certify that we have read
the dissertation prepared by William Albert Mitchell
entitled Informational Constraints in Optimal Foraging: Theoretical
Development and Field Experiments with Hummingbirds

and recommend that it be accepted as fulfilling the dissertation requirement
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Final approval and acceptance of this dissertation is contingent upon the
candidate's submission of the final copy of the dissertation to the Graduate
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direction and recommend that it be accepted as fulfilling the dissertation
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Michael Rosemary
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25 April 1986

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William A. Mitchell

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ABSTRACT

I consider two types of foraging situations. In the first type, the forager knows the location and quality of no more than one food item or habitat at a time. I call this myopic foraging. In the second situation, the forager may know the location and quality of more than one food item or habitat at a time. I call this periscopic foraging. I develop theoretically both models and the predictions generated by each. Myopic models predict that foragers should have a so-called "bang-bang" control with respect to the choice of food types. Periscopic models predict that foragers will have a continuous control with respect to the choice of food types. I experimentally tested for the presence of each type of control in a field study that employed hummingbirds feeding on artificial resources. As predicted by the theory, the transition of behavior from picky to opportunistic was significantly sharper for the myopic than for the periscopic foragers. Furthermore, theory predicts that there should be some range of relative values of the rich and poor food types over which the myopic foragers are opportunistic, while the periscopic foragers exhibit a partial preference. This prediction was supported by the data.

I predicted that the partial preferences of periscopic foragers would result from the hummingbirds exploiting those poor quality feeders which were located nearest to the best foraging path among rich feeders. The data supported this prediction. Periscopic foragers also

performed as predicted by becoming more selective on rich feeders as the densities of both rich and poor feeders increased.

I developed a model of optimal sampling behavior that hypothesized birds have evolved in an environment of exploitative competition. The model predicted a rule of departure from a resource patch that depended on the presence or absence of nectar in a sampled as well as the expected quality of the nectar. Hummingbirds performed according to the model's predictions.

CHAPTER 1

INTRODUCTION

Optimal foraging theory is actually a collection of theories developed within the adaptationist paradigm or research program. Each theory is characterized by two kinds of hypotheses. The first kind of hypothesis expresses how the biologist thinks fitness is a function of one or more inputs, such as energy consumed, matings performed, risk of predation, etc.. The second kind of hypothesis expresses how the biologist thinks the environment, including other organisms, constrains the inputs, or domain of the fitness function. The theory, in conjunction with additional, or auxiliary hypotheses (Lakatos 1978) generates predictions which can be tested in the field or laboratory.

If the empirical results do not favor a theory, it may be overthrown completely in favor of a very different theory, or it may be modified and retested. If optimal foraging theory is overthrown, it may be replaced by an alternative from within the adaptationist program or by a theory from a different research program. The latter event, however, is either rare or non-existent for two reasons: (1) the current vitality of the optimization paradigm, and (2) the lack of other research programs which address similar problems in the evolution of adaptive behavior.

The status of optimal foraging as a paradigm or research program (Lakatos 1978), rather than a theory is clear from the observation that it is not possible to refute the conjecture that animals optimize their foraging. The refutation of one specific theory can always give way to the proposition of another optimization theory hypothesizing different constraints or fitness relations. If, however, most of the theories are empirically refuted, then the research program is degenerate and ripe for overthrow by another, more successful, program. Conversely, if adaptationist theories are relatively successful, then the program must be reflecting reality.

The fate of a research program should depend on the empirical tests of well developed, comprehensive, theories. Optimal foraging currently comprises a variety of models, some of which have been tested (see the review of Krebs 1983). But the similarities and differences between the models are not always made clear in the context of their theoretical development. This can lead to some inappropriate tests of theories. Empiricists do not always seem clear as to where the predictions which they purport to be testing come from. On the other hand, theoretical development often seems to ignore obvious hypotheses.

Optimal foraging has been criticized for a number of reasons. Many of the criticisms are not criticisms of the research program itself, but rather how the program has been applied thus far. For instance, Myers (1983) states that most of the theory assumes that the animal possess perfect knowledge of its environment. Even if this were true, which it is not, (see the rest of this paper) the level of

information the animal possesses could be theoretically altered by simply changing or introducing constraints. Some critics claim that optimal foraging does not consider the effects of constraints or trade-offs imposed by the existence of predators or other non-foraging activities or limited cognitive abilities (Janetos and Cole 1981). Clearly, however, the whole point of an optimization problem is to solve for an extremum subject to a set of constraints.

I have several objectives in this paper. One is to develop theoretically the consequences of a certain kind of hypothesis made on the constraint function in the optimal diet problem. Second, I wish to contrast the predictions of this model with the predictions of the most common optimal diet model in the literature. Finally, I shall test the predictions of both models. I shall not claim that they are mutually exclusive. They are not. I shall simply try to clarify the conditions under which either should be applied and then test them under those conditions. I will conclude that both models are useful in understanding foraging behavior.

The Current Status of Optimal Foraging Theory

MacArthur and Pianka (1966) originally constructed an optimal foraging and optimal habitat selection theory to explain and predict community level phenomena. They were interested in how animals which actively forage for discrete food items in discrete habitats should adaptively modify their foraging behavior, and, consequently, their magnitude of interaction. Theories of foraging behavior soon diverged

from theories of community structure as behavioral ecologists began to study the former as an interesting problem in its own right. With a few exceptions (Pulliam 1986; Pimm et. al. 1985) the two categories of theories have remained apart.

Pulliam (1974) analyzed a stochastic form of the optimal diet problem in which he assumed that the resource items are distributed independently as Poisson processes. His consumer knows the location of one resource item at a time. At each resource encounter the consumer must decide whether it should spend some time handling the resource item or continue searching for something better. Search time per item is a function of prey density and it is usually fixed. So is handling time per item. Some recent developments allow for the possibility that the forager may be able to improve its searching or handling efficiency as a function of prey encounters (McNair 1981). Others model the case in which prey are dependently distributed in the environment (McNair 1979). Some models treat the case of a forager which must spend time with a prey item before it can evaluate the item's quality (Hughes 1979) The case of encounter rates decreasing as prey are consumed has also been modelled and tested (Brown and Mitchell, MS). One feature which all of these models have in common is the assumption that forager encounters the food items one at a time.

A few models, however consider a different situation. They treat the case of a forager which can view several resources at one time. The motivation for these models has come primarily from fish and nectarivore studies.

Aquatic ecologists proposed that fish may select from among several prey (aquatic arthropods) the item of largest apparent size, where this measure is a function of actual size and distance from the forager (O'Brien et. al. 1976, but see Gardner 1981). Pyke (1981) proposed a similar mechanism for hummingbirds selecting flower inflorescences. The apparent size hypothesis is probably best considered a hypothesis about how a proximate mechanism of feeding works. Its prediction does match that of an optimization hypothesis if larger prey yield more energy per unit of handling time than smaller prey.

Waddington (1982) used the term "simultaneous encounter" to indicate the situation in which a forager sees several food items at once. He applied the term "sequential encounter" to the case when the forager sees only one food item at a time. He also proposed a behavioral rule by which a forager which simultaneously encounters food items can do better than it would by moving randomly among food items. This rule states that the forager should move to the resource item which yields the highest caloric reward per unit time, where the latter quantity includes handling and travel time to the item. His model predicts that when resources are randomly and independently distributed, foragers will not necessarily use food types in the proportion in which they occur in the environment; that is, foragers will show a partial preference for better quality food items.

Stenseth and Engen (1985) consider a general model of optimal foraging in which the forager is confronted with a set of options from

which it must choose one. The options are not limited to accepting or rejecting a single food item which has been encountered, but may include accepting one of several food items or even one of several groups of food items. One option which is always available to the forager is to reject all food items and continue searching for a better set of options. This is a very general model which can make a variety of predictions, depending on the specific parameters. One of the very non-intuitive predictions is that, in some cases, the forager will reject certain items as they become abundant.

Myopic and Periscopic Foragers

The dichotomy of simultaneous and sequential encounter is useful. But it should be nested within the more general problem of understanding how a forager obtains information and uses it. For instance, a forager which can see only one food patch at a time may nonetheless know the locations and qualities of several from past experience. If the food patches renew after they have been exploited, the forager may revisit patches without having to search for them anew. Although the forager encounters its food patches sequentially, its memory allows it to forage as though it were encountering them simultaneously. Here, the important distinction is the information state of the forager.

Consider the case of an animal which exploits discrete resources or resource patches. The information available to this animal may place it in one of two categories. In the first category

is an animal which knows the location and quality of, at most, one resource or patch at a time. This animal discovers the information upon encountering the resource or patch after searching. I call this myopic foraging. In the second category is an animal which knows the location and quality of more than one resource or patch at a time. This animal can either see several resources at one time or it has a memory of where resources and patches occur in the environment. I call this periscopic foraging. These two categories of information generate two different models of optimal resource use.

Most optimal foraging theory can be classified as myopic. The most cited treatment of optimal diet theory is that by Pulliam (1974). Subsequent developments and embellishments often begin with the framework provided by Pulliam's paper (McNair 1979, 1981, Krebs et. al. 1983). All of these assume that the forager searches the environment for food items which are located one at a time. Upon encountering a food item, the forager must decide whether it should take that item and spend some amount of time handling it or pass the item by and continue searching for something better. The model assumes that the animal has been selected to maximize its rate of energetic intake. If average encounter rates, handling times and energetic values of different, recognizable types of food are known, the optimal decision rule is straightforward. The myopic forager should reject the item if it can expect to find and exploit a better food item within the amount of time it takes to handle the one it has encountered. Otherwise, the forager should consume the encountered item.

Organisms to which the myopic models have been applied and whose behavior has been compared to the model's predictions include seed eating birds and mammals (Pulliam 1986, Brown and Mitchell MS), and mud-flat feeding birds (Goss-Custard 1977). There are other examples discussed later, but these exemplify the physical situation which produces myopic foragers. For instance, seeds are often small, inconspicuous and frequently dispersed in soil or litter, making it difficult for a forager to see more than one seed at a time. Red-shank which feed on mudflats for mud-dwelling invertebrates probe the substrate for their prey. One worm or arthropod is found at a time during a search that may involve many probes. Neither of these situations allow the forager to gain access to the kind of information which will allow it to forage periscopically. A bird confronted with a seed or a worm only knows the handling time and value of that item and the expected time required to search for other, perhaps better, kinds of food.

A periscopic forager is confronted with a set of food items whose qualities and locations it knows. It can also estimate the cost of travelling between food items in the set. Thus, the periscopic forager's problem is to choose some subset of known items to visit and the order in which to visit them.

An animal should be selected to do an activity if the marginal benefit to fitness is greater than the marginal cost to fitness, that is to say, if the net effect is to increase fitness. If fitness is an increasing function of energy consumed and, as in simple foraging

models, a foraging activity can be assumed to affect only the energy consumed, then an activity should be performed if the marginal gain in energy exceeds the marginal loss in energy. Some of the predictions of periscopic foraging differ from the predictions of myopic foraging because the marginal costs of including food items in the diet differ between the two models. I shall elaborate on this in the two sections below in which I treat the myopic and periscopic models and their predictions. However, in order to clarify these discussions, it will be useful to distinguish between two kinds of effort or time expenditure, which I call directed and undirected.

Directed effort is the time which a forager spends exploiting one specific kind of food or resource. The handling time of most optimal diet models falls into this category. Time which a forager spends handling one food item cannot be spent searching for or handling items of other food species.

Undirected effort is the time which a forager spends on all food or resource types simultaneously. Search time of most diet models can be considered as undirected effort since this time must be spent if any food items are to be eaten and the forager is searching for all food types simultaneously.

My purpose in defining these two new terms is that, in some models discussed below, directed and undirected effort do not always correspond to handling and search time. In a periscopic model, travel time between food items counts as directed effort. In some models of foraging behavior which include the effects of sampling resources for

their values, handling time may count as undirected effort.

In the following section, I present the myopic foraging model in its standard linear form. Although it is usually presented as an unconstrained optimization problem in which the rate of energy intake is the surrogate of fitness, I give it as a constrained optimization problem. This treatment facilitates my discussion of modified myopic models in which fitness is not simply a function of the energetic values of resource items, but may also include the value of nutrients.

CHAPTER 2

FITNESS AND CONSTRAINT FUNCTIONS

An optimal foraging model is defined by two kinds of functions, a fitness function and a set of constraint functions. Myopic and periscopic foraging models differ with respect to their constraint functions, not their fitness functions. However, because the predictions of a model depend on both types of functions, I will discuss both below.

Fitness is the per capita rate of population growth, the value of which depends on the amounts of various resources exploited. In general, fitness is a function of non-foraging as well as foraging activity. Although some workers (Myers 1983) believe that incorporating many activities into one fitness function may be prohibitively difficult, the task may be accomplished under some hypotheses (Mitchell and Brown MS). Since it is my goal to compare the influence of different informational constraints on the predictions of optimal foraging theory, I will be concerned with fitness functions whose arguments are some kinds of food values, such as caloric energy or nutrients.

Let there be a vector of values, \underline{y} , reflecting the properties of food. One property would be the number of joules of energy in the food; another would be nitrogen; another, calcium; etc.. Define the

fitness function, $G(\cdot)$ to be a parametric-valued function of the vector, \underline{y} . It is not necessary to know the exact effect of each component of \underline{y} on the value of G in order to understand the qualitative foraging behavior of individuals. It is, however, necessary to make some assumptions or hypotheses about the qualitative effect of \underline{y} on $G(\underline{y})$.

Formally stated, these assumptions are,

$$\frac{\partial G}{\partial y_i} > 0 \quad (1)$$

$$\frac{\partial^2 G}{\partial y_i^2} < 0 \quad (2)$$

$$\frac{\partial^2 G}{\partial y_i \partial y_j} > 0 \quad (3)$$

The first assumption states that it is possible to define fitness as a non-decreasing function of the amount of some food value ingested. By food value I mean energy or some nutrient. The second assumption is a rule of diminishing returns. It states that there can not be increasing marginal returns to fitness as the amount the exploited food value increases. Other ecologists (e.g. Real 1980) have also made this assumption with regard to the effects of resource exploitation on fitness. The third assumption states that the influence of one input on fitness is augmented by an increment in the value of another input to fitness. For example, the marginal effect of

a nutrient on fitness increases as a function of the amount of energy which the forager consumes. If these three assumptions can be made, then the fitness function is convex in the space of the quantities of energy and nutrients consumed (Chaing 1974)

A convex fitness function will have concave isopleths (lines of equal fitness) (fig.1). The concavity is important in the optimization problem because it, along with the convexity of the constraint functions (to be discussed below), and the first-order conditions of the optimal solution, give the second-order conditions for an optimum.

The next step is to describe fitness as a function of the quantities of food items taken. The forager controls its intake of nutrients and energy by its choice of food items, and different types of food generally contain different amounts of these constituents. Hence, we consider a graph of G in the space whose axes are the numbers of food items of each type exploited.

For simplicity, consider the case of two kinds of food, R_1 and R_2 . Let x_1 and x_2 be the quantities of each consumed by a forager. Each item of R_1 and R_2 contain certain quantities of energy and nutrients. The amounts contained by an item of R_1 relative to an item of R_2 determines the graph of fitness as a function of quantities of each food type taken. Given the assumptions (1-3) the fitness isopleths will be linear or concave, but never convex (fig. 2). They will be linear if the vectors denoting the energetic and nutrient contents of items of R_1 and R_2 are dependent (that is, if they point in the same direction in the space whose axes are the amounts of resource

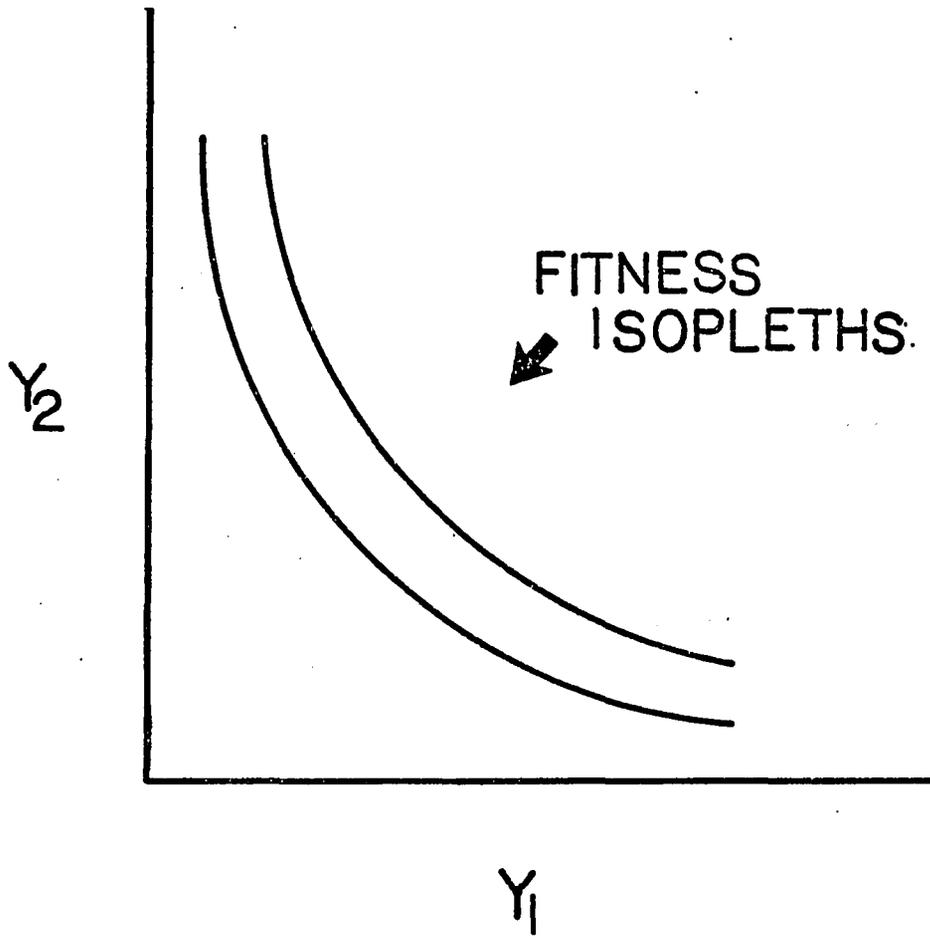


Figure 1. Fitness isopleths in the space of food attributes.

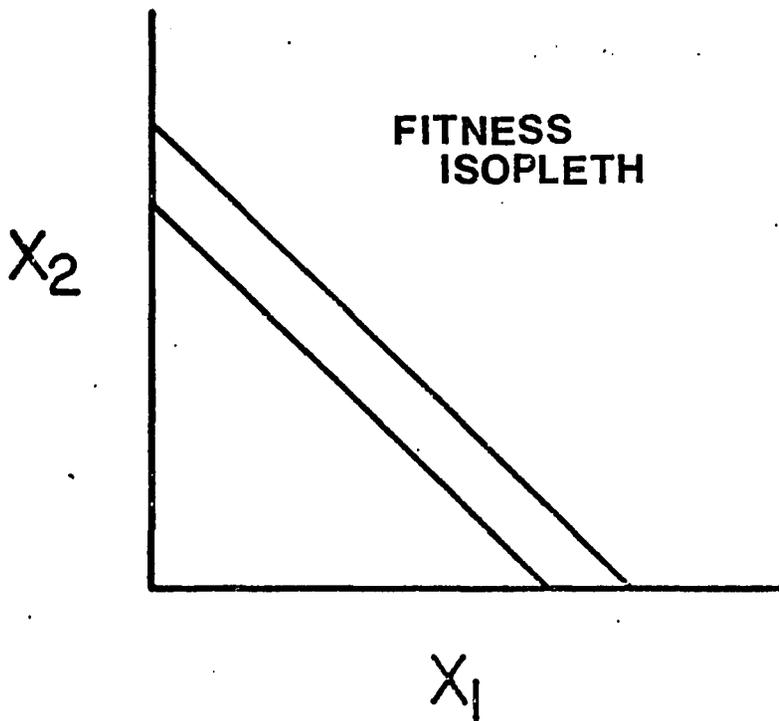
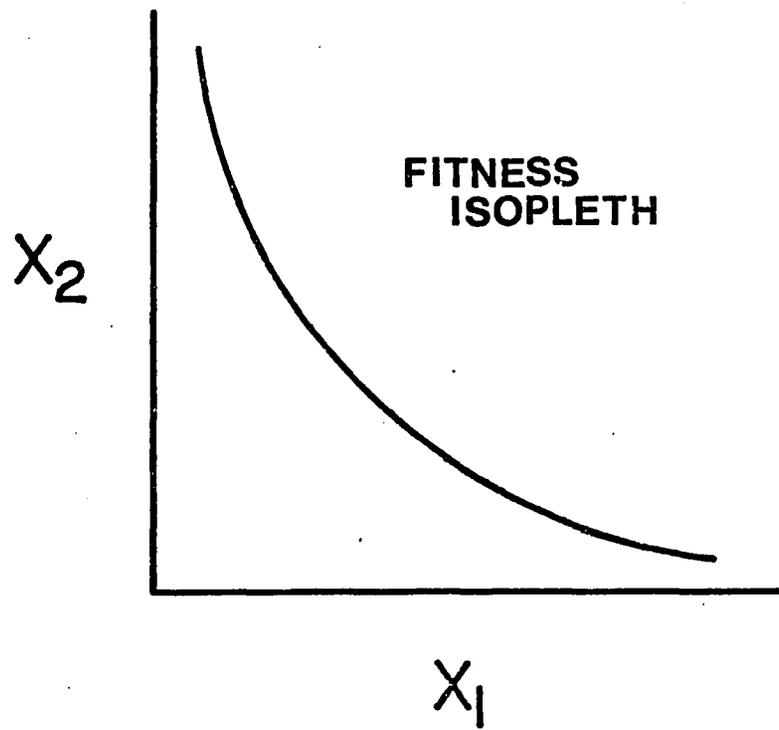


Figure 2. Fitness isopleths in the space of diet components.

values in a single food item.). Otherwise, they will be concave. If the only assimilable content of items of R_1 and R_2 is energy (or some single nutrient), then the fitness isopleths are linear in the graph whose axes are the quantities of food items consumed. Most models of optimal foraging assume that the only important constituent of the food is energy (MacArthur and Pianka 1966, Pulliam 1974, Pyke, Pulliam and Charnov 1977, MacNair 1979, Krebs et. al. 1983). Thus, most models deal with fitness functions whose isopleths are linear.

The Constraint Functions

The amount of food which an animal can consume within a certain amount of time depends on the temporal cost of exploiting the food. When there is more than one kind of food, then the forager will generally experience trade-offs in the numbers of each it can exploit. These limitations and trade-offs are expressed in the constraint functions of an optimal foraging problem. Below, I give two different kinds of constraint functions. One corresponds to myopic foraging and the other to periscope foraging.

Myopic Constraints

Recall that the definition of a myopic forager is one who knows the location and expected quality (food content) of no more than one food item at any one time. After encountering a food item, it must decide whether to spend some time handling and consuming that item or to pass the item by and continue searching for something better. The important result of this assumption is that there will be one linear

inequality constraint for each type of food potentially in the diet. In this section, I construct these constraints for the case in which there are two different categories of food. First, consider the two ways in which a myopic forager spends its time: it searches for food items and it eats food items. When it searches for food items it can search for all types simultaneously. But when it eats (or handles) a food item it can only handle one item, hence one type, at a time. Because the cost of search is shared among all food types, it is not possible to separate the per capita temporal costs of exploiting different foods. Hence, it is necessary to include a different constraint for each type of food which may be eaten.

Each constraint denotes the maximum number of one food type which can be eaten as a function of the numbers of items of other types which are eaten. This constraint incorporates the per capita search cost and handling cost of the food type to which it refers; but it will include only the per capita handling costs of other food types because they exact no additional cost of search. Thus, the per capita search cost of a food appears only in its own constraint. The per capita handling cost, however, appears in all of the constraints since handling one item always precludes searching for and handling other items.

Now I will make the constraints explicit functions of the per capita search costs, handling costs, and the total foraging time which I call T . Call the two food types, R_1 and R_2 . The search cost of an item in one of these categories is simply the amount of time it takes a

searching forager to encounter an item. This will likely be a random variable, but if the food items are distributed independently and identically according to a Poisson process then the mean search time can be used (Pulliam 1974). This assumption means the the search times of food types will be distributed according to a negative exponential function and that the distribution of search time for the n^{th} item is independent of the time required to find the m^{th} ($m=n$). With rare exceptions (McNair 1979), most models of optimal diet theory include this assumption either explicitly (Pulliam 1974) or implicitly (Sih 1978; Pyke, Pulliam and Charnov 1977).

Another assumption of most diet models is that the expected search costs are constant; that is, the per item search cost of food does not increase as the forager depletes the food. This assumption will often be unrealistic, in which case the revised myopic model's predictions differ from published predictions (Brown and Mitchell MS). Pulliam suggested that search cost will be constant if the forager moves directionally through the patch and does not try to re-exploit a depleted area of the environment. I will retain Pulliam's assumptions in this work and make the average search cost of an item of R_i a constant which is inversely proportional to original density of R_i before the forager depletes the resources. So, if n_i is the density of R_i , then the per item search cost for $R_i = a/n_i$ where a is a search speed and efficiency constant.

The other cost of exploiting an item of R_i is the handling cost which I write as h_i . Let x_i be the number of R_i which the forager

consumes within the time period, T . For $i=1,2$, the x_i 's must satisfy the following constraints,

$$(a/n_1 + h_1)x_1 + h_2x_2 - T < 0 \quad (4a)$$

$$h_1x_1 + (a/n_2 + h_2)x_2 - T < 0 \quad (4b)$$

Any diet, (x_1, x_2) , which satisfies both inequality constraints (4a) and (4b) is called a feasible diet. The optimal forager will choose the feasible diet that yields the highest fitness.

A constraint is said to be active at a point if it is equal to zero. It is called inactive at a point if it is less than zero. If both constraints are active, then the forager takes every item of both food types which it encounters; that is, the forager is opportunistic. If only one constraint is active, then the forager has a preference for the food type corresponding to that constraint. The preference can either be partial or complete. A complete preference means that the forager rejects all items of one food type that it encounters. In other words, it is picky. A partial preference means that the forager takes some, but not all, of the unpreferred food items that it encounters.

In the next section I put the myopic constraint functions together with the linear fitness functions and the non-linear fitness functions in order to derive the predictions of myopic optimal foraging.

Predictions of Myopic Foraging: Linear Fitness Function

If the fitness function is linear then an optimal myopic forager will have a "bang-bang" control (Bryson and Ho 1975). This means that the proportion of items of a food type which is taken by the myopic forager is a discontinuous, or step function of the model's parameters. Furthermore, if the constraints in (4a) and (4b) are the only constraints which describe the feasible diets, then the myopic forager will use an "all-or-nothing" rule of accepting food items of a category. This means that it will either accept all of the items or reject all of the items of a given type of food; thus, it will never have a partial preference (Pulliam 1974). In the next section I discuss a case due to Pulliam (1975) in which the myopic behavior will be a "bang-bang" response, but not an "all-or-nothing" response.

When there are only two types of food, then the feasible set of diets and the isopleths of the fitness function can be graphed as in figure (3). The picture shows that only two solutions are possible: opportunistic behavior (having no preference) and picky behavior (having a complete preference). A picky forager will take only the food with the highest ratio of value to handling cost (v_i/h_i). In figure (3) this is food type R_1 . The picky diet means that the energetic benefit of taking an item of R_2 is less than the energetic cost. The energetic benefit of taking an item of R_2 is v_2 . The energetic cost of taking an item of R_2 is simply the decrement in the energetic return from taking R_1 that results from time spent handling the item of R_2 . In order to find an expression for this cost, first

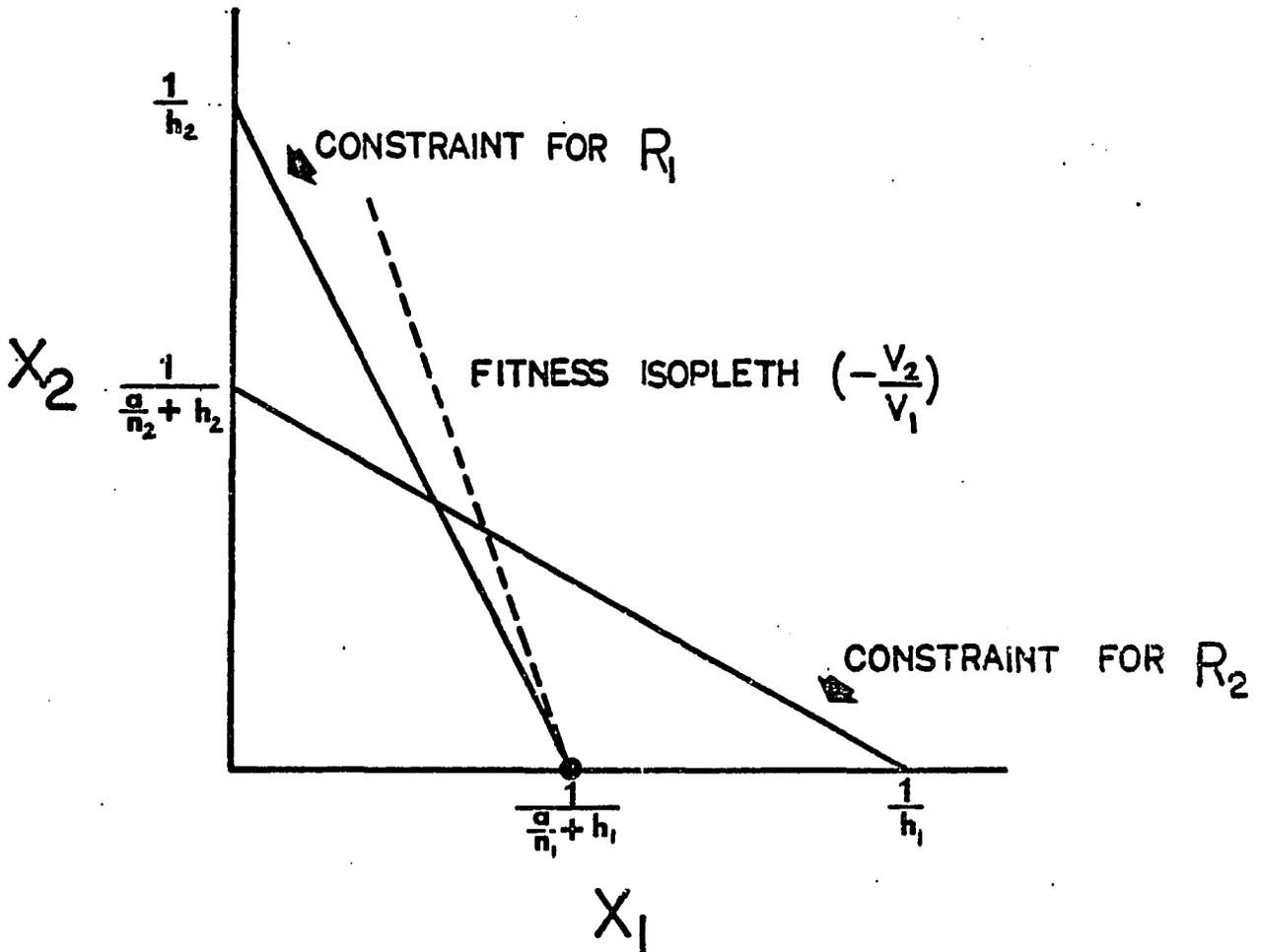


Figure 3. Myopic constraint with a linear fitness function. -- The only possible optimal diets reside on corners of the feasible set of diets. In this example, the optimal diet is the choice of pickiness on resource 1.

consider the rate at which the forager can acquire energy by searching for and handling items of R_1 . This rate is,

$$(1/ar_1 + h_1)^{-1}v_1 \quad (5)$$

where a is a constant of search efficiency. The expression in the parentheses is the sum of the per item search cost, which is a linear function of density (r_1), and the per item handling cost. The inverse of the total per item cost of taking R_1 is the number of R_1 which can be consumed per unit time. Multiplying this number by v_1 gives the amount of energy acquired per unit time when the forager only consumes R_1 . The energetic cost of handling an item of R_2 is the product of its handling time, h_2 and the rate of energetic return in expression (5). This product is also called the marginal cost of using R_2 . The marginal benefit of using an item of R_2 is larger than the marginal cost if,

$$v_2 > h_2(1/ar_1 + h_1)^{-1} \quad (6)$$

If the inequality (6) is satisfied then the optimal myopic forager should accept the item of R_2 which it has encountered. Conversely, the criterion for rejecting an item of R_2 is that the inequality of (5) be reversed. Note that this criterion does not depend on the abundance of the R_2 . So, if R_2 is not part of the optimal diet at one density of R_2 , this model predicts that it will not be in the optimal diet at any density of R_2 . This prediction can change, however, if we alter one

assumption of the model presented above. Now assume that the forager cannot instantaneously distinguish the type of resource that it has encountered. Instead, the forager must spend some time handling an item before it knows whether the encountered item is of type R_1 or R_2 . Hughes (1979) analyzed a model with this assumption and found that it predicted that the acceptance of the poorer quality resource depended on its abundance: poor resources should be rejected when rare and accepted when common. I will now present Hughes' discrimination time model.

Assume that, after it has encountered a food item, a forager must spend a certain amount of time distinguishing whether the item belongs to category R_1 or R_2 . Call this discrimination time, c . Also assume that the discrimination time, c , can be used to "process" the food for consumption. That is, discrimination time is part of the time which must be allocated by a forager to handling a food item if it is to be eaten. But in this model, this part of the handling time is also incurred by a forager who chooses to reject the item once the item has been distinguished as belonging to the category of poor quality resources. Consequently, the abundance of poor quality resources affects the rate at which a forager can acquire energy, even if the forager chooses to be picky on the rich resources. This means that the marginal cost of taking a poor quality resource is a function the abundances of both rich and poor resources and not just rich resources as it was in expression (6). The inequality comparable to (6) that must

be satisfied for the optimal myopic forager to take an encountered item of R_2 is,

$$v_2 > h_2(ar_1v_1/(1 + ar_1h_1 + ac(r_1 + r_2))) \quad (7)$$

where c is the time that a forager must spend handling an item before it can identify the type of item it has encountered. If the forager chooses to consume the item it had just identified, it would be forced to spend an additional h_1 time units doing so. In this case, the criterion for accepting an item of R_2 is a function of the abundance of R_2 : the greater the abundance, the more likely it is to be accepted in the diet. The reason for this is that the discrimination time, c , counts as undirected effort since it must be spent on every item whether or not the item is consumed. Note that the model with discrimination time still possesses linear constraints. And, the only optimal decision rule is still an "all-or-nothing" rule of bang-bang control.

The Compression Hypothesis

The predictions of MacArthur and Pianka's Compression Hypothesis are easy to visualize in the context of the model which lacks discrimination time. These predictions are that interspecific competition contracts the range of habitats used but either expands or does not change the range of prey used within the exploited habitats (MacArthur and Pianka 1966). The different optimal directions of response for diet and habitat choice follow from the different way in

which exploitation changes the picture in figure 3. Consumption of a food item such as a seed causes a decrease in abundance and thus alters the constraint. Exploitation of a habitat reduces the value of that habitat and thus alters the slope of the fitness isopleth. The former change may shift the optimal diet from picky to opportunistic. The latter change may shift the habitat use from opportunistic to picky.

The habitat shift may be more likely to occur than the diet shift if the populations occur at equilibrium numbers. The individuals in equilibrium populations will have zero fitness which they cannot improve upon by a shift in behavioral strategy. This means that they are already exploiting all the types of resources from which they can obtain a positive net return. Therefore, if these individuals are subject to competitively reduced densities in their preferred resources, they cannot improve their fitness by expanding their diet to include additional categories of poorer quality resources. Thus, the myopic model of foraging predicts that individuals in equilibrium populations (with zero per capita growth rates) should not increase the number of resource types they exploit. In fact, because the forager is forced by competition to exploit fewer habitats, it may encounter fewer (hence, exploit fewer) types of resources if resources are randomly and independently distributed among habitats.

Myopic Constraints - Nonlinear Fitness Function

Now I consider the case in which the fitness function, G , is a nonlinear function of the amounts of each food ingested. Rapport (1971) introduces the idea of concave fitness isopleths into a

graphical foraging theory. Their importance is that they result in the prediction that a myopic forager can possess partial preference with a continuous control. Recall (1) and (2) which give fitness as an increasing function of the amounts of different foods ingested. These assumptions result in isopleths of the G function that are concave curves in the graph whose axes are the numbers of each resource type exploited. The nonlinearity of G has three effects on the optimal myopic behavior: (1) the myopic diet may include partial preferences; that is, the forager may accept some proportion between one and zero of the items it encounters in a certain category, (2) the myopic strategy will no longer change in a "bang-bang" fashion, but will change continuously with a continuous change in the model's parameters, and (3) the partial preference of a resource may decline if the density of that resource increases while the density of other resources remains constant. The derivation of these results follows from an optimization problem in which a convex fitness function is maximized subject to linear inequality constraints. The presentation of the model follows.

Let the fitness function, $G(\cdot)$, be a convex, increasing function of the vector (x_1, x_2) , which gives the quantities of food items consumed from each category: This is simply a restatement of assumptions (1-3) with the number of resource categories limited to two. The optimization problem is to maximize this nonlinear function subject to the constraints (4a) and (4b).

A solution can be found by the method of Lagrange multipliers. This technique involves adjoining the constraints, each with a

multiplier, to the fitness function to obtain the Lagrangian,

$$L(x_1, x_2, \lambda_1, \lambda_2).$$

$$L(x_1, x_2, \lambda_1, \lambda_2) = G - \lambda_1 C_1 - \lambda_2 C_2 \quad (8)$$

The necessary conditions for a candidate point (x_1, x_2) to yield a maximum for the function $G(x_1, x_2)$ subject to $C_1(x_1, x_2)$ and $C_2(x_1, x_2)$, are

$$\partial L / \partial x_1 = 0 \quad (9a)$$

$$\partial L / \partial x_2 = 0 \quad (9b)$$

and the complementary slackness conditions,

$$\lambda_i = 0 \text{ if the } i^{\text{th}} \text{ constraint equals zero (} i = 1, 2 \text{)} \quad (9c)$$

The sufficient conditions follow from the fact that the feasible set given by the constraints (4a) and (4b) is convex and the isopleths of the function G given by (1-3) are concave (see Chaing 1974 for this form of the conditions). For the problem stated above, the sufficiency conditions also assure the maximum obtained at (x_1, x_2) is a global maximum.

The point (x_1, x_2) yields a local maximum for the function G if no allowable variation from that point yields a higher value for G . One way to express this fact is to say that the gradient of G evaluated at (x_1, x_2) can be expressed as a positive linear combination of the gradients of the active constraint evaluated at the same point. The

coefficients of the gradients of the constraints correspond to the Lagrange multipliers, $\$_1$ and $\$_2$. This is the relationship given by the first-order conditions for a maximum in (9a-c).

The gradient of G is a continuous function of the vector (x_1, x_2) . This means that the conditions (6a-c) can be satisfied for a diet that is given by a partial preference. Recall that a diet (x_1, x_2) shows a partial preference diet if the vector has no zero component and only one constraint is active at that point. Say, for example, that only the constraint C_1 is active at (x_1, x_2) . Then the complementary slackness condition (6c) states that $\$_2 = 0$. Thus, the first order condition becomes,

$$\partial G / \partial x_1 - \$_1 (\partial C_1 / \partial x_2) = 0 \quad (10a)$$

$$\partial G / \partial x_2 - \$_1 (\partial C_1 / \partial x_1) = 0 \quad (10b)$$

Solving for $\$_1$ in each of the above equations, equating the expressions, and rearranging gives,

$$\frac{\partial G / \partial x_2}{\partial G / \partial x_1} = \$_1 \frac{\partial C_1 / \partial x_1}{\partial C_1 / \partial x_2}$$

This equation states that the optimal diet is the one at which the relative marginal values of the resources to fitness equal the marginal trade-offs imposed by the constraints on the possible exploitation of resources (Fig. 4).

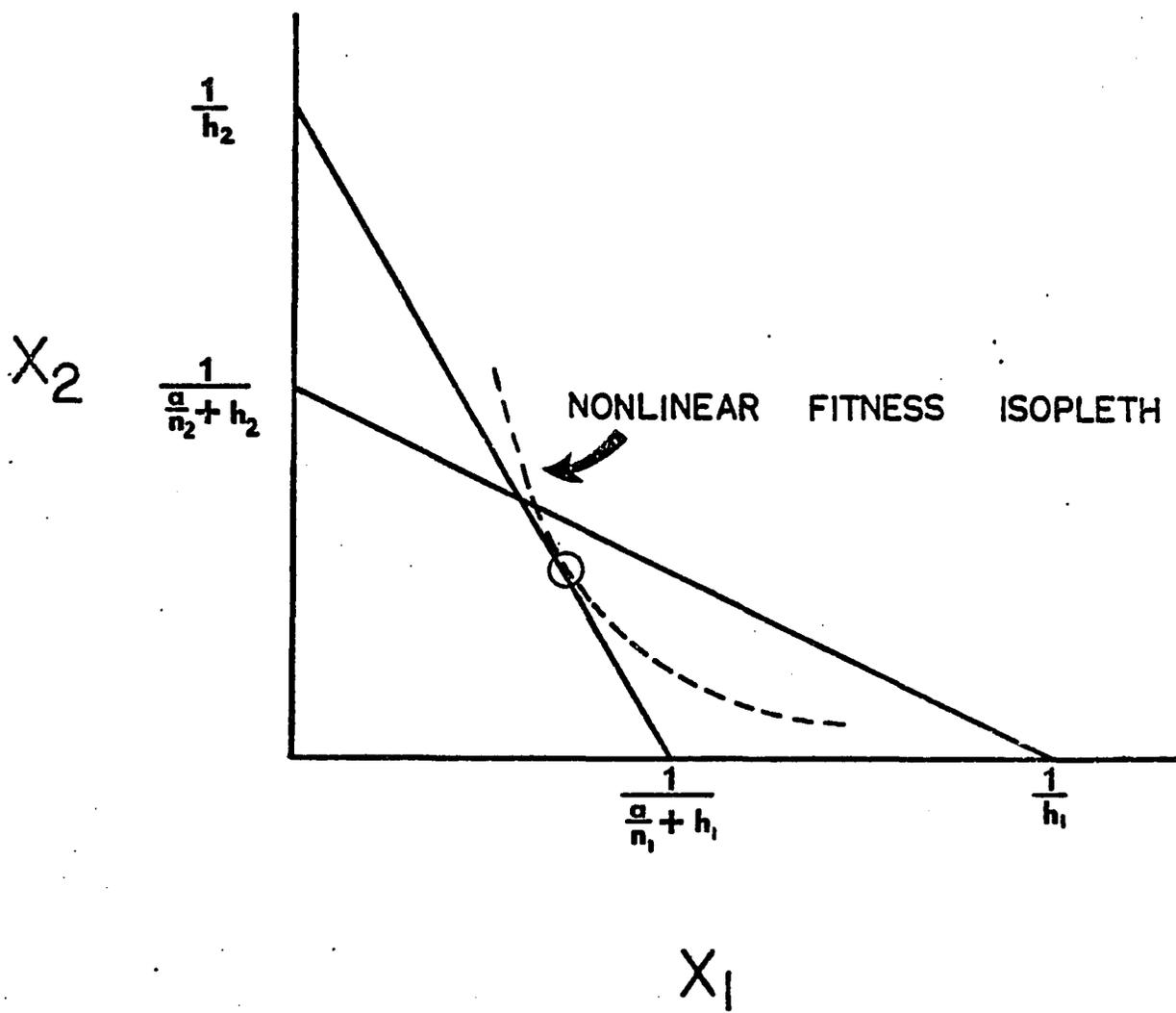


Figure 4. Myopic constraints with a nonlinear fitness function. -- Decreasing marginal returns in each food type generate concave fitness isopleths and allow for the possibility of optimal diets which are partial preferences and which do not reside at the intersections of constraints.

Myopic Model With Nutrients Included as Constraints

Pulliam (1975) included the effects of nutrients on the optimal diet in a different way than I have. He assumed that a forager requires some threshold amount of nutrient. If it acquires less than the threshold requirement, then it dies. If it acquires more than the threshold requirement, then it survives, but it gains no extra fitness by obtaining more of the nutrient. Under this assumption, the best way to include nutrient requirements is by making them constraints which must be satisfied by the optimal forager. I complete my discussion of the myopic model by giving a modified version of Pulliam's analysis next.

Pulliam's model does not explicitly include the effects of search time, but the prediction of a partial preference which he derives does not depend on this fact. In fact, the model with nutrient constraints can be set up similarly to the former myopic model with only the addition of the new constraints.

$$\text{Maximize: } x_1 v_1 + x_2 v_2$$

$$\text{Subject to: } (1/a_{n_1} + h_1)x_1 + h_2 x_2 - T < 0$$

$$h_1 x_1 + (1/a_{n_2} + h_2)x_2 - T < 0$$

$$\underline{z}x > \underline{w}$$

$x = (x_1, x_2)^t$, where superscript 't' means transpose.

$z = m$ by 2 matrix containing the amounts of m different nutrients in each item of resource 1 and 2.

$w = (w_1, \dots, w_m)$, where w_j denotes the minimum threshold requirement of nutrient type j in the diet.

The first two constraints are the same time constraints imposed on the myopic problem when there were no nutrient constraints. The remaining constraints indicate the animal's dependence on a set of nutrients.

For some sets of parameter values, this model predicts that a forager will possess a partial preference for one of the food types. Since the constraints are all still linear, however, it still predicts "bang bang" control. Now, however, the corner solutions do not always correspond to the behavior of the forager consuming all or none of the items of a given food type it encounters. If, as in figure 5, a nutrient constraint generates a feasible set of diets which does not include the diet which maximizes the amount of energy consumed, then the optimal feasible diet will reside on a corner formed by the intersection of a time constraint and the nutrient constraint. Thus, the forager will consume all items of one resource type it encounters and some proportion less than one of the items of the resource type on whose time constraint the optimal feasible diet resides. This result, although produced by a bang-bang control system will be a partial preference.

Sampling Behavior by a Myopic Forager

I have not discussed one problem which must be considered by any forager, and especially a myopic one: that is the problem of how it obtains its estimates of resource values, resource densities, and handling times. The decision rules of the myopic forager depend on its knowing, or estimating, these parameters. Because a myopic forager cannot see or know the locations of a set of unexploited resource

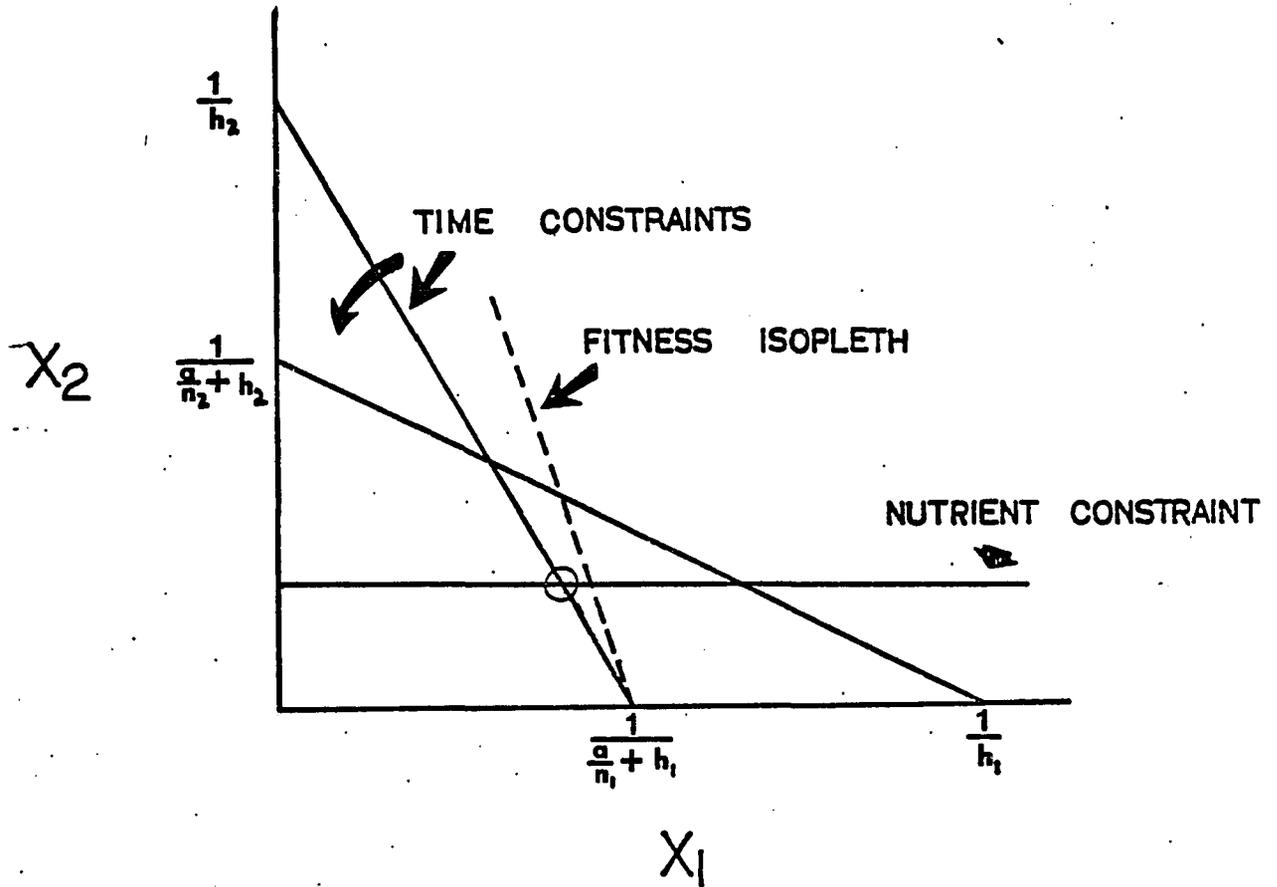


Figure 5. Nutrient constraints in the myopic problem. -- The inclusion of a nutrient constraint allows for the occurrence of a partial preference under bang-bang control.

items, it must use its past experiences to estimate future encounter rates with resources. The myopic forager will encounter resource items stochastically which means that over any period of foraging time it may encounter resources in markedly different proportions than they exist in the environment. A forager which is constantly trying to assess the expected future encounter rates with resources may change its assessment within a foraging period. If such a change in the estimate of encounter rates produces a change in the optimal decision rule, then it may appear that a myopic forager has a partial preference, when, in fact, it does not.

The empiricist can try to distinguish between a true partial preference on one hand and an adjusted 'bang-bang' control on the other by considering the sequential pattern of acceptance and rejection of resource items. If the forager is adjusting a 'bang-bang' control, then one of two patterns should occur. The forager may decrease its estimate of rich items if it has not recently encountered one. This may cause it to stop being picky and start accepting poor items in the middle of a foraging bout. Or, it may increase its estimate of rich items if it has recently encountered some. This may cause it to stop being opportunistic and start rejecting poor items.

A myopic forager with a partial preference will respond to stochastic encounter rates differently. If the forager has a partial preference because of a nonlinear fitness function, then there are diminishing marginal returns in each resource. This means that, other things being equal, the more of one type of resource the forager has,

the less valuable is another item of that same resource. Thus, if the forager happens to encounter and consume a disproportionate number of R_1 , then the marginal value to fitness of R_1 decreases. This makes the forager reduce the probability that it consumes the next item of R_1 , or increase the probability that it consumes the next item of a different resource that it encounters. These predictions differ from the previous case. There, a poor resource item was more likely to be taken after the other resource had not been encountered for a while. Here, a poor resource is more likely to be taken after the other resource had been encountered and exploited.

Some Myopic Predictions

In the experimental part of this paper, I report on the tests of a number of predictions, two of which come from the discussion of myopic constraints above. I chose to test these predictions because they draw the sharpest contrast with the predictions of periscopic foraging theory.

Prediction 1. A myopic forager will have a 'bang-bang' response to a change in the relative values of resources whose only content is energetic.

Prediction 1a. If the myopic forager with linear fitness isopleths appears to show a partial preference, then the forager should be more likely to accept poor items after it has not recently encountered rich items.

Prediction 2. The myopic forager should be opportunistic for some range of marginal values of the resources even when those marginal values are not equal.

CHAPTER 3

PERISCOPIC FORAGING

First, I will give the general statement of the periscopic diet model. Then, I will derive the predictions for the case of resources which are randomly and independently distributed. These are the same conditions which Pulliam (1974) assumed in developing his myopic model.

Statement of the Periscopic Foraging Problem

Let n_1 and n_2 represent the number of items of R_1 and R_2 resource items in a food patch. Let the total number of resource items be represented by $n = n_1 + n_2$. For any given spatial array of n resource items there is an n by n cost matrix, C , with elements, c_{ij} , where each element denotes the cost in time of traveling from resource item r_i to resource item r_j . The indices refer to individual items in the patch, and not to different resource types. I assume for the rest of the discussion that travel cost, c_{ij} , is proportional to the Euclidean distance between the resource items.

The forager will choose a foraging path among some number of items equal to or less than n . I can represent the forager's choice of path by a control matrix Q with elements q_{ij} . An element $q_{ij} = 1$ if the forager chooses to travel directly from resource item i to resource item j . Otherwise, $q_{ij} = 0$. A necessary constraint on the control

matrix Q is that it must represent a completely connected graph. That is, a resource cannot be traveled from unless it has been travelled to. The only exception to this rule is the first resource item visited which I assume for simplicity is visited without cost. A second constraint on the control matrix is that it is non-cyclic. This simply means that the forager does not re-visit a resource item.

When a forager chooses some foraging path given by the control matrix Q , it generates a state, which is the vector of the number of items of R_1 and R_2 exploited. Let x_1 be the number of items of R_1 and x_2 be the number of items of R_2 exploited. Then, (x_1, x_2) is the state. In biological terms, (x_1, x_2) is the diet.

As in the myopic problem, let T denote the total available time during which the animal may forage. Let v_1 denote the energetic food value of an item of R_1 , and let v_2 denote the energetic value of an item of R_2 . The perisopic foraging problem is to maximize the value of the state generated by the choice of a foraging path among not more than n items, subject to the condition that the summed travel costs (in time spent) must be less than or equal to total available time, T . Or, stated differently:

Given an n by n matrix of travel costs, $C = \{c_{ij}\}$,

Maximize $v_1x_1 + v_2x_2$,

by choice of the control matrix $Q = \{q_{ij}\}$, $q_{ij} = 0,1$

Subject to: (1) Q describes a non-cyclic, connected graph

(2) $q_{ij}c_{ij} - T < 0$

Because the periscopic forager can know the location of its resource items, it can base its diet choice on the known cost of traveling between and exploiting items. Recall that the marginal cost to a myopic forager of adding a resource item of type R_2 was simply the handling time of R_2 times the rate at which the richer resource, R_1 could be harvested. Thus, the marginal cost of all items of R_2 were equal. The marginal, or incremental cost of adding an item to a periscopic diet is not the same for all items of a given resource type because it depends on the location of that item relative to other items included in the foraging path described by the sequence, (r_1, \dots, r_1) .

I will call a diet feasible if the numbers of items, $x_1 + x_2$, in it can be travelled to and handled in no greater time than T . For any given array of resource items, there will be a set of feasible diets. Call the set of feasible diets D . Each yields a point in (x_1, x_2) space. The set of feasible points, D , can be circumscribed by a convex polygon (fig. 6). The particular shape of the polygon depends on the cost matrix C . The vertices of the polygon are important because they constitute the candidates for the optimal diet. Each one of them will be the optimal diet for some range of relative values of the resources, R_1 and R_2 . A diet forms a vertex if it contains the most items of at least one resource, and does not contain the fewest items of any resource, compared to any linear combination of any other diets in the feasible set.

Figure 6 illustrates how the polygon might look and why the vertices are the only candidates for the optimum when the fitness

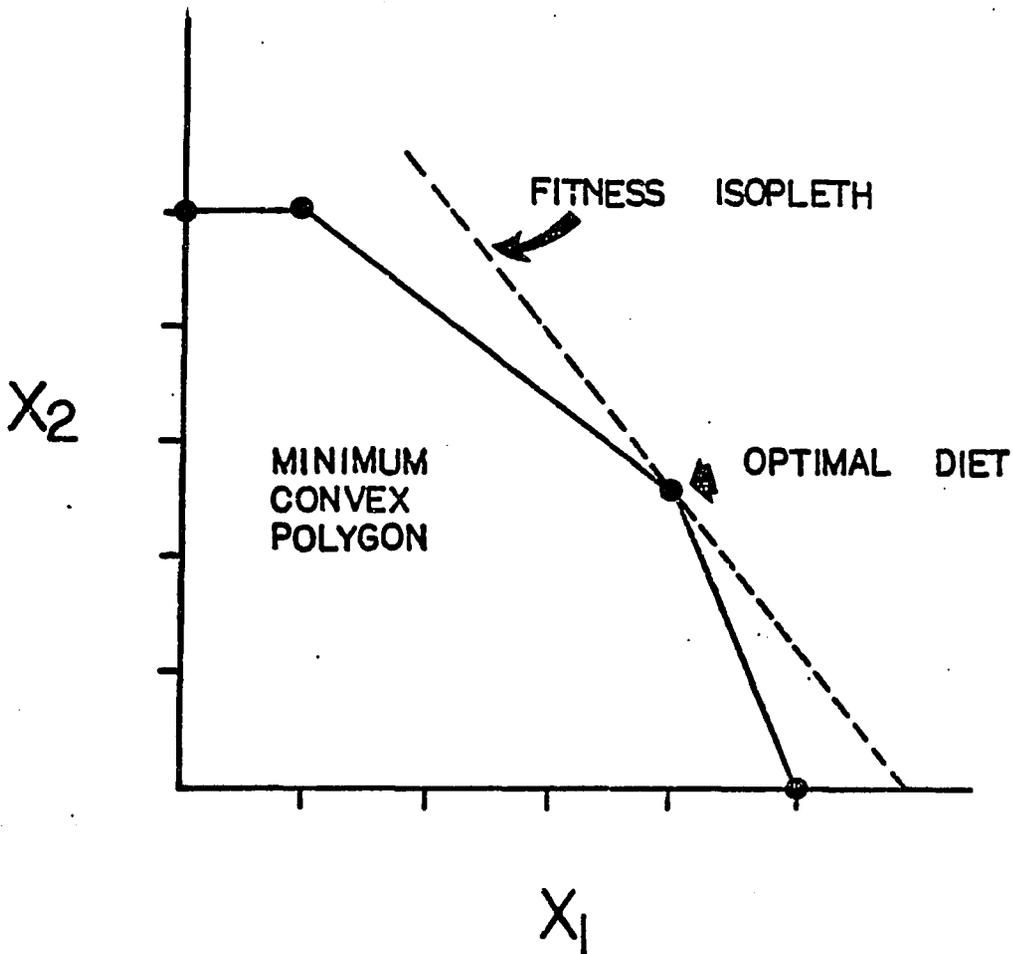


Figure 6. A set of feasible periscopic diet. -- All diets which are feasible to a periscopic forager can be circumscribed by a minimum convex polygon, the vertices of which form the candidates for the optimal periscopic diet. The particular shape of the polygon depends on the particular array of food items in the environment.

is linear. Given an abundance of R_1 and R_2 , there are many possible configurations for the polygon and many possible subsets of diets which might form the vertices of the polygon. This is because the trade-offs involved in obtaining items of the different resource types depend on the directed cost of travel, which is variable depending on the particular arrangement of items. Nonetheless, if we know the abundances of the resources then it is possible to make some qualitative predictions about the optimal periscopic diet and how it is different from the optimal myopic diet. Some of these predictions must be framed in terms of the statistical expectations of the diets because so many different configurations of the constraint set are possible. Next, I will state each prediction of periscopic foraging followed by its derivation from the model.

Predictions of the Periscopic Foraging Problem

Prediction 3

Periscopic foragers should not have a "bang-bang" control, instead, they should have partial preferences which change continuously with a change in the relative values of resource types. In order to see this, first consider the case in which both resources have the same value ($v_1=v_2$). In this case, the periscopic forager would maximize its fitness function, $G = x_1v_1 + x_2v_2$, by simply maximizing the number of items it exploits, irrespective of the type of items they are. The expected proportion of the diet comprising a given type of resource would be the proportion of items in the environment which were of that

type. So far, this prediction is identical to the one made by the myopic model. But, whereas the myopic model predicts that the forager can be opportunistic even when resources are not identical in value, the periscopic model predicts that the forager will have a partial preference whenever resources differ in value.

Consider a resource item indexed by the superscript i . The resource item, r^i will be included in the optimal periscopic diet if the value of G generated by the best control matrix, \underline{Q} , including r^i is larger than the value of G generated by the best control matrix, \underline{Q} which does not include r^i . The probability of this event occurring is larger for r^i in the rich resource category than for r^i in the poor resource category; the only expected difference in the values of G between the two cases (r^i rich and r^i poor) is in the values of r^i since resources are assumed to be distributed randomly and independently. Thus, the per capita probability of rich resources being included in the diet is higher than the per capita probability of poor resources being included in the diet. Furthermore, the only differences in the per capita probabilities of exploitation depend on the relative values of the resource types.

Prediction 4

The poor resources which are taken by a periscopic forager are those which have the smallest incremental, or additional travel cost. Often, these will be the poor resources located nearest to the rich items. The reasoning for this predictions is as follows.

The directed cost of an item to a periscopic forager is the additional travel cost beyond that which the forager would have to incur anyway in order to consume the best diet which did not include the resource item under question. If prediction 3 is correct, then the periscopic forager should tend to visit more rich than poor items. This means that the poor items located nearest the best travel path among rich items will tend to have the lowest additional directed costs of travel. Generally, the poor items located nearest rich items should have a higher probability of being consumed than poor items located far from rich items. This situation contrasts that of myopic foragers for which all poor items have the same directed cost of exploitation.

Prediction 5

The likelihood of an item being taken increases with the value of nearby items. This prediction is just a more general statement of prediction 4. But, it goes beyond prediction 4 in that it says that the likelihood of a given rich feeder being taken depends on the value of nearby poor items. Because some rich items will usually not be taken, the forager should discriminate between them on the basis of the value of other items which can be reached by a travel path which includes the rich item under consideration. If the value of a poor item near a rich item increases, then the periscopic forager should be more likely to include both the poor and rich item in its diet.

Prediction 6

An increase in the densities of both rich and poor resources

should cause the periscopic forager to increase its pickiness on the rich resources. The higher the density of resources, the larger the number of resources which can be travelled to and exploited within the constraining time period T . This causes an outward shift in the boundary of the convex polygon circumscribing the set of feasible diets. For the diets on the boundary of the polygon, the time spent travelling among items will decrease while the time spent handling items will increase. This means that the total costs of different diets on the boundary will be more reflective of their relative handling costs when the diets comprise a larger number of items. In other words, as abundances increase, the effect of travel cost decreases relative to the effect of handling cost. As the handling cost becomes more important the expected proportion of the optimal diet comprising rich resources will increase if the rich resource is defined as the one with the highest ratio of value to handling time. In the limit, when resource densities become so high as to make travel time negligibly small, then the constraint is linear and the model predicts that the forager will be completely picky on the richer resource (figure 7).

Prediction 7

A periscopic forager should be less picky on rich resources if rich and poor resources are randomly dispersed in the same patch than if they are in separate patches. When rich and poor resources are located in the same patch, some of the travel cost of poor resources is

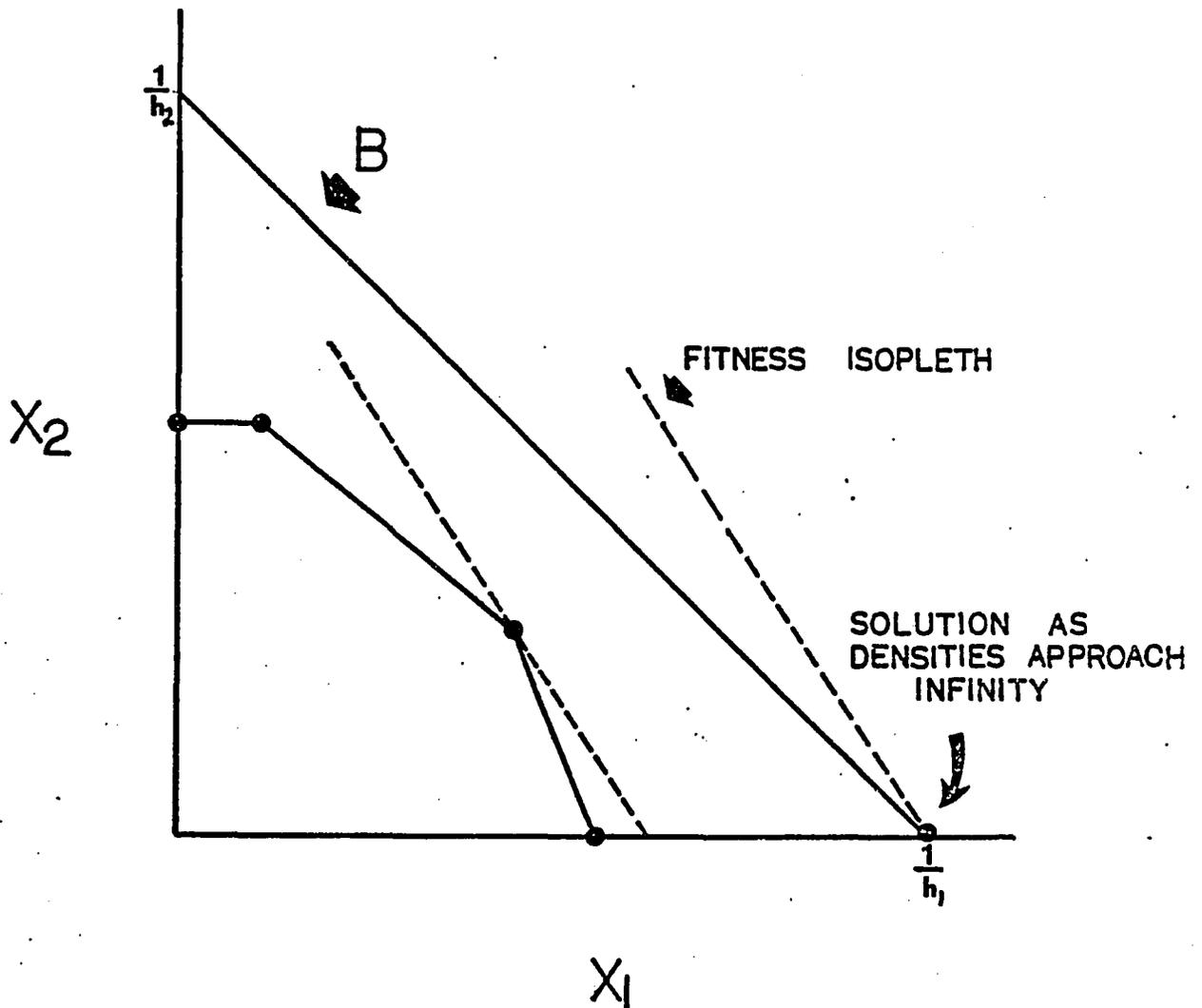


Figure 7. Effect of densities on the periscope constraints. -- At higher densities, the feasible diets comprise more food items. When the forager exploits more food items within a fixed period of time, it spends relatively more of that time handling food and less time travelling among food. Therefore, at higher densities, the constraints are more influenced by the handling costs of different diets. As travel time becomes negligible, the forager will become picky on the food type which yields the highest ratio of energy to handling time.

shared by the rich. When rich and poor resources are located in separate patches, all of the travel time among poor resource takes away from time that could be spent travelling among rich resources. Hence, the diets which are intermediate in their proportions of rich and poor items are unlikely to be vertices of the convex polygon which circumscribes the set of feasible diets. Instead, pickier diets are the likely candidates for the optimum.

This prediction assumes that rich and poor patches are not separated by too great a distance. If they were, then a forager who, for some reason, found itself in the poor patch at the beginning of the foraging period might be better off remaining in the poor patch rather than incurring the travel cost of getting to the rich patch. In this kind of coarse-grained situation, other considerations, such as the proximity of nesting sites, might play a role in determining the forager's diet.

Prediction 8

When rich and poor resources are located in separate patches a periscopic forager should change its diet less in response to a change in the relative values of resources than when rich and poor resources are intermixed in the same patch.

This prediction is derived from the same considerations of the periscopic constraint discussed under prediction 7. When rich and poor resources are located in separate patches, the marginal cost of taking a poor resource includes the travel cost between patches. The relative

value of the resources must be nearly equal before the forager should consider taking much of the poor resource. Indeed, if the forager does take both resource types with an equal probability, it should still consume only one type on any given foraging bout.

CHAPTER 4

EXPERIMENTS

I experimentally tested my predictions with free-living hummingbirds in the Chiricahua Mountains of southeastern Arizona during the summers of 1981-1983. In 1981 and part of 1982, I worked at Rustler's Park (elevation 2800m). During the remainder of 1982 and 1983, I worked at the Southwestern Research Station of the American Museum of Natural History. The research station is located in Cave Creek Canyon at an elevation of 1500m).

The Rustler Park site was situated in a sparse stand of pine near a meadow containing Iris and Delphinium. Although Iris can support some foraging by Broad-tailed hummingbirds (Selasphorus platycercus) in good years it had already passed its season of nectar production by the time I began my experiments. Delphinium blooms in the late summer at this site and its rich nectar (1.3M sucrose) supports a variety of hummingbird species, the commonest of which are Broadtailed, Rufous (Selasphorus rufus), and Magnificent (Eugenes fulgens). I completed experiments in Rustler Park before the peak of the Delphinium bloom in the middle of August.

The research station site was situated in an open area bordered by a stream. Although dense stands of Penstemon barbatus can be found

in Cave Creek canyon, there were neither Penstemon nor dense clusters of any other flower species commonly used by hummingbirds at the research station. Most of the hummingbirds which visit the station from early spring through autumn subsist on sucrose solution supplied in hummingbird feeders by the human residents of the canyon.

The Birds

I worked with Magnificent hummingbirds in the Rustler Park experiments. Magnificent is a large hummingbird (6.5g) with a long bill (6 cm) and long wings relative to the body weight giving it a low wing disk loading (Feinsinger and Chaplin 1976). Some workers (Feinsinger and Colwell 1979) classify hummingbirds with this suite of characters as high-reward trapliners -- birds which feed on widely dispersed flowers containing very rich nectar at the base of very long corollas. As is the case for most such birds, Rivoli's does not typically defend territories and, thus, are excellent birds to observe in experiments of individual optimal foraging.

I observed Blue-throated (Lampornis clemenciae) and Black-chinned (Archilocus colubris) hummingbirds at the research station during 1982. In 1983, there were virtually no individuals of Blue-throated at my study site. I recorded data on Black-chinned during this summer.

Tests of Predictions 1,2,3,4 and 5

Resources

I constructed specially designed hummingbird feeders to present

to the birds as resources. I closed one end of a plastic tube with a tight-fitting plastic bolt. I clamped this with a clothespin to a wooden dowel stuck vertically into the ground. Then I coated the base of the dowel with 'stickem' to prevent crawling insects from invading the feeder. I injected 20 ml of sugar water into the feeder with a tuberculin syringe.

Feeder Arrangement

In both the myopic and periscopic experiments I placed 16 feeders in eight pairs with 1 meter separating members of a pair. The pairs were separated by approximately 3m between nearest pairs. Two of the pairs contained two rich feeders each, two others contained two poor feeders each and the remaining four pairs contained one rich feeder and one poor feeder.

I varied the exact location and arrangement of feeder types and pairs every 15-20 minutes to prevent the birds from learning to associate a given location with a quality of food. In the experiments in which I allowed the birds to forage periscopically, I placed a colored ribbon on each feeder. The color of the ribbon indicated the molarity of the 20 ml of sugar water contained in the plastic tube on that day. The color blue always indicated a molarity of 1.0. The color orange indicated a molarity equal to one of the following values: 0.8, 0.67, 0.5. The value of the orange feeders only varied between days, not within days. I replicated the 0.8 and 0.5 treatments twice, and the 0.67 treatment three times.

In another set of experiments, I forced the birds to forage myopically by removing all the ribbons from the feeders. Thus a bird had to fly to the feeder and sample the sugar water to ascertain the quality of the feeder. The time spent flying to the feeder qualifies as undirected effort since the bird did not realize the type of food item it was approaching. Time spent drinking the sugar water after it has been sampled counts as directed effort, since that time is dedicated to using only that one type of resource. I replicated the 0.67 treatment twice and the 0.8 and 0.5 treatments three times.

My myopic experiment differs in detail from that proposed by Pulliam (1974). In his model, the forager searched for food items, which, when encountered were immediately identifiable. In my myopic experiment, the food items could be seen at a distance but not identified to type. However, because the qualities of several food items are not simultaneously known from a distance, the forager qualifies as myopic and in both cases a bang-bang response is still predicted.

Data Collection

Each day on which I recorded data, I initially filled the feeders at 7:00 AM with the appropriate concentrations of sucrose solutions. I allowed the birds 45 minutes to an hour to learn the combination of sucrose solutions. Undoubtedly, all eventual participants in my experiments did not have a chance to sample the feeders during this period. I account for this possibility in the data analysis I describe below.

I began recording data after 8:00 AM and continued for several hours until 11:30. After this time, the birds were allowed access at the study plot to a commercial feeder containing 0.5M sucrose solution.

I recorded the sequence of feeders a bird visited after it entered my experimental plot. For each feeder, I included the type of feeder (rich or poor) and what kind of feeder it was paired with (rich or poor). After the bird left the plot, I inspected each feeder it had visited and recorded how much, if any, sugar water remained. Then, I refilled each depleted feeder with the appropriate concentration of sugar water.

Rarely, more than one bird at a time foraged in the patch. I did not include these few data in the analysis if two birds tried to feed from the same feeder or if one bird fed from a feeder which another bird had visited. When a bird which had successfully foraged in the plot was chased from it, I recorded the reason for its departure.

Accounting for the Birds' Sampling Behavior

Some birds in my experiment may not have had the opportunity to sample the feeder qualities before my observation period began. These birds may have varied their feeding behavior within a single feeding bout or visit to my experimental plot as they acquired new information. In particular, myopic birds were confronting a patch of artificial flowers in which all the flowers looked identical. Without previous experience they may have treated all the flowers identically until they found one which was better, after which time they would adjust their

evaluation of the general patch quality. Such an adjustment might suffice to change their decision rule regarding the acceptance or rejection of poor feeders. I tried to account for the possibility of the birds revising their decision rules after sampling a rich feeder by including in the analyses only those data recorded after the bird had sampled a rich feeder. I did this for both the myopic and periscopic experiments discussed in this section. Below, I discuss the impact this has on the results. I also present a table which includes the results before and after I account for this sampling behavior.

Account of Raw and Sampling Adjusted Data

Table (1) shows the total numbers of rich and poor feeders taken at each value (molarity) for the poor feeders, in both the myopic and periscopic experiments. I have included in the table the numbers both before and after I eliminated the visits preceeding and including the first rich feeder visited. The percentage composition of the diet remains virtually unchanged for the periscopic results. That is, the periscopic birds did not change their rules for accepting feeders after they had sampled the sugar water in a rich feeder. Myopic foragers were, however, much more likely to accept a poor feeder before they had sampled and fed from a rich feeder. This pattern held when the sucrose solution in the poor feeders was 50% or 67% as concentrated as that in the rich feeders. When the sucrose solution in the poor feeders was 80% as concentrated as that in the rich feeders, the myopic birds accepted most of the poor feeders they encountered, either before or

Table 1. Numbers of rich and poor feeders taken at different values of poor feeders. -- Numbers in parantheses are the number of feeders probed but rejected by the myopic birds.

Periscopic Experiments

Quality of Poor	Raw Data			Sampling Adjusted*		
	Rich	Poor	(% Poor)	Rich	Poor	(% Poor)
0.5M	169	26	13%	122	16	12%
0.67M	262	88	25%	185	54	23%
0.8M	236	142	38%	181	118	39%

Myopic Experiments

Quality of Poor	Raw Data			Sampling Adjusted		
	Rich	Poor	(% Poor)	Rich	Poor	(% Poor)
0.5M	128 (3)	32 (115)	20%	95 (3)	8 (107)	8%
0.67M	110 (0)	44 (71)	29%	83 (0)	34 (66)	29%
0.8M	173 (3)	163 (15)	49%	125 (2)	140 (14)	53%

after they had encountered a rich feeder. Thus the myopic foragers appear to have increased their evaluation of the density of rich feeders after encountering a rich feeder. Periscopic foragers did not need to adjust their estimation of the density of rich feeders during their foraging bout because they could see at the outset what that density was.

I used the data which were adjusted by excluding visits prior to and including the first rich feeder to test the predictions 1 through 5. First, I consider predictions 1 and 3 together since they contrast the expected myopic and periscopic responses to a change in the relative values of resources.

Predictions 1 and 3

The first of these states that a myopic forager should have a bang-bang control. Prediction 3 states that a periscopic forager should have a continuous control. I evaluated the predictions by analyzing the occurrence of pickiness, opportunism and partial preferences.

In the myopic experiment, visits were classified as picky, opportunistic, or displaying a partial preference (table 2). A picky visit is one in which the bird rejected all of the poor feeders which it encountered. An opportunistic visit is one in which the bird accepted all of the poor feeders which it encountered. A visit displaying a partial preference is one in which the bird accepted some poor feeders which it encountered and rejected others.

Table 2. Picky, opportunistic, and partial preference behavior during individual myopic visits. -- Number and percentage of bouts in each category.

Quality	Raw Data			Sampling Adjusted		
	Picky	Opportun.	P. P.	Picky	Opportun.	P. P.
0.5M	14 (42%)	0 (0%)	19 (58%)	25 (76%)	0 (0%)	8 (24%)
0.67M	11 (41%)	5 (19%)	11 (41%)	14 (52%)	5 (19%)	8 (30%)
0.8M	0 (0%)	33 (75%)	11 (25%)	same as raw data		

Table 3. Picky and non-picky behavior during individual periscopic visits. -- Both the number and percentage of each kind of visit is given.

Quality of Poor Feeder	Raw Data		Sample Adjusted Data	
	Picky	Non-Picky	Picky	Non-Picky
0.5M	25 (76%)	18 (24%)	30 (71%)	12 (29%)
0.67M	25 (34%)	48 (66%)	33 (49%)	35 (51%)
0.8M	6 (12%)	44 (88%)	8 (17%)	40 (83%)

In the periscopic experiment, visits were classified as either picky or not picky (table 3). A picky visit is one in which the bird exploited only rich feeders. A visit is considered not picky if the bird exploited both rich and poor feeders. Periscopic birds could not be classified as opportunistic using the same criterion as for myopic birds because it is impossible to specify how many poor feeders a periscopic "encounters" on any visit.

At each treatment of sucrose concentration in the poor feeder, 70% to 75% of the myopic visits were either picky or opportunistic. When the sucrose solution in the poor feeders was only 50% as concentrated as that in the rich feeders, none of the myopic visits were opportunistic, and about three-quarters were picky. When the sucrose solution in the poor feeders was 80% as concentrated as that in the rich feeders, none of the myopic visits were picky, and about three-quarters were opportunistic. When the sucrose solution in the poor feeders was intermediate in value (67% as concentrated as that in the rich feeders) there were both picky visits (52%) and opportunistic visits (19%).

Two possibilities exist for explaining the presence of both picky and opportunistic visits at the intermediate value of poor feeders. The first possibility is that, while individuals use a bang-bang control, different individuals have different estimates of encounter rates with resources or handling times of resources. The second possibility is that individuals do not employ a bang-bang control, but accept each encountered poor item with some probability,

p, where p is a parameter between 0 and 1. This strategy would generate a distribution of behaviors over all three categories (picky, opportunistic, and partial preference).

The myopic model suggests that the first possibility is the better one. That is, the myopic model predicts that the distribution of behaviors cannot be generated by a single partial preference strategy in which foragers accept each poor item with a fixed probability between 0 and 1. A chi-square analysis support the myopic model. There were significantly more visits classified as either picky or opportunistic than predicted by the null model of a constant partial preference (table 4).

In the periscopic experiments, there were picky visits at all three treatments of sucrose concentration in the poor feeders. In this respect, the periscopic results differ from the myopic in which, as predicted, there were no picky visits at the high relative value of the poor feeders. Indeed, because the periscopic model predicts a gradual response to changing relative resource values, the percentage of visits which were picky should change less abruptly for periscopic than for myopic foragers. I tested this with a log linear model in which the theory predicts a significant interaction between forager type (myopic or periscopic), poor feeder quality (0.5M, 0.67M, 0.8M), foraging behavior (picky or not picky). The interaction was significant ($G=8.0$, $P<0.05$).

Persicopic foragers also differed from myopic in their behavior at the intermediate concentration of sucrose solution (0.67M) in the

Table 4. Frequencies of foraging behaviors of myopic foragers at the intermediate value of poor feeders.

	Picky	Partial Preference	Opportunistic
Expected under null hypothesis	6.3	17.6	1.1
Observed	13	7	5

*P < 0.05

Table 5. Frequencies of foraging behaviors of periscopic foragers at the intermediate value of poor feeders.

	Picky	Not Picky
Expected under null hypothesis	21.9	37.1
Observed	23	36

$$\chi^2 = 0.09$$

poor feeders. Unlike myopic behaviors, the distributions of behaviors in the case of periscopic foraging (picky or not picky) could be generated by a single strategy in which the foragers exploited poor feeders with a fixed probability of acceptance (table 5).

Prediction 2

This prediction states that myopic foragers should be opportunistic over a range of relative resource values. When the poor resources were 80% as valuable as the rich resources, 75% of the visits were opportunistic. The remaining 25% of the visits showed a partial preference. The total percentage of the diets of myopic foragers in this treatment which comprised poor feeders was 53% (table 1).

Prediction 1a

This prediction is that if the myopic forager with linear fitness isopleths displays a partial preference, then the forager should be more likely to accept a poor item after it has not recently encountered a rich item (this prediction is derived from the hypothesis that the myopic forager reassesses encounter rates with rich resources as a result of its experience in the food patch).

Myopic birds encountered rich and poor feeders randomly since they could not distinguish feeder type until they had probed the feeder. That is, the likelihood of encountering a poor feeder immediately after encountering a rich feeder was the same as the likelihood of encountering a poor feeder immediately after encountering a poor feeder; the probability of each occurrence is 0.5. Thus, if the

prediction is true, most of the poor feeders which were accepted in a partial preference visit should have been accepted immediately after an encounter with a poor feeder. At the intermediate value of poor feeders (0.67M) 16 poor feeders were accepted during partial preference visits. Of these, 14 were accepted immediately after encounters with poor feeders ($P < 0.05$). There was no significant trend in the pattern of acceptance of poor feeders during partial preference visits when the poor feeders were only 0.5M. However, when the poor feeders contained sucrose solutions of 0.8M, the trend in acceptance pattern of poor feeders during partial preference visits suggested a different hypothesis concerning the use of information by myopic foragers. Ten of the 14 poor feeders rejected during partial preference visits at this concentration came immediately after encounters with rich feeders. Although this result is contrary to the prediction above, it is consistent with the hypothesis that these birds increased their estimates of encounter rates with rich resources upon an encounter with a rich resource. Upon increasing their estimate of the value of a patch, they were more likely to reject an encountered poor feeder.

Prediction 4

This prediction states that periscopic foragers should be more likely to take poor resources located near rich resources than poor resources located far from rich resources. The data from the periscopic experiments support this prediction. A periscopic forager was more likely to take a poor that was paired with a rich feeder than a poor feeder that was paired with a poor feeder ($P < 0.05$, $n = 121$).

Prediction 5

This prediction states that the likelihood of a periscopic forager taking an item increases with the value of nearby items. As I stated in the theoretical section, this prediction is simply a generalization of prediction 4. The data support this one as well. The periscopic forager was more likely to take a rich item paired with another rich item than it was to take a rich item paired with a poor item ($P < 0.05$). And, as Table 6 shows, the probability that a periscopic forager took a rich feeder paired with a poor resource increased with the value of the poor resource.

A Further Test of Prediction 4 and a Test of Prediction 6

For this set of experiments, I observed Rivoli's Hummingbirds foraging from my experimental feeders in a study plot in Rustler's Park. As in the previous experiments, I re-filled each feeder after a bird exploited it. I performed two kinds of manipulations: (1) changing the overall densities of both rich and poor feeders, and (2) changing only the incremental travel cost (directed effort) of obtaining poor items. I altered the densities in two ways: (1) increasing the number of each type of feeder from 5 to 10 on a 20m by 30m plot, and (2) decreasing the plot size from 20m by 30m to 20m by 15m when there were ten rich and ten poor feeders on the plot. I altered the incremental travel cost of taking poor feeders by moving them closer to the rich feeders (with one meter separating them) from an otherwise random spatial distribution. The random distributions were generated by randomly assigning feeders grid positions using a

Table 6. Account of rich feeders taken from pure rich pairs and mixed rich and poor pairs by periscope birds.

Quality Of			% From
Poor Feeder	Pure Pairs	Mixed Pairs	Pure Pairs
0.5M	74	48	61%
0.67M	109	86	56%
0.8M	91	90	50%

random number table. These treatments included ten rich and ten poor feeders each and were arranged as follows:

Treatment 1: rich and poor feeders randomly placed on 20m by 30m plot.

Treatment 2: rich and poor feeders randomly placed on 20m by 15m plot.

Treatment 3: rich feeders paired with poor feeders on 20m by 30m plot.

Treatment 4: rich feeders paired with poor feeders on 20m by 15m plot.

Prediction 4

This prediction stated that periscopic foragers should be more likely to take poor feeders which are near rich feeders than poor feeders which are far from rich items. This prediction would be supported if the periscopic birds were less picky when rich and poor feeders were paired than when they were randomly arranged. The birds behaved as predicted when the feeders were arranged on the larger 20m by 30m plot. The diet was 72% rich feeders when feeders were randomly arranged, but only 55% rich feeders when rich and poor feeders were paired. The difference is significant ($P < 0.05$). On the smaller 20m by 15m plot, the decline in pickiness due to pairing rich and poor feeders was small (78% to 73%) and statistically insignificant.

Prediction 6

This prediction states that increasing the densities of both rich and poor resources should cause an increase in the proportion of the periscopic diet comprising rich resources. The first increase in density from 5 to 10 feeders of each type on the plot produced a significant increase in the percentage pickiness on the rich feeders

Table 7. Effect of resource density on the pickiness of periscope
Magnificent hummingbirds.

Low Density	Intermediate Density	High Density
52%	72%	78%

(58% to 72%). Figure 7 shows that the second increase in density caused by halving the plot size from 20m by 30m to 20m by 15m resulted in a statistically nonsignificant increase (72% to 78%).

Test of Predictions 7 and 8

I tested these two predictions in the summer of 1982 at the Southwestern Research Station. Both Blue-throated and Black-chinned hummingbirds were regular visitors to my study plot during this season. I established two rows of ten feeders each. The rows were parallel and separated by 4 m. I separated feeders within rows by 2 m. Rich feeders contained 1.0 M sugar water and poor feeders contained either 0.33 M sugar water or 0.67 M sugar water depending on the treatment.

There were two arrangements of rich and poor feeders. In one, the rows contained five rich and five poor feeders each, mixed randomly within the row. In the other arrangement, the rows contained ten feeders of one type, either rich or poor.

My purpose in arranging the feeders in rows was to try as much as possible to equalize the incremental travel cost of taking feeders within a patch. My purpose in separating the rows by four meters was to make the travel cost between patches greater than the incremental travel cost between feeders within a patch.

The four treatments of this experiment were: (1) rich and poor feeders intermixed in the same row with poor feeders at 0.33M, (2) rich and poor feeders intermixed in the same row with poor feeders at 0.67M, (3) rich and poor feeders separated into different rows with poor

feeders at 0.33M, and (4) rich and poor feeders separated into different row with poor feeders at 0.67M.

Prediction 7

This prediction states that a periscopic forager should be less picky on rich resources if rich and poor resources are randomly dispersed in the same patch than if they are distributed in separate patches. The data from the Blue-throateds' foraging support this prediction. When the poor feeders were at 0.33 M, the average partial preference was 81% rich in the intermixed patch and 94% in the pure stand. When the poor feeders were at 0.67 M, the average partial preference was 58% in the intermixed patch and 75% in the pure stand (table 8). Both results are significant ($P < 0.05$).

The data from the Black-chinned's foraging support this prediction in one of the two possible comparisons. The average partial preference was virtually identical in the intermixed (84%) and pure stands (85%) when the poor feeders contained 0.33 M sugar water (table 8). However, when the poor feeders contained 0.67 M sugar water, the average partial preference was significantly less in the intermixed patch (65%) than in the pure stand (87%). Again, the lack of significance is not troubling: make the poor, poor enough, and the birds should stop caring about other, minor matters.

Prediction 8

This prediction states that the response to a change in relative values of the resources should be less when resource types are

Table 8. Responses of Black-chinned and Blue-throated to an increase in the quality of poor feeders in intermixed and pure patches.

Pickiness on Rich Feeders				
Quality of Poor Feeder	Black-chinned		Blue-throated	
	Intermixed	Pure	Intermixed	Pure
0.33M	84%	85%	81%	94%
0.67M	65%	87%	58%	75%

in distinct patches than when they are intermixed in the same patch. Table 8 gives the results of this test. When rich and poor resources were in separate patches, the Black-chinned response to an increase in the value of poor feeders was virtually nil (an insignificant increase in pickiness from 85% to 87%). However, when rich and poor resources were intermixed in the same patches, the Black-chinned diet became significantly less picky as the poor feeders became more valuable (65% picky compared with 84% picky). Hence, the Black-chinned data support the prediction.

Table 8 also gives the results for the Blue-throated response to changing values of the poor resource under the two treatments of mixed and separated resources. When resource types were in separate patches, Blue-throated decreased pickiness from 94% to 75% in response to an increase in the value of the poor resource. When resource types were intermixed in the same patches, Blue-throated decreased pickiness from 81% to 58% in response to an increase in the value of the poor resource. This corresponds to a decrease of 24 percentage points. The comparative Blue-throated responses differed in the proper direction but not by a statistically significant amount.

CHAPTER 5

SAMPLING BY PERISCOPIC FORAGERS

Two categories of exploitative competition may be distinguished by whether exploitation changes the constraints or the fitness isopleths in the optimal programming problem. Exploitation of seeds, insects and other food items usually depletes the abundance of a resource and thereby alters the constraints. Exploitation of a habitat usually reduces the expected value of that habitat type and, thereby, alters the slope of the fitness isopleths. When a hummingbird feeds from a flower, the effect of exploitation is more similar to that of habitat depletion. Subsequent visitation from other hummingbirds will involve wasted directed effort caused by the colorful flower which remains on the plant. Because an empty flower looks like a nectar-containing flower, hummingbirds may be subject to strong selective pressure to incorporate a type of Bayesian sampling into their foraging behavior.

In this section, I consider the question of how a forager should use new information, acquired while foraging, about the quality of resources or resource patches. Many foragers will have expectations about the costs and benefits of using certain resources or habitats before they begin a foraging bout. But these same animals will adjust their evaluations of resource qualities in light of information they

gain while foraging. One example of this kind of behavior is the animal who re-evaluates the quality of a food patch it is currently foraging in. The kind of information the animal may be interested in is the number of resource items encountered and the amount of time spent in the patch (Green 1980). The degree to which the patch is exploited depends on the forager's new evaluation of patch quality.

Sometimes, however, the forager may employ information in a more sophisticated manner than merely using it to estimate the density of resources. For instance, if there were some underlying mechanism which could generate predictable pattern in the distribution of usable resources, then it would behoove the forager to be capable of detecting the pattern. An example of this kind of information use is the detection of so-called "hot spots" by nectarivores. Zimmerman (1981) found that nectar distribution tends to be clumped. That is, the likelihood of a flower having nectar in it depended on the presence of nectar in nearby flowers. Bees use this information by leaving areas in which they had visited several empty flowers in succession. This behavior would be non-adaptive if nectar were distributed independently among flowers.

The reason why nectar is distributed non-randomly does not matter for Zimmerman's hypothesis. All that does matter is the benefit accruing to the animal which responds accordingly. If, however, a hypothesis is made about the mechanism which generates a nonrandom distribution of nectar among flowers, then a more sophisticated behavioral prediction can be made. It is possible to imagine two such

hypotheses. One proposes that the nectar distribution is the result of the plant or plants producing nectar in 'hot' and 'cold' spots, perhaps because of local and microhabitat differences. Another hypothesis proposes that the pattern is at least in part generated by other foraging nectarivores. If the absence of nectar in a flower means that it has already been visited by a nectarivore, then it also means that nearby flowers have probably been visited.

The second hypothesis is particularly interesting because it introduces an evolutionary response to a selective factor mediated through two other agents; a resource and a competitor for that resource. This hypothesis of competitor induced pattern makes a prediction that the first hypothesis does not make: not only should a forager be more likely to leave a patch after finding a sampled flower empty, but the probability that it leaves should depend on the value the nectar the forager would have consumed had the flower been full.

Consider the following situation. Let there be patches of flowers (perhaps inflorescences) in which different flowers possess nectars of different sucrose concentrations. Also let the birds be periscopic in that they can distinguish different qualities of flowers at a distance. In order to simplify the situation, assume that there are only two flowers in a patch. Let v_i , and h_i represent the energetic value and handling time, respectively, of a flower i ($i=1,2$). Let there be $n > 1$ patches. If a bird visits a patch, it may do one of three things: (1) visit both the rich and poor flower, (2) visit only the rich flower, and (3) visit only the poor flower. The more flowers

a bird visits within a patch, the less time it has for flying between patches, because there is some time constraint, T , within which it must do all of its foraging.

Given that a bird flies to a patch, it should attempt to exploit the rich flower. Whether or not the bird exploits the poor flower depends on the incremental benefit and cost of that exploitation. The incremental benefit is v_2 . The incremental cost is the amount of energy which could not be acquired foraging in other patches because the bird spent an additional amount of time in this patch. The additional time spent in a patch where the poor flower is used, is the handling time plus the additional flight time required to deviate from the shortest path from the rich flower to the next visited patch.

The sequence in which the flowers are exploited is not important since there is no reason to exploit the flowers in order of decreasing rank (v_i/h_i). Hence, the bird does not experience a reduced rate of energetic intake during its stay in the flower patch. It is true, however, that the more items chosen and, hence, the longer the total time the bird spends in the patch, the lower the overall rate at which energy is acquired in that particular patch.

The prediction of this model is that the bird should either take both flowers or only the rich flower, but not the poor flower alone. This prediction does not yet include the effect of the other nectarivores' feeding behavior on the decision rules. Now consider the case in which a hummingbird is subject to exploitative competition.

Each competitor will be attempting to maximize its fitness by its choice of foraging behavior, including its choice of which flowers in a patch to exploit. In the model above, the optimal number of items taken depended on the exploitation efficiency and travel efficiency of the forager. These parameters may vary for different foragers, either conspecifics or heterospecifics. But, if the assumption can be made that all visitors to the resource patch rank resource items in the same way, then all visitors to the patch will exploit the flower with the highest rank. No flower of rank, $j < k$ will be exploited if flower k is not exploited.

In light of this decision rule, a bird may use the absence of nectar in one flower to inform it regarding the likelihood that there is nectar in the other flower. In particular, if the bird samples the poor flower first and finds no nectar, then then it should find no nectar if it were to sample the rich flower. If the bird samples the rich flower first and finds no nectar, there may or may not be nectar in the poor flower depending on whether the previous visitor to the patch exploited both flowers or only the rich flower. The conditional probability that the rich flower is empty given that the poor flower is empty is greater than the conditional probability that the poor flower is empty given that the rich flower is empty. Thus, we should see that an opportunist (a forager wishing to use both flowers) should be more likely to leave after finding the first sampled flower empty if that first flower is poor. This leads to the following prediction: once a flower of rank j has been found empty, the bird should not waste effort

investigating flowers of rank higher than j . In the following section I present an experimental test of this prediction.

Experimental Design

I tested the prediction by observing Magnificent hummingbirds foraging on experimental feeders in Rustler park, Chiricahua mountains. I performed the experiments on a 20m by 30m plot with the same feeders described in the previous section. I placed 8 pairs of feeders in the plot. The pairs were separated by about 3 to 5 meters. Feeders within the pair were separated by about one meter. Each pair comprised one feeder marked with blue flagging tape and one feeder marked with orange flagging tape.

In the experimental arrangement, the probability that a feeder was full did not depend on the presence of nectar in its neighbor. I placed the following arrangement of nectar in the eight pairs of feeders: Two pairs contained feeders which were both filled with sugar water. I filled the blue feeders with 1.0 M sucrose solution and the orange feeders with 0.5 M solution. Two other pairs contained one empty blue and one empty orange feeder, each. Two pairs contained one blue feeder filled with 1.0M sucrose solution and one empty orange feeder. Finally, the last two pairs contained an empty blue feeder and an orange feeder filled with 0.5M sucrose solution.

The experimental pattern is contrary to my hypothesis of the distribution of nectar in nature; there, I expect exploitative competition to impose a positive correlation between the presence and absence of nectar in nearby flowers. Furthermore, the experimental

set-up includes an equal number of pairs in which the rich and poor feeders occur as the "unexploited" member of the pair. This also contradicts my hypothesis since I expect that the optimal foraging of competing individuals in nature will leave more exploited patches in which poor flowers remain unexploited.

The reason I designed my experiment purposely to be 'unnatural' is that I wanted to test the prediction by tricking the birds into doing the wrong thing, owing to the artificiality of the situation. If the birds respond in a manner which is adaptive for the natural situation as I hypothesize it to be, they will treat the information gained by sampling as though it indicated a positive correlation between the presence of nectar among neighbors. Thus, their response will not simply show that they can learn to jump through empirical hoops, but reveal instead an underlying adaptive capacity linked to an expected natural pattern.

Results

The results support Zimmerman's prediction that the absence of nectar in one flower should discourage foragers from probing nearby flowers (Recall that Zimmerman's prediction does not yet include the sampling behavior specialized for exploitative competition). When the first feeder visited contained sugar water, 67% of the time the bird visited the second feeder. When the first feeder visited was empty, the bird visited the second feeder only 38% of the time. The

difference is significant ($X^2 = 8.24$, $P < 0.05$, $n = 99$) and in the direction of the prediction.

The results also support my prediction which stated that information gained from the poorer feeder should have a greater influence on the probability of a bird's leaving a pair than information gained from the richer feeder. In the 29 samples in which the low quality feeder was first visited, the Chi-square value for a test of independence between the presence of solution in the first feeder visited and the probability of visiting the other feeder was 10.18. This is a highly significant value by the proper one-sided test. In the remaining 70 samples in which the high-quality resource was first visited, the Chi-square value was 1.20 which is insignificant. So, as predicted, the decision rule based on Bayesian-like sampling appears to be more important when the low-quality resource is used as the sample by the hummingbird.

Discussion of the Results of the Sampling Experiments

Magnificent hummingbirds used information on the presence or absence of sugar water in artificial flowers to determine the departure rules from a resource patch comprising two artificial flowers. Not only do they avoid spending additional effort in a patch containing a feeder they know to be empty, but the weight which they give the information depends on the prior quality of the empty feeder. I had predicted the latter result by hypothesizing that the birds have been selected to detect pattern imposed on resources by exploitative competition from other optimally foraging birds.

Birds showed a more sophisticated response than would be expected by the hypothesis of Zimmerman (1981). He simply suggested that nectarivores recognized the existence of areas in which a larger proportion of flowers contained nectar, which he called "hot spots", and areas in which a smaller proportion of flowers contained nectar, which he called "cold spots". He proposed that nectarivores could use this information to avoid wasting effort on flowers which were unlikely to contain nectar. The cause of the nonrandom distribution of nectar among flowers is not relevant to Zimmerman's model. It may be due to local spatial differences in the allocation effort by the plants to produce nectar. Or, it may be due to foraging by previous visitors who would not tend to distribute their foraging effort randomly among all flower patches in the environment. Clearly, the results of my experiment suggest that the second manner in which cold spots may be generated is much more important to hummingbirds than the first.

These results suggest another possibility. The periscopic forager can maximize the information it has on the state of exploitation of unencountered resources by encountering the poorer resources first. Hummingbirds, for instance, may often choose to visit the worst flower they are willing to accept in the patch before they visit any better flowers. In this way they could avoid wasting effort sampling better flowers whose condition they can discern from the condition of the poorest acceptable flower. However, other foraging considerations may prevent a hummingbird from gaining maximum use of this structure in its environment. For instance, in a world of

considerable interference competition, the birds may be selected to go for the richer resources first before they are engaged by another bird in a chase or fight. My experimental results did not show that the birds preferred to visit the poor feeder first; but my experimental design could not ensure that birds which first visited rich feeders, also intended to visit the poor feeder.

CHAPTER 6

DISCUSSION

My experimental results support the view that useful theories can be constructed by making adaptationist hypotheses on the foraging behavior of animals. The results corroborate predictions of a comprehensive foraging theory which accounts for the type of knowledge available to a forager. The manner in which a forager responds to a change in the relative values of its resources depends on how many items it knows the location and quality of. If it knows, at most, the location and quality of one food item at a time, as well as the average quality of the environment, then it has a discontinuous, or "bang-bang" response. If, however, it knows the quality and locations of more than one food item at a time, then it has a more gradual response if resources are distributed randomly and independently. I call these two types of foraging myopic and periscopic, respectively.

Periscopic foragers are predicted to show a partial preference when the qualities of different types of food are not the same. Periscopic hummingbirds showed such a partial preference. The cause of the periscopic partial preference is that the incremental cost of adding a poor quality food item depends on the spatial location of that item relative to the best path that does not include the item. Thus, the incremental cost differs among poor quality items. My experimental

results supported the prediction that periscopic birds were more likely to exploit poor items located near rich items than poor items located far from rich items.

The same argument works with the likelihood of a given rich item being exploited. The incremental cost of taking a given rich item depends on the additional cost of travel due to taking the item. This incremental cost is lower if the value of nearby items is higher. My experimental results show that the likelihood of a rich feeder being taken is positively related to the quality of nearby feeders.

Myopic foragers are not predicted to have a partial preference when the qualities of different types of food are not the same (assuming that fitness isopleths are linear). They are supposed to either accept or reject every poor resource item which they encounter. Some hummingbirds in the myopic experiments did show some partial preferences. But these also showed a statistically significant tendency to accept or reject a poor resource in a way that depended on what kind of resources they had recently encountered. Thus, it seems unlikely that the partial preferences were simply mistakes. Instead, the sequential pattern of partial preferences supports the hypothesis that the myopic birds were adjusting their expected future encounter rates based on their foraging experience.

Also as I predicted, the birds responded to the manipulations of resource distributions. Periscopic birds were pickier when resource types were distributed in different patches than when they were distributed intermixed in the same patch. They also showed less

sensitivity to the quality of poor resources when those resource resided in a different patch than rich resources.

One of the best substantiated predictions of myopic foraging is that the forager should become picky on the best resource as the densities of all resources increase. A periscopic forager should also become pickier (though in a gradual, not discontinuous fashion) on the best resource as densities of resources increase. My periscopic hummingbirds responded as the theory predicted. I did not, however, consider an interesting variation on this problem. In the case where handling times are different for the two resources, the optimal periscopic forager may switch its preference as the densities of both kinds of resources increase. At low densities the polygon circumscribing the feasible diets should be determined primarily by the travel costs among resource items. Handling time will be relatively unimportant since few items will be handled. If densities are equal then the expected optimal periscopic diet will reflect the relative values of the resources (the slope of the isopleths). At high densities, the shape of the polygon will often be skewed to reflect the difference in per capita handling costs of the resources. In this case, the expected optimal periscopic diet will favor the resource with the highest ratio of per capita value to handling cost. The resource with the highest energetic value to handling cost may not have the highest energetic value. If not, the periscopic forager may switch preferences with a change in total resource density.

In the real world, foragers may frequently have, at best, a priori estimates of the expectation of the resources quality. They may have to 'test the waters' of a resource or a resource patch before they gain additional information about its quality. A myopic forager may be able to acquire this information with relatively little cost. Once the myopic forager encounters the item, it can immediately begin to exploit it. Or, if it is selecting patches, it can immediately begin to exploit the patch. Upon exploiting the resource or patch, it may be able to discern quickly the return on its investment in handling the resource or patch. If the return is very low, the forager can immediately decide to leave the patch and continue searching for something better. Thus, the initial lack of information regarding the quality of resources may be immaterial to a myopic forager if it can quickly discern quality upon encountering the resources.

A periscopic forager, however, cannot acquire information about a resource until it has paid the cost of travelling to the resource. This cost depends on the location of the resource relative to the best travel path not including it. Therefore, a lack of information regarding the quality of resources will usually impair the ability of a periscopic forager to forage efficiently since it will be forced to waste directed effort on food or patches which it would not have chosen to exploit.

This feature of periscopic foraging has the potential of increasing habitat separation between potentially competing species. If one habitat type is being exploited by a competitor species, then

the expected value of that habitat is lowered to an individual. A perfectly sampling myopic forager, however will only make its decision about foraging in a habitat based on the actual value of the habitat, not the expected value (Brown and Rosenzweig MS). The periscopic forager, on the other hand, will not make the additional effort of travelling to a habitat if the expected value of the habitat is not sufficiently large relative to the additional travel effort. Thus, while a periscopic habitat specialist may sample a few unpreferred habitat patches which are close to its best travel route among preferred patches, it will not risk the additional directed effort of visiting and sampling those unpreferred habitat patches far from this travel route. Conversely, a myopic habitat specialist will sample all patch types in the proportion in which they occur in the environment and feed in those unpreferred patches which have not been depressed in value below some threshold quality.

In some situations, the forager does not have the option of sampling the value of the habitat and deciding whether or not to continue foraging. In others, the option is useless because the forager is unable to predict its future fitness gains in the habitat based on past experience. In this case periscopic abilities of foragers should decrease habitat separation among competing species which are specialist for different habitat types. In order to see this, first consider the theory of myopic habitat selection when directed effort is fixed.

Rosenzweig (1981) shows that there are regions in the state space of competitor densities in which the optimal behavior of individuals is to select only the preferred habitat. In other regions of the state space, the individuals of one or both species should be completely opportunistic with respect to habitat type. In other words, the myopic foragers show a bang-bang all-or-nothing response with respect to habitat choice.

Periscopic foragers, however, should not show a bang-bang response of habitat selection in response to combinations of species' densities since the effect of densities is simply felt through the value of the habitats to individuals. And, the previous discussion in this paper supports the prediction that the control of periscopic foragers is not necessarily discontinuous with respect to resource or patch quality.

Periscopic hummingbirds are able to mitigate the problem confronting them regarding the uncertain quality of some resources. When the pattern of resource quality is, at least in part, imposed by the adaptive foraging behavior of other individuals, these birds are capable of using a type of Bayesian decision rule that tells them the likelihood that one flower is exploited as a function of whether nearby flowers have been exploited.

The interest of this test is that it substantiates two often controversial kinds of hypotheses. One kind is, like the others tested in this paper, an optimization hypothesis. Optimal sampling behavior has been suggested by other workers to be important in nectarivore

feeding (Zimmerman 1981) as well as in foragers in general (Iwasa et. al. 1981). The other kind of hypothesis is a competitive hypothesis. The birds responded to the information of the presence or absence of nectar in my feeders as though the absence were the result of exploitation by optimal foragers. They did this in spite of the fact that their response was inappropriate given the resource distribution I had experimentally established. These results suggest that it is possible to use optimization hypotheses to help test competition hypotheses.

I have tried to present myopic and periscopic foraging as two different ways in which an animal may exploit resources or habitat patches, not as clashing theories or paradigms. The biologist who wishes to apply optimal foraging theory to his study organism must take into account, or make a hypothesis about, the amount of information which the forager can acquire.

I hypothesized that the birds could utilize the information which the flowers go to some trouble to make available to them. Overall, the hypothesis appears successful. The hummingbirds perform as predicted by the model of periscopic foraging when they can know the location and quality of more than one food item at a time. On the other hand, when they know the location and quality of only one food item, they perform as predicted by myopic foraging theory. The result is that the domain of optimal foraging theory can be expanded to include a greater variety of foraging situations than it has typically claimed. There is nothing in the nature of either optimization

mathematics or the hard core of the adaptationist program which can account for the hobbles scientists have placed on this approach to understanding animal behavior.

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