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Optimal Foraging Strategies and Hunter-Gatherer Research in Anthropology: Theory and Models

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Introduction

Optimal foraging strategy theory offers a generalized and realistic approach to the analysis of hunter-gatherer behavior. The theory provides a cluster of simple models, partially derived from neo-Darwinian postulates, which produce operational hypotheses about foraging behaviors expected in different environmental circumstances. Some of these hypotheses are nonintuitive. These and other qualities argue for the use of these models in anthropological research. This chapter describes the assumptions and theory of this approach, and outlines models that deal with diet breadth, use of a heterogeneous habitat, patterns of movement in a heterogeneous habitat, and group size and settlement patterns. These models focus on patterns expected if foragers behave so as to obtain a high net rate of energy acquisition while foraging. Because they provide explicit predictions about the behaviors, given energy optimization assumptions, they can be used to disentangle the relative importance of this and other selective influences acting on the formation of behavior. I shall also note points where data and analytic judgment are necessary to adapt this approach reliably to human ecology study.

The potential anthropological importance of this approach rests in its generality. The models seem to provide predictions, based on a limited number of parameters, which identify basic qualities of adaptive solutions to recurrent environmental features. For instance, central place aggregation in species as diverse as fish, birds, and primates appears to be a common foraging adaptation which reduces the costs of finding and successfully recovering foods that are abundant but clumped together and unpredictable in location (Horn 1968; Schoener 1971:395-96). Consequently, when obvious constraints are allowed for, the models are fairly insensitive to phylogenetic context. This generality argues for their use in hunter-gatherer research. Furthermore, the operational qualities of the theory mean that its analytic scope and reliability in anthropological investigation are open to empirical assessment.

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The theory discussed here is adapted from ecology. Despite recent applications in ethnographic study (E. A. Smith 1978; Winterhalder 1977 1980a n.d. ab) and in archeology (Jochim 1976; Keene 1979ab 1980; Wilmsen 1973), and considerable promise (Thomas, Winterhalder, and McRae 1979), caution is urged for its use in anthropology. For instance, some of the archeologists cited have assumed a simple interpretation of optimal foraging models to be true for humans, and then elaborated more complex interpretations on this basis, that is, prior to tests of the foraging models themselves. In contrast, Winterhalder (1977) found the optimal foraging approach heuristically very valuable, but noted that assumptions of the theory are not always applicable, and that specific models are sometimes not reliable for predicting human foraging behavior. Consequently, this chapter has as its purpose: (1) identification of the assumptions that lie behind application of evolutionary ecology to anthropological subjects; (2) clear statement of the analytic decisions faced by an anthropologist using this theory; (3) identification of models and hypotheses that are particularly appropriate in human ecology investigation; (4) isolation of points where, despite the semideductive nature of the approach, significant data are required to apply it reliably; and (5) some indication of the analytic shortcomings and promise of these models. Available human ecology analyses using specific models are cited where appropriate.

I hope to establish that the theory provides a theoretically coherent framework for the investigation of the ecology and evolution of hunter-gatherer behavior, generalized with respect to behavioral category and environmental context. As a result the models should perform well in investigating the environmental factors contributing to the behavioral diversity of hunter-gatherers.

Evolutionary Ecology

The optimal foraging models discussed here are part of evolutionary ecology theory developed over the past fifteen years (see Pianka 1978 for a summary). This theory relies on the observation that neo-Darwinian assumptions (Cody 1974; Pianka 1978:13-14) and simple graphical or algebraic models (Levins 1966 1968:3-9) are often adequate to predict selected aspects of an organism's behavior.

Evolutionary ecology deals with a broad array of topics, including resource procurement (Krebs and Cowie 1976; Pyke, Pulliam, and Charnov 1977; Schoener 1971); life history and mating (Brown 1975:166-75; Orians 1971:536-38; Stearns 1976); and avoiding predators (W. D. Hamilton 1971; Orians 1971:540-41; Pulliam 1973). Each area is broken into more specific behavioral categories for analysis. For instance, foraging is usually considered in terms of four overlapping sets of questions: diet breadth and choice of items, foraging space, feeding period, and foraging group size. These sets of questions focus on individuals or groups of individuals of a single species, but analysis at this scale can be considered the "microecological theory" (Pyke, Pulliam, and Charnov 1977:140) of behavior producing population phenomena such as interspecific competition, predation, and trophic relationships (e.g., Orians 1975). The division of behavior into these four categories rests on analytic convenience; it does not necessarily mirror a similar partitioning of life processes by the organism.

An important facet of the development of ecological research since 1960 lies in the type of questions asked. Orians (1971:529-30) has discussed this shift of perspective with respect to analysis of territoriality. Prior to 1960 the major research question was, What is the function of territoriality? Investigations centered on behaviors occurring in territories and produced a list of activities associated with defended space. The functional orientation did not, however, yield results which could be generalized or which, in the case of birds, for example, directed attention to data "that could explain the diversity of avian territorial systems rather than just describe them" (Orians 1971:530). In 1964 Brown reformulated the question, and significantly altered the success of the inquiry: "Brown's major contribution was to point out that the way to explain the diversity of territorial systems was to ask the question in the form, What factors select for increased aggressiveness with respect to space?" (Orians 1971:530; see also Brown and Orians 1970: 246-54). It emerged that a major variable--the density and predictability of resources--accounts for much of the behavioral variability of avian species with respect to territoriality (Brown 1964). Resource-based hypotheses were promulgated prior to Brown's analysis, but, stated in the functional form, they did not suitably link observations with theory.

Two shifts in the rephrasing of this question underlie the microecological elements of evolutionary ecology. First, there is an emphasis on individual-level selection and adaptation (Lewontin 1970; Williams 1966). Second, there is a shift to analysis of the mechanisms and conditions which interact to produce adaptive processes. Less attention is given to classification of the functional results of evolution or to correlation of these with environmental features.

It is possible that the tendency in human ecology research to state questions in functional terms similarly impedes the identification of environmental variables useful for analyzing the evolution of behavior. This chapter describes models which pose questions about foraging in the form suggested by Brown--in terms of selection and individual-level adaptive behavior. Explicit attention is given to procedures for testing sets of alternative hypotheses. The focus here is on foraging, but the approach parallels that of Durham (1976b) on warfare.

Assumptions and Concepts of Optimal Foraging Theory

Adaptation and Optimization

The optimization concept derives from the postulates of synthetic evolutionary theory. Pianka (1978:12) states, "*Natural selection and competition are inevitable outgrowths of heritable reproduction in a finite environment*" (italics in original). Direct and indirect competition for resources gives advantages to organisms that have efficient techniques of acquiring energy and nutrients which can be turned into offspring or used to avoid predators (Pianka 1978:12). Pianka's statement identifies the "source" of optimal phenotypes and the three arenas of behavior usually considered: resource acquisition, reproduction, and predator avoidance (see Crook, Ellis, and Goss-Custard 1976:262). Optimization pertains to the efficiency, relative to time or energy costs, with which these activities are performed, with the assumption that increased efficiency relative to a standard of performance leads to a relative increase in fitness.

The extensive use of optimization or maximization principles in ecology has led to a serious debate about their merits (Maynard Smith 1978; Lewontin 1979a 1979b). Here it is assumed that an optimality principle provides a structured and contingent guide to the expected direction of evolution by selection. It is structured because, with specification of auxiliary conditions and parameter values, hypotheses about the development of particular behaviors can be devised; contingent, because no set of conditions or derived hypotheses can be stated which have theoretical generality sufficient to qualify as evolutionary universals. Further, optimality analysis assists in identifying the products of selection at the expense of attention to other evolutionary processes.

It is assumed in the biological literature that adaptive phenotypes result from natural selection acting over time to produce changes in the gene pool of a population. Selection acts through its effects on the reproductive fitness of individuals. The focus on genetic adaptation is, however, an unnecessary restriction. The evolution of foraging strategies can reside in the realm of sociocultural behaviors and yet be analyzed by evolutionary ecology models (Campbell 1965; Durham 1976a; Pyke, Pulliam, and Charnov 1977:138). Genetic differences among individuals presumably have no significant effect on the behavioral variability relevant in ethnographic studies of human foraging behavior. Consequently, it is necessary to assume only that foraging is characterized by recurring variability; that the "successful" variations are consciously or unconsciously adopted by individuals; and that the "selected" behavioral variants are passed from parent to offspring or between generations by other persons (cf. Lewontin 1970:1).

As Cody (1974:1156) states, it is somewhat tautologous to invoke optimization in an evolutionary context. Selection is sometimes defined as producing the optimal or best-adapted phenotype. Nonetheless, optimum phenotypes hypothesized by ideal models ignore a variety of effects manifest in the real world. It is possible, for instance, that the constraints of history, chance, or competing goals (Cody 1974:1156) prevent the evolution of phenotypes that are ideal relative to certain goals of behavior. Selection or adaptation may more or less adroitly track but not approach conceivable optima. Appropriate preadaptations may not be available; conditions in the environment can change; or conflicting adaptive goals may be set up by alternating environmental states, or by the necessity to harvest two resources for which the "optimal" strategies are mutually exclusive. Evolutionary ecology analysis becomes interesting when it attempts to specify the optimal pattern of behavior in a particular situation, or when it attempts to assess the constraints that multiple goals or historical circumstances place on an organism's ability to achieve a particular optimum.

In the human case two points arise concerning the possible disjunction between modeled optima and observed behaviors. First, much of the historical constraint on nonhuman organisms stems from the fortuitous nature of mutations and preadaptations, and from relatively inflexible behavioral abilities. Genetic evolutionary change can be slow relative to change in environmental features. This constraint is partially relaxed in the human case owing to behavioral flexibility and to the possibility of rapid cultural innovation in response to particular ecological circumstances. Second, humans have cultural goals which take on the status of social imperatives by virtue of their residence in the coherent systems of belief and meaning which pervade and structure much behavior (Geertz 1973; Slobodkin 1977). It is possible that constraints on optimal (as opposed to biologically minimal) solutions to particular adaptive problems from this cultural source are significant. The balance of the two influences--biological flexibility and cultural constraints--on the realization of optimal behaviors is not easily determined. Little empirical information and few theoretical guidelines are available (cf. Durham 1976a).

Foraging

Foraging refers inclusively to tactics used to obtain nonproduced foodstuffs or other resources, those not directly cultivated or husbanded by the human population, although they may in some senses be conserved or managed (Feit 1973). Foraging may involve hunting, trapping, netting, snaring, gathering, or other techniques. The word hunting implies that the forager is directly and immediately involved in the capturing or killing of animal prey.

The focus here on the foraging practices of hunter-gatherers is not based on recognition of a traditional category or the desire to isolate a manageable set of examples. These criteria would imply the misapprehension that hunting and gathering behavior represents a uniform or simple class of subsistence adaptations (Martin 1974). Rather the restriction identifies a set of behaviors amenable to analysis using evolutionary ecology concepts much as they would be used by biologists. Two criteria bound this class, aside from the previously stated condition that the resources be nonproduced. First, the choice of foraging largely obviates the need to consider money. This circumvents the problem of mixing "currencies" (see below) of different conceptual status. The second criterion is the restriction to subsistence. The models described here can thus employ a limited form of cost-benefit comparison, evaluating both the costs and benefits associated with particular activities in commensurate ecological units (primarily calories).

Strategy Analysis and Temporal Scales of Assessment

Strategy analysis links a certain kind of explanation to an evolutionary time scale (Pianka 1978:15; Mayr 1976b:360-63). It looks for the origins of complex behaviors in the effects of selection in patterned environments (Levins 1968). Despite emphasis on long-term adaptation, strategies are not fixed. Considering a series of intervals in which an organism must make decisions, Schoener (1971:375) states, "At the beginning of each, the animal assesses its strategy in the face of alternative future conditions whose probabilities are known (i.e. genetically programmed), but whose exact manifestation is unknown." The assessment includes the organism's immediate physiological state and its evaluation of present and impending environmental conditions. The environment changes as do the requirements of the organism during its life cycle. The strategy concept recognizes that behavior is patterned but that organisms need to evaluate and reach decisions appropriate to changing circumstances.

In the human case, it is usually not appropriate to rely on rates of genetic change under natural selection to establish the temporal parameters of the evolution of a behavioral strategy. Instead the focus must be on the long-term accumulation and integration of experience by cultural means. Information passed from generation to generation by culture provides much of the strategic framework within which specific choices and options are exercised by individuals or groups of human foragers. Thus the emphasis in ethnographic studies of optimal foraging is on the long term relative to sociocultural processes rather than to genetic processes.

Besides the evolutionary time scale of the strategy approach, there is another appropriate time interval for assessing aspects of behavioral optimization. This is the duration of the relevant behavioral pattern, its interval of recurrence (or, more precisely, the duration of the behavior's immediate and postponed effect on fitness or some other goal). An optimization interval may be based on an obvious environmental quality such as seasonality. But evolutionary processes are sometimes bound up with less easily recognized intervals which arise from the interactions between environmental variability and the life history processes affected by selection. It is usually assumed in optimal foraging studies that short-term maximization of net energy intake while foraging is an acceptable approximation of an organism's long-term goal, one producing optimal results over the longer periods as well. But this need not be the case. Assessment intervals are always important unless foraging "behavior at one point in time does not alter the optimal (foraging) behavior at a later point in time" (Pyke, Pulliam, and Charnov 1977:139; see also Katz 1974:761).

Three situations in which short-term evaluation of foraging cannot be extrapolated in a simple manner to a longer time span are identifiable (Pyke, Pulliam, and Charnov 1977:139-40): (1) First are cases where a behavior commits the organism to a particular activity or location for an extended period. Unless the fitness or adaptation results are uniform from beginning to end, evaluation should encompass the whole period. Foraging effects following from the choice of a camp or settlement location are an example. (2) In the second class the present behavior of the organism alters the environmental conditions which will affect later foraging efforts. For example, if there is exclusive use of a resource, the organism may adopt foraging behaviors which avoid complete local harvest in favor of returning at some future time. (3) The third class encompasses environmental changes which are independent of the organism's activity and more or less unpredictable. The organism may mix foraging with exploration, although the latter does not contribute in an immediate sense to energy maximization. Exploration behavior may reduce the efficiency of foraging but provide the organism with information instrumental in later foraging efforts.

Each of these three cases involves a more general observation: optimal strategy analysis is an attempt to specify the effects of complex fitness- or goal-related behaviors relative to theoretically derived predictions. This makes it important, with respect to both the predictions and the observations, to attend to the time interval over which the immediate *and* delayed costs and benefits accrue to the organism considered. Identifying these intervals can be difficult, and requires that the investigator know the "natural history" of the population being studied and the long-term properties of its environment (Winterhalder 1980b).

The strategy concept, and the necessity of evaluating behaviors over an interval that accurately represents their aggregate effect on the organism, introduce an effectiveness component into analysis by requiring that optimal (efficient) behaviors be evaluated over a relatively long time interval. Highly efficient short-term behaviors may not be effective over the longer period in which organismal or habitat variability occurs. Conversely, an effective adaptation over some time span may not always be the most efficient (Slobodkin 1973). In adaptation studies it is generally necessary to balance assessment of efficiency and effectiveness (Vayda and McCay 1975:295-97).

Modeling

Behavioral phenomena combine multiple elements of ecology and population biology and genetics (Levins 1966:421). The problem is to simplify complex adaptive systems so that they retain essential and interesting (i.e., nontrivial) features, but at the same time become analytically tractable. Modeling has proven a useful solution. Levins (1966:422; cf. Schoener 1972:391) notes that ideally a model would simultaneously achieve generality, realism, and precision, but that this is rarely possible. Most types of modeling sacrifice one of the three qualities, with the choice depending on the nature and goals of the investigation. The models cited in this chapter emphasize realism and generality. They are expressed in differential calculus or graphical form, and functions are assumed to be linear, increasing or decreasing over some range--convex, concave, or the like--rather than having exact specifications. The resulting predictions are generally expressed as inequalities (Levins 1966:422-23) or in ordinal rather than cardinal rankings. The hypotheses are commonly comparative and qualitative.

The simplifying assumptions and constraints of all models make it possible that the results are an artifact of the procedure. Levins (1966:423) suggests a partial solution to this difficulty in characterizing models as "robust" or "nonrobust": "we attempt to treat the same problem with several alternative models each with different simplifications but with a common biological assumption. Then, if these models, despite their different assumptions, lead to similar results we have what we can call a robust theorem" (Levins

1966:423). Robustness is a quality of the modeling procedure, and hence somewhat independent of empirical confirmation or refutation of specific hypotheses. Most of the hypotheses outlined below come from models which are robust for biological applications. They may also be robust with respect to *some* aspects of human behavior, but testing will be necessary to establish that robusticity is correlated with empirical confirmation in both the nonhuman and the human cases.

A second important concept in modeling is that of "sufficient parameters" (Levins 1966: 427-30), abstractions of multiple, more detailed variables. For analysis it is necessary to generate sufficient parameters which (1) are reduced in number; (2) summarize most of the information at the level of concern; and (3) retain as much information from other, more detailed levels as possible. Examples of sufficient parameters in foraging analysis are resource qualities such as dispersion pattern or predictability, or adaptive criteria such as foraging efficiency or effectiveness. The utility of sufficient parameters lies in their condensation of information, but this also introduces imprecision and an inability to reconstitute lost information (Levins 1966:429).

In summary, there are three kinds of imprecision that enter into models emphasizing generality and realism: (1) They omit factors which have small effects or which have large effects but only in rare cases. (2) They are vague about the exact form of mathematical functions in order to stress qualitative properties. (3) The many-to-one property destroys information about lower levels (Levins 1966:429-30). The necessity to simplify, to stress qualitative properties, and to develop sufficient parameters gives foraging models a unique status. A model is not a theory or hypothesis, nor is it true or false. "The validation of a model is . . . that it generates good testable hypotheses relevant to important problems" (Levins 1966:430).

Confirmation of Hypotheses

A strength of optimal foraging theory lies in its attention to hypothesis testing. Consequently, it is important how one confirms or refutes an optimal behavior hypothesis and how one interprets the meaning of either outcome. I will take up the latter point after discussing specific models; here I discuss tests and their interpretation (see also Dyson-Hudson and Smith 1978).

Cody (1974:1156-57) outlines two ways of testing for optimal solutions to the problems of time and energy allocation in natural situations. The first is comparative, and most valuable in situations where it is difficult to isolate the active selective forces or likely outcomes in order to build a model. In this instance one defines and measures several variables of interest in one locality. These could be community traits (e.g., number of species occupying a certain trophic level) or behavioral attributes of a population (e.g., diet breadth). The measured variables are then compared with those of a second, environmentally similar situation or species with an independent evolutionary history, and "if we find extensive similarities or convergences we can infer that selection has reached optimal solutions in both fields [cases], despite differences in history, time scales, and genetic origins" (Cody 1974:1157). This approach is widely used in anthropology, e.g., in the comparative studies of "band societies" (Damas 1969c; Lee and DeVore 1968).

An alternative test is to compare the natural situation with predictions based on models designed to replicate certain important features of the natural system (Cody 1974: 1157). This approach has been less used in anthropology.

Many foraging strategy models are based on geometric representations of the relationships of foragers to resources, with solutions found by graphs or by differential calculus

(Cody 1974:1157). Graphs have the advantage of simplicity. As an example, MacArthur and Pianka (1966:604) note that the details necessary to construct exact curves in their diet breadth models are usually unknown, and would vary from case to case in any event. Nonetheless, graphing allows the derivation of interesting results in the form of comparative and qualitative predictions. In complex mathematical models, predictions can easily become sensitive to poorly understood parameters (Schoener 1971:376). The proper analytic balance between simple and less simple models is for the investigator to judge, but "ultimately, our ability to test relationships like these [predicted by optimal foraging models] would seem to depend on retaining the simplicity in such models when confronting the real system" (Werner and Hall 1974:1044).

It is important when using this approach to recall that the model and hypothesis represent an analytic compromise mediated by the technical and logical constraints of analyzing the multiple interacting variables. The conflicts generated by the necessity to simplify and generalize are irreconcilable, but it is important that they are about methods, not reality, and that models are meant to assist understanding, not to duplicate nature (Levins 1966:431).

Application of Optimal Foraging Models

Choice of a Currency

According to Schoener (1971:369): "The primary task of a theory of feeding strategies is to specify for a given animal that complex of behavior and morphology best suited to gather food energy in a particular environment." Schoener identifies a three-step procedure: (1) a currency must be chosen; (2) an appropriate cost-benefit function must be adopted; and (3) the function must be solved for an optimum.

The first problem is to decide what is to be maximized or minimized, i.e., the currency must be identified (Schoener 1971:369). In biological terms, the most fundamental evolutionary property of an organism is reproductive fitness. It is rarely feasible to measure this. In foraging studies it is usually assumed that fitness varies directly with the rate of net energy intake which can be achieved while foraging (Pyke, Pulliam, and Charnov 1977:138-39; Krebs and Cowie 1976:99), although a variety of factors (summarized by Schoener 1971:372) can intervene to influence this relationship. An increased rate of energy intake while foraging can enhance viability of the organism or its ability to produce and provision offspring, but indirect effects are also significant. The time and energy that an organism invests in foraging are generally unavailable for other activities, and foraging may expose it to predation or other hazards. Thus "the profit an animal acquires in feeding must be weighed against the loss of time, while feeding, to participate in activities such as search for mates or predator avoidance" (Schoener 1971:371; see also Pianka 1978:148-49; Krebs and Cowie 1976:99; and Pyke, Pulliam, and Charnov 1977:139).

The sociocultural goals which pervade human behavior do not diminish the importance of efficient and effective foraging behavior in the maintenance of viable populations. Energy efficiency, assessed by a net rate of acquisition during foraging, need not be strictly covariant with human adaptive success, however defined. But it does provide a useful, proximate measure of adaptive behavior with both empirical and theoretical importance, and broad applicability (see Smith 1979b).

There are several rationales for emphasizing an energy currency. First, the environment may be one with absolute energy limitations, on either a periodic or a constant basis. This is especially likely for the larger omnivores or carnivores, including humans. General biome productivities (e.g., Leith 1973), however, are a very crude measure of the energy circumstances affecting a particular population. Attention must focus on productivity available to the population, relative to its requirements. Availability includes such factors as the absolute amount of the resource, fluctuations in its abundance, its distribution, difficulties of harvesting it, and the role of intra- and interspecific competitors. The case for energy limitations can be advanced if historical evidence shows shortages directly. The converse, short-term studies indicating relative freedom of a group from energy shortages are not reliable evidence that selection pressures capable of influencing foraging behaviors do not or have not existed (Smith 1979b; cf. Vayda and McCay 1975).

Secondly, the relationship between energy and time on the one hand, and fitness or some other measure of goals, on the other, can be left hypothetical. This procedure invokes the scarcity postulate of evolutionary (Pianka 1978:12) and microeconomic theory (Robbins 1932). In this case the utility of that postulate in developing models is focal, and demonstration of absolute shortages is secondary.

Human behavioral flexibility expands the list of activities that compete with foraging for time and energy. Included are behaviors not normally associated with fitness in nonhuman organisms--the desire for leisure, status, social interaction, and accumulation of wealth. Humans must invest time and energy to maintain coherence and cross-generational continuity in their social and cultural systems, on which adaptive behavior depends. Additionally, there is the manufacture of essential technologies. These activities require time and energy, and thus contribute to the selective pressure for efficient foraging.

The operational reasons for using energy as a currency are also important. Persistent or at least periodic energy shortages are likely to have been significant for human populations throughout their history and in many different habitats. Adaptations producing efficient foraging should thus be a consistent aspect of hunter-gatherer behavior, and hence an important area for the comparative and historical investigation of human adaptation. This is not to assert the primacy of energy-related adaptations for all cases (Vayda and McCay 1975:295-97); rather it suggests that such adaptations will be, with fair regularity, important in many cases. Energy flow is common to the functions and structural attributes of diverse human groups and ecosystems, and provides a quantifiable variable around which each can be analyzed within the context of the other (Adams 1978:298).

Finally, there is analytic convenience. The energy currency is amenable to clear operational study and quantification; it is used frequently because it is a component of adaptation which can be isolated and reliably assessed. The factors contributing to the observed behavioral variability within and among human foraging populations are multiple and interact in complicated ways. A major operational merit of the energy currency is that it is possible to determine with some confidence to what extent optimization with respect to the energy efficiency of foraging is the operative influence on the formations of certain behaviors.

Energy is not the only significant aspect of food resources; nutritional qualities are important. In most ecological studies it is assumed that energy is the most important component of food (Schoener 1971:369), and the significance of nutritional factors has rarely been established (Pyke, Pulliam, and Charnov 1977:139). Pyke, Pulliam, and Charnov (1977: 138-39) conclude that the use of energy as the sole currency is justified for most of the studies they review, but there are cases where it is fairly clear that nutritional or other factors predominate, in avian species (Davies 1977:1026, 1032) and for humans (Harpending and Davis 1977:280; Keene 1980; Meehan 1977a; Montgomery 1978:64; Rappaport 1968). It is possible that carnivores will be less influenced by nutrient constraints than are herbivores, as the latter must cope with the complex allelopathic defenses of plants in addition to their lower nutritional quality.

Optimal foraging models exist which take nutrients to be the currency (Belovsky 1978; Keene 1979ab 1980; Pulliam 1975; Rapport 1971), and a goal of optimal foraging studies is to develop models capable of handling currencies more complicated than energy (Pyke, Pulliam, and Charnov 1977). For the present, given the paucity of foraging studies on humans, cautious use of an energy currency will be likely to produce extensive and fairly reliable, if ultimately incomplete, insights.

Cost-Benefit Functions: General

Schoener (1971:177-79; see also Krebs and Cowie 1976:100; Pyke, Pulliam, and Charnov 1977:139-41) divides foraging into four decision sets: optimal diet breadth; optimal foraging space; optimal feeding period; and optimal foraging group size. These categories separate questions about (1) which items the forager will consume from those available; (2) where in the spatial environment the forager will seek food resources; (3) the times when foraging will occur; and (4) the circumstances in which foragers will form groups for pursuit of food resources.

These decision sets and their arrangement in a hierarchy are for the convenience of the investigator (Krebs and Cowie 1976:100). The categories may or may not approximate those used by the organism as it assesses foraging decisions, although analysis using the separate categories is based on an *assumption* that the forager makes decisions as if the different sets are "approximately independent" (Pyke, Pulliam, and Charnov 1977:140). The investigator should remain sensitive to the fact that the choice of a decision set, or, if more than one is chosen, the arrangement of the sets in a hierarchy, and the design of a model commit him or her to analytic constraints which may or may not be appropriate. Such decisions must be justified with respect to the population and situation analyzed.

These analytic constraints are potential targets of criticism of optimal foraging models (Krebs and Cowie 1976:98). In anthropology the problem has been cogently identified by Sahlins (1976:82-83) in his criticism of "the fallacy of an a priori fitness course" in evolutionary (or sociobiological) analysis. Lewontin (1977:28-29) criticizes the unwarranted "*ceteris paribus*" assumption. Still, all behaviors are complex, and they are related to multiple aspects of the environment and to other behaviors of the organism. Constraints must be identified and their existence in analytic procedures accepted if evolutionary study is to proceed beyond description and broad statements about functions. It is difficult in any situation to decide what should be taken as constraint and what then analyzed as adaptation. The quality of the analysis depends on the thoroughness with which the researcher knows the population and the skill with which that knowledge is incorporated into the analysis. Constraints can be chosen which reduce the problem in particular cases, but "in general, there is no recipe for determining just what the currency and constraints should be in a particular situation, and it will always be the job of the naturalist to understand the biology of an animal sufficiently well to know which currency is being optimized" (Pyke, Pulliam, and Charnov 1977:138; see also Crook, Ellis, and Goss-Custard 1976:265-66). Anthropological analyses of particular sociocultural groups do not escape this difficulty, although research such as that reported in this volume should eventually provide some general guidelines.

In the description of foraging models that follows I have adopted Schoener's (1971) foraging decision categories, although models dealing with optimal feeding period will not be discussed.

Optimal Diet

Models of optimal diet are concerned with the forager's choice of food items and with the range or variety of items that are harvested in different environmental circumstances. Most foragers are faced with a broad array of potential resources, and most are selective to some degree. Models of optimal diet analyze that selectivity. They are designed to predict for a given organism and habitat the answers to questions such as these: What items will a forager prefer? Which will be passed up even when located? Will the diet breadth be broad or narrow? In what environmental circumstances will the diet breadth expand or contract? Which items will be added to or dropped from a changing diet? Before discussing a model that helps to answer these questions, I must introduce some terminology.

First, a forager can be a generalist or a specialist. An organism is a generalist if it consumes a relatively large range or diversity of food types; if it has a variety of feeding behaviors; or if it is capable of extracting energy from diverse food sources, as is an omnivore (Schoener 1971:384). Specialists can be defined by any of the inverse qualities.

A second set of terms relates to spatial characteristics of the environment and an organism's behavior. The definitions used here follow Pianka (1978:263) and Wiens (1976: 82-84). Environments that are heterogeneous, having a discontinuous distribution or mosaic of resources, are termed patchy. Conversely, environments containing well-mixed, similar, or evenly distributed resources are homogeneous or uniform. Patchiness can exist on any spatial scale and can be defined with respect to multiple environmental features. Consequently, a definition of patches must be relevant to the organism and the behavior being analyzed (Wiens 1976:83); although patches are delimited by the physical differences in the environment, they must also reflect the array of resources and hazards influencing the organism and its evolution.

An important descriptive feature of patchiness is grain. Grain is a relative measure. It is determined either by comparing environments or by assessing the behavior of an organism or population in an environment. Organisms that structure daily activities so as to encounter and exploit different patches in the actual proportion in which they occur use the environment in a *fine-grained* manner. Conversely, organisms that make disproportionate use of certain components of heterogeneous environments employ space in a *coarse-grained* manner. These definitions refer to the extremes of a continuum of possible behaviors. Coarse- or fine-grained use may result because the scale of the relevant environmental features is very large or very small relative to the size and mobility of the organism. Thus patches such as a meadow and adjacent woodlot have a large grain size relative to a mouse but a small grain size relative to a human. Whereas fine- or coarse-grained behavior is based on functional aspects of an organism's behavior in an environment, small or large grain size expresses a structural relationship between the organism and its environment (see Wiens 1976:85).

The diet breadth model examined here was developed by MacArthur and Pianka (1966; MacArthur 1972:61; Pianka 1978:263-66) for an environment that is fine grained with respect to the organism's foraging movements. A random search by the organism would encounter the resources in the actual proportion in which they occur. Although the organism searches in a fine-grained manner, it selects only certain prey to pursue and exploit, and therefore harvests the environment in a coarse-grained manner (Pianka 1978:264). From an array of fine-grained encounters the diet breadth model is designed to determine the selectivity of resource use practiced by an optimal forager. The model also assumes that organisms consistently do or do not take a certain resource type.

The foraging effort is divided into two phases: time spent searching (T_s); and time spent pursuing, capturing, and eating the prey (T_p). The functional difference is that all items are searched for simultaneously but are pursued singly. When an item is encountered the forager must decide whether to pursue it or to continue searching for more desirable prey. If a forager has *n* resource items in its diet, we can ask in what circumstances it should enlarge, or possibly reduce, the diet by one type. If prey are ranked by net rate of energy return from those with the highest to those with the lowest, the rule is that prey types should be added until the additional pursuit time necessary for including the next type is greater than the savings in search time.[1] At this point including an additional resource type produces a net increase in the cost per unit of resource intake.

The graphical form of this model is given in figure 2.1. Prey are ranked on the abscissa from highest to lowest yield per unit of time or energy cost. ΔS measures the *change* in search time per unit of harvest as the diet is enlarged, stepwise, to include a greater number of the resource types encountered. As more of the encountered items are pursued, the average time to find an acceptable item decreases. On the other hand, as less desirable or harder to catch items are added, the costs of pursuit increase. Thus the average pursuit time (ΔP) grows as the diet breadth enlarges. The organism benefits--in terms of net energy intake relative to time or energy investment in foraging--by expanding or contracting its diet breadth to that represented by the intersection of the ΔS and ΔP curves.

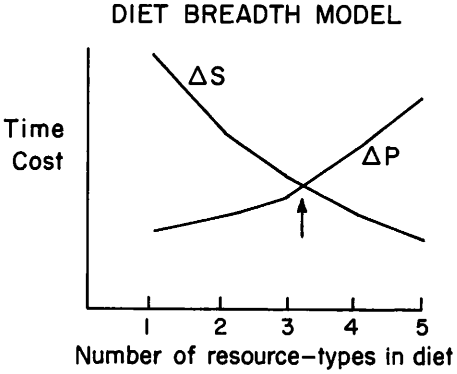

Figure 2.1. MacArthur and Pianka Optimal Diet Breadth Model. The ΔS curve plots decreasing average search costs, and the ΔP curve increasing average pursuit costs, as an increasing number of resource types are added to the diet. Cost here is expressed in terms of time, though it could be in terms of energy. Resources are ranked by their value to the organism in terms of the currency, or cost-benefit measure, adopted. The optimal diet breadth occurs at the intersection of the two curves. After MacArthur and Pianka 1966.

The predictions derived from this model are based on the positions and slopes of the ΔS and ΔP curves, or changes in these over time. A variety of influences on the forager's behavior can be conceived of as affecting or acting through these components of the model. For instance, if the encounter rate with items that are fairly easily pursued is low, the

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[1] In their original model MacArthur and Pianka (1966) ranked prey types by numbers harvested per unit time. Schoener (1971:308) subsequently pointed out that this ranking implicitly assumes prey types are of equal value, and that the model does not guarantee an optimal solution if this condition is violated. The problem can be obviated if prey types are ranked by net energy gained per unit of pursuit time. Later formulations of the model (Pianka 1978:263-66; MacArthur 1972:61-62) point out that time and energy are interchangeable as measures of cost, and they measure returns in harvest or yield rather than numbers of prey.

search curve (ΔS) will be high relative to the pursuit curve (ΔP), and the organism should consume many of the prey types encountered. On the other hand, when encounter rates are high (the ΔS curve is low), the forager should be selective and pursue only the highly ranked prey. An optimal forager is selective in a rich environment; less discriminating in a poor one.

Changes in the environment, or in forager or prey behavior, can be reflected in the model's predictions. This is done by manipulating the curves to mimic the relevant factors. If, for instance, prey density increases, search time should decrease, shifting the ΔS curve downward and narrowing diet breadth. The ΔP curve remains stationary; pursuit time is not affected by prey density. The same change in the ΔS curve would occur if the forager became more efficient at searching. Converse circumstances would lead to an increase in diet breadth. This model also indicates that prey items should be added to or dropped from the diet sequentially and in the order of their ranking. Items taken by an optimal forager when the diet is narrow will continue to be taken as it enlarges; conversely, diet breadth will always decrease by a stepwise restriction to highly ranked items which were included in the more generalized diet.

In the results derived so far, we have assumed changes in prey species abundance to be proportionate for all resources. The environment became richer or poorer overall. But variation in the density of a single resource species will produce different effects depending on how the species is ranked. If the resource is highly ranked (within the existing diet breadth), an increase or decrease in its density should cause the diet breadth to contract or expand, respectively. If, however, it is ranked low, outside of the diet breadth, fluctuations in its abundance will have no effect on the optimal forager's diet. In terms of the model (figure 2.1), what happens to the ΔS curve to the right of its intersection with ΔP is irrelevant. In fact, "whether or not a food type should be eaten is independent of the absolute abundance of that type and depends only on the absolute abundances of food types of higher rank" (Pyke, Pulliam, and Charnov 1977:141).

The predictions about forager behavior which can be derived from the diet breadth model may be listed as hypotheses:

A. An optimal forager with a high search-cost/pursuit-cost ratio will tend toward a generalized diet breadth. Conversely, a forager with a high pursuit-cost/search-cost ratio will tend toward diet breadth specialization.

B. Any factor which causes an increase in the search costs of an optimal forager will produce a stepwise enlargement of its diet breadth. Conversely, a factor decreasing search costs will lead to a restriction of diet breadth.

C. Any factor reducing pursuit costs of the optimal forager will produce an enlargement of its diet breadth. Conversely, a factor increasing pursuit costs of a forager will produce diet breadth specialization.

D. An optimal forager highly specialized for searching, pursuit, or both will be relatively insensitive to factors affecting diet breadth. Conversely, organisms generalized for search, pursuit, or both will evidence fairly large changes of diet breadth in response to changes in search or pursuit costs.

E. The diet breadth of the optimal forager will be affected only by changes in the abundance of highly ranked resource items. In particular, if the absolute abundance of highly ranked resources is unchanged, the diet breadth of an optimal forager will not respond to an increase in the density of a resource which is ranked outside of its extant diet breadth.

Pyke, Pulliam, and Charnov (1977:141) note that similar results have been derived more or less independently at least nine times; they are therefore fairly robust. Reviews of field and laboratory analyses of foraging behavior using these hypotheses can be found in Krebs and Cowie (1976); Krebs (1977); Pyke, Pulliam, and Charnov (1977); and Davies (1977). Winterhalder (1977 n.d.b) applied this model in a detailed analysis of Cree foraging behavior and found a fairly strong confirmation of its hypotheses.

Optimal Foraging Space

Optimal foraging space models examine the spatial characteristics of an organism's foraging relative to particular resource distributions (Schoener 1971:386). Some models also consider the spatial aspects of inter- and intraspecific interactions stemming from resource use. Specific questions include home range size (Clutton-Brock and Harvey 1978b: 192; Hamilton and Watt 1970; McNab 1963); whether a forager should or should not be territorial (Brown 1964; Hamilton and Watt 1970; Verner 1977); selection of foraging areas in a heterogeneous environment (MacArthur and Pianka 1966; Pianka 1978:265-66); and selection of a foraging pathway (Charnov 1976a; Charnov, Orians, and Hyatt 1976).

If prey are motile two extreme types of strategy can be identified: "sit and wait" and "widely foraging" (Pianka 1978:260-62). The former is expected when prey are dense and highly mobile, and the predator has a low resting energy requirement. In contrast, the widely foraging strategy is appropriate for an organism with a high resting metabolic requirement (including the energy requirements of nonforaging dependents), or one which depends on sedentary and low-density prey. Foraging space models indicate that territories (defended areas) should arise for individual foragers only when resources are of intermediate density and sufficient stability that the organism can acquire a net energy gain from exclusive use (Brown 1964; Hamilton and Watt 1970). Both ethnographic (Dyson-Hudson and Smith 1978) and primate (Clutton-Brock and Harvey 1977:16) studies provide evidence in support of this model. The models discussed below address two questions: choice of feeding areas in a patchy habitat, and choice of an optimal foraging pathway.

Many environments are characterized by a discontinuous, coarse-grained array of the resources or factors that affect the forager, and organisms should have behavioral patterns which reflect the heterogeneity of environmental conditions that facilitate or impede their essential activities. A model proposed by MacArthur and Pianka (1966) specifies the number of patch types that an optimal forager would include in its foraging itinerary (see figure 2.2). This model assumes that the environment is coarse grained, that patch types have different resource qualities, and that the mosaic is of a scale which affects the organism. The forager searches for the patch types in a fine-grained manner, but searches for and pursues prey only within certain patch types. Thus exploitation of patch types is coarse grained.

Patch types are ranked on the abscissa from the most to the least productive, measured by decreasing "expectation of yield" relative to time or calorie costs (Pianka 1978:265-66). Again, foraging is divided into two phases. Hunting time (or energy) within a patch type represents both search time and pursuit time (or energy) as defined in the model in figure 2.1 (Pianka 1978:265). Average hunting time (ΔH) increases with the number of patch types included in the foraging itinerary because progressively less suitable patch types are harvested. ΔT represents the time spent traveling between or searching for acceptable patches. ΔT is a decreasing function of the number of patch types the organism includes in its foraging itinerary out of those that it must traverse.

This model predicts that the optimal forager will expand the number of patch types

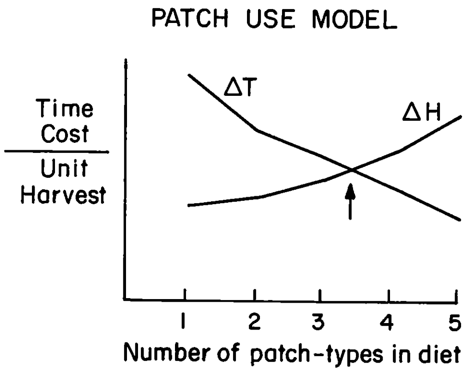

Figure 2.2. MacArthur and Pianka Optimal Patch Choice Model. The *ΔT* curve measures decreasing average between-patch travel time, and the *ΔH* curve increasing average within-patch foraging time (both per unit of resource taken), as an increasing number of patch types are added to the foraging itinerary. Cost here is expressed in terms of time, though a measure of energy could be used. Patch types are ranked by their value to the organism in terms of the currency, or cost-benefit measure, adopted. The optimal set of patch types for the forager to harvest is indicated by the arrow. After MacArthur and Pianka 1966.

included in its foraging itinerary until the increase in the average hunting time or energy (per unit yield) within the next patch type is greater than the average decrease in travel time or energy (per unit yield) between patches achieved by adding that next patch type. In graphical terms (figure 2.2) the optimal diet includes all patch types up to the intersection of the *ΔT* and *ΔH* curves.

This model is not fully analogous to that for diet breadth. We cannot substitute patch types, which may be relatively stationary, for motile resource items, because the forager can learn the location of favorable patch types in its range and adjust its "search" pathway accordingly (Pyke, Pulliam, and Charnov 1977:144). The nonrandom search path among patches implied by such learning is a violation of the fine-grained search assumption of the model. If favorable patch locations are known, the forager can reduce its average travel costs by avoiding encounters with unfavorable patches. Thus the outcome of knowing the location of high-ranked patch types is a greater specialization of patch type use.

The hypotheses that can be derived from the patch use model are more complicated than those in the diet breadth case. A uniform increase of resource density lowers both *ΔT* and *ΔH* curves, making predictions about changes in optimal patch use difficult. *ΔH* is lowered because the search within a patch becomes easier; *ΔT* is lowered because patches included in the foraging itinerary will be productive for a longer period of time, reducing the amount of travel between patches. Organisms which are pursuers (have a large pursuit-time/search-time ratio) should be relatively more affected by the decrease in travel time than by the decrease of hunting time within a patch. (Within the patch the greatest portion of their time is spent in pursuit.) Consequently, they are more likely than searchers to specialize with respect to patch types as food density increases (MacArthur and Pianka 1966:606; Pianka 1978:266). Increased mobility of the forager has the same effect as increasing the density of prey, and would thus generate the same prediction.

The relative size of patches (grain size) is also important in this model. If two environments are similar in the proportion (by area) and quality of their patch types, but differ in the size of patches, the model predicts that a forager will use the environment with the larger patches in a more specialized way. The reasoning behind this is explained by Pianka (1978:266).

Charnov (1976a; see also Charnov, Orians, and Hyatt 1976; Parker and Stuart 1976) has formulated a model predicting how an optimal forager will move in a patchy habitat. While the MacArthur and Pianka (1966) model cited above specifies which patch types an optimal forager will include in its diet, Charnov's "marginal value theorem" predicts when a forager should leave the patch that it is in. The theorem thus helps to determine the optimal forager's pattern and rate of movement among the patches being harvested.

This model is based on the observation that the activities of a forager often reduce the numbers or capturability of prey in its immediate vicinity. Charnov, Orians, and Hyatt (1976:247-48) call this "depression." It can occur in three ways. "Exploitation depression" results from the depletion, by harvesting, of the resources at a site. If easily discovered resources are taken first, then concurrent with diminishing abundance the forager must obtain its harvest from a residue of items that are increasingly difficult to locate or capture. "Behavioral depression" results from the increased wariness of prey which become aware of the forager's presence. "Microhabitat depression" results when alerted prey move to habitats where they are less conspicuous, or otherwise more protected. This kind of movement is expected to result from the coevolution of the forager and the prey. In each of these cases the marginal value theorem is applicable.

Charnov (1976a) begins with these assumptions: Food is encountered by the forager within patches. The forager must also travel between acceptable patches. Within a patch the forager "depresses" the rate of food intake as it forages; the quantity of food harvested rises over time to an asymptote, at which point the patch is exhausted and the rate of intake zero. Patch types are distributed randomly in the habitat, and the forager has a low probability of return in short time intervals to any one. Finally, the forager behaves so that its net rate of energy intake while foraging is maximized.

With these assumptions Charnov (1976a:131-33) derives the following theorem: "The predator should leave the patch it is presently in when the *marginal capture rate in the patch . . . drops to the average capture rate for the habitat*" (italics in original). This result is depicted graphically in figure 2.3. The average capture rate is represented by a straight line, with positive slope. The net energy intake for each of two patch types (A and B) is also shown. These curves represent assimilated energy less the costs of search, pursuit, and capture. The x-coordinates of the points of tangency of lines parallel to the average capture rate (T_A and T_B) represent the optimal time to spend in each patch. If the organism remains beyond these times, its net rate of energy intake drops below the habitat average or what it could expect if it moved on. Thus an optimal forager abandons patches before they cease to be productive, and abandons them sooner the higher the overall quality of the environment. An optimal forager also leaves in its trail a series of patches of uniform quality (Krebs and Cowie 1976:102).

The marginal value theorem highlights the knowledge that a forager must have in order to forage optimally. To assess the point at which to leave a patch the organism must "know" how well it is doing in that location (i.e., the shape of the depression function) and on average how well it could expect to do in surrounding patches (Charnov, Orians, and Hyatt 1976). This implies that considerable information about the environment is stored by the organism. The advantage of familiarity with habitat patchiness is one reason to expect a violation of the fine-grained search assumption of the MacArthur and Pianka patch use model (figure 2.2).

Resource depression, and the microgeographic experience required to adjust to it, raise the question of the exclusive use of foraging space. The interval between depression of a patch and the time when it can again be profitably foraged is called "return time"

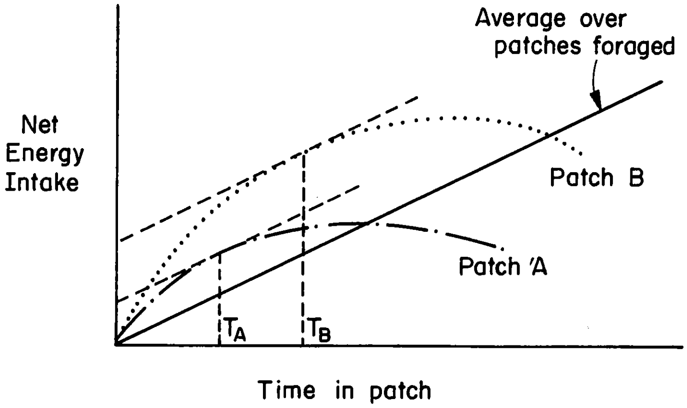

Figure 2.3. Charnov Marginal Value Theorem. Net energy intake within a patch for two patch types is shown as a function of time (curves *A* and *B*). Energy intake within a patch grows at a decreasing rate as the forager depresses the resource availability for that location. The straight line from the origin represents the average capture rate assessed over the full set of patch types included in the foraging itinerary. The optimum time to spend within a patch type is found by constructing the highest tangent to the patch depression curve that is parallel to the line representing the average capture rate for the patch types visited. In this case the optimum times to spend in patch types *A* and *B* are represented on the x-axis by T_A and T_B, respectively. After Charnov 1976a.

(Charnov, Orians, and Hyatt 1976:256). A forager must in some sense "know" an area in order to adjust its return times to patch recovery and hence optimal use, giving an advantage to foragers maintaining home ranges or territories (Steward 1977:53). Charnov, Orians, and Hyatt (1976:256-57) suggest that this kind of reasoning may help account for "passive" territoriality. In addition, the forager remaining in a certain range can become familiar with locations which provide shelter, escape, or other microgeographic advantages (Orians 1971:531). It is important that humans can, if they wish, share information with immigrants. Thus people can shift around over the landscape without suffering a shortage of the information needed to forage optimally, so long as at least one person maintains continuity of knowledge about an area.

In summary, the MacArthur and Pianka model specifies how an optimal forager chooses which patches to harvest from the larger habitat mosaic; the marginal value theorem model specifies the way in which an optimal forager moves among those patches. The hypotheses which can be derived from these models are as follows:

A. An optimal forager with a high pursuit-cost/search-cost ratio will react to an increase in resource density by a stepwise decrease in the number of patch types included in the foraging itinerary.

B. An optimal forager in a habitat with small-grained patch types will tend toward generalized use of available patch types. Conversely, a forager in a large-grained habitat should tend toward specialized use of patch types.

C. An optimal forager will abandon a locality or patch before its resources are depleted, and specifically will abandon it at the point that the marginal return in that patch is equal to the average return from the set of patch types being foraged.

D. The optimal forager leaves behind it a foraging pathway of patches of uniform resource quality.

E. An increase in resource densities will reduce the amount of time that an optimal forager spends in a given patch, i.e., will increase its rate of movement among the set of patch types being foraged.

Experimental or field studies on optimal foraging responses to patchy environments are summarized in Pyke, Pulliam, and Charnov (1977); Krebs and Cowie (1976); and Cowie (1977). Winterhalder (1977 n.d.b) found that the constraints incorporated in the patch use model are not always appropriate in the context of Cree foraging; the same analysis produced indirect and qualitative support for hypotheses derived from the marginal value theorem.

Group Formation and Optimal Foraging

Much recent work in evolutionary ecology attempts to isolate ecological factors which affect individuals through the context of their group membership and which can be incorporated into models predicting group size and structure. Initially three hypotheses are pertinent: (1) group formation may hinder individual foraging but has other, compensatory effects; (2) groups form in response to concentration of food without an effect on the efficiency or effectiveness of individual foragers; and (3) aggregation increases the efficiency or effectiveness of individual foragers (Schoener 1971:392).

The third hypothesis is the most interesting in the present context. Smith (1980), for instance, has gathered extensive field data showing that Inuit hunting group size is adjusted so as to maximize the net energy return per individual for a variety of hunt types. There are a number of ways that group foraging could be of advantage to individual foragers (Orians 1971:538-41; Schoener 1971:393-96). Clumped foragers may increase the effective density of prey by flushing, or groups of foragers may be able to take larger prey by cooperative search or pursuit. A third advantage of group foraging may lie in an increased ability to defend an area for exclusive use (Hamilton and Watt 1970; Schoener 1971:394).

A fourth advantage of group foraging is the prevention of foraging overlap. If a population of foragers in a certain area moves through it as a group they will more likely encounter, or be able to adjust their routes to encounter, areas not already searched by individuals and discovered to be empty, or areas already harvested and to some extent depleted. Individuals foraging alone (and not in territories) will always encounter a habitat with resources fairly uniformly depleted by other individuals foraging singly (uniform depletion is predicted by the marginal value theorem). Thus individuals foraging in groups should in some circumstances be more efficient because groups are more effective at locating undepleted resource areas (Cody 1974:1162-64).

A fifth potential advantage of group foraging is the ability to monitor a large area for prey and to exchange information at a central place. This situation is most likely when the resources are heterogeneously and erratically distributed, but abundant relative to the requirements of the group being considered (Schoener 1971:395-96; Clutton-Brock and Harvey 1977:15).

In the cases cited the benefits of group formation accrue to foragers that obtain and consume their own food. By contrast, in hunter-gatherers and some social carnivores (Thompson 1975), there is often a widespread sharing of foodstuffs and a division of foraging labor, mediated by cultural systems of reciprocity in the case of humans (Sahlins 1972). The effects of such differences in behavior on the use of these models are difficult to specify outside of particular cases. I simply point out that certain features of human behavior could constitute a problem vis-à-vis the human application of some models.

The model of group formation that I will discuss (see figure 2.4) is adopted from

Horn (1968; see also Orians 1971:532-36). It varies the distribution and predictability of food resources relative to the dispersion of the foraging population in four cases. The geometric distance from the forager to a food source, weighted by the probability of finding food at a particular point, is established for each case. The optimal pattern of forager dispersion is the one which requires the individual organisms to travel the smallest distance to locate food successfully. The actual or potential resource points, the number of foraging organisms, and the quantity of food resources are the same in all cases.

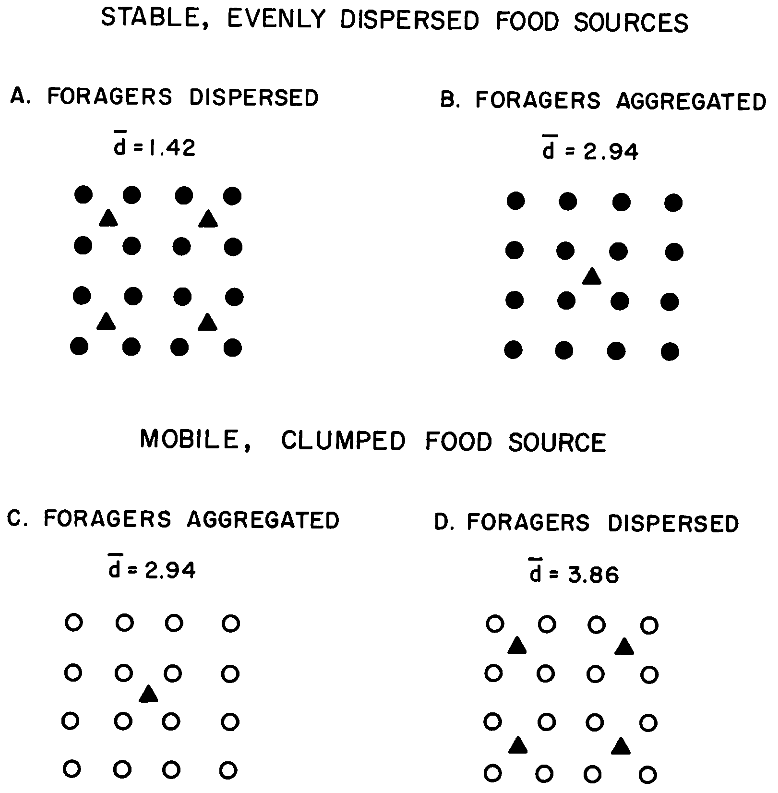

Figure 2.4. Horn Model for Optimal Forager Group Size and Dispersion. Triangles represent foraging group locations; solid circles the locations of dispersed, stable resources; and open circles the transient locations of clumped, mobile resources. The mean round-trip distance from forager to resource points weighted by the probability of successfully locating food is given by $\bar{d}$. After Horn 1968.

If food resources are evenly distributed and stable, optimal foragers will then tend toward regular dispersion of individuals or small social units (figure 2.4A; $\bar{d}$ = 1.42), rather than toward aggregation at a central point (figure 2.4B; $\bar{d}$ = 2.94). Conversely, if resources are mobile and unevenly distributed or clumped (i.e., concentrated transiently at only one of the resource points and moving unpredictably among all of them), the optimal strategy is aggregation of the foraging population at a central location (figure 2.4C; $\bar{d}$ = 2.94), rather than toward dispersion (figure 2.4D; $\bar{d}$ = 3.86).

The mathematical interpretation of this model assumes that no information is exchanged among the foragers. Horn (1968:690) notes, however, that if the distribution of resources is aggregated and their location unpredictable, then the exchange of information at a central location gives an added advantage to the aggregation of foragers. The human ability to communicate about situations displaced in space and time thus favors aggregation in this case. The situation producing dispersion of individual foraging organisms or units is also that which favors the evolution of territorial behavior (Orians 1971:533-35). Foraging from a central place, or refuging, is the subject of a number of interesting models (Hamilton and Watt 1970; Morrison 1978; Orians and Pearson 1979). Wilmsen (1973:6-10; Heffley, chapter 6, below) has considered the anthropological application of this model in detail; its hypotheses are the following:

A. Optimal foragers living in an environment with evenly distributed and stable resources will tend toward regular dispersion of the smallest viable social units.

B. Optimal foragers living in an environment with resources which are clumped and unpredictably located (mobile) will tend toward aggregation of social units at a central place.

Interpreting Confirmation and Refutation

The foraging models outlined provide fairly realistic hypotheses about the characteristics of foraging, given optimization assumptions. The predictions about forager behavior in different environmental circumstances are based on a limited number of sufficient parameters, and to a large extent the success of the technique hinges on the nature of these parameters. They are amenable to quantitative research, and are also general enough to serve as vehicles for a variety of specific effects that could be important in the development of foraging behaviors. Thus search and pursuit times can be observed and measured, and they can carry into the model consideration of factors as diverse as changing prey densities or improvements in forager technology.

In this section I want to outline the possible interpretations that can accompany the confirmation or refutation of an optimal foraging hypothesis. The discussion assumes that the relevant parameters have been estimated or measured, including information on the microgeography or patchiness of the forager's habitat; on prey densities and population qualities such as distribution and fluctuations; and on the time and energy costs and energy returns of different aspects of foraging behavior. The actual foraging patterns of the organism should also be known, and the analysis should cover a suitable time interval. Not all studies will or can meet these conditions, but they should receive attention, since a strength of optimal foraging theory is its operational assessment of alternative hypotheses. The approach generates an agenda of information necessary for ecological analysis of complex behaviors; often the requisite data only partially overlap with those usually collected in human ecology studies.

It is initially necessary to decide what constitutes an acceptable "fit" between predictions and observation. This is largely a matter of judgment. Rarely will fit be exact, nor should it be. The models consider evolutionary tendencies or trends; they isolate single-goal behaviors from the larger arena of behavior; they analyze portions of those goals (represented by certain cost-benefit functions which are possibly interacting or hierarchical); and they abstract from the complex, fluctuating environmental situation wherein the organism is subject to competing goals and constraints. The logical limitations of the approach and the necessity to abstract from a complex situation are matched by the difficulties of gathering exhaustive and accurate field data. Nonetheless, to avoid vitiating the heuristic strengths of optimal foraging theory, it is necessary to demand a fairly close fit when testing a hypothesis. It is essential to maintain a balanced commitment to the situation and to ideas about how it can be described and analyzed, and to preserve regard for complex and sometimes recalcitrant data in the fact of a simple but comprehensive and compelling theory. This can be accomplished in evolutionary studies only by a continual reluctance to be comfortable with a fit that is close or suggestive (see also Schoener 1972:389-90).

On the other hand, confirmation of the fit between a prediction and observation is not in itself a fully reliable test of a hypothesis, unless the prediction is unique (not possibly generated by other models, currencies, or factors). This is rarely the case. Confirmation cannot prove that the factors identified in the model are the causative ones in the formation of the behavior because it does not exclude all alternative hypotheses (Charnov 1976b:149-50; Krebs and Cowie 1976:112). The methodology of optimal foraging research and its operational specificity, however, allow one to search for ways by which apparently complementary hypotheses can be distinguished (Krebs 1977; Verner 1977). This provides a way of evaluating the relative contributions of differing factors or processes to the evolution of observed behaviors.

A failure to confirm an optimal foraging hypothesis can initiate a series of procedures which themselves provoke insights. The model or its sufficient parameters may fail to capture essential elements of the situation. The constraints affecting the immediate behavioral capabilities of the organism and its evolutionary history, or the effective features of its environment, may be inadequately recognized. Adjustments designed to achieve a better fit must be done with a careful interplay of the theory and the data. There is a temptation to correct deficiencies of a model in ways (e.g., by incorporating additional variables) that make its predictions less specific and therefore less amenable to refutation, whatever their improved accuracy (Lewontin 1979a).

It is also possible that the environment in which the assessment is made is not similar to the one in which the behaviors evolved. In effect the test conditions may not be appropriate (Krebs and Cowie 1976:113). An organism's environment and the qualities of its food resources are continually changing, so that the extant situation is never precisely that in which selection acted to produce existing behaviors (Orians 1971:516). Deciding what constitutes or has constituted the natural or significant habitat of an organism is a difficult task (Krebs and Cowie 1976:113; Winterhalder 1980b). This problem can be avoided to some extent by choosing appropriate time intervals for assessing foraging behaviors and their evolution, a procedure greatly assisted in the human case by historical records.

Another possibility is that the wrong optimization goal or currency has been chosen. The nutrient or some other, perhaps social, value of food resources may be more important than calories in certain cases. When the assumed selective influence is stated through a simple, operational model that yields hypotheses amenable to refutation, it is possible to demonstrate that one selective influence (e.g., energy capture) is of less importance than another. Belovsky (1978) and Caraco and Wolf (1975) provide excellent examples of this point. The predictions of the models with certain assumptions will not always be correct, but if carefully evaluated even incorrect predictions can usually prove informative, and assist in disentangling the multiple interacting factors affecting human behavior.

Use of this approach in data collection and interpretation, then, results in a test of the assumptions and constraints contained in the model and the procedure used to evaluate specific hypotheses. Such tests can be informative about the evolution and function of behavior, but do not confirm the general proposition that nature optimizes or that behavior is adapted (Maynard Smith 1978).

Conclusion

There is considerable disagreement in anthropology about the best sources of information for gaining insight into the hunting and gathering adaptation of prehistoric hominids. Hall (1977) and Thompson (1975), and earlier Schaller and Lowther (1969), have emphasized the usefulness of analogies with social carnivores, while Washburn and DeVore (1961), Reynolds (1966 1968), and Teleki (1975) have focused on various primate species, especially baboons and chimpanzees. A generalized ecological approach, based on vertebrate ecology, was suggested by Bartholomew and Birdsell (1953). Ethnographic information has always been used more or less explicitly in the formulation of conceptual models about early hominid lifeways (Martin 1974; Ember 1978). And, increasingly, systematic observations of extant hunter-gatherers are being used to develop concepts and data that will assist archeologists in the interpretation of prehistoric remains (R. A. Gould 1978; Jochim 1976; Yellen 1976). There is little way of deciding a priori which information source provides the greater or more accurate insights. It is certainly not clear that contemporary hunter-gatherers should be our preferred or exclusive models. Extant populations of foragers exist only in certain habitats, and their lifeways have been altered by contact with agricultural and industrial peoples. Aside from the difficulty of representativeness, there is simply little good information on contemporary hunter-gatherers.

The usefulness of diverse information sources is not always recognized, perhaps because an encompassing framework for ecological and evolutionary analysis has not been developed in anthropology. Washburn (1976:xv-xvi) insists on the uniqueness of human foraging with the claim that it is unlike that of any other social carnivore or primate. At one level this is undeniable. However, little is gained by emphasizing uniqueness at the expense of valuable sources of theory and information which arise in comparative studies of ecological adaptation. With respect to foraging behaviors, where similar conditions of resources pertain, all species, including humans, face the common problem of their efficient and effective harvest. The research approach developed here does not claim behavioral similarity of different foragers, but it does assert comparability with respect to the ecological factors affecting their behavioral variability. In place of assertions that hominids behaved *as if* they were baboons, or social carnivores, or !Kung San, we need an evolutionary framework which can (1) relate behavioral patterns to environmental properties through realistic models; and (2) encompass the diverse and individually only partially satisfactory information sources available to anthropologists interested in elaborating and refining understanding of hominid adaptive behavior.

Evolutionary ecology will not resolve the differences among these information sources; it does provide a framework of sufficient breadth and cohesiveness to pursue their systematic study. Useful results will probably emerge through the eclectic use of families or clusters of interrelated models, where each model is simple, analytically tractable, and addressed to a specific and fairly limited topic, and where as many as possible are robust or achieve robusticity through their overlapping relationships with one another (Levins 1966:430-31; Schoener 1972:391).

Optimal foraging theory is rich in the need for empirical confirmation. The analytic choices open to the investigator are many, indicating both the operational breadth of the approach and a present shortage of suitable information about human foraging. The investigator can choose among different currencies, different cost-benefit functions, different (perhaps hierarchical) combinations of those functions, or short- or long-term optimization approaches. Each choice will reflect initial impressions about important selective factors or adaptive goals, the significant environmental features or qualities of the forager, the differential importance of various kinds of foraging behaviors or kinds of behavioral optimization, and the temporal qualities of the behaviors and their development. It may become possible to identify a particular currency that accounts for a major portion of the behavioral diversity in most cases, or to conclude that some models are more commonly applicable or reliable than others, or to isolate the conditions under which short-term models are sufficiently accurate for analytic purposes. Advances such as these, with the insights they imply, will come primarily from ethnographic and archeological research using the perspective discussed here.

3

The Application of Optimal Foraging Theory to the Analysis of Hunter-Gatherer Group Size

Eric Alden Smith

The size and composition of social groupings among human hunter-gatherers, and in particular the ecological determinants of group size and structure, have been topics of theoretical interest in anthropology for quite a number of years (Steward 1936; Birdsell 1968; Yellen and Harpending 1972; Damas 1969c; Wobst 1974). This chapter presents the general approach developed by evolutionary ecology (Emlen 1973; Pianka 1978) to explain group size, emphasizing the models and ideas falling under the rubric of optimal foraging theory (Pyke, Pulliam, and Charnov 1977; Schoener 1971). In addition, comparable as well as contrasting positions taken by anthropologists are surveyed. Finally, in order to demonstrate more clearly what the application of evolutionary-ecological theory to an anthropological problem might entail, one simple hypothesis on foraging group size is derived and subjected to empirical test with data drawn from recent fieldwork on Inuit (Canadian Eskimo) hunting strategies.

The Evolutionary Ecology of Group Size

The evolutionary-ecological theory of social groups begins with the assumption that groups are expected to form only when group membership is on the average associated with greater reproductive success for each individual group member than is solitary living (Brown 1975:72ff., 134ff.; Alexander 1974:328). Evolutionary ecology so far recognizes four major forces leading to the formation of groups: (1) foraging strategies; (2) reproductive strategies; (3) predator avoidance; and (4) certain types of competition. Changes in any or all of these selective categories can affect the costs and benefits of various forms of social organization. Although I will be stressing foraging strategies, I want to emphasize that we can expect several factors to interact in any specific case. Thus, the different categories of selective forces may select for different types of group structure in the same population; for example, foraging considerations might favor solitary living, reproductive advantages might be associated with small groups of kin, and predator pressures might select

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