

Anthropological Applications of Optimal Foraging Theory: A Critical Review¹

by Eric Alden Smith

HUMANS HAVE SPENT the bulk of their evolutionary history in foraging economies. In appreciation of this fact, anthropologists have endeavored to establish the general rules that apply to this mode of economic organization in the hope of explaining observed differences and similarities in hunter-gatherer societies and of accounting for both the persistence and the eventual transformation of this once universal way of life. A promising source of insight into these matters is available in the models of optimal foraging theory developed by evolutionary ecologists.

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THE CONTEXT

Anthropological interest in preagricultural economies dates back at least to such 19th-century social evolutionists as Tylor, Morgan, and Engels. Although this interest in reconstructing the early "stages" of cultural development was stifled by the anthropological reaction against grand evolutionary schemes early in this century, the seminal work of Steward (1936, 1938, 1955, 1977) on hunter-gatherer subsistence and social organization chartered a new approach to foraging societies—an approach based largely on ecological concepts of adaptation.

Following Steward's lead, ecological research on hunter-gatherer societies has grown tremendously in the last few decades, and a large corpus of both ethnographic and archaeological studies in this tradition has accumulated (important collections and reviews include Lee and DeVore 1968, 1976; Bicchieri 1972; Damas 1969a; Cox 1973; Netting 1977; Bettinger 1980; Hayden 1981; Williams and Hunn 1981). While this research exhibits growing methodological sophistication and empirical rigor, the accumulation of ever more detailed case studies of hunter-gatherer subsistence systems presents anthropologists with a staggering diversity that the Stewardian framework of cultural ecology can cope with only in the most rudimentary fashion.

One response to this situation has been to eschew the application of general theory altogether and concentrate all one's energies on analysis of particular empirical cases. While careful empirical studies are essential, general failure to articulate data with theory would seem to place such research in the realm of natural history rather than science. At best, such natural history can be viewed as (empirical) knowledge in search of (theoretical) understanding. Another response to the problem of diversity has been to advance "general models" of hunter-gatherer subsistence and social organization that are based on inductive generalization from "representative" cases. The foremost example of this is the widespread portrayal—in textbooks as well as scholarly articles—of the !Kung San as the archetype for hunter-gatherers, thus allowing the wealth of carefully collected information on a single ethnographic case to obscure the incredible diversity found among foraging societies (cf. Martin 1974, Wobst 1978, Smith and Winterhalder 1981).

Given this unappealing choice between atheoretical particularism and inadequate generalizations, it is understandable why some anthropologists have recently become interested in optimal foraging theory. I shall summarize some of this theory and review a representative selection of studies applying it to

the analysis of human foraging strategies. In doing so, I hope to demonstrate that optimal foraging theory can satisfy the demand for a deductive theory that is simultaneously general in scope and capable of explaining particular empirical cases. Foraging theory may also offer an opportunity to “translate” some aspects of orthodox cultural ecology into a more rigorous format, making them susceptible to both logical scrutiny and empirical test and thus integrating ecological studies of human foraging into the general context provided by current evolutionary and ecological theory.

THE LOGIC OF OPTIMAL FORAGING THEORY

Optimal foraging theory has developed primarily over the last 15 years and is now one of the more active areas of research in the field of evolutionary ecology (see reviews in Pyke, Pulliam, and Charnov 1977, Krebs 1978, and Pianka 1983). This body of theory represents an attempt to develop a set of models general enough to apply to a broad range of animal species yet rigorous and precise enough to explain details of behavior exhibited by a particular forager. Discussion of particular optimal foraging models (below) serves to illustrate the form and content of this approach, but some general features of the theory deserve mention here.

First, foraging theory is anchored by a set of assumptions derived from current views of adaptation via natural selection. Specifically, it assumes that foraging behavior has been “designed” by natural selection to respond to changing conditions in a way that yields the greatest possible benefit for the individual forager’s survival and reproductive success (Darwinian fitness). Thus, foraging models focus on the costs and benefits accruing to individual actors from their decisions, avoiding the group-benefit assumption so common in anthropology and generally ignoring the complexities of “kin selection” that interest sociobiologists.

Since the costs and benefits of different foraging options are difficult or impossible to quantify in increments of fitness, proxy currencies (presumed correlates of fitness) are employed. Most foraging models assume that foragers will be selected to behave so as to maximize the *net rate of return* (of energy or nutrients) *per unit foraging time*. This assumption seems reasonable under a variety of conditions, including the following: (1) available food energy is in short supply (fitness is energy-limited); (2) specific nutrients are in short supply (fitness is nutrient-limited); (3) time for adaptive nonforaging activities is scarce (fitness is limited by time available for nonforaging activities); or (4) foraging necessarily exposes the forager to greater risks (fitness costs due to predation, accident, climatic stress, etc.) than do nonforaging activities (for further discussion, see Schoener 1971; Orians 1971; Smith 1979; Winterhalder 1981a, 1983b). While the first two of these selective contexts are obvious and widely recognized, the second two are not so often appreciated—yet they point to “opportunity costs” of gathering energy or nutrients that may be widespread. This indicates that a forager need not be facing the specter of food shortages or be attempting to maximize the total amount harvested in order to benefit from efficient foraging strategies. In sum, time shortages or various environmental hazards can select for efficient foraging choices just as readily as can the threat of starvation.

The second general feature of foraging theory is its explicit optimization approach to theory building. This approach has almost inevitably involved some borrowing of terminology and analytical methods from fields that have a longer history of optimization analysis, such as microeconomics, decision theory, and operations research. Optimization analysis is quite widespread in current evolutionary biology—and quite controversial as well (e.g., Cody 1974, Sahlin 1976, Maynard Smith 1978, Oster and Wilson 1978, Lewontin 1979, Gould and Lewontin 1979, Clutton-Brock and Harvey 1979). Without going

into the details of this controversy, it seems reasonable to say that optimization assumptions should be viewed as potentially useful starting points for building models and generating testable hypotheses rather than as Panglossian conclusions about the operation of the real world (see Maynard Smith 1978). In order to generate explanations of any sort, one must make some assumptions about how the world is put together. Our current understanding of natural selection makes certain types of optimization assumptions plausible guides to theory building—but we must recognize that, although they often lead to insights otherwise unattainable, optimality models are simply shortcuts to understanding the world, and shortcuts may sometimes lead one astray. Like any optimization analysis, an optimal foraging model must specify a currency (such as energy), a goal (such as maximizing foraging efficiency), a set of constraints (factors that limit the range of options for the duration of the process studied), and a set of options (choices left open to the actor). Each of these elements is clearly present in the models reviewed in this paper.

A third general feature of foraging theory is the use of mathematical and graphic representations to reduce the complexity of real-world constraints and options to a limited number of “sufficient parameters” (Levins 1966, Winterhalder 1981a). The mathematical format of foraging models is usually quite simple, allowing rather straightforward deduction of hypotheses. Typically, a few parameters are specified to represent environmental and physical constraints (such as prey density or travel time), and another few parameters represent strategic options (such as degree of dietary specialization). The emphasis is on employing mathematics for the rigorous deduction of hypotheses from a small number of assumptions rather than on detailed simulation of the behavior of particular systems.

Finally, foraging theory further simplifies its analysis by dividing its subject into discrete choice categories and by focusing on broad strategies while generally ignoring details of perceptual mechanisms, predation tactics, and the like. Classifying foraging behavior into a set of discrete decision categories allows both models and data to be simpler and more tractable. The major analytical categories in current foraging theory include diet breadth (prey choice), patch (microhabitat) choice, time allocation, foraging-group size, and settlement location—in other words, what to eat, where to forage, how long to forage, with whom, and where to live (see table 1). Since foraging theory is intended to be general, the focus is on strategic rules of this sort rather than on the particular tactics used by any forager in carrying out these strategies (e.g., optimal diet models predict the set of resource types harvested, not the tactics used in harvesting each). While application of a foraging strategy model to a specific case may require detailed understanding of the natural history of that case, it would serve little purpose to complicate the model itself in such a way that it precisely fit this one case but had no general applicability.

Although foraging theory assumes that foragers’ decisions are guided by criteria that produce outcomes consistent with those favored by natural selection, there is no reason to believe that any species inherits alternative foraging strategies via direct genetic transmission. Models in evolutionary ecology typically avoid specifying the mechanics of ontogeny and genetics in making predictions about the fit of phenotypes to their environments (Stearns 1977:140; Maynard Smith 1978). The broad assumption in foraging theory that natural selection has “designed” foragers to respond adaptively to changing opportunities is consistent with this tradition and decidedly not a form of genetic determinism. Nevertheless, the neo-Darwinian basis of foraging theory raises questions about its applicability to human beings. Certain critics have contended that the application of such models to humans is an exercise in loose analogy and that such “ecological determinism” represents a “fallback position” from stronger forms of genetic determinism and sociobiology (Boucher et al. 1978; Gould 1980:265).

Actually, there are several ways in which application of foraging theory to human foragers might be justified. First, the issue of proximate mechanisms—the manner in which humans might come to exhibit foraging strategies that maximize components of fitness—can be ignored, predictions from the theory being directly tested against observed patterns of behavior. This is the standard approach in evolutionary ecology, since the manner in which other species learn to forage is at least as mysterious as the human case. This first approach would lead one to view foraging strategies as one arena for evaluating the general claim that, regardless of the complex mechanisms of learning and enculturation, our species's behavioral tendencies are fundamentally a product of natural selection and should therefore be expressed in a manner that will maximize fitness (e.g., Alexander 1974, 1979; Irons 1979; Hawkes et al. n.d.).

A second view holds that while a partial concordance between neo-Darwinian predictions and human behavioral phenotypes is to be expected, this results from a distinct process of *cultural* evolution (Durham 1976, 1978, 1982; Richerson and Boyd 1978; Pulliam and Dunford 1980; Pulliam 1981; Boyd and Richerson 1982). In this view, while the capacity for culture and the general rules governing cultural transmission have evolved through natural selection acting on genes, the cultural variation evident in foraging (and a multitude of other human practices) is subject to the forces of cultural selection and transmission and hence is not directly predictable from the theory of natural selection as applied to traits controlled by Mendelian inheritance. Since the theory of cultural evolution is in its infancy, it is not yet clear what effects this separate "design force" should be expected to have on observed patterns of foraging behavior. In fact, subscribers to this second view generally disagree not with the predictions generated from optimal foraging theory, but only with a neo-Darwinian interpretation of their confirmation in the human case.

Finally, a third view justifies the application of foraging theory to humans by portraying ecological optimization theory as simply a version of standard (neoclassical) economic logic

applied to production systems in certain types of nonmonetized economies (Orlove 1980, McCay 1981, Winterhalder 1982). This last view is probably the most congenial to anthropologists, although it can be criticized for begging the question of how human foragers come to possess the specific preferences (utility functions) they exhibit (Smith 1983, Stephens and Charnov 1982, Hawkes et al. n.d.). In any case, given the variety of assumptions one can draw on to justify application of foraging theory to humans, critics of such applications must be wary of tarring all practitioners with the same theoretical brush.

To sum up, optimal foraging theory represents an attempt to specify a general set of "decision rules for predators" (Krebs 1978) based on cost-benefit considerations that are in turn deducible from first principles of adaptation via natural selection. A substantial and rapidly growing number of experimental and field studies of many different species have been conducted (see reviews in Pyke, Pulliam, and Charnov 1977, Krebs 1978, Kamil and Sargent 1981). Because of the generalized nature of foraging models, and perhaps because of their economic orientation, a number of anthropologists have concluded that the theory might be relevant to analysis of human foraging behavior. The following three sections discuss selected foraging models and representative attempts to apply them to human societies.

DIET BREADTH AND PREY CHOICE

A key problem in foraging theory concerns prey choice and diet breadth: out of the array of available prey types, which ones should an efficient forager attempt to harvest? The same basic answer, termed the "fine-grained diet-breadth model," has been derived repeatedly, beginning with the seminal papers by MacArthur and Pianka (1966) and Emlen (1966) that founded the field.

TABLE 1
MAJOR DECISION CATEGORIES OF OPTIMAL FORAGING THEORY: STRATEGIC GOALS, DOMAINS OF CHOICE, COST-BENEFIT CRITERIA, AND MAJOR CONSTRAINING VARIABLES

DECISION CATEGORY	STRATEGIC GOAL	DOMAIN OF CHOICE	COST-BENEFIT CRITERIA	SOME MAJOR CONSTRAINING VARIABLES
Diet breadth	Optimal set of resource types to exploit	Which types to harvest, once encountered	Return per unit handling time for each type, overall return on foraging (including search time)	Search and pursuit abilities of forager, encounter rates with high-ranked types
Diet breadth with nutrient constraints	Same as above	Which and how many of each prey type to harvest	Minimum cost for meeting nutritional requirements	Nutrient requirements, abundance of prey types, procurement costs
Patch choice	Optimal array of habitats to exploit	Which set of patches to visit	Average rate of return with patch types and average over all patches (including travel time between patches)	Efficiency ranking of patch types, habitat richness, travel time between patches
Time allocation	Optimal pattern of time allocated to alternatives (patches, etc.)	Time spent foraging in each alternative	Marginal return rate for each alternative, average return rate for entire set	Resource richness, depletion rates for each alternative
Foraging-group size	Formation of optimal-sized groups for foraging	Size of groups to join for foraging under specified conditions	Average per capita rate of return at each group size, marginal cost and gain to joiner or group members	Return-rate curves for each group size under each condition, possibilities for group formation, rules governing division of harvest
Settlement pattern	Optimal location of home base for foraging efficiency	Settlement location of each foraging unit (individual or family)	Mean travel costs and/or search costs per unit harvest	Spatiotemporal dispersion and predictability of major resources, effects of cooperation and competition

THE FINE-GRAINED DIET-BREADTH MODEL

The fine-grained diet-breadth model assumes, first, that a forager encounters available prey types "at random"—that is, in the same relative proportions throughout the foraging area. This is the assumption of a "fine-grained" environment, as contrasted with a "patchy" environment, in which prey are distributed (and encountered) in a heterogeneous fashion. Second, total foraging time is partitioned into two mutually exclusive and exhaustive categories: *search* time (generalized over all prey types, in accordance with the random-encounter assumption), and *handling* times (the average time spent pursuing, capturing, processing, and consuming one item of each prey type once encountered). Thus, it is assumed that foragers search for all prey items simultaneously and that once a prey item has been encountered and the decision to pursue has been made the time spent handling it is unavailable for searching. Third, the forager is assumed to rank prey types along a single dimension of profitability, measured as net energy or food value obtained per unit handling time. This last assumption obviously may not be valid if prey types differ greatly in their nutritional value to the forager (see "Limitations," below).

As is illustrated in figure 1, the partitioning of foraging time into search and handling times generates two opposing cost curves. As a forager widens its diet by adding prey types of lower rank (i.e., higher handling time per unit return), handling costs averaged over the entire diet increase; search costs decrease because less time is spent searching for acceptable items. This fundamental trade-off between search costs and handling costs defines a unique and optimal set of prey types for any foraging system fitting the assumptions of the fine-grained diet-breadth model. For any particular situation, then, the optimal diet is achieved by "adding" prey types in descending rank order until the expected return (e.g., in calories) per unit foraging time is maximized.

Although heuristically attractive, the MacArthur-Pianka diet-breadth model (fig. 1) has been superseded by more rigorous and general formulations. In the algebraic version proved by Charnov (for a detailed development, see Charnov 1973, 1976a; Charnov and Orians 1973), the fine-grained diet-breadth model states that any prey type j is in the optimal set if and only if

its net energy return (E_j) per unit handling time (h_j) is greater than the average return rate (including search time) for all prey types of higher rank, that is,

$$\frac{E_j}{h_j} > \frac{\sum \lambda_i \cdot E_i}{\sum \lambda_i \cdot h_i + 1} \quad (1)$$

where λ_i is the encounter rate with each prey type. (For a formulation more closely parallel to figure 1, see Schoener 1974.)

The fine-grained diet-breadth model generates a number of testable predictions, some of which run counter to widely held notions in ecological anthropology. First, as the availability of high-ranked prey types fluctuates, the optimal diet breadth shrinks or expands: increased availability should result in more specialized diets, while scarcity of high-ranked items favors a more generalized diet. ("Availability" refers here to *encounter rate*, which may often differ from actual environmental abundance.) Second, prey types should be added to or dropped from the diet in rank order of handling efficiency, with low-ranked types moving in and out of the forager's "consumption mix" while the higher-ranked types are invariably pursued when encountered. Third, and least obvious, the inclusion of a prey type in the diet should depend only on the availability of higher-ranked prey types, *not* on its own availability. That is, as long as changes in abundance do not affect a prey type's handling efficiency, no type with a handling efficiency lower than the overall foraging efficiency (excluding that type) should be taken, however common it becomes. (This is strictly true only if recognition time upon encountering this prey type is zero—see Hughes 1979; Krebs 1978:29.) Conversely, high-ranked types should be harvested even if they are rarely encountered, as long as the expected return from handling them is higher than the expected return if they are passed by in favor of different prey. Thus, the *rank* of a prey type predicts not how common it will be in a forager's diet, but only whether it will be taken when encountered; to predict the number of prey harvested, we need to specify the encounter rates of prey types as well as their rank orders. It follows that we cannot use the commonness or rarity of a prey type in a forager's diet to predict whether it will remain in the diet under altered conditions: one prey type may be highly ranked but rarely encountered and thus rarely harvested (and thus seemingly "unimportant"), while a staple that is abundant but ranked low in handling efficiency may suddenly be dropped from the diet if higher-ranked resources increase in availability (cf. Hawkes and O'Connell 1981). These rather counterintuitive predictions have many implications for the explanation of variation in the harvesting choices of human foragers.

ANTHROPOLOGICAL APPLICATIONS

Until very recently, anthropologists who have considered the general issue of hunter-gatherer dietary choice have rarely employed explicit models or other well-defined theoretical constructs. (Important exceptions include archaeologists who have employed algebraic models and linear programming to predict dietary strategies [e.g., Jochim 1976; Keene 1979, 1981, 1982; Reidhead 1979; Earle and Christenson 1980]; space considerations preclude a review of these approaches here, but see "Limitations," below.) While those convinced of the autonomy of culture have stressed the unique, symbolic logic of dietary preferences, ecological anthropologists have postulated a large variety of competing adaptive rationales for food choices. Thus, human foragers have been portrayed as minimizing effort, maximizing efficiency, minimizing risk, maximizing dietary diversity, or assuring sustainable yields—or even as pursuing several of these goals simultaneously (see reviews in Bettinger 1980, Hayden 1981, and Smith 1980). Empirical studies have shown that some human foragers are extremely selective in their use of available resources while others are much less so,

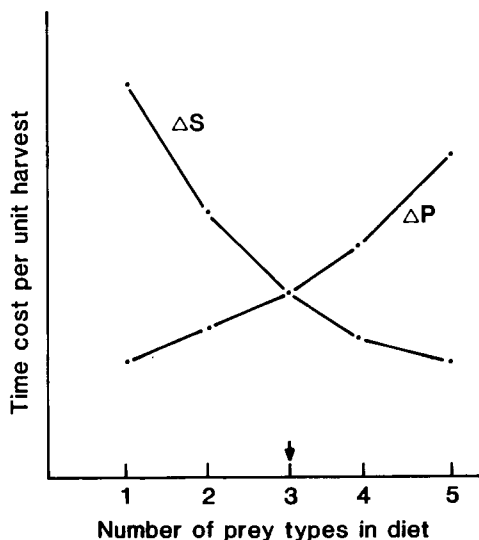


FIG. 1. The MacArthur-Pianka diet-breadth model. The ΔS curve plots decreasing search costs per unit harvest and the ΔP curve increasing handling (pursuit) costs per unit harvest as prey types are added to the diet (in descending rank order of net return per unit handling time). The optimal diet includes all prey types to the left of the intersection of the two curves (arrow). This diet minimizes total time costs per unit harvest. (From MacArthur and Pianka 1966, as modified by Schoener 1971 and Winterhalder 1977, 1981a.)

yet there is no agreement on how to explain this diversity in general terms.

The diet-breadth model offers hope of accounting for much of the observed diversity in hunter-gatherer resource choice in terms of a few general principles, and it generates much more precise predictions about resource utilization than does standard anthropological theory. This model is also notable for the crucial role it assigns to procurement costs (handling and search times), which are often ignored by other analyses (Hawkes and O'Connell 1981).

A number of archaeological studies have examined prehistoric dietary choice in the framework provided by the diet-breadth model (e.g., Perlman 1976, 1980; Bayham 1979; Lewis 1979; O'Connell and Hawkes 1981; Yesner 1981; Bettinger and Baumhoff 1982; O'Connell, Jones, and Simms 1982). While in these cases foraging theory has served as a useful device for generating hypotheses, archaeological applications are inherently limited by the lack of direct measures of either foraging costs or harvest rates. In some cases this can be remedied by using data from ethnographic analogues or experiments, but often an educated guess is the only option open to the archaeologist using foraging theory. Hence, while ethnographic tests of these models are still possible it is important for ethnographers and archaeologists to cooperate in determining the applicability of the theory to human production systems (Smith and Winterhalder 1981:12). Because of the crucial nature of ethnographic evidence, this review will concentrate on ethnographic tests of foraging models.

Ethnographic applications of the fine-grained diet-breadth model include the work of Winterhalder (1977, 1981b) on the boreal-forest Cree, O'Connell and Hawkes (1981, n.d.) on the Alyawara of Australia, Gage (1980) on Samoan horticulturalists, and Hames and Vickers (1982), Hawkes, Hill, and O'Connell (1982), and Hill and Hawkes (1983) on four Amazonian Indian populations. All of these studies conclude that the diet-breadth model is a useful explanatory device, though not consistent with the field data in every detail. Findings from three of these studies are briefly summarized below. While the number of production systems analyzed is still limited, the diversity of environments (subarctic forest, subtropical desert, volcanic island, and tropical forest) and subsistence types (hunting-fishing-trapping, plant gathering, mixed hunting and horticulture, and pure horticulture) included suggests that the model may be widely applicable.

The most direct anthropological test of the diet-breadth model to date is that of Hawkes, Hill, and O'Connell (1982) on the Aché of eastern Paraguay. This study confirmed that the Aché would suffer a decline in foraging efficiency if they dropped from their diet any one of the 16 resource types they harvest and that the return rate per unit handling time for the lowest-ranked resource is nearly identical to the overall return rate on foraging time (fig. 2)—both findings precisely in agreement with the model. The interpretation of this apparent confirmation has, however, several problematic aspects: (1) Can the Aché actually perceive the difference in overall foraging returns from the optimal set (872 kcal/hr) versus a set that drops the lowest-ranked prey type (871 kcal/hr) or even the four lowest-ranked types (821 kcal/hr)? Would Aché with these slightly suboptimal diet breadths suffer from reduced fitness? (2) The diet-breadth model specifies *net* energy returns (calories captured minus calories expended) as the currency, but the data measure only gross returns; would inclusion of energy costs alter the outcome of the test? (3) The study duration is short (three and a half months); would seasonal changes in prey availability be great enough to alter the optimal diet breadth, and if so would Aché prey choice reflect this? (4) It is likely that Aché men and women (like most or all hunter-gatherers) have quite different foraging capabilities and specialties and thus should have different optimal diets (Kim Hill, personal communication); would disaggregated data still support the model? (5) The diet-breadth model assumes a random-encounter pattern, yet Hawkes et al. do not verify this for the Aché case and even apply a patch-choice model to analyze the same data; to what degree is simultaneous search and random encounter in a homogeneous habitat actually characteristic of the 16 resources in the optimal set? These are all questions generated by considerations of foraging theory itself. Fortunately, Hawkes et al. have recently conducted more fieldwork among the Aché and should be able to address some or all of these issues with extensive new data.

Hawkes et al. go on to discuss the oft debated importance of hunting vs. gathering, noting that Aché foragers gather plant foods even though hunting is very productive and efficient and arguing that this is because that particular resource mix yields better returns on foraging time than a specialized (pure hunting or pure gathering) strategy would. This leads them to question

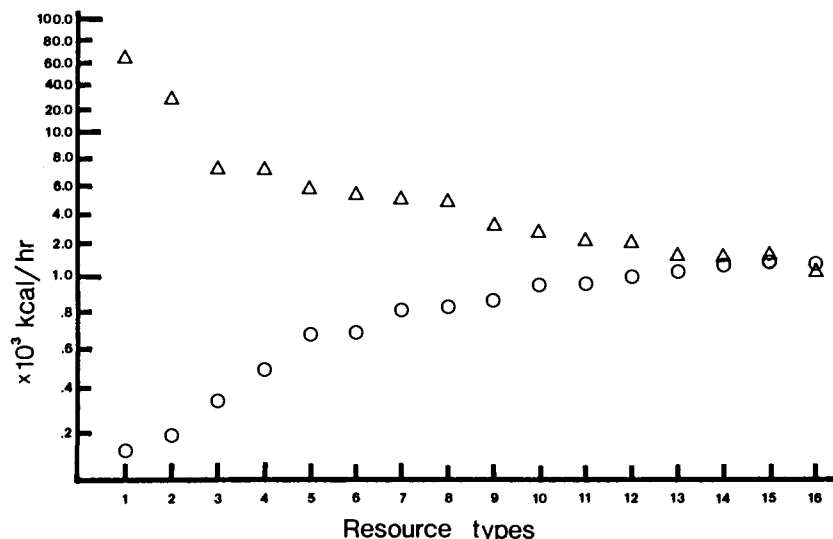


FIG. 2. Aché diet breadth and foraging efficiency. The upper curve (triangles) plots the caloric returns per unit handling time for each resource type taken (ordered by rank, as in fig. 1), while the lower curve (circles) plots the overall return rate to foraging (including search time) that is obtained as the types are added to the diet in rank order. The optimum diet breadth occurs at the intersection of the two curves. (Modified from Hawkes, Hill, and O'Connell 1982.)

the orthodox view that hunter-gatherers generally rely on gathering because it is a low-risk, high-return activity and hunt only to obtain the luxury of meat. If their argument is correct, anthropologists have been too quick to conflate the relative *reliability* of gathering with its relative *efficiency*. It remains to be seen whether the variable importance of gathered vs. hunted resources seen in different foraging societies reflects the optimal (most energy-efficient) resource mixes dictated by varying ecological and technological constraints in each case.

Hames and Vickers (1982) utilize the diet-breadth model in a comparative analysis of three Amazonian Indian groups: the Siona-Secoya of Ecuador and the Ye'kwana and Yanomamö of Venezuela. Given the patterns of anthropogenic depletion of game that are known to occur in Amazonia (Vickers 1980), they note that high-ranked prey species will be less abundant (1) around older settlements and (2) in the hunting zones closest to a settlement. They use this variation in prey availability to test two hypotheses generated from the diet-breadth model. The first hypothesis is that as high-ranked prey species are depleted over time the diet should expand to encompass more low-ranked species, and it is borne out for the one settlement for which diachronic data were available. Here, although deer (a formerly taboo item) is the only new species added to the diet, a marked shift in the proportion of high-ranked to low-ranked prey was noted over a six-year period, especially in the hunting zone closest to the village, where low-ranked game constituted only 4% of all kills when the village was first studied but had increased to 41% six years later. The second hypothesis is that diet will be broader in hunting zones closer to a village (where high-ranked prey are less abundant), and it receives support in all four cases (table 2).

In some respects this study is only an indirect test of the diet-breadth model. First, since the data were not collected with optimal foraging theory in mind, Hames and Vickers lack any direct measures of prey handling times and encounter rates. Thus, they are forced to estimate prey efficiency rankings on the basis of their impressions, informants' statements, and especially prey size (which is a dubious proxy for efficiency rank). Second, the hypothesis of shifts in the proportions of broad categories of prey (high-ranked versus low-ranked) is not derived rigorously from the diet-breadth model, as Hames and Vickers (1982:367, 373) recognize, and the special assumptions required to generate this hypothesis from the model may not hold (this is a criticism I can make of my own attempts to test the diet-breadth model—see Smith 1980:chap. 6). Third, no statistical tests are presented to demonstrate that the observed patterns are consistent with a process of optimal prey choice, and it could be argued that they arose by some more random or density-dependent process—although given the quantity of data on time allocation and hunting success Hames and Vickers present I find this last criticism rather implausible.

Despite these caveats, the study is a valuable one for dem-

onstrating some of the types of questions and analyses that foraging theory can generate. It is to the credit of both the optimal foraging approach and these two researchers that the unresolved questions, and the data needed to resolve them, can be clearly and explicitly discussed. Furthermore, in their conclusion Hames and Vickers point out the contrasts between the optimal foraging perspective and the "prudent predation" view of native game management proposed by certain other anthropologists studying Amazonia (e.g., Ross 1978) and stress the advantages of the former for explaining both short-term and long-term changes in foraging strategies.

As part of his study of boreal-forest Cree foraging strategies, Winterhalder (1977, 1981b) has demonstrated an intriguing correspondence between some predictions of the diet-breadth model and historical changes in Cree subsistence patterns. Employing the basic distinction between search costs and handling costs, he argues that technological changes have produced three relatively distinct periods in Cree history, each with a different optimal diet breadth (fig 3). Under aboriginal conditions, both search costs and handling costs were relatively high, as Cree foragers searched for prey on foot and by paddled canoe and pursued game with bow and arrow, rawhide snares, and fish-hooks. With their participation in the fur trade, Cree obtained a variety of tools, such as rifles, wire snare, and fishnets, that greatly reduced pursuit costs across a broad range of prey types. Since search technology remained almost unaltered, the model's prediction is that Cree diet would have expanded noticeably—and this is what the rather meager historical data seem to indicate. Finally, the recent adoption of motorized transport (snowmobiles and outboard engines) has resulted in greatly reduced search costs but little change in pursuit costs (since prey, once encountered, continue to be pursued primarily on foot). Winterhalder's hypothesis that the diet should be considerably narrower than in the fur-trade era is consistent with evidence of contemporary specialization in a few high-ranked species (primarily moose, beaver, hare, and fish).

Although Winterhalder's historical application of the diet-breadth model is a preliminary one and of necessity based on limited data for earlier periods, it demonstrates that foraging theory is capable of dealing with relatively long-term changes in technology and subsistence patterns in an innovative and enlightening fashion (see Hames and Vickers 1982 for a similar demonstration). This suggests that the theory is indeed applicable in archaeological, and perhaps even paleontological, contexts.

PATCH CHOICE AND TIME ALLOCATION

Whenever resources are distributed and encountered in a spatially heterogeneous pattern, the resource distribution can be said to be *patchy*. In patchy environments, foragers face two

TABLE 2
DIET BREADTH AMONG FOUR AMAZONIAN INDIAN GROUPS AS A FUNCTION OF DISTANCE OF KILL SITES FROM VILLAGES (HAMES AND VICKERS 1982)

STUDY GROUP AND PERIOD	LOW-RANKED SPECIES ^a		SPECIES OF ALL RANKS ^b	
	Near zone ^b	Far zone ^b	Near zone ^b	Far zone ^b
Ye'kwana (1975-76)	6	1	11	5
Yanomamö (1975-76)	2	1	6	10
Siona-Secoya (1973-75) ^c	2	1	9	5
Siona-Secoya (1979) ^c	7	0	15	5

^a Three ranks of prey (high, intermediate, and low) were defined for each study group, primarily on the basis of meat yield. The figures given here are for the total number of species taken, regardless of frequency. Bird species are not included here or in the original.

^b Three zones were defined for each village, but data for the intermediate zone are not included here. The near zone = 0-4 km from the village for Ye'kwana and Yanomamö and a mean of 5 km from the village for Siona-Secoya. The far zone = over 9 km for the former and a mean of 25 km for the latter.

^c The same village of Siona-Secoya was studied during the two periods by the same ethnographer.

related optimization problems: which set of patches to forage in and how long to forage in each. Although a general model that can deal with both problems has not yet been constructed, foraging models have suggested some answers for each.

THE PATCH-CHOICE MODEL

Although MacArthur and Pianka (1966) presented a model of patch choice, it had a number of features that have prevented its widespread application (see discussion in Charnov 1973, Charnov and Orians 1973). The model is similar in form to their diet-breadth model in postulating a trade-off between declines in yield per unit time spent foraging in patches (as patches of lower and lower quality are added to a forager's itinerary) and a decrease in travel time between patches (as fewer patches are passed by). As with the diet-breadth model, the optimal solution is to add patch types to the itinerary until total foraging time (within-patch as well as between-patch) per

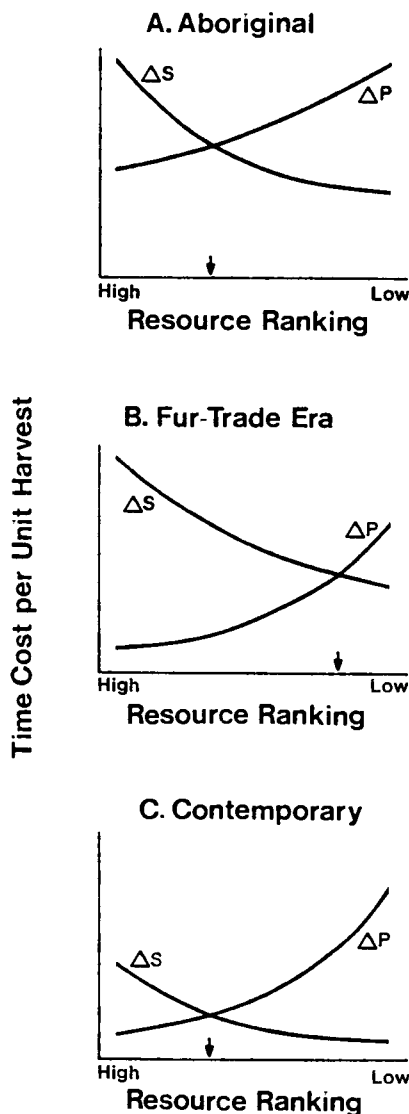


FIG. 3. Optimal diet breadths hypothesized for boreal-forest Cree in three historical periods. Under aboriginal conditions (A), both search and handling or pursuit costs were relatively high, resulting in a rather narrow diet breadth. In the recent past (B), with involvement in the fur trade, pursuit technology became more efficient, but search costs remained high, favoring a relatively wide diet breadth. In the contemporary period (C), the use of motorized transport and efficient manufactured pursuit devices keeps both search and pursuit costs low, resulting in a relatively narrow diet breadth once again. (After Winterhalder 1977, 1981b.)

unit harvest is minimized. However, the MacArthur-Pianka patch-choice model does not specify how long a forager should stay in each patch or what effect foraging has on the stock of resources found in each. The most reasonable interpretation of the assumptions guiding the model is that patches contain resources that are harvested at a constant rate over some time period but foragers leave a patch when the last item in their diet is harvested and the expected or marginal harvest rate suddenly drops to zero (Eric Charnov, personal communication; Charnov and Orians 1973:69-70).

These assumptions may fit certain human foraging situations, as when easily located prey items such as plants or sessile animals are being harvested from certain types of patches (e.g., nuts from a grove of mongongo trees or clams from a beach). Under such conditions, it is reasonable to consider the MacArthur-Pianka patch-choice model, but quite different conditions might pertain to other types of patches. For example, foraging per se might have little or no effect on prey availability within some types of patches, the rate of return remaining constant for some period until conditions changed. Under these conditions, which may be quite rare but perhaps pertain to certain migrant and superabundant resources (e.g., salmon or caribou), the optimal strategy is simply to locate oneself in the patch with the highest rate of return and remain there until conditions change, perhaps sampling other patches periodically to redetermine the patch rank ordering (Krebs 1978:40). This can be termed the "single best patch" situation. A third and theoretically more interesting set of conditions is found when foraging within a patch causes a gradual but continual decline in the return rate for that patch. This case—the classic economic situation of "diminishing returns" to inputs of time or labor—is treated by a foraging model termed the marginal value theorem.

THE MARGINAL VALUE THEOREM

The marginal value theorem was first proposed (and mathematically derived) by Charnov (1973, 1976b; Charnov and Orians 1973). Unlike the MacArthur-Pianka patch-choice model, the marginal value theorem takes the set of patches utilized as a given and asks what pattern of time allocation to each patch in the utilized set would be optimal, in the sense of offering the highest overall rate of energy capture. It makes the explicit assumption that the foraging process gradually depletes the resource level in any patch and that this causes a monotonic decline in the net return rate from that patch (e.g., as prey become harder to locate). The critical variable to be optimized is hence the point on this curve of diminishing returns at which the forager should depart for another patch. Assuming that the foraging period in any one patch is short relative to renewal time, the optimal solution is to leave each patch when the marginal capture rate (i.e., the instantaneous capture rate at the end of a foraging period within that patch) is equal to the overall mean capture rate (averaged over the entire set of patches utilized, including travel time between patches) (fig. 4).

Several predictions follow from this model. First, the optimal forager should leave any patch when it is depleted to the point where foraging elsewhere will yield higher returns per unit time (taking travel costs into account). Second, since optimal time allocation to any patch is a function of average yields for all utilized patches, as the overall productivity of a habitat (set of patches) rises less time should be spent in any one patch and conversely (declining productivity increases optimal patch-stay times). A similar prediction holds with changes in travel costs, with lower costs being equivalent to higher productivity and conversely. Finally, any patch not yet in the utilized set should not be added unless it can yield a marginal rate of return equal to or greater than the average rate for the utilized set (Charnov and Orians 1973:53-54; see my figure 4). This last prediction

suggests that it might be possible to employ the marginal value theorem to define optimal patch choice: a forager should add patch types to its itinerary as long as the return rate curve for that patch passes above the ray defining the mean return rate for all utilized patches (fig. 4). However, this specification would require detailed information on changes in interpatch travel time as a function of changes in the set of utilized patches. Anthropologists interested in the marginal value theorem should also be aware of recent discussions concerning the limitations and range of applicability of this model (see McNair 1982, Stephens and Charnov 1982, and references therein).

ANTHROPOLOGICAL APPLICATIONS

Models of optimal patch choice and time allocation have many interesting anthropological implications. Several researchers have remarked on these, and a few have analyzed empirical evidence on human foraging in light of the models. In reviewing these studies, I move from the more general discussion to the more detailed and empirically focused analyses.

The most general issue concerns resource conservation. Many ecological anthropologists (and others) have argued that human foragers consciously practice conservation of their prey, pointing to game taboos in Amazonia (e.g., Ross 1978) and rotation of hunting territories in subarctic North America (e.g., Feit 1973) as striking examples of indigenous resource management. An opposing view argues that what Hardin (1968) has called the "tragedy of the commons" is a phenomenon that can afflict hunter-gatherers as well as nonforagers and cites the mass extinction of many New World vertebrate species at the end of the Ice Age as a case of "Pleistocene overkill" (Martin 1973) resulting from Paleo-Indian colonization of the Americas.

Resolution of these competing claims requires detailed empirical study beyond the scope of this paper. However, it is

worth pointing out that optimal foraging theory offers a different, and perhaps more general and enlightening, view of these issues. The assumption of foraging theory that individuals will seek to maximize net returns per unit foraging time suggests that planned conservation will be limited to cases in which individual foragers or small economically integrated groups have more or less exclusive control over resources within a foraging area. Unless such effective territorial control is present—and it rarely is among nonsedentary hunter-gatherers (Lee 1972, Dyson-Hudson and Smith 1978)—restraint in resource harvest by one individual or group will often be to the profit of another individual or group, and effective conservation will be impossible.

Does it follow that foraging models predict inevitable resource depletion and support the tragedy-of-the-commons theme in general and the plausibility of the Pleistocene-overkill scenario in particular? The answer is probably no, although this depends on both the form in which resource depletion is expressed in the within-patch return rate curves and the time-scale over which resource utilization is examined.

If patches are characterized by return rates that do not drop until the prey within them are exhausted—as in the MacArthur-Pianka patch-choice model—then short-term extinction will result unless countered by conservation or the ability of some of the prey to escape detection or find refuges. For other types of patches, however, short-term foraging optimization will have effects that greatly reduce the probability of prey extinction. In the single-best-patch situation (see above), foraging has no effect on prey availability in the short run, by definition. If prey abundances, and hence return rates, fluctuate randomly, foragers should sample other patches, from time to time and leave the first patch whenever they encounter a patch with higher returns—presumably leaving a remnant prey population behind (or having been left behind themselves, in the case of

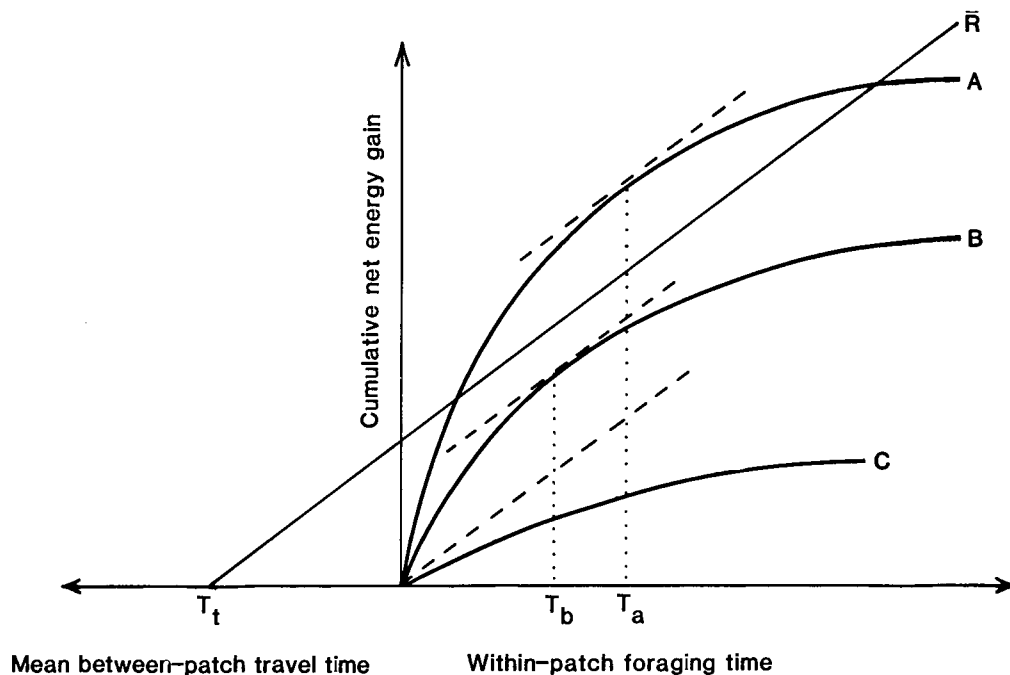


FIG. 4. The marginal value theorem for time allocation to a set of patches characterized by foraging-induced diminishing returns. The curves labeled A, B, and C plot the declining marginal (instantaneous) net return rates for the three different patches during foraging episodes. The average capture rate for the entire set of utilized patches, including time spent traveling between patches (T_t), is represented by a line of slope \bar{R} . The optimal time allocation to each patch is found by constructing the highest line tangent to the return rate curve for that patch that is parallel to (has the same slope as) \bar{R} (broken lines). A (dotted) line from this point of tangency perpendicular to the time axis intersects this axis at the optimal time allocation for that patch (T_a , T_b). This solution (1) equalizes the marginal return rate for each utilized patch with the mean return rate for the entire set of such patches (\bar{R}) and (2) maximizes \bar{R} for this particular set of patches. Any patch whose return rate curve does not pass above the mean return rate curve—for example, patch C here—should not be utilized, since the point of tangency (as defined above) is at the origin (i.e., the optimal time allocation = 0). (Modified from Charnov and Orians 1973 and Charnov 1976b.)

migrant prey). Finally, if the patches are characterized by diminishing return rates due to foraging-caused depletion, then the marginal value theorem is applicable. Again, as long as there are other, richer patches to exploit, total prey extinction within the patch is highly unlikely. Rather, the marginal value theorem predicts that foragers will leave a patch when its rate of return is low relative to other patches—which should generally be well before the favored prey types in that patch are exhausted. Indeed, to exploit prey to local extinction under these conditions requires exceedingly inefficient foraging, as it requires the forager to approach an asymptote of zero rate of return. It is important to note that this is true even when the forager in question is a single-species specialist.

It can be plausibly argued that the conditions under which the Pleistocene overkill is supposed to have occurred—foragers colonizing a heterogeneous game-rich habitat and expanding rapidly along a front into virgin territory—are precisely those for which the marginal value theorem predicts the most rapid movement between patches and hence the least likelihood of prey extinctions in the short term, given the high payoff for moving on to new pastures before local exhaustion can occur (Winterhalder 1977, 1981a). Any extinctions from overhunting imply either nonoptimal behavior or a situation that is not characterized by diminishing returns. Alternatively, prey extinction could have followed an extended period of “settling in” and local population growth, but this sort of process is very different from the “advancing front” model postulated in the overkill scenario (Martin 1973, Mosimann and Martin 1975).

The marginal value theorem demonstrates that certain phenomena which have the effect of conserving resources may well arise from simple self-interest (efficiency maximization) even when there is no territoriality or other guarantee of exclusive use. If exclusion of competing foragers can be instituted to some degree, optimal foraging practices may quite closely mimic rational conservation measures. Feit (1973:122) writes of the Waswanipi Cree:

Waswanipi regulate the harvests of animals and the production and distribution of animals as well . . . by rotational hunting. By not occupying a given hunting territory every year the hunters allow the population and harvests of animals to grow. . . . From year to year hunters constantly evaluate the state of the animal populations on the land they hunt, and any drop in the success of the hunt, the number of animals sighted or the number of animal signs seen, is taken as an indicator of overhunting. . . . Rotation of territories then is the critical mechanism for managing the size of the animal population.

Hunting-territory rotation may well have the effect of managing prey populations and preventing overhunting, but is it *designed* to do so? Given the drastic and unpredictable fluctuation that has been documented for populations of most prey species in the Subarctic (e.g., Knight 1965, Winterhalder 1977), it is difficult to see how a strategy of long-term resource management could repay the costs to individual foragers of foregoing immediate returns for uncertain future returns.

If we view hunting-territory rotation as time allocation on

a large spatiotemporal scale, the argument can be rephrased in terms congruent with foraging theory. As Feit himself notes, the concentration of hunting effort in a rotational system, by reducing search and travel costs and increasing harvest rates, may well have the effect of “maximizing harvest efficiency.” I suggest it is more reasonable to view the Waswanipi rotational system and similar practices in other foraging societies as primarily devices to increase foraging efficiency and optimize time allocation, only incidentally having the effect of “managing” prey populations. This should of course be considered as a hypothesis to be tested rather than as a conclusion.

There have so far been no attempts to test the marginal value theorem or other patch-choice models with anthropological data in any rigorous fashion. However, several studies have demonstrated human foraging behavior that is consistent with these models. Winterhalder (1977, 1981b) has discussed Cree foraging data in terms of the marginal value theorem, showing that Cree will abandon snarelines and trapsets before depleting an area of all hare, muskrat, or beaver and suggesting that this is done because patches that would give a higher return on foraging effort are available—yet he recognizes that the data are not sufficient to falsify the competing hypothesis of resource conservation. O’Connell and Hawkes (1981, n.d.) have analyzed quantitative data on Alyawara patch choice and argued that the pattern of choices generally leads to optimal time allocation, especially if the need to gather information on changing habitat productivity is taken into consideration. Hames (1980) has demonstrated that Yanomamö roughly equalize the return on hunting effort from different hunting zones surrounding a settlement and has argued that they utilize hunting-zone rotation as a strategy to maximize yields per unit foraging time.

My own research on Inuit (Canadian Eskimo) foraging strategies (Smith 1980) included an assessment of time allocation to marine vs. terrestrial habitats. The hypothesis tested was that habitats with higher average return rates will receive greater allocations of foraging time. Since this prediction uses average rather than marginal returns to alternative allocations and assumes that depletion curves of these alternatives are roughly parallel, it cannot be considered a robust prediction of the marginal value theorem, but it is a plausible correlate under the given assumptions (see figure 4). Alternatively, this can be conceptualized as a single-best-patch situation, in which the ranking as best patch alternates between the two habitats. The data on Inuit time allocation, covering 25,500 hunter-hours of foraging, demonstrate a striking seasonal reversal of the relative profitability of marine and terrestrial hunting (table 3). In summer and fall, when canoes with outboards allow easy mobility along the coast but travel on the tundra is difficult, marine hunting is given greater emphasis and yields much higher returns, both absolutely and per unit foraging time. After freeze-up, while considerable hunting occurs on the sea ice or at the floe edge, terrestrial hunting is emphasized, with

TABLE 3
SEASONAL TIME ALLOCATION TO MARINE VS. TERRESTRIAL HABITATS AMONG
INUIT FORAGERS (SMITH 1980)

SEASON	MARINE		TERRESTRIAL	
	Time (hr.) ^a	kcal/hr. ^b	Time (hr.) ^a	kcal/hr. ^b
Summer (July–September)	4,958	3,390	589	1,950
Fall (October–mid-November)	664	2,350	556	1,560
Winter (mid-November–March)	1,989	1,760	6,747	4,030
Spring (April–June)	915	1,030	9,103	1,730

^a Forager-hours of effort allocated to the particular habitat, as sampled in the study period (August 1977–July 1978).

^b Average per capita net return rate, as defined in Equation 2.

snow cover allowing efficient access to caribou, freshwater fish, and other inland resources. A more detailed (month-by-month) analysis reveals the same pattern of reversals in time allocation matching reversals in efficiency rank order (Smith 1980: chap. 7).

In summary, a variety of results are in agreement with the general hypothesis that human foragers preferentially allocate foraging time to locales with higher yields and respond to shifts in relative yields with appropriate shifts in time allocation. Optimal foraging models offer a way of interpreting spatial patterns of resource utilization without invoking assumptions of long-term conservation goals. More detailed tests of patch-choice and time-allocation models are needed, however, to assess their value for interpreting human foraging economies.

GROUP FORMATION AND OPTIMAL GROUP SIZE

The adaptive significance of sociality is a central concern of current evolutionary theory (e.g., Alexander 1974, Wilson 1975, Bertram 1978), and group living and cooperative foraging are conspicuous features of human evolutionary history (e.g., Isaac 1978). Anthropologists have long been interested in defining the ecological forces favoring social cooperation in prehistoric as well as ethnographically described societies of hunter-gatherers (see review in Smith 1981). The selective factors acting on group formation and social interaction are undeniably complex, and multiple factors must determine these attributes in the case of both nonhuman and human foragers. With humans, historical and cultural factors undoubtedly greatly complicate analysis of the expected patterns of social interaction involved in foraging. Nevertheless, foraging theory may provide some valuable insights into this problem. Here I emphasize the testable hypotheses about group formation that can be generated using the optimal foraging approach and review the few existing anthropological applications.

At least three possible relations may exist between foraging strategies and group formation (modified from Schoener 1971): (1) group formation may have a neutral or negative effect on individual foraging efficiency but have other adaptive advantages; (2) groups may aggregate in response to resource concentrations, with no direct benefit arising from cooperative foraging; or (3) individuals foraging cooperatively may enjoy increased foraging efficiency. The first case may be important in many hunter-gatherer societies, where group living offers advantages for long-term reciprocity and reproductive strategy that outweigh short-term losses in foraging efficiency. The second case may range from temporary aggregations at locations with abundant resources to longer-term effects on settlement patterns (see discussion of Horn's model, below). The third case, in which groups form because of the advantages of cooperative foraging, may arise in several ways. Group formation may increase the per capita harvest rate by facilitating location of prey, by permitting division of labor in capturing prey, or by reducing the degree of foraging-area overlap (Schoener 1971, Cody 1971). Group foraging may also allow foragers to reduce *variance* in food capture rates (Caraco 1981, Pulliam and Millikan n.d.). Groups foraging from a central place and exploiting unpredictable food patches may increase per capita foraging efficiency through passive or active information sharing (Horn 1968, Ward and Zahavi 1973, Schaffer 1978, Smith 1981, Waltz 1982).

Thus, foraging strategies can affect group formation in a variety of ways and at two levels (at least): the foraging group and the settlement system. Although anthropologists have speculated on the role foraging strategies might play in structuring hunter-gatherer groups (see review in Smith 1981), detailed applications of foraging models to data on human group formation are much rarer. Three studies, one focused on settle-

ment patterns and the other two on foraging groups, are summarized here.

Settlement pattern. The geometric model of optimal dispersion formulated by Horn (1968) focuses on an idealized division of food resource distributions into two polar categories: stable/evenly dispersed resources and mobile/clumped ones. If each forager chooses an optimal settlement location with the goal of minimizing mean round-trip travel costs (weighted by the probability of locating any resource clump), the two resource distributions clearly favor two different settlement patterns. For stable/evenly dispersed resources the optimal pattern is dispersal of foragers in minimal social units, while for mobile/clumped resources it is aggregation in a central location (fig. 5). Any intermediate resource distribution would favor a correspondingly intermediate settlement pattern.

Several anthropologists (Wilmsen 1973; Winterhalder 1977, 1981b) have discussed the implications of the Horn model for studies of hunter-gatherer settlement patterns. The first detailed application of the model to hunter-gatherer data is that by Heffley (1981), who has examined aboriginal settlement patterns among three Northern Athapaskan Indian societies. Briefly, she found that in each society, settlement size and degree of aggregation changed dramatically over the annual cycle and that the "settlement patterns chosen appear to be . . . those which minimized travel costs (energy and time), given the foods available and their distributions" (p. 144). Although this test lacks any quantitative measure of travel costs, the Horn model does appear to be a useful explanatory device. However, it is worth noting that cultural attributes such as information-sharing networks and food storage introduced some complications not foreseen in the model.

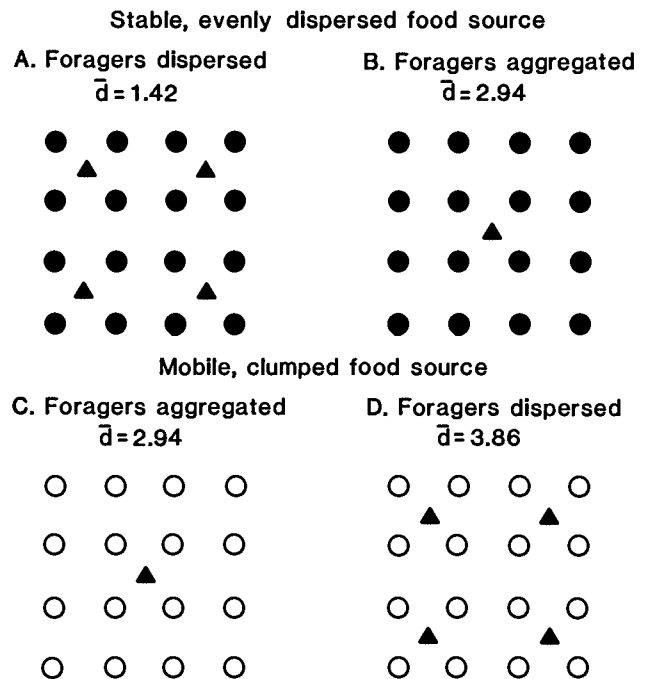


FIG. 5. The Horn model for optimal settlement pattern. Forager locations (settlements) are represented by triangles, the location of evenly dispersed, spatiotemporally stable resources by darkened circles, and the location of clumped, mobile resources by open circles. The mean round-trip travel cost from settlement to resource locations, weighted by the probability of locating the resource, is given by \bar{d} . This cost increases as resources become more mobile, clumped, and thus unpredictable in location. Travel costs per forager are minimized by a pattern of dispersed settlement where resources are stable/evenly dispersed and by centralized aggregation where resources are mobile/clumped, with intermediate resource distributions favoring intermediate settlement patterns. (After Horn 1968.)

Foraging-group size. Given the basic assumptions of optimal foraging theory outlined above, foraging groups should be expected to form whenever cooperative foraging yields higher benefits *per forager* than does solitary foraging. There is some ambiguity here, however, since several types of situations may arise in which individual interests are in conflict. Sometimes, for example, a forager could do better by joining a group than by foraging alone even though addition of this member to a group would depress the per capita returns for other members. Depending on their needs and abilities, individuals may differ regarding the group sizes that would maximize their per capita returns from foraging (Durham 1981). In such cases of conflicting interests and/or optima, the resulting compromise may take many forms, depending on specific constraints affecting decision makers. There have been very few attempts to model the effects of social interactions and conflicting interests on foraging strategies, although some recent progress has been made using concepts from game theory (Pulliam and Caraco n.d.). Before turning to the anthropological evidence relevant to this issue, I want to present two simple models of optimal foraging-group size in order to isolate some of the major determinants of both optimal size and conflicting individual preferences.

Both models apply to a population of foragers sharing a central base (camp, settlement, etc.) and making foraging trips of duration t away from this base, foraging alone or in groups of size n (where n reflects foragers' preferences in some way and is the primary variable of interest) and then returning to the base, where the harvest may be shared or divided in various ways. Although, as noted above, the optimal or preferred size of the foraging group may differ from one forager to another, for simplicity I will assume here that individuals who have the option of foraging together possess identical optima. How is the optimal group size defined? This will depend on several factors, but one of the most important is the *sharing rule* that governs disposition of the harvest.

Where the catch is equally divided among the members of any foraging group, who may then allocate their shares to immediate dependents or others (a pattern found among many hunter-gatherers, including the Inuit foragers whom I studied), we might expect each forager to attempt to join groups that will maximize the expected net energy return rate per capita, defined as

$$\bar{R}_n = \frac{\sum^n (E_n - E_r)}{t \cdot n}, \quad (2)$$

where E_n and E_r stand for food energy acquired and metabolic energy expended, respectively, and n and t are as defined above (Smith 1980, 1981). According to this formulation, which we might call the simple per-capita-maximization model, all foragers should prefer to be members of foraging groups of optimal size \hat{n} , defined as the group size for each foraging situation (patch, prey type, foraging period, etc.) that maximizes \bar{R}_n . Elsewhere I have presented and tested a variety of more specific hypotheses derived from this model (Smith 1980, 1981). The most obvious is that modal group size for each foraging situation should equal \hat{n} .

The simple per-capita-maximization model is a useful beginning, but it fails to predict what will happen when the interests of individual foragers conflict. Even when individuals have the same optimum, such conflicts may arise. If $\hat{n} = 1$, or if the number of foragers at the central place equals \hat{n} (or some whole-number multiple of \hat{n}), each individual's optimum can be realized, but when these special conditions do not apply some or all foragers must make compromises. For example, where the pool of foragers equals $\hat{n} + 1$ and each forager wishes to maximize his own net return rate (\bar{R}_n), once a foraging group

of size \hat{n} has formed the "odd person out" must decide whether he prefers to forage alone or in a group of size $\hat{n} + 1$. Under the stated conditions, his preference will be to join the group if and only if

$$\bar{R}_{\hat{n}+1} > \bar{R}_1. \quad (3)$$

In fact, whenever foraging groups are formed one at a time and the decision is whether to forage alone or become the n th member of a group, the optimal preference rule for per capita maximizers is to join if

$$\bar{R}_n > \bar{R}_1. \quad (4)$$

(Of course, if more than one foraging group is being formed, Equation 4 is too simplified, and the forager will prefer to "shop around" for the option offering the highest return.)

Once a *member* of a foraging group, however, a per capita maximizer will view things rather differently. Using the previous example, we expect a member of a foraging group of size \hat{n} to prefer to exclude any additional foragers. More generally, the preference rule for members is to favor additions to a group of size $n - 1$ as long as

$$\bar{R}_n > \bar{R}_{n-1}. \quad (5)$$

It follows that a conflict of interest between members and joiners will arise whenever

$$\bar{R}_{n-1} > \bar{R}_n > \bar{R}_1, \quad (6)$$

—that is, whenever the n th addition to a group will receive a higher per capita return from group foraging than from solitary foraging but will diminish the existing members' shares. Under the assumptions governing the simple per-capita-maximization model, the conflict of interest defined by Equation 6 should be a rather common occurrence. This model does not address the question of how such a conflict will be resolved; to predict this, we would obviously need to consider a number of factors structuring social interactions which lie outside of foraging theory proper.

As I have said, the simple per-capita-maximization model assumes an equal division of the group catch among members of the foraging group. Different sharing rules can produce quite different predictions concerning optimal group size and the situations defining conflicts of interest. One other sharing rule reported to apply to at least some resources among many hunter-gatherers will be considered here: settlementwide sharing. In this situation, the harvest is not divided among the members of a foraging group, but instead is returned to the home base (camp) and pooled with the catch of other groups and individuals residing there. Under such a sharing rule, the share each individual gets is a function of the total catch of all coresident foragers. Assuming equal division of the total catch from i foraging groups and j solitary foragers among N coresident "camp" or "band" members, this individual share equals

$$\frac{\sum^i n\bar{R}_n + \sum^j \bar{R}_1}{N}, \quad (7)$$

where \bar{R}_n is the net per capita return rate for n foragers over some foraging period, as defined earlier.

What is the optimum foraging-group size (\hat{n}) under these conditions? In the simplest case, in which only a single foraging group forms, the decision is whether to join the group or forage alone. The goal is to maximize the total return rate averaged

over all foragers in the band—the denominator in Equation 7. This currency is maximized by adding an n th member to the foraging group (and thus reducing the number of solitary foragers from k to j) as long as

$$n\bar{R}_n + \sum \bar{R}_i > (n-1)(\bar{R}_{n-1}) + \sum \bar{R}_i \quad (8)$$

(See Hill and Hawkes 1983 for a similar model but one with somewhat different assumptions and predictions.)

Equation 8 is a precise way of saying that where settlementwide equal sharing prevails, one's share is maximized by joining a foraging group as long as one's contribution to the group catch is larger than the catch one can obtain on one's own during the same period. This formulation presents a clear alternative to the simple per-capita-maximization model presented earlier. First, under settlementwide sharing the optimal group size (\hat{n}) is not always the size that maximizes each individual's per capita return rate (\bar{R}), but may often be larger than that (Hill and Hawkes 1983, Smith n.d.). Second, when settlementwide equal sharing prevails members of any foraging group will maximize their eventual returns by following the same preference rule for group size as potential "joiners"—that is, Equation 8 expresses the optimal decision rule for *all* foragers in the sharing network, and conflicts of interest over group size per se are avoided. (Which sharing rule is optimal and under what conditions one or the other will develop are separate issues. Also, this conclusion only applies under the specific assumptions governing Equation 8.)

While data for quantitative tests of such predictions are not inherently difficult to obtain, I am aware of only two studies that directly test hypotheses of optimal foraging-group size. Hill and Hawkes (1983) present data on the Aché that are inconsistent with both of the above models. Aché primarily hunt alone but form "pursuit groups" (temporary foraging groups) when they encounter certain prey types (white-lipped peccaries, coatis, and monkeys) and do so by calling for assistance when they sight these species. Hill and Hawkes's data show that individuals would maximize their own catch by pursuing even these species alone, while the band-level harvest would be maximized by forming pursuit groups as large as 12. The actual frequency distribution of pursuit group sizes is quite flat—there is no predominance of either large or small groups. Hill and Hawkes conclude that the apparently random distribution of foraging-group sizes they observed among the Aché is probably due to physical constraints on movement and communication and the need to maintain dispersal for efficient foraging with most prey types. Given the band-level sharing pattern characterizing meat (Kaplan et al. n.d.) and evidence that Aché

rarely fail to call for assistance when they encounter group-hunted species (Hill and Hawkes 1983), it seems likely that the band-maximization model is more applicable here than the simple per-capita-maximization model.

I have tested several hypotheses concerning optimal foraging-group size with data on Inuit hunting groups, focusing on the prediction that the modal group size in each type of hunting is the size that maximizes individual returns (Smith 1980, 1981, n.d.). For the ten hunt types examined, the per-capita-maximization hypothesis is supported in at least four cases and comes close in four additional cases (table 4). The two most problematic hunt types (beluga and winter caribou) are those with the largest mean group sizes, the greatest concentration of resources, and the closest approximation to a pattern of settlementwide sharing—but for these and other hunt types the band-maximization model fares no better than the per-capita-maximization model (Smith n.d.).

Although the results of these two studies provide rather equivocal support for optimization models of foraging-group size, there are several obvious complicating factors that render any overall evaluation of the approach premature. Insufficient sample sizes, small differences between the return rates for modal and predicted group sizes, and other statistical problems must be considered (Smith 1981: 64). In addition, the expectation of an exact match between modal and optimal group sizes for a single season assumes either that there are no year-to-year fluctuations in foraging conditions or that foragers have perfect information and can track shifting optima precisely. It is more realistic to expect that human foraging strategies, based as they are on individuals' own experiences in previous years plus culturally stored and transmitted information, will often be keyed to fairly long-term expectations and thus may violate predictions assuming short-term optimization. In short, simple models that view variation in group size as a device to maximize individual foraging efficiency and assume that foragers possess perfect information are perhaps best treated as starting points, with inconsistent results serving to suggest where further analysis of the determinants of group size is needed (cf. Durham 1981).

Models of optimal foraging-group size can be used to reflect more broadly on questions of anthropological concern. One example will serve to illustrate this potential. Canadian Inuit traditionally formed their largest camps in winter, and the usual explanation for this aggregation has pointed to the adaptive value of large groups of hunters for cooperative hunting of seals at their breathing holes in the sea ice (e.g., Balikci 1970: 58; Damas 1969b: 51). If the data from Inujjuaq (Smith 1980, 1981, and table 4) are at all representative, we can conclude that hunting groups much larger than 4–5 men would be sub-

TABLE 4
INUIT FORAGING-GROUP SIZE IN RELATION TO HUNT TYPE AND PER CAPITA NET
RETURN RATES (SMITH 1980, 1981)

HUNT TYPE (SAMPLE SIZE)	GROUP SIZE RANGE	MEAN GROUP SIZE	MODAL GROUP SIZE	NET CAPTURE RATE (KCAL/HUNTER/HR.)	OPTIMAL SIZE (R_{max})	NET CAPTURE RATE (KCAL/HUNTER/HR.)
Lake jigging (60).....	1–10	2.8	1	1,770	1	1,770
Ocean netting (69).....	1–5	1.6	1	21,350	1	21,350
Jig / goose (25).....	1–6	2.6	1	3,290	1	3,290
Spring goose (53).....	1–7	2.4	1	3,400	3	3,410
Ptarmigan (27).....	1–6	1.5	1	1,170	1	1,170
Lead / floe edge (54).....	1–10	2.7	1	2,210	2	2,340
Breathing-hole (19).....	1–8	3.9	4	1,350	3	4,120
Canoe seal (36).....	1–8	2.9	2	3,400	1	3,980
Beluga ^a (6).....	5–16	10.3	5–6	4,760
Winter caribou ^a (10).....	1–7	4.0	3,5	10,500	6–7	12,710

^a No modal group size occurs in the sample of beluga hunts, and group size frequencies peak bimodally for winter caribou hunts; for both of these hunt types, maximal net capture rate is averaged over two group sizes in order to meet a sample criterion of at least two hunts per return rate calculation.

optimal for breathing-hole hunts. Relevant demographic data and model life tables (Weiss 1973: table 25-40; Keene n.d.: table 3) indicate that a camp of 20-25 Inuit would usually contain this many adult males. This is substantially below the 50-200-person size range reported as characteristic of Inuit winter camps in the Central Arctic (Damas 1969b:51). Hence, quantitative data on group foraging efficiency are inconsistent with the standard ecological explanation for Inuit winter aggregation, and we need to reconsider the role foraging ecology may play in structuring this settlement pattern.

One suggestion is that larger groups of hunters provide more *reliable* returns from breathing-hole hunting and that this reliability compensates for their lower efficiency (Durham 1981:224-25). Another alternative hypothesis is that the fielding of multiple hunting parties, coupled with pooling or extensive sharing of the catch, is critical for reducing the variation in daily food supplies at the household level and that large camps are a way of assembling multiple parties and sharing networks (cf. McGhee 1972: 124). Both of these alternatives assume great importance for risk reduction, but risk (variation in daily food supply) can also be reduced by food storage at the household level. A third possibility is that large camps function as "information centers" to facilitate resource location and to coordinate foraging efforts so as to reduce or eliminate foraging area overlap (see theoretical discussion on this point above and in Smith 1981 and Moore 1981). Testing these and other alternative hypotheses would require detailed information on sharing networks, risk sensitivity, daily harvest statistics, breathing-hole distributions, the role of food storage, and the like. Accordingly, we can see how optimal foraging models, by allowing us to frame our hypotheses in a falsifiable form, are useful even when they fail to explain all we hoped they would in that they focus the search for additional determinants and thus stimulate further research.

LIMITATIONS AND FUTURE DIRECTIONS

Despite its qualified successes in analyses of nonhuman foragers and the recency with which it has been applied to humans, optimal foraging theory has been subjected to criticism by both biologists and anthropologists. Before concluding this review, then, certain key criticisms and limitations of the approach need to be discussed, along with suggestions as to the likely future directions for research on human foraging strategies. In briefly surveying these issues, it is important to keep in mind that foraging theory is not a finished product or dogma, but very much an evolving entity: foraging theorists are continually testing and revising their models and hypotheses and are generally well aware of the problems inherent in any analysis of complex, dynamic phenomena in terms of simplified and abstract models.

SIMPLIFICATION

Perhaps the most general criticism of foraging theory concerns the simplicity of the models and their failure to take into consideration the complexities of the foraging process. This criticism may seem especially cogent to anthropologists, who are well aware of the cognitive complexity of human foraging decisions and the unreality of simple optimization criteria in the face of culturally mediated norms and values. However, whether or not an analytical simplification is warranted cannot be determined in any absolute terms; rather, it depends on the goals of the analysis and the state of development of the discipline.

Levins (1966, 1968) has argued persuasively that any attempt to construct a model of some facet of nature must face up to the "modeler's dilemma": much as we might like it to, no model can simultaneously maximize generality, precision, and realism. Emphasizing any one of these virtues will usually exact

a cost—for example, increasing the realism of our assumptions or mechanisms will often reduce the range of conditions to which the model can be applied or the precision of the predictions it will generate. Thus any use of models involves some implicit or explicit ranking of these three attributes by the modeler. The optimum toward which we aim our models will be determined—as in any optimization problem—by a combination of goals (what are the strategic objectives of our research? how do we plan to test the model?) and constraints (what relevant theories are available? what kinds of data can we hope to collect?).

Although optimal foraging models can be adjusted, to some degree, to emphasize one or another attribute or combination of attributes (see Moore 1981: 196-97; Winterhalder 1981a), I would argue that in comparison with orthodox cultural ecology most existing models emphasize generality and precision at the expense of realism. Hence, the approach is most attractive to those ecological anthropologists who favor a strategy of explaining particular cases in terms of general theory, utilizing rigorous testing of hypotheses. Those who favor detailed, realistic analysis of particular foraging societies as an end in itself or more qualitative analyses will find foraging theory less appealing.

REDUCTIONISM

Many criticisms of the application of foraging theory to humans focus on the dangers of borrowing a theory developed in biology to explain phenomena in the domain of social science. Lee (1979:434), for example, has argued that "mechanical models drawn from animal behavior and animal ecology, however sophisticated, cannot do justice to any but the simplest of cultural ecological phenomena." Similar judgments are commonly expressed by anthropologists wary of the dangers of biological reductionism (see Keene 1983 for an extended version). These criticisms rarely cite empirical evidence as grounds for rejecting the extension of foraging theory to humans, tending instead to appeal to a priori issues such as the genetic determinism allegedly underlying any model from evolutionary biology. As I have pointed out, such reductionist assumptions are neither necessary nor frequent in optimal foraging studies, and hence criticisms of this sort are usually misdirected.

Since humans develop and transmit alternative foraging strategies through cultural systems that have no parallel in the nonhuman world, it is certainly possible that the logic of foraging theory is inapplicable. In the absence of any well-developed and empirically tested theory of cultural evolution, however, it seems premature to reject the application of foraging models to humans on these grounds. Given the complicated decision making and information processing assumed in many foraging models and the often explicit links to micro-economic theory, it might more plausibly be argued that foraging models are better suited to human foragers than to less intelligent species.

A related criticism scores foraging theory for being limited to analyses of individual decisions. For these critics, the individual focus is a distorting reductionism that factors out the complexity of social interactions and obscures "the social dialectic that exists between the needs of the individual and the needs of society" (Keene 1983). This type of criticism strikes me as plausible but misplaced. Optimal foraging theory certainly is not suited to the task of accounting for all the social interactions and constraints that structure foraging decisions. However, few if any scholars employing it have suggested that it is. Rather than reject the approach because it is not a complete framework for considering foraging in a social context, we might consider how it might be articulated with other explanatory frameworks to provide a more comprehensive view.

It is also important to remember that until simple models of foraging strategy have been empirically tested, we really don't know to what extent they might succeed in accounting for observed patterns—regardless of any dogmatic statements to the contrary.

Criticism of foraging theory for focusing on the level of individual decisions is logically linked to several venerable, ongoing, and perhaps unresolvable debates concerning the validity of reductionism and “methodological individualism” in a variety of disciplines (such as economic anthropology, evolutionary theory, psychology, political economy, and sociocultural anthropology, to name only the more relevant fields). To a large degree, the merits of a “top-down” versus a “bottom-up” approach remain a matter of preference, not yet being amenable to strictly logical or empirical assessments.

COST-BENEFIT CURRENCY

A more tractable criticism concerns the validity of the simple currency of energetic efficiency employed in most foraging models. The charge here is that the reliance on energy harvest rates is misleading for a potentially large number of cases in which other nutrients or nonfood qualities of prey are of equal or greater importance (Keene 1981, 1983; Cashdan 1982; Jochim 1983; cf. Pyke, Pulliam, and Charnov 1977:143). Actually, several models of diet breadth incorporating nutrient constraints have been presented with the aim of rectifying this limitation (e.g., Pulliam 1975, Altmann and Wagner 1978, Belovsky 1978, Rapport 1981). Among anthropologists, the problem of multiple nutrient (and nonfood) requirements has been tackled with linear programming models adapted from microeconomics (see reviews in Reidhead 1979 and Keene 1979, 1982). Nevertheless, the great majority of optimal foraging studies in biology and anthropology continue to employ a simple energy-time currency. The reasons are obvious: models with simple currencies are easier to construct, manipulate, and test. But is this simplification justified? There is not room to review the relative advantages of complex and simple currencies in any detail here, but Levins's model of models (see above) is relevant to this issue. While the complex currencies of linear programming appear to be more precise and realistic, they accordingly reduce the generality of the conclusions one can draw from particular applications.

Furthermore, the gains in precision and realism may prove to be partly illusory: (1) Nutritional needs and the effects of deficiencies over various time spans are poorly understood at present (Keene 1981:187). (2) Multiple currencies whose components must each be precisely measured inevitably increase the probability of random and systematic error in empirical evaluations. (3) One can question the realism of models that require foragers to assess the relative benefits of 100 mg of niacin, say, vs. 50 mg of calcium. (4) The assumption of most linear programming models that foragers search for different prey types one at a time seems less realistic than the assumption of the fine-grained diet-breadth model that search is generalized over all prey types within a patch (Smith 1980:281–82; Durham 1981:221; O'Connell and Hawkes n.d.). (5) The use of nutritional needs to predict foraging choices requires either that foragers predict the future with great accuracy or that they sacrifice much efficiency in order to minimize daily (or monthly) variation in nutrient intake. In sum, the benefits of linear programming models, like those of any increase in model complexity, are quite mixed (cf. Hawkes et al. 1982:395 n. 3). Nevertheless, they do offer one way to pursue the optimal foraging approach where the simple energy-time currency seems, or proves, unreasonable. Complex currencies should be most useful for foragers relying heavily on plant foods (which tend to vary in nutritional composition more than do meats), for those with major raw-material needs such as hides for clothing, and of course for those whose foraging articulates with a market economy.

An important criticism of foraging theory concerns its limited temporal and spatial scale (Pyke, Pulliam, and Charnov 1977: 139–40; Katz 1974; Moore 1981; Jochim 1983, n.d.; Keene 1983). The time-scale of optimization should vary with the ultimate goal (fitness and/or utility functions) of the forager and the patterns of environmental variation and behavioral capabilities pertaining to a particular adaptive problem. Fitness and survival are lifetime measures, while foraging models typically maximize short-term return rates. Obviously, short-term maximization is easier to incorporate into both models and empirical tests, but it is a perfect surrogate for long-term measures only so long as “behavior at one point in time does not alter the optimal behavior at another point in time” (Pyke et al. 1977:139).

It is not always clear how one should apply this rule to particular situations, but suggestions have been made about the types of situations in which short-term optimization assumptions will be inappropriate (see Pyke et al. 1977:139–40; Winterhalder 1981a:17–18). For some of these situations it may be possible to formulate simple models that can predict the long-term optimization solution (e.g., Katz 1974; Craig, Angelis, and Dixon 1979). The effect of cultural transmission on the time-scale of optimization is not yet known, but given the human capacity for foresight and cultural storage of information it seems intuitively likely that deviations from short-term foraging optimization will be more prevalent in our species than in noncultural ones. This of course provides an excellent opportunity for theory construction and empirical research in ecological anthropology.

Criticisms of the restricted spatial scale of current foraging models are less common but perhaps equally important in the human case. While existing models generally assume that individual foragers (or small groups) act in isolation, abundant ethnographic evidence points to the importance of regional interactions in structuring and constraining foraging behavior—presumably as a result of the tremendous capabilities for information flow in a cultural species. Although work extending the spatiotemporal scale of foraging theory has scarcely begun, it promises to be quite productive and interesting (e.g., Moore 1981) and will certainly increase the anthropological utility of the theory.

UNCERTAINTY AND RISK

The final set of criticisms to be considered here concerns the limitations of deterministic models given the stochastic nature of the foraging environment. That is, most existing models in foraging theory ignore the existence of stochastic variation by assuming that foragers can obtain perfect knowledge of relevant features of the environment and that they are concerned only with maximizing mean returns, regardless of variation around the mean. The criticism of determinism (in this particular mathematical sense) is directly analogous to ones that have been raised in microeconomics and decision theory (e.g., Simon 1957; Hey 1979, 1981). As in these latter fields, stochastic variation in the foraging process presents two distinct problems (Stephens and Charnov 1982; cf. Knight 1921, Hey 1979): *uncertainty* due to imperfect information and *risk* due to the consequences of unavoidable variation. These are sometimes conflated by both critics and model users, but they have rather different implications and therefore deserve to be considered separately.

Whenever a forager has less than perfect information about present and future states of the environment as these influence foraging costs and benefits, it cannot be certain of the optimal strategy for a particular situation. It must then either choose the strategy that has greatest probability of being optimal (if it can estimate that probability), “play it safe” with a compromise mix of strategies, or invest some time and effort in sam-

pling the environment in order to increase its information fund. The last option is probably one that is commonly chosen, and foraging theorists have recently begun considering the role of sampling, especially the trade-off between the costs of obtaining more information and the benefits of increased certainty (e.g., Oaten 1977, Krebs, Kacelnik, and Taylor 1978, Hughes 1979, Green 1980, Orians 1981). Existing work thus demonstrates that the unrealistic assumption of perfect information can be attacked directly by building models that relax this assumption. Once again, however, the modeler's dilemma suggests that we can increase the realism of our models only at some cost to their precision or generality. Imperfect-information models are indeed generally more complicated, predict a greater number of possible outcomes, and require that a larger number of variables be measured in empirical tests.

The problem of risk concerns not uncertainty per se, but the effect of variation in foraging returns on the forager. Even when it is possible to estimate precisely the probability distributions of foraging returns under different conditions (via sampling, information sharing, or the like), a forager may benefit from adopting strategies that are adjusted to the variation in foraging returns and not just the expected (mean) returns. In the terminology of decision theory, such a forager is said to be "risk-sensitive" and may be either "risk-averse" (concerned with reducing or minimizing variation) or "risk-prone" (attracted to increased variation) (Caraco 1981, Keeney and Raiffa 1976). Most foraging models, including the ones discussed earlier in this paper, are deterministic, assuming that the optimal solution maximizes the mean return rate from foraging regardless of the impact of the associated variance. How realistic is this feature?

It has been suggested that "an overriding concern of many human foragers, in fact, may be to minimize risk (maximize the reliability of food procurement) rather than to maximize the efficiency with which any food nutrient is acquired" (Cashdan 1982:1308; see also Durham 1981; Keene 1981; Gould 1982; Jochim 1982, 1983, n.d.; Wiessner 1982). Since precise evidence on this point is generally lacking, a statement like Cashdan's should be considered a hypothesis rather than an empirical generalization. It is also an incomplete hypothesis until some constraints are specified (e.g., since the minimum of zero variance could always be achieved by refraining from any foraging, the actual goal must be to choose from the set of possible options the solution that will satisfy food needs with minimum variance or the option with the optimal mean/variance combination, as discussed below). Nevertheless, a plausible case for the importance of risk can be made. Especially where food storage is ineffective or costly and temporal variation in resources is substantial, we might expect human foragers to deviate from the pattern of simple efficiency maximization.

Growing awareness of the potential importance of risk-sensitive foraging has recently led to a flurry of activity among foraging theorists. Models treating foraging decisions as risk-sensitive are now available for most of the standard decision categories, including prey choice (McNair 1979, Caraco et al. 1980), patch use (Green 1980, Stephens and Charnov 1982, McNair n.d., McNamara 1982), group size (Thompson, Vertinsky, and Krebs 1974; Caraco 1979a, b; Pulliam and Millikan n.d.), and time allocation (Caraco 1980).

One general conclusion that has been reached by several theorists (Caraco, Martindale, and Whittam 1980, Pulliam and Millikan n.d., Stephens 1981) is that risk-sensitive strategies can be predicted from the relation between the expected benefits of alternative choices and the forager's minimum requirements over some reasonable time period (e.g., the period within which starvation would occur if the minimum were not obtained). This finding has been formalized as the "extreme variance rule" (Stephens and Charnov 1982): to minimize the probability of falling critically short of required food intake, always choose the strategy with the *minimum* variance when expected returns are *greater* than the critical requirement, and

always choose the strategy with the *maximum* variance when expected returns are *less* than this requirement.

The prediction that conditions of scarcity should elicit risk-prone choices may strike many as counterintuitive, but it can be explained by the idea that under conditions of extreme food shortage a forager should be willing to take greater risks (accept greater variation) in order to increase its chances of obtaining a return at the upper end of the probability distribution—and hence, perhaps, above its minimum requirements. However, further work has shown that the extreme variance rule should hold only when the available alternatives all yield the same mean return but exhibit different amounts of variation around that mean. A more general model, of which the extreme variance rule can be shown to be a special case, has been developed by Stephens and Charnov (1982) and can be used to predict which of the mean/variance combinations available to a forager is optimal—that is, minimizes the probability of falling below minimum requirements (fig. 6). Stephens and Charnov suggest that, under realistic assumptions about the stochastic distribution of alternatives available to foragers, risk-sensitive optima may often differ little from optima predicted by simpler efficiency-maximization models and that actual risk *minimization* may be quite rare. This result suggests that deterministic

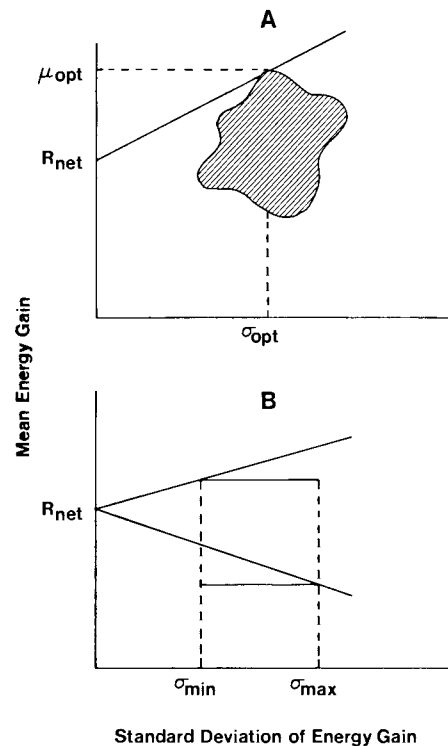


FIG. 6. A, a general model of risk-sensitive foraging choices. The forager is assumed to choose from some set of available alternatives defined by paired means and standard deviations of energy gained over some finite period of time (hatched area). The goal is to choose from the available set that combination of mean and standard deviation that will minimize the probability of obtaining less than R_{net} —the net energy required to survive this period. The optimal choice is found by constructing the line from R_{net} (indexed on the mean gain axis) to the available set that has the steepest positive slope; the optimal mean/standard-deviation pair occurs at the point of tangency. B, the special case of A in which options differ in their variances but not in their means. The rule given in A still applies, but in this case it can be summarized as the "extreme variance rule": if the expected gain of the options is greater than R_{net} (upper line), choose the option with minimum variance, but if the expected gain is less than R_{net} (lower line), choose the alternative with maximum variance. (Both graphs after Stephens and Charnov 1982.)

foraging models may actually be quite robust in their predictions, even when foragers behave in a risk-sensitive fashion.

Although the various stochastic models of foraging have not yet been applied to human foragers, the fact that they can be developed answers some of the criticisms anthropologists have raised against optimal foraging theory. Ironically, stochastic models may be less critical for humans than for other species, given our expanded cognitive and cultural capabilities for reducing uncertainty and buffering variation (e.g., through information exchange, food storage, and trade). In any case, application of models of risk-sensitive foraging provides one avenue to future developments in human foraging strategy analysis. Other likely areas of future development, spurred by the criticisms discussed above, include paying much greater attention to the effects of social interactions on individual optimization and linking the optimization framework to larger-scale problems in ecological anthropology and political economy such as the evolution of hominids, hunter-gatherer population dynamics, resource intensification and agricultural origins, ethnic interactions, conservation and resource management, and sociopolitical change (for some initial attempts along these lines, see Moore 1981; Hill 1982; Bettinger and Baumhoff 1982; Smith n.d.; Winterhalder 1981c, 1983a).

CONCLUSIONS

The models of optimal foraging theory surveyed in this article are drawn from the field of evolutionary ecology and analyze foraging strategies as the joint product of environmental and behavioral "givens" (constraints) and the goals and choices exhibited by foragers attempting to maximize the benefits obtained per unit foraging time. As discussed herein, the recent application of these models to human foragers has been justified in several ways: by the renewed claim that our species's behavior is fundamentally a product of Darwinian adaptation, by the assumption that *cultural* evolution mimics many of the results of natural selection, and by the portrayal of foraging theory as a variety of economic logic applied to production choices in nonmonetized foraging economies.

The predictions that flow from optimal foraging theory are at once more general and more precise than is typical of most research in ecological anthropology. As a result, hypotheses are subject to fairly direct empirical support or refutation, and theory building can proceed rapidly. Because foraging theory allows for the generation of great diversity from a few general decision rules, it offers hope of parsimoniously explaining the heterogeneity of human foraging strategies that has proved such a stumbling block for orthodox cultural ecology. Dietary specialization or opportunistic omnivory, individualistic production or communal effort, nomadism or sedentism, dispersed settlement or nucleation—all these oppositions and more can potentially be accounted for within the unified framework provided by foraging theory. The theory can also be used to generate explanations or predictions out of reach of intuitive arguments or to predict the likely behavioral patterns of extinct foraging societies or hominid species, given some knowledge of their technology and environment.

It must be recognized that, like any other "middle-level" theory, optimal foraging models offer a less than complete perspective on the diverse patterns of foraging behavior exhibited by humans (or by wolves, bees, or hummingbirds, for that matter). Obviously, foraging theory should not be used unaided if we hope to comprehend the full richness of human foraging in all its dimensions—ecological, economic, social, and cognitive/symbolic. In addition, existing foraging strategy models exhibit some specific shortcomings and limiting assumptions that require attention, as discussed above. It would be unfortunate if enthusiasts were to apply the models to particular cases in "cookbook" fashion. It would be even more unfortu-

nate if the limitations of foraging theory were to lead anthropologists to dismiss it before its potential had been empirically assessed.

Despite its limitations, optimal foraging theory has distinct advantages and may accomplish much within its modest explanatory framework. The research summarized here, representing some initial applications of the theory to human economies, gives a preliminary indication of the anthropological potential of this approach. Given these results, foraging theory promises to improve our understanding of human foraging behavior in significant ways. I suggest that it will be even more useful if extensive efforts are made to integrate it with other analytical approaches. If human foraging behavior results from a combination of optimizing decision rules and complex socioecological constraints, then we can hope to construct theory that combines these rules with general principles of adaptation and culture process, paying heed in our analyses to the unique environments, systems of production and exchange, and social formations characterizing particular societies. In this manner, we may be able to generate more powerful and comprehensive explanations of hunter-gatherer behavioral diversity than have heretofore been achieved.

Comments

by ROBERT L. BETTINGER

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Smith properly discounts the common objection that optimal foraging models are simplistic and reductionist; the point of science, provided we grant that anthropology is a science, is to simplify the real world by distinguishing between extraneous facts and informative data. This, as Kuhn (1962) points out, is the job of paradigms and, in a more specific sense, of theories. Whether this necessary simplification is justified is measured in terms of how well important data are accounted for and the parsimony of the accounting. It is incumbent on those who reject optimal foraging models on the grounds that they are too simple to provide an equally parsimonious explanation of the behaviors in question or to show why these behaviors are unimportant. Without this demonstration, such criticisms are just so much carping.

More legitimate are reservations regarding the degree to which optimal foraging models can be applied to specific anthropological problems. Since these models are energetically based, at its simplest the problem entails measurement of caloric returns and expenditures for particular resources. In archaeology, where there are uncertainties about the tactics employed in resource procurement, this is complicated enough. The uncertainties are compounded as estimates of search time within specific patches and the distribution of patches within habitats are added. It remains to be seen whether the rapid accumulation of these uncertainties in even the simplest of models will render optimal foraging models useful as anything more than rough analogies in archaeology; in the end, optimal foraging may find a role in paleoanthropology similar to that of systems theory—more as a way of looking at things than as a source of rigorous quantitative models.

The situation is more favorable in ethnography, and it is probably not far wrong to suggest that one of the more powerful uses of optimal foraging models, particularly those of diet breadth, patch selection, and foraging interval, is in relation to ethnohistoric situations in which contact changes of environment and technology effect changes in native hunter-gatherer adaptation. The studies of Winterhalder (1981) and O'Connell and Hawkes (1981) are of this sort, and one suspects that optimal foraging theory would provide equally illuminating insights into postcontact adaptive change (e.g., cessation

of seed gathering) in California and the Great Basin. Of course, the principal advantage of ethnographic settings is the ability to measure or infer from historical accounts return rates and resource distributions.

It is worth noting in this regard that the ethnographic hunter-gatherers at our disposal for studies of this sort constitute a peculiar sample of global hunter-gatherer adaptations through time. It has, of course, long been axiomatic that contemporary hunter-gatherers are unusual in the sense that they occupy marginal habitats. I would argue, nevertheless, that the foraging behaviors of nearly all these groups might be more characteristic of optimal habitats. This is because few if any of these groups support themselves exclusively by foraging for wild plants and animals and as a rule the number of individuals regularly exploiting these resources is substantially less than in late precontact times. Hunting and gathering under these conditions are likely to be productive, at least for short intervals, as resource abundance may be relatively high and competition for resources low—although postcontact concentration near European settlements to a degree acts to offset this. In these circumstances it is more likely that a forager will be acting optimally by maximizing the rate of food intake per unit of time invested. Under more pristine circumstances, in contrast, one suspects that the abundance of resources would in many cases be lower, owing to exclusive reliance on them, while the area in which they could be obtained would be restricted by competing foragers in the surrounding region. As rate of return and habitat availability drop, it may often be that a highly selective forager, optimizing rate of return per unit of time, would fail to meet his subsistence needs over some critical period, while a less selective forager accepting suboptimal rates of return would satisfy his (cf. Schoener 1974:4170).

The point is that most of the optimal foraging models that have been devised and actually put to the test define optimality in terms of rate of return and assume no limiting constraints of caloric intake or habitat availability. It is my guess that these models are less universally applicable than believed and that the behavior of hunter-gatherers more crowded in space might be more closely approximated by models into which such constraints might be built—linear programming, for example.

Smith's closing point—that optimal foraging models should not be prematurely dismissed—is especially well taken. Even where these models fail to predict subsistence behavior, they will sharpen our perception of the economic, political, and social structures that may take precedence over caloric efficiency in determining adaptive strategies. We have only begun to examine potential anomalies of this sort. Agriculture is generally conceded to be very high in cost, yet some agriculturalists in the American Southwest, accepting these costs, exploit only the least costly wild plant and animal resources and ignore others that are more costly yet apparently still less expensive than cultivars. In California, acorn procurement—evidently very high in cost—persisted historically long after most traditional subsistence activities had disappeared.

Understood not as iron-clad laws violated only by fools courting extinction, but merely as expectations that follow when specific goals are pursued, optimal foraging models seem certain to play a pivotal role in future studies of human adaptation.

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Smith has done an excellent job of synthesizing the literature on optimal foraging theory. Because it is recent (nonexistent fifteen years ago), novel, and controversial, those working with, especially, human foragers appear to be divided into two camps: those who ignore/oppose it and those who appear to devote all of their attention to it. However, Smith himself cautions that optimal foraging models are shortcuts and that they can lead

scholars astray. I do not see them as a replacement for the more traditional ("realistic") kind of study; rather, they should be viewed as an additional tool for our ethnographic foraging. Smith seems to agree when he argues that optimal foraging theory not be employed in isolation; would that this were so. In fact, his table 1 not only excludes social and cultural cost/benefit criteria, as well as sociocultural constraining variables, but gives no indication as to when or how these latter considerations would be "plugged in." It is this sort of simplification that has annoyed, turned away, and even infuriated those who prefer more detailed studies that can be compared among themselves. My point is not that optimal foraging theory should be discarded in favor of these, but rather that it is very easy to fall into the pattern of applying its models in cookbook fashion.

A couple of additional examples associated with history and contextual information point up yet other difficulties. For instance, Smith criticizes Feit's view that the Waswanipi actually "manage" their resources, arguing instead that they are simply increasing foraging efficiency. While I agree that there has been no long-term resource management, Feit's work among the Waswanipi was done in the 1960s and '70s, at a time when it would have been difficult to claim that these Indians were not both aware of the need and competent to manage their resources. Thus, Winterhalder's dilemma as to whether the people of Muskrat Dam Lake were increasing foraging efficiency or practicing resource conservation would seem to be a false dichotomy. Couldn't they have been doing both? And why didn't Winterhalder ask the people why they shifted to other patches? Both studies, while they do contain a limited amount of historical data, illustrate the error of assuming that the habits of recent groups reflect those of aboriginal people. In some cases this may be so, but how can we be certain in the absence of cultural-historical and demographic data?

Smith seems to ignore certain key variables when, viewing foraging-group size among the Central Inuit, he attempts to account for the marked discrepancy between the ecological expectation of 20–25 persons in winter camps and the reported 50–200. Beginning early in the 20th century, Inuit had access to store goods and credit; such access would have had the potential for making large groups relatively risk-free (Damas 1969c:119–21). Furthermore, the introduction of guns reduced caribou herds in some areas after the 1920s but made coastal seal hunting easier, thereby increasing returns (Balikci 1964:51–57, 71). Thus, the existence of larger groups should not be surprising.

Optimal foraging theory does have possibilities, and I do not believe that it should be ignored. If it is to be of value, however, far more robust models will need to be constructed—i.e., they must not treat fundamental cultural factors from other aspects of the system as trivial or capable of being held constant.

by VALDA BLUNDELL

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Smith endorses the anthropological application of optimal foraging models because, he claims, they allow us to predict behaviour and to "build theory." As I understand him, the logic of this research strategy is as follows: If we assume that individual foragers "will seek to maximize net return per unit foraging time," then we can construct models that permit us to predict certain behaviours in a range of human hunter-gatherer societies. According to the theoretical assumptions of evolutionary ecology, such maximizing behaviour will occur under certain conditions as the result of Darwinian selection for strategies that maximize individual fitness. Such "conditions" include those in which foragers confront "time shortages," "environmental hazards," or "the threat of starvation." Given

adequate observational data, we can determine whether these predicted behaviours do, in fact, occur.

My query to Smith is: Where does such a research strategy take us? Is a belief that maximizing behaviour results from selection for fitness necessary for this strategy, or will other assumptions lead to the same models? For example, does a behaviourist assumption that via conditioning humans will learn to emulate more efficient foragers lead to the same predictions (cf. Alland 1975:69–70)? Early in his paper Smith clearly states that foraging theory “is anchored by a set of assumptions derived from current views of adaptation via natural selection. Specifically, it assumes that foraging behavior has been ‘designed’ by natural selection to respond to changing conditions in a way that yields the greatest possible benefit for the individual forager’s survival and reproductive success (Darwinian fitness).” However, a bit farther on he suggests that one could get to optimal foraging models via alternative theoretical routes: “Actually, there are several ways in which application of foraging theory [he must mean “models” here] to human foragers might be justified.” He then lists not only the theory of natural selection, but also theories of cultural evolution and neoclassical economics. Although it would seem that each of these theoretical approaches predicts foraging strategies that “maximize fitness,” the processes that these theories advance to explain such behaviour are quite disparate. However, Smith dismisses any interest in evaluating these competing explanations, stating that “the manner in which humans might come to exhibit foraging strategies that maximize components of fitness . . . can be ignored, predictions from the theory [again, he must mean “models” here] being directly tested against observed patterns of behavior.”

Given Smith’s theoretical pliancy, what do we learn by testing foraging models? What does it mean, for example, when the behaviours predicted by such models are “not consistent with the field data” or are “equivocal” as in the case of the applications he summarizes? Does it mean that certain actors are not maximizing fitness (because the conditions necessary for Darwinian selection to operate are not present or because of overriding influences of multiple constraining variables), or does it perhaps mean that the underlying assumptions of ecological anthropology, or some other theory, are wrong? The point, of course, is how we are to know which of these may be the case in a given situation.

For these and other reasons I would argue that as anthropologists we must go beyond prediction to a search for the laws that underlie the behaviour we observe. Our research strategies must permit us to compare the relative merits of alternative explanations of observed behaviour. As Smith is well aware, many anthropologists find the Darwinian assumptions of evolutionary ecology, when applied to humans, highly implausible. Alland (1975:59), for example, sees certain formulations of this “school” as tautologies, arguing that “to say that adaptive traits are those which are present in systems, or that those traits which are present in systems are adaptive, adds nothing to our understanding of process.” Alland and others question the plausibility of theories that ignore the maladaptive aspects of human behaviour and the influence on behaviour of mental structures. “Humans,” he writes (p. 68), “are the only species in which too much thinking may lead to false solutions.” On the basis of my own fieldwork among Australian foragers, and along with other so-called structural ecologists, I have suggested that an understanding of behaviour must be integrated with an understanding of brain-based cognitive models (Blundell 1980, 1982).

It is not, however, my intent here to evaluate the relative merits of the theoretical assumptions of the optimal foraging theorists, the mentalists, or, indeed, the structural ecologists. Rather, I wish to argue for research strategies that return hypothesis testing to the level of theory by clearly specifying how

the results of tested predictions will affect the credibility of the basic theoretical assumptions. This I find lacking in the research strategy that Smith has described. Smith does not return in his critique to assess the assumptions of theories of natural selection (or those of the competing theories of cultural evolution or neoclassical economics). While prediction in science is possible without explanation, I do not think we should ignore questions regarding the processes that underlie human behaviour. If humans do, under certain conditions but perhaps not under others, “maximize components of fitness,” then I consider it important to ask why and how this comes about. If anthropologists who advocate the theories of evolutionary ecology do not evaluate the implications of their findings for their assumption of Darwinian selection for fitness, their view of “how the world is put together” will remain, as Alland warns (1975:69), a “just-so story” rather than a plausible scientific explanation of human behaviour.

by ELIZABETH CASHDAN

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Smith has provided an excellent review of optimal foraging theory and its anthropological applications. Attempts to use the models and theory of other disciplines often rely on a textbook knowledge of the other field and risk being seriously out of date. Smith’s review, however, is current and is a useful guide to new developments in the field. I find his reply to the theory’s critics convincing and his appraisal of the theory’s limitations refreshing.

The criticism that optimal foraging models are too mechanistic to apply to humans is especially interesting, since they are based on models from microeconomics. I think Smith may be right in suggesting that “it might more plausibly be argued that foraging models are better suited to human foragers than to less intelligent species.” I suspect that the genesis of this criticism lies in the fact that optimal foraging theory, like microeconomic theory, views individuals as strategists, hence paints a rather unappealing picture of human nature. And because the models are general ones, as Smith points out, many variables are of necessity left out. The formalist-substantivist debate in economic anthropology, which I think had some of the same roots, presented two options: formal models from microeconomics or substantivist description. A productive response would have been the development of new formal models by anthropologists to deal with the societies and problems of concern to them. Ecological anthropologists can learn from this old debate; if the models don’t fit, make new ones. “Substantivist” cultural ecology is not the only alternative.

Studies of hunter-gatherers have been long on empirical generalizations and short on real theory. For this reason, the current interest in optimal foraging theory is most welcome. Archaeologists who try to understand the Pleistocene by generalizing from ethnographic descriptions have faced the problem that all extant foragers have direct or indirect contact with nonforagers and with the products and markets of the world capitalist system. But this is no cause for despair. While we cannot view modern foragers as “representatives” of prehistoric foragers, the real point is to understand the ways in which environmental and cultural variables interact and influence one another. Modern foragers are as relevant to this effort as their ancestors, and these relationships, once they are understood, should enable us to understand the behavior of foragers in a wide range of contexts, including the Pleistocene. Optimal foraging theory shows promise in enabling us to uncover these relationships. The study by Winterhalder (summarized by Smith above) is a good example because it uses changes in search and pursuit time brought about by modern technology as a way of testing predictions derived from the diet-breadth model.

Like Smith, I think that the models of optimal foraging theory can yield important insights into the behavior of human foragers. However, I am concerned that rigorous "tests" of optimal foraging theory have been oversold. Empirical tests of these models have shown that in most cases predictions are "fairly close" to observed behavior. How much observations must differ from the models' predictions for the models to be reasonably rejected is impossible to say, because these are deterministic models and they ignore the probabilistic character of the evolutionary process. To reject a probabilistic hypothesis one needs not only an expectation, but also some indication of the magnitude of variation about it. This we do not have. For this reason, and because the models are very general (hence "unrealistic"), attempts to falsify them with precise caloric data may be a waste of time. Such models are useful not because they are directly testable, but because they generate insights. Several of the examples discussed by Smith (not least those from his own work) illustrate well how such insights may be generated and creatively applied.

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In this comprehensive discussion of optimal foraging theory, Smith shows that one of its weaknesses lies in the choice of a simple energy-time currency. It is clear that this choice allows the construction of a general and comprehensive model which describes the strategies employed. However, as the author points out, it may, in specific cases, lead one to draw wrong conclusions. More careful comparative analyses of actual nutritional situational values and control values would provide a better basis for an understanding of foraging strategies. Especially where seasonal fluctuations diminish the variety of normally mixed diets and create temporary nutritional bottlenecks, the food-acquisition strategies observed can thus be better explained. I believe it is not correct that little is known about the interdependence between nutritional deficiencies and the manifestation of appetite (partial hunger) or craving for specific substances; "nutritional wisdom" has been greatly underrated, and the abundant literature on the topic has been largely neglected by anthropologists (but see Silverstone 1976 and Kare and Maller 1977).

In hazardous environments and in regions where, apart from the general problem of adequate energy supply, the further problem of the adequate availability of specific nutrients exists, special, seasonal hunting and gathering activities should not be viewed as aspects of primary energy acquisition. It can be very meaningful to expend large amounts of energy in order to obtain small quantities of vitamin C, certain essential amino and fatty acids, or specific minerals. Thus, the exclusive gathering of up to 100 kg of lily bulbs per family by Siberian hunter-pastoralists over many weeks in autumn (Vainshtein 1980:194-97) cannot be considered primarily as a means of energy acquisition; it is pertinent that in the arctic zone there is preferential gathering of edible plants with the highest content of vitamins, and notably ascorbic acid (Rodahl 1944, Porsild 1953). Other nomadic populations, such as peripatetics who often sell their goods and services to patchily distributed customers in exchange for food (Rao and Casimir 1983, n.d.), sometimes adapt their migrations, in certain seasons, to the availability of fresh fruits rather than to the availability of their principal energy source, wheat flour.

Linear programming (Calavan 1976, Keene 1981, Johnson and Behrens 1982), which takes into account fluctuations in nutritional status as well as a broader spectrum of nutritional needs, often constitutes a better analytical method. Where precise control value figures for specific communities are unavailable, the Recommended Dietary Allowances (1980) represent

a good basis for the comprehension of nutritional control values, and when a given community has a staple food its chemical analysis can help identify eventual nutritional deficiencies. If ecological constraints are also taken into consideration, it is easier to recognize the mechanisms which trigger specific (e.g., seasonal) foraging activities aimed at maximizing the intake of certain essential nutrients.

A broader theory of optimal foraging which considers specific, often seasonally fluctuating nutritional problems is still lacking. More intensive collaboration between nutritional physiologists, food chemists, and anthropologists would most certainly help create such broader perspectives.

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Traditionally, anthropological models of human behavior have been relatively weak because they have not been derived from explicit and well-developed theories. The models that Smith reviews are important not only because of their particularly interesting predictions about human behavior, but also because of their solid foundation in a specific theory. That this theory is a biological one is disconcerting to some, but for anthropologists interested in the development of more general theory biology is one of the most logical sources of ideas.

The relationship between biology and the social sciences has been a long and complex one, one in which a variety of concepts have been exchanged (Hirschleifer 1977, Worster 1979). The recent flurry of interest in sociobiology and optimal foraging theory on the part of anthropologists has been balanced by the interest in cultural transmission among biologists (Bonner 1980, Mundinger 1980). It is important to both disciplines that this exchange continue. Anthropological uses of optimal foraging theory should generate much of interest to evolutionary ecologists. The models that ecologists currently use are only a small subset of the total range possible. There is considerable room for anthropologists to develop models that are not only more precise, but more general as well. In the examples of the use of optimal foraging theory discussed by Smith, anthropologists have been conservative and uncreative in their adaptation of the theory to the human animal, even though biologists admit that current optimal foraging models are not well suited to omnivores such as humans, who have the ability to alter their diet in numerous ways by the application of technology to storage, food processing, and the manipulation of food resources (Hespenheide 1980). Furthermore, models that do not apply to most humans now living cannot be considered very general.

Anthropologists truly interested in optimal foraging theory might be expected to look to models coming from microeconomics, a field that has a long background in the development of models of human time/energy allocation under conditions of varying supply and demand. Already, significant insight into human subsistence change has been gained by the use of simple marginal-cost models, models that have the capability of being applied to both foraging and agricultural economies (Christenson 1980, 1981; Earle 1980; Hastorf 1980, 1983). Less flexible, but following similar lines, are linear-programming models (Keene 1982; Reidhead 1979, 1981). What these economic optimization studies have lacked is a firm tie to a body of theory. It is in this area that optimal foraging theory can make its most useful contribution.

Looking farther afield, the development of an anthropological theory of time/energy allocation in subsistence raises the issue of how labor is allocated in other areas of behavior. There is evidence of strong pressure for minimization of subsistence

effort in some contexts but not in others (e.g., Christenson 1981:218), and a significant question is how variation in labor allocation to subsistence affects that allocated to protection, child rearing, ritual, and other necessary activities. The application of optimal foraging theory to humans raises many significant and interesting questions. For that reason alone, it can be said to have made a major contribution to anthropology.

by BRUCE COX

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Smith reports on Winterhalter's (1981b) work on the diet of the Indians of Ontario's Severn River, in particular his hypothesis (p. 90) that in the 19th century they were restricted to hunting a small number of species by limitations in their hunting technology. I want to supply information from another Algonkian group that bears on this hypothesis.

During the 1700s, the major Hudson's Bay Company posts were served by shifting groups of Cree hunters known collectively as the Homeguard. The Homeguard hunted geese for the posts in spring and fall and sometimes ptarmigan in the winter. Two factors recommend them as a test case. First, their harvesting equipment was similar to that of the 19th-century Severn River people. They travelled by canoe or dogsled and used muskets, bows and arrows, snares, weir fish traps, and deadfalls (Rich 1949:117–18, 139, 163–68; cf. Winterhalter 1981:89). Second, they were better known than other natives of this period. Two sorts of evidence remain to tell us about the breadth of Cree diet: instances of overharvesting and starvation.

James Isham's and Andrew Graham's substantial accounts of life at Hudson's Bay Company posts in the 1700s both mention the Homeguard's "improvidence." Isham writes: "I have found frequently Indians to kill some scores of Deer [caribou] and take only the tongues or heads, and let the body or carcase go Drift with the tide, therefore I think it's no wonder . . . their being starved" (Rich 1949:81). Graham writes that natives killed caribou in great numbers at crossing places, often leaving "the carcasses [to] drive with the stream" (Williams 1969:121). These accounts suggest that the Homeguard may have hunted too few species, leading to inefficient foraging. Isham's second theme, starvation, is even better attested.

Isham notes that the Homeguard who wintered near the forts were often "starved and in want of food" (Rich 1949:80). Graham reached similar conclusions (Williams 1969:191–92). Isham also includes a phrasebook for use with "Indians Coming in the Winter to Trade." This Cree phrasebook begins with an Indian complaining, "I am starved no Deer to be got" (Rich 1949:63). Furthermore, another Company servant told a parliamentary committee in 1749 that "if the [Homeguard] Indians bring no Game in they are in that case generally allowed half a pint of oatmeal [each] a Day, which is given them to keep them from starving" (House of Commons 1765:215). Winter relief of this sort came to be seen as a normal cost of doing business. This entry from Fort Churchill's account books is typical of those from many other years: "Expended . . . this Winter to support and cloath starved Natives" (HBC 1764).¹ Early spring could also be a hungry time, as this entry from Fort Churchill's journal for March 8, 1725, shows: "Munday her came in all our Indian goos hunters they haveing come near two months to soon they haveing little or nothing with them . . . and I am afraid they will be very hungry before geese comes itt being almost 2 months before we can expect any" (HBC 1725).

¹ I wish to thank the governor and committee of the Hudson's Bay Company for permission to quote from their archives and the Social Sciences and Humanities Council of Canada for their assistance.

Taken as a whole, these instances accord well with Smith's claim for restricted "diet breadth" during the early years of the fur trade. The Homeguard Cree seemed to have relied heavily on a few species, especially caribou, ptarmigan, and migratory waterfowl. (The posts may have encouraged this as well.)

I have also found indirect evidence that the Homeguard Indians were seeking to broaden the range of species they harvested during this period. This comes from the records of Fort Churchill's goose hunts (HBC 1722–62). After the spring or fall hunts, the goosehunters were allowed to choose the trade wares they wanted in proportion to the number of geese they bagged. They chose a wide variety of trade wares, including perennial favourites like tobacco, knives, and blankets. Ice chisels and hatchets, however, changed in popularity over the period. Early on they were seldom chosen, but later they were traded in almost every year. Ice chisels were traded on only 5% of the 38 hunts before 1742, but on fully 50% of the 38 hunts between 1742 and 1762. Similarly, hatchets were traded on 66% of the hunts after 1742 and on only 3% before. Both tools were needed in setting fishing nets under winter ice (Rich 1949:167–68). The increased popularity of both tools may show that the Homeguard were trying to extend their winter diet breadth, as Smith predicts they would do. Smith's colleague Winterhalter (1981:90) hoped for a "partial confirmation" of his hypothesis concerning harvesting priorities among early Algonkians. That is all I can provide, since we cannot rule out extraneous factors such as the effect of *European* harvesting priorities. Nevertheless, the Homeguard deserve to be considered as a test case in the ongoing debate on this topic.

by RADA DYSON-HUDSON

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Smith's critical review clearly demonstrates both the strengths and the limitations of the application of optimal foraging theory to human behavior. This body of theory, based on the assumption that individuals will choose foraging behaviors that maximize their Darwinian fitness, has developed a set of models that predict optimal choices in particular situations: which of the available array of prey species a forager should attempt to harvest, which patches to forage and for how long, and how many conspecifics to forage with. Optimal foraging models focus on the level of individual decisions and are based on a number of simplifying assumptions which ignore the stochastic nature of the environment. The use of an energy-time currency (net rate of return per unit of foraging time) rather than multiple currencies is another simplifying assumption. It cannot be dismissed as "caloric obsession" (Vayda and McCay 1975:295), however, because, as Smith points out, it does not require that calories be the limiting factor; it also applies to situations in which time for nonforaging activities is scarce and in which foraging involves risks related to time spent in foraging.

Smith's review of anthropological studies that test these models shows that this body of ecological theory has stimulated interesting ethnographic research. In fact, human foraging behavior tends to conform to predictions based on these models from evolutionary ecology, an indication of the impact of natural selection on human behavior. (I find theories of cultural selective processes acting through selective retention of variations in behavior [e.g., Durham 1976, 1982] unconvincing because the mechanisms of cultural transmission are not adequately dealt with.)

Most of the ethnographic studies cited in Smith's review are of foraging societies, although Gage (1980) applies optimal foraging theory to diet choice of Samoan horticulturalists. However, predictions about behavioral responses to uncertainty and risk—e.g., that conditions of scarcity should elicit risk-prone choices—are clearly applicable to agricultural and even in-

dustrial societies. Smith's excellent review should stimulate attempts to apply models from evolutionary ecology to a wider range of human societies.

by BRIAN HAYDEN

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This is a good review of optimal foraging theory, its assumptions, its usefulness, and its potential. I am especially glad to see second-generation models of optimal foraging theory beginning to incorporate risk minimization as a factor accounting for foraging decisions. I would extend this and suggest that a number of foraging decisions may also reflect concerns for maintaining specific techniques and exploitation knowledge in individual or group foraging repertoires. I specifically have in mind techniques that might only be useful in times of starvation. To ignore these techniques altogether in normal times would be to run the risk of forgetting them, resulting in greater risk of starvation in times of resource shortage (see Colson 1979, Hayden 1981; Dincauze 1982 discusses how quickly basic technology can be forgotten).

Those interested in critiques of optimal foraging theory should read Durham (1981).

Smith's discussion of territoriality and group size shows nicely why groups should leave foraging areas long before resources begin to become overexploited, as opposed to the mystified views of Woodburn (1968:106) and others. However, I think that, in contrast to the individual-advantage viewpoint, a good argument can be made that bands actually did determine who would have access to resources within the band range (see Wiessner 1983) and that group size was kept within limits that would not overexploit critical resources. There may have been temporary increases in group size, but I suspect that these took place only under temporary conditions and occurred when the resident group believed that the resources would not be permanently depleted. To recast Lee's observations, whenever an overt or tacit consensus emerged that there were too many people in the band range using resources there would be a significant rise in the frequency of quarrels, fights, and disputes. In this view, quarrels and fights are mechanisms built into band communities to help regulate man:land relationships. Other bands which recognized these situations and respected the resident group's assessments of man:land relationships and its authority to make such assessments would be permitted to exchange group members and "visit" for varying lengths of time (see Meyers 1976). Groups that did not would be considered hostile and would be forcibly prevented from using the area's resources.

Another consideration influencing group size is defense. While foraging strategies may play a key role in many species, the revenge feuding and overt hostilities which characterized almost all hunter-gatherers not in the shadow of more advanced cultures may have been important in individuals' decisions to band together in groups rather than forage as independent nuclear families. I am convinced that the level of conflict among hunter-gatherers was considerably higher than most current general models suggest, but to document this would require too much space here.

Optimal foraging theory is extremely useful for examining how synchronic foraging systems work and for identifying the factors on which individuals base foraging decisions. However, there is nothing in optimal foraging theory to account for long-term changes in subsistence or technology during the Paleolithic. To address these problems, other models (e.g., models based on biological changes or recurrent stresses) must be used, and ideally they can be integrated with optimal foraging theory to yield a more useful construct of Paleolithic subsistence (see Hayden 1982 for an elaboration of this point).

Smith: OPTIMAL FORAGING THEORY

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Smith's review is a lucid description of a sophisticated application of ecological theory to humans. Optimal foraging theory has given us useful insights into the behavior of foraging peoples, and its refinement promises more and better understanding.

For those of us not primarily interested in human foraging, the special case of the use of optimal foraging theory is interesting mainly as an example of methods of theory construction. As such, the paper should be interesting, even to those who are least persuaded of the applicability of the evolutionary biologist's theories to humans, for its clear sketch of how optimal foraging theorists conceptualize their problems, develop theory, and test it. Some of the methodological issues in evolutionary ecology itself are fairly subtle, among them the rationale for using deliberately simplified mathematical models. The application of the evolutionary ecologist's theory to humans raises additional issues, such as how to take account of culture and human cognitive capacities. Smith clearly explains and ably defends the optimal foraging theorists' reasons for making the methodological choices they do.

For the purpose of making this contribution of optimal foraging theory clearer, I want to expand on two points that Smith makes in a narrower context.

The first of these is made in the context of comparing optimal foraging theory with conventional microeconomic explanations of similar phenomena. Evolutionary ecological models do bear a close resemblance to microeconomic theories, but there is one important difference. Evolutionary theory includes a way to predict what preferences organisms should have, whereas economic theory takes preferences as given. A similar criticism can be made of neofunctional human ecology, which depends on the concept of adaptation without having an explicit theory of a process that generates adaptation. Human behavior is a product of genetic and cultural dispositions, skills, and capacities and their joint interactions with environmental contingencies. The genetic and cultural determinants of behavior are in turn caused by some set of historical or evolutionary processes. Whether or not a theory of the evolution of human preferences or human adaptation can ultimately be drawn from neo-Darwinian theory is perhaps an open question. What is clear is that any satisfactory explanation of human behavior must have a theory that does the work Darwinian theory does in optimal foraging models, among other applications of it to humans (Rosenberg 1980 makes this argument with great generality). A theory of that behavior that is complete, even in principle, must include an explanation of how genetic and cultural influences on behavior come to be the way they are.

The second point is a related one. Of what use is theory from evolutionary biology if we know in advance that culture rather than genes is responsible for the variations in human behavior we see? Smith gives one answer to this question; it is often useful to ignore the proximal details of the causes of behavior, so long as appropriate constraints are imposed on the evolutionary model. From the point of view of optimization under natural selection, it may be a matter of detail whether a trait is proximally caused by learning, genes, or culture or a mixture of all three. However, it seems to me that strictly neo-Darwinian models serve an extremely important function even in cases in which they are almost certain to fail to explain behavior. They give us one clear benchmark hypothesis against which to compare alternatives. If culture and other human mental attributes require theories different from neo-Darwinism, then it must be shown in some detail how such alternatives work and how their predictions differ from those of neo-Darwinism. Even the stoutest critics of the application of evolu-

tionary theory to humans admit that biology at least imposes broad constraints on human behavior. Surely hypotheses such as optimal foraging theory must ultimately be incorporated into any theory of human behavior to explain these constraints. In the meantime, this and similar "narrow-constraint" hypotheses serve to challenge critics to explain how alternatives to them might be formulated and tested. This is not to say that alternatives to narrowly neo-Darwinian models bear some special burden of proof against models derived from biological theory, but only that progress in understanding human behavior will be favored by having all the candidate explanations formulated as clearly and completely as are the neo-Darwinian ones.

Taking the two points together, the methodological virtue of neo-Darwinian theoretical models is the development of reasonably precise and testable hypotheses from a set of fundamental causal processes, using formal mathematics to clarify the logic of the models and extend their deductive power. By demonstrating the utility of this method for the special case of human foraging, Smith's and his colleagues' work invites its extension to other fields of human behavior and to other proposals for the fundamental causes of that behavior.

by ERIC ABELLA ROTH

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This article and previous critical evaluations of optimal foraging theory by Smith and his colleagues (see Smith and Winterhalder 1981) have convinced me of the value of this approach for anthropological studies. As these authors see it, the theory's value lies both in what it does and in what it does not do. First, it provides a general, heuristic model of hunter-gatherer socioecology that avoids the pitfalls of historical-particularistic case studies. In particular, it avoids the latter's emphasis on case-specific detail, which militates against meaningful cross-cultural comparisons. Second, it is built upon clearly defined, testable assumptions, thus fulfilling Popper's criterion of falsifiability (Ayala 1976). This point is particularly important, for invalidation of any of the theory's basic assumptions can lead to investigations of evolutionary dysfunction, a major topic today in biology (Diener 1982).

What the theory does not do is equally important. It does not sink into the morass of biological reductionism into which, sometimes despite the best intentions, sociobiologists are inevitably drawn. As a result, it does not yield to direct but useless comparisons between human and nonhuman behavioural patterns. Finally, it does not assume that some populations are capable of identifying minute differences of caloric return from differing foraging strategies. By not making this erroneous assumption we are spared having to distinguish between "smart" and "dumb" populations, terminology today best reserved for inanimate objects, e.g., bombs.

Despite these advantages, optimal foraging theory has not yet generated an empirical data base to substantiate its basic claims. Nevertheless, Smith deserves much credit for his careful account of the correct and incorrect application of the model's theoretical framework to the study of human foragers.

by STEVEN R. SIMMS

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Smith's paper is a good overview of a controversial subject. He offers several timely points of clarification. Given my general agreement with him, I will restrict my comment to archaeological applications of foraging models.

Smith points out that archaeological applications are limited by the difficulty of knowing the costs of procurement in prehistoric contexts. While he is literally correct, the inherent

deficiencies of archaeological data can have positive consequences. The lack of *precise* cost data forces archaeologists to stand back from the models and attempt to find the appropriate level of applicability for the data at hand. While cost data (expressed as calories per hour, for example) are at first glance *ratio*-level statistical data, they do not have to be used as such. Indeed, given the deficiencies of cost data for archaeological situations, it is better to begin by using them on an *ordinal* level. This approach directs attention toward the development of simple, general explanations that capture the essentials of a complex situation.

My work (dissertation in preparation) has produced cost data on Great Basin resources that are very robust at the ordinal level. For the intended applications, the error expected in some of them is not great enough to affect the relationships between specific resources or classes of resources. Thus, with archaeological data, it is often easier to see that foraging models should be used not so much as a means of predicting highly specific day-to-day behavior, but as a tool for developing rules and constraints that generally predict the character of foraging decision making. Our task should be not the duplication of the behavioral complexity we all know exists, but the simplification of that complexity.

Archaeological data on prehistoric resource abundance are typically incomplete. This makes it difficult to determine the search-time component of cost, because search time is primarily a function of the availability and abundance of a resource. However, research has shown that an understanding of post-encounter costs, without *detailed* knowledge of search time, can make useful contributions to the study of foraging behavior. Given the weaknesses of archaeological data on resource abundance, we should investigate how much can be understood with a knowledge of postencounter costs alone. This approach is useful for general theory building because often in our appeals to the complexity of human behavior we bypass the investigation of simple relationships that may explain much more than we initially suspect. Thus, the very weaknesses of archaeological data insure archaeology's role in the development of general theory about human behavior.

That a foraging model predicts behavior by reference to currencies as simple as time and energy does not mean that the behavior is *determined* by those variables. Behavior (human or nonhuman) is always complex, the product of numerous proximate causes and processes. Nevertheless, it is essential to consider whether a complex pattern can be predicted and *explained* by reference to some simple rules.

Smith mentions the diversity in theoretical perceptions and research goals in anthropological applications of foraging models. Yet among critics there is a clear tendency for this healthy diversity to be reduced to the common denominator of vulgar environmental determinism. Anthropology's assessment of applications of evolutionary ecology to humans has been primarily negative and defensive, appealing to the complexity of human behavior to deny them any value. Many of the "reasons" (e.g., behavioral plasticity, free will, inventiveness, and human capriciousness) for rejecting the approach are, however, empirical questions begging to be addressed with an open mind. An understanding of man's place in nature depends upon such investigation.

by W. A. STINI

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Not the least of the reasons for the interest of anthropologists in optimal foraging strategies is the capacity of such theories to integrate the research interests of social/behavioral and biological anthropologists with those of archaeologists, providing genuine opportunities for the deployment of a wide range of

anthropological expertise in attacking a problem of fundamental concern. The linkage of human bioenergetics to the decision-making process made possible by this integration should not be viewed as reductionist, since those engaged in its pursuit are well aware of the uniqueness of human problem-solving behavior. Just as "the longest journey must start with a single step," solutions to complex problems require the formulation of simplifying models. Seldom does the model predict more than a small segment of the phenomenon it is constructed to explain. The essence of good theory is that it can generate testable hypotheses. Each model is a testable hypothesis and thus must always be considered tentative. If the attempt to identify the most effective means of satisfying fundamental biological needs is reductionist, so be it, but if one adopts that position very little besides "behavioral stamp collecting" is possible. Admittedly, human interaction in a cultural setting is a complicated process that has proven beyond the scope of any quantifying model. That should not, however, be taken as a priori proof that all elements of that interaction are intractable.

Evidence of past behavior can be obtained by analyzing elements of human interaction that leave physical traces or can be reconstructed through contemporary analogies. Both methods of reconstructing the past rely upon less than exhaustive sampling of the repertoire of interaction. The value of models that permit mathematical testing is that they do make probability statements possible. However, anyone familiar with the rapid decline in the probability of an event with the addition of other events on which it is dependent will realize how seldom it is possible to verify cause-and-effect relationships involving several intervening variables. Simple models are necessary because even the normal variation inherent in all biological traits will obscure the meaning of all but the most obvious relationships. This is one of the problems alluded to by Smith in his discussion of the "modeler's dilemma." It is in this connection and not in the area of biological determinism or reductionism that I think the most serious problems with optimal foraging theory applied to human behavior are to be found. This is not because of the superorganic nature of human culture, but simply because the development of cultures has provided human populations with so many options for the solution of the problem of survival. Moreover, when biologists attempt to identify an optimal foraging strategy it is generally within the context of a known set of nutritional requirements that can be satisfied through exploitation of the species's native habitat. The best models can be constructed where the range of food sources is finite and known. Humans are essentially obligate omnivores with great dietary versatility. In addition, most humans live in habitats much different than the one in which they evolved. Thus, they could hardly be expected to exhibit the same sort of predictable alterations of behavior seen in less adaptable species. The course of human evolution appears to have been a unique sequence of adaptations that relaxed environmental constraints, shifting the balance in favor of facultative as opposed to obligate responses to all sorts of stimuli (Stini 1975). As the range of responses available increases, the ability to predict which one will ultimately be chosen decreases. This is one reason that humans have proven to be so unpredictable and that the social sciences are so frequently criticized as purveyors of pseudoscientific conclusions. Human problem-solving ability is unparalleled in any other species. Also unique is the range of information sharing and storage seen among all human populations. Ideas diffuse from one group to another, altering behavior with a swiftness not seen in other species, where a far greater proportion of behavior is genetically determined.

These criticisms are not meant to discourage development of hypothesis-testing strategies provided by optimum foraging theory. It is unlikely that its use to reconstruct the behavior of extinct populations will yield valid conclusions. However, where

data can be collected in contemporaneous populations and comparisons made in different ecological conditions, important insights into the roots of variation in human behavior may be forthcoming.

Reply

by ERIC ALDEN SMITH

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In my review, I hoped to convey to an anthropological audience the essential features of optimal foraging theory, probe the promise as well as the problems this theory brings to the study of human foraging strategies, and assay some preliminary attempts to apply optimal foraging models in anthropological contexts. Most of the comments suggest that I have managed to achieve these goals. In replying, I will avoid engaging in a detailed, point-by-point discussion or rebuttal of issues raised by the commentators. Instead, I want to stress certain central themes and points of controversy or misunderstanding.

I took some pains to make clear that different rationales can be and have been offered to justify the application of optimal foraging theory to humans: neo-Darwinian, cultural evolutionary, and economic theories all offer frameworks capable of anchoring optimization models of the type discussed to a general explanatory scheme. While this circumstance is hailed as one of "healthy diversity" by Simms, Blundell decries it as "theoretical pliancy" that begs important questions about the causes of human behavior. Actually, this is simply an expectable state of affairs when an immature discipline (anthropology) begins borrowing from a somewhat more mature field (evolutionary biology) a set of models that contain elements borrowed from yet another, rather divergent field (neoclassical economics). Blundell is right to ask whether these, and perhaps other, different frameworks are equally capable of justifying the optimal foraging approach (but wrong to conclude that I would "dismiss" any interest in answering that question, a conclusion that must have been reached by confusing my *description* of an existing theoretical position for a *prescription* I do not actually offer). Attempting an answer to this important question would require another essay, but I believe Richerson presents a critical argument in this regard: the optimization or maximization assumptions contained in any sort of decision model or psychological concept like operant conditioning are inherently incomplete explanations for the existence of behavioral patterns and must be coupled to evolutionary theory (genetic and/or cultural) in order to achieve theoretical closure. In the meantime, anthropologists are sure to find a diverse set of reasons to justify their application of optimal foraging models. While I encourage the continuing search for a convincing linkage between a general theoretical scheme and the middle-level models themselves, I do not think we have to wait for this in order to make progress in understanding human foraging strategies, and I want to reemphasize the present theoretical diversity among anthropological practitioners of the optimal foraging approach.

Several commentators raise the issue of the testability of optimal foraging predictions. All science—indeed, any system of knowing—faces epistemological problems of limits to certainty and difficulty in evaluating conflicting results. I agree with Roth that falsifiability of predictions is an important criterion for science and one that foraging models can meet better than other approaches currently employed by ecological anthropologists, but I have conflicting feelings about Cashdan's argument that quantitative tests of optional foraging models have been "oversold." On the one hand, I have seen many of

my own predictions falsified for reasons I suspect are often matters of sample size or research design. On the other hand, logic and scientific experience demonstrate that rigorous, quantitative tests are much surer routes to falsification—and hence to theory building—than are more judgmental or intuitive approaches. One problem, of course, is that rigorous tests assume that most variables are under experimental control—a condition that few ethnographers, and no paleoanthropologists, are capable of meeting. Yet I refuse to accept Cashdan's advice that we forego such tests. I am convinced that the testing process—imperfect as it is—both forces us to collect better data and checks the tendency to evaluate competing explanations in terms of the prestige and polemical abilities of their advocates. The only solution I see to this dilemma, other than a miraculous increase in the quality of anthropological data or the subtlety of our testing methods, is to require that alternative explanations be subjected to the same rigorous tests that those generated by foraging strategy models undergo.

The problems of testing are obviously compounded when the data are drawn from prehistoric contexts. I argued that extensive ethnographic tests are necessary before we can be confident that the general approach will be worth applying archaeologically or paleontologically. Bettinger and Stini are more pessimistic about the prospects for using the models as any more than "rough analogies," while Simms presents a counter-view based on his own success in interpreting prehistoric patterns of resource use in the Great Basin. I suspect that experimental and ethnoarchaeological techniques will be crucial for paleoanthropological applications of the models, and that Simms's prognosis is thus closer to the truth—but I leave it to the prehistorians to argue this point.

I argued at several points in the paper that social, economic, historical, and cultural variables could and should be integrated into optimal foraging hypotheses or at least articulated with these in some systematic fashion. The commentators seem to have rather disparate views about the prospects for such integration. Bishop is the most critical, charging that I and others have ignored or trivialized sociocultural variables in our devotion to ecological determinism. But we have to be careful to distinguish what *has* been done from what *can* be done. For example, Bishop's criticism of table 1 for excluding sociocultural factors is somewhat misplaced, since the table summarizes models primarily developed by ecologists, not anthropologists. Furthermore, factors such as travel costs, return rates, and settlement size (not to mention "rules governing division of the harvest") are all directly affected by technology, social organization, and even ideology. The whole point of Winterhalder's argument concerning historical changes in Cree diet breadth is the way in which we might use optimal foraging theory to explain the effects of technological and economic change on resource choice. So if existing efforts at integrating sociocultural variables into foraging strategy models are weak, they are surely not as weak as Bishop implies, and I don't believe it takes a visionary to foresee how this direction could be pursued with greater diligence.

The crucial issue is really *how* we can most effectively integrate ecological and sociocultural variables. I do not think that simply asking informants why they make particular choices, as Bishop recommends, is a viable answer—although neither Winterhalder nor to my knowledge any other ethnographer using foraging models has failed to collect and consider this sort of information. I also have serious reservations concerning the socioecological logic of Bishop's explanation for the occurrence of large Inuit camps and Hayden's more general arguments on band size. I do not see how arguments such as these can be reconciled with foraging theory or with contemporary ecological and evolutionary theory in general. Briefly, the central problem is that evolutionary ecology (along with neoclassical economic theory) predicts that individually optimal strategies will prevail over those optimal for the social group

in most cases where these conflict. Bishop and Hayden, it seems to me, impute adaptive function to variables such as group size at a higher level than can be theoretically justified. Hence, while I believe optimal foraging theory can be domesticated by incorporating sociocultural variables, I am dubious about attempts to functionalize it in the rather unproductive traditions of sociological and ecological functionalism.

Several commentators urge anthropologists to construct entirely new models of human foraging strategies. I am in sympathy with this suggestion but also consider an initial period of testing existing models useful and sensible and not to be castigated as "conservative and uncreative" as Christenson argues. While I certainly agree with Casimir and other commentators that specific resources may often be acquired for their specific nutritional value (or even symbolic value) rather than for their energy value, I am doubtful that complex models of the linear-programming variety are the best way to analyze human subsistence strategies. It is relatively easy to build complex models that incorporate a host of constraints and goals, but this will not usually generate the sort of insight and understanding that simpler but carefully constructed models can produce. In many cases, in order to get realistic predictions from complex models we must first obtain most of the answers we were originally seeking, quickly reducing the procedure to an exercise in curve fitting. Simple models obviously leave out many factors, but in many cases the missing factors may have little effect relative to the cost of including them; until the simple models are tested, we have no solid basis for rejecting them as *too* simple.

In conclusion, I urge ecological anthropologists to test existing models *and* formulate new ones. We should not view existing models as truth revealed just because they were published in the pages of *Theoretical Population Biology*. On the other hand, we should not dismiss them a priori because they do not make reference to calcium needs, lineage solidarity, relations of production, and binary oppositions. If existing models are found wanting or incomplete, we should strive to build models that incorporate the best features of optimal foraging theory (parsimony, logical rigor, and testability) while integrating the anthropological variables we suspect are important. If we can combine the spirit (not necessarily the letter) of optimal foraging theory with the unique concerns of anthropology, we will certainly have accomplished something worthwhile.

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