FOOD AND EVOLUTION

Toward a Theory of Human Food Habits

EDITED BY MARVIN HARRIS
AND ERIC B. ROSS

TEMPLE UNIVERSITY PRESS
Philadelphia

1987

12

BRUCE WINTERHALDER

The Analysis of Hunter-Gatherer Diets: Stalking an Optimal Foraging Model

MY TITLE ALLUDES TO HUNTING. THE IMAGERY IS DELIBERATE: I intend a somewhat predatory engagement with the subject. How do ecological factors affect hunter-gatherer decisions about the harvest of non-produced food resources? What are the ecological strategies of the food quest? And, especially, how does one go about asking these questions? What is a productive or heuristically useful research procedure? I will suggest that the analytic process is a little like foraging itself. The inquiry is, in a sense, the quarry.

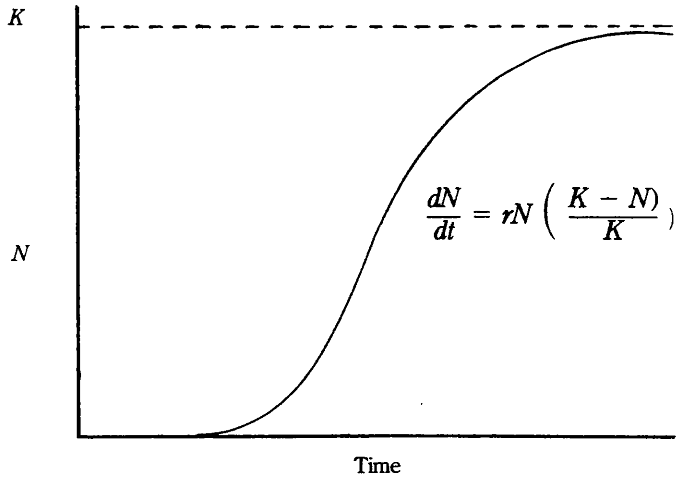
This paper has three parts: (1) a brief statement about the methodology of evolutionary ecology that focuses on assumptions and attempts to convey a particular attitude toward this kind of invesgiation; (2) a quick summary of applications, giving evidence that the assumptions are not so unrealistic nor the effort so unrewarding as they may seem after the first part; and (3) an exploration that attempts to extend the models while showing more precisely what they cannot do.

A Brief Historical Digression

I will begin indirectly, with an older but similar biological model, the logistic equation, developed first by Verhulst in the 1840s but promoted and popularized by Pearl in the 1920s. The history of the equation (Kingsland 1982) contains lessons about the strengths and limitations of foraging models.

The logistic is a systematic expression of a set of biological relationships (Figure 12.1). It has an easily visualized graphic form, the *s*-curve. It can be stated as an intuitively appealing equation of several variables. It also raises some hard, though usually implicit, questions. What kind of scientific status do we give to a creature like this? For what is it best used?

FIGURE 12.1. The Logistic Curve and Equation



NOTE: See Hutchinson (1978) for a definition of the terms in the equation.

Verhulst was after a calculating device (“*logistique*”) derived from first principles. He had practical problems in mind—the limitations of Belgian farmland, for one. In contrast, Pearl developed the formula directly from empirical data and promoted it as a Law, comparable “in a modest way” to Boyle’s and Kepler’s laws. Pearl devoted much of his scientific work to showing that population-growth data sets fit the logistic curve. This required second-order corrections in the equation and some creative attention to the data as well. Pearl’s promulgation of the equation in this manner led to clamorous debates, as economists, statisticians, and demographers pointed out that its assumptions were artificial and that the fudging required to preserve its lawfulness was counterproductive.

Others approached the equation differently. Lotka realized the potential of closely investigating the r term. His pursuit of that component led to formulas relating population growth rates to age structure. The logistic gave Lotka entry to demographic questions going beyond the equation itself. He said of it: “An empirical formula is . . . not so much the solution of a problem as the challenge to such a solution. It is a point of interrogation, an animated question mark” (quoted in Kingsland 1982:42). Gause (1934) realized that the growth-resistance term—$(K - N)/K$—expressed competitive processes like those envisioned in Darwinian natural selection. He extended the model to two competing species and used it as a tool for the analysis of resource competition and co-existence. In his experimental work he attempted to estimate model parameters directly, but he did not confuse the equation with a realistic portrayal of nature.

The debates provoked by Pearl are forgotten; the approaches developed by Lotka and Gause permeate evolutionary biology. Kingsland’s summary indicates why:

> The logistic curve cannot be tested by comparison with observations, as one would test a scientific hypothesis, for it is neither a law nor a hypothesis, but a logical argument based on a variety of assumptions. By looking at deviations from the logistic curve, however, one can refine these assumptions to gain a more accurate understanding of how a population behaves. The logistic can therefore be useful as a tool of research even though it is not a realistic description of growth. (Kingsland 1982:41)

Optimal foraging models are valuable in much the same way—not as lawful statements about reality, but as structured forms of inquiry, more interesting to stalk than to live by.

Assumptions, Procedures, and Two Basic Models

Optimization as a Working Principle

Optimization is the outcome of selection in a finite environment. Resource competition gives the edge to organisms more efficient at gaining energy and nutrients to expend on more foraging, the search for mates, or avoidance of predators and hazards. This is a neo-Darwinian article of faith, although competition is remarkably difficult to observe in nature (Connell 1975; Schoener 1982; Wiens 1977).

The extensive use in evolutionary ecology of optimization and cost-benefit assessments has led to a serious debate about their validity and merits (Gould and Lewontin 1979; Lewontin 1978; Maynard Smith 1978). I argue (Winterhalder 1981a:15) that optimization principles provide a structured, contingent, and partial guide: an entry to inquiry rather than an acceptable proposition about nature. They are structured because they allow one to devise hypotheses or predictions about adaptive behaviors in well-defined conditions. They are contingent because no set of conditions has complete theoretical generality. They are partial because they assist one in speculating about selection at the expense of attention to other aspects of the evolutionary process. In general, they make explicit and thus open to scrutiny a widespread form of functionalist reasoning (Smith and Winterhalder 1981).

The optimization principle relevant to what follows is this: human foragers will adopt behaviors that allow them to achieve the highest possible net rate of energy capture *while foraging.* Note the phrase "while foraging." It circumvents the assumption that hunter-gatherers attempt to maximize (or minimize) resource use in general. It leaves open the question of how long an organism forages. It is a postulate of scarcity for analytic purposes, not a statement about actual scarcity. It is a formal, operational way of stating a commonsense hypothesis: hunter-gatherers will have developed behaviors that make them as skillful and successful as is possible in the capture of game or harvesting of plants, relative to their effort. I will return below to the question of how long they forage.

The expectation of optimal results is more heuristic than realistic. Natural design highlights the efficacy of selection, but a careful look often shows that nature is "tinkered" together, to use Jacob's (1977) metaphor. Constraints arise from history, chance, and competing goals (Cody 1974). The appropriate pre-adaptations or phenotypic variance may not be present. Environmental fluctuations may impede or reverse directional evolution. Or the optimal responses for concurrent goals may conflict. Nature is less facile, it is messier, and it is not so single-minded as the methods of the evolutionary ecologist. Thus, the constraints themselves may be "more interesting and more important in delimiting pathways of change than the selective force that may mediate change when it occurs" (Gould and Lewontin 1979:581). Optimization analysis sensitive to this possibility is the best way to uncover the effects of such constraints.

The issue of constraints raises one of mechanism. Although Darwinian in origin, optimal foraging models can predict the effects of the selection of behavioral variants not associated with genetic variance (see discussion in Durham 1976; Orlove 1980; Pulliam 1981; Pyke, Pulliam, and Charnov 1977; Richerson 1977).

Simple and Compound Currencies

An optimization assumption requires a currency. Here again there is debate. A simple energy currency is used widely. It addresses several possibilities (Smith 1979): (1) energy may be periodically or chronically scarce; (2) foraging may expose the hunter-gatherer to greater-than-average hazards; or (3) foraging may divert valuable time from other activities. Energy, unlike some nutrients, is an immediate, recognizable need and hence a likely proximate guide to foraging behavior.

If, however, resources have several significant nutritional or non-food attributes, or complementary effects, then compound or linear programming models are required. Resources assessed by multiple attributes are not easily ranked; those with complementary effects cannot be assigned a value independently of one another (Rapport 1980; Westoby 1978). Few researchers have asked in what circumstances simple or compound currency models are more appropriate. In general, the foods of carnivores are of a high quality and roughly comparable in their nutrient mix. Attaining sufficient energy is likely to subsume other requirements (but see Speth and Spielmann 1983). The mixed diet of an omnivore may be nutritionally adequate even if "chosen" on the basis of an energy currency, but here nutrient considerations are more salient. The low and uneven quality of plant foods makes a presumptive case for compound currencies when these predominate in the diet.

Compound currencies require linear programming models, but I am wary of the view that complex nutritional models are more desirable because they appear to be more realistic. They incorporate more elements, but whether they accurately take account of them is more difficult to decide. Few of the input variables are known precisely (see Chapter 6), and although detailed, results can quickly become sensitive to these poorly understood parameters. Ethnographic study (Johnson and Behrens 1982) has shown that specific auxiliary information is needed to "calibrate" a linear programming model to particular circumstances and questions. Simple models are hedged with analytically penetrable uncertainties. As structured questions, their virtues diminish as their structure escapes comprehension.

Whatever the currency, most foraging models are deterministic. They are based on average or "expected" values and do not allow for the possibility that decisions respond to stochastic variability in the factors affecting foraging. I will return below to the question of stochasticity and risk (see Jochim 1982).

Models as Creatures That Are Good to Think

We seek, then, simple models that are good to think. These are not theories or hypotheses. Neither are they true or false in the manner of a lawful statement. Rather, they are valuable because they "generate good testable hypotheses relevant to important problems" (Levins 1966:430). A comprehensive theory about a subject is composed of a family of these models, each with its idiosyncracies. Thus, for modeling purposes "foraging" is artificially divided into "decision sets" (Krebs and Cowie 1976:100; Pyke, Pulliam, and Charnov 1977:140) related to such factors as diet breadth, foraging space, foraging period, and group size. Each model is uniquely relevant to a few questions and a small set of conditions. Models are not always clearly hierarchical, overlapping, or complementary. It is disconcerting to some that foraging theory works with such a motley set of individually limited tools, as if restricted applicability and the necessity to be selective were themselves a rebuke to the whole approach.

But this confuses something like a law, which is meant to be an accurate and universal representation, with something like a structured question. If models are the latter—good to think—then better many thoughts than a few.

The methodology, then, is built on (1) an optimization (or scarcity) assumption, to be distinguished from a belief that actual scarcity is a general condition; (2) a simple energy currency, tractable to those of us who can think about only a few things at a time; and (3) simple models meant to guide inquiry about a phenomenon, not to depict it.

The Diet-Breadth Model and the Marginal-Value Theorem

To exemplify this approach I will describe two key models. Consider a predator with prey scattered randomly through its environment. The diet-breadth model specifies the set (which and how many types) of resources this forager should pursue in order to achieve the highest net rate of energy intake while foraging (MacArthur and Pianka 1966; Pyke, Pulliam, and Charnov 1977:141). The assumptions of this model are as follows:

Currency:

1. The organism has the goal of maximizing its net rate of energy intake while foraging.

Constraints:

2. Prey are encountered randomly; the type encountered is independent of the last type encountered.
3. At a particular diet breadth, the organism always does or does not take a prey item; that is, there are no partial preferences.
4. Prey types have a stable ranking by net energy value per unit of pursuit and handling costs; that is, the quality of each prey type can be evaluated independently of other types.
5. Foraging can be divided into searching and pursuit phases, which are independent; that is, the predator searches for all prey jointly but pursues them singly.
6. Prey density is constant in a foraging interval; that is, the forager does not reach the end of its foraging range or overtake a constant rate of prey renewal during a foraging interval.
7. The benefits and costs associated with resources are treated as expected values, without relevant stochastic variance.

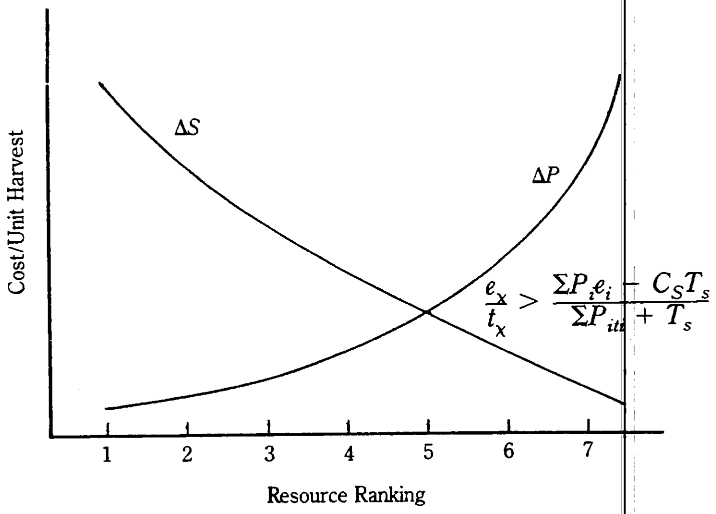
Despite its appearance, this is not a paralyzing list.

In graphic form (Figure 12.2), addition of each potential prey type reduces average search costs by an increment (ΔS) that can be plotted. The average pursuit and handling time per unit of prey increases by an increment (ΔP) because the less desirable prey added are more difficult to capture or less rewarding when secured. The optimal diet includes all ranked prey types down to the last for which the incremental savings in search costs are larger than the incremental loss due to added pursuit costs (i.e., the last before the intersection of the curves). Virtually any factors that might affect foraging can be adapted to this "systematic argument" to form a hypothesis. Thus, decreased overall habitat richness raises average search costs and expands diet breadth by stepwise addition of items of lower rank. Or, increased pursuit capabilities lower average pursuit costs, with the same effect. An especially important prediction is the following: presence of a resource in the optimal diet is independent of its abundance. It depends rather on its rank, and on the abundance of items of higher rank.

The algebraic form specifies that an item x should be added to the diet only if its return relative to pursuit and handling costs (e_x/t_x) is greater than the average for the diet containing all items of higher rank. In other words, the optimal forager elects to pursue an item if and only if it does not expect, in the same interval of time, to both locate and capture a more valuable item.

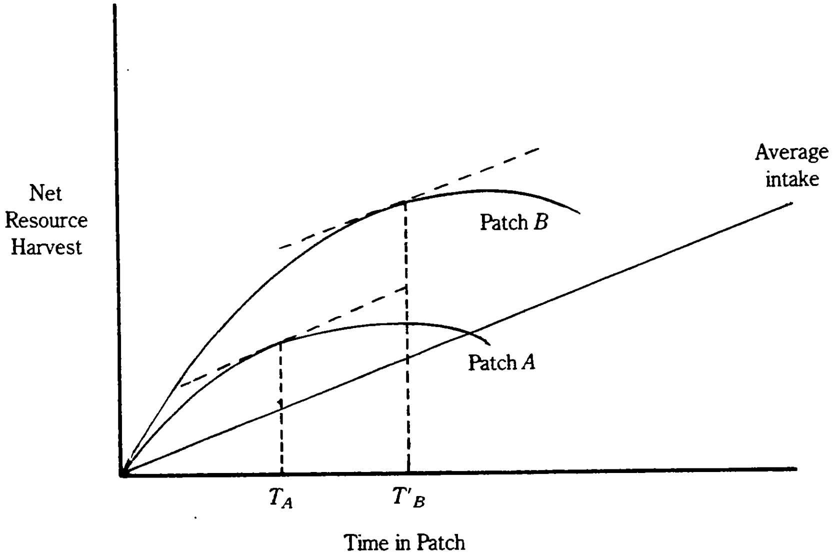
The second model is the marginal-value theorem (Figure 12.3; Charnov 1976; Charnov, Orians, and Hyatt 1976). This model answers the question,

FIGURE 12.2. The MacArthur and Pianka (1966) Diet-Breadth Model and Equation



NOTE: See Schoener (1974) for a definition of the terms in the equation.

FIGURE 12.3. The Marginal-Value Theorem



NOTE: See Charnov 1976.

when should a forager leave one discrete patch to travel to another? The assumptions are:

Currency:

1. The forager attempts to maximize its net rate of energy intake.

Constraints:

2. Food is encountered within habitat patches.
3. Patches are encountered randomly.
4. Patches are not revisited before their resources recover from exploitation.
5. Travel between one or more patch types is non-productive or lost time.
6. As an organism forages within a patch, it depresses the rate of food intake because the prey become scarce or wary, or because they flee to other locations.
7. The relevant variables are characterized by expected value.

The model predicts that the optimal forager will leave a patch being harvested when the marginal capture rate there drops to the average rate of intake for the habitat. At this margin, the predator will do as well or better by seeking out an unexploited locale, even though some effort will be lost in traveling there. The optimal forager abandons particular spots before prey are fully depleted, and the higher the overall quality of the environment, the sooner it abandons them.

Anthropological Studies

I have tried to convey the assumptions and constraints that give optimal foraging theory its strength and also rather strongly restrict the range of issues that it may help to resolve. Whatever its attractiveness as an exercise in structured inquiry, or problem stalking, the success of optimal foraging theory depends on the guidance it offers in actual analyses. I will restrict a brief discussion to several ethnographic analyses that use simple currency models, and I will stress relevance to important problems rather than testability of hypotheses (see also Chapter 13). Smith (1983) presents a detailed review of the ethnographic research based on foraging theory; Keene (1979, 1981) and Reidhead (1979, 1980) focus on linear programming models and archaeological research. Yesner (Chapter 11) and Cohen (Chapter 10) give additional examples of the use of the models.

Cree Foraging

The first anthropological fieldwork guided by these models was my work with the boreal forest Cree-Ojibwa in 1975 (Winterhalder 1981b, 1983a, 1983b). For a year I traveled with Cree-Ojibwa foragers, timing and assessing the energy expenditure of foraging activities, mapping on airphotos their movement through the vegetation mosaic, weighing game captured, and discussing the tactics of foraging with my companions. The results were a modest confirmation of the diet-breadth and marginal-value theorem hypotheses and a more certain demonstration that the assumptions of another model, the patch-choice model (MacArthur and Pianka 1966), were frequently violated in the Cree-Ojibwa case.

For instance, historical changes in diet breadth give comparative evidence that fits the predictions of the diet-breadth model (Winterhalder 1981b, 1983b), and the qualitative dynamics of Cree-Ojbiwa foraging appear to confirm the marginal value theorem hypothesis. A forager nearly always leaves a localized patch of beaver, muskrat, or hare in search of another location before that patch is exhausted of capture opportunities. Equally interesting is the negative result. Using the MacArthur and Pianka (1966) model for patch choice, I predicted that habitat use would be quite generalized. In fact, not all patches containing sought game can be exploited. Anyone who has attempted to walk in thawed muskeg or to hunt a large, skittish herbivore like a moose in thick brush will understand immediately. And contrary to model assumptions, patches are not encountered randomly. The Cree-Ojibwa forager knows a wide landscape of vegetation communities intimately. Moreover, Cree-Ojibwa foragers do not always adopt the patch-to-patch pattern incorporated into the model. Because they know that some prey move in this manner, the foragers search for tracks in the interstices between patches, a practice that is more efficient and improves the chances of successful pursuit.

Fortified with these limited successes, I suggested that foraging theory might also shed light on a key issue in hominid paleoecology (Winterhalder 1981c). Using the competitive exclusion principle, some paleoanthropologists have argued that there could be no more than one sympatric hominid species. In this view, the response of a partially cultural hominid to a like competitor would be to expand its use of resources and hence to exclude the less efficient of the two species. However, a derivative result of the diet-breadth and patch-choice models, the "compression hypothesis" (Schoener 1974), shows that although the diets of the two competitors might become more general, their use of habitat patches would specialize, producing the ecological and ultimately the evolutionary divergence necessary for joint survival. Cultural flexibility would only facilitate the selective processes for the optimal response of each species: niche divergence in the use of micro-habitats.

I have argued as well that the Pleistocene overkill hypothesis of Martin—that human foragers newly arrived in North America around 11,000 B.P. caused massive extinctions of big game species (review in Webster 1981)—can be questioned using the marginal value theorem. The situation outlined by Martin—highly efficient hunters in a heterogeneous environment rich in game species and with a virtually unlimited frontier—are exactly those in which depletion of localized patches of prey is least likely. Such foragers would have moved quickly through the habitat, skimming the most easily obtained prey in each location before moving on. Each patch left behind would retain a breeding population.

Inuit Foraging and Group Size

In fieldwork with the Inuit on the northeast coast of Hudson Bay, Smith (1981) has used optimization approaches to analyze ecological determinants of hunter-gatherer group size and structure. The Inuit provide a classic but untested example of ecological adaptation—the winter aggregation of small hunting parties to engage in cooperative hunting of seals at their breathing holes. Since studies by Boas in the 1880s, anthropologists have noted that a seal visits several breathing holes unpredictably. It has been argued that a successful harvest requires that hunters station themselves at as many of the holes as possible. By plotting group sizes against measurements of their energy efficiency, Smith was able to test this proposition. For seal hunting, his evidence shows a peak of individual efficiency at 3 hunters, corresponding to a winter camp of about 20 persons (1981: 62). This is much smaller than the 50 to 200 persons observed by Boas and others, suggesting the influence of factors besides this one. Overall, in 5 or 10 hunt types, Smith found a positive and statistically significant correlation between hunting group size and foraging efficiency. Where the energy optimization hypothesis failed, alternative factors like apprenticeship of children or partnerships to reduce foraging hazards apparently were operating.

Tropical Foragers: The Aché

Hawkes, Hill, and O'Connell (1982) have shown that foraging choices of neotropical Aché living in Paraguay match reasonably well those predicted by the optimal diet model. Whether plant or animal, a resource appears to enter the optimal diet set of the Aché by virtue of its pursuit and handling costs and the abundance of foods of higher rank as expected. That set will usually include some plants as well as animals. This answers the central question, "Why do hunters gather?", especially those that apparently could live well on meat alone.

These conclusions are qualified somewhat by the Aché division of labor, in which males pass up encounters with highly ranked plants and females with highly ranked animals, lowering the average foraging of each . Where the energy-optimization hypothesis failed, alternative factors like apprenticeship of youths or partnerships to reduce foraging hazards apparently were operating.

Tropical Foragers: The Yanomamo, Ye'kwana, and Siona-Secoya

In a neotropical example, Hames and Vickers (1982) have examined data on the diet choice of Yanomamo, Ye'kwana, and Siona-Secoya foragers. These people forage radially (see Orians and Pearson 1978) from their gardens and villages. Hames and Vickers have made comparative observations on diet choice as prey are depleted adjacent to the village and as radial foraging effort grows. The observed practices of taking only more valuable game at greater distances from the village are broadly in accord with predictions. Resolution of disputes (Ross et al. 1980) about the effects of ecology on the lifeways of tropical horticulturalists may well come from interpretations and data like these.

Marine Fishermen in New Jersey

Finally, McCay's (1981) analysis of a marine inshore fishery on the east coast of the United States is the first explicitly to set optimal foraging theory into the context of a market economy. Some optimal foraging predictions were consistent with harvest decisions made by the fishermen, but these were a rather restricted part of a complex of choices influenced by personal values, economics, and politics. McCay argues that New Jersey fishermen *are* foragers, but they exist in an enveloping political economy that rather strongly restricts the insights available from foraging theory alone.

Opportunity-Cost Models

The above-mentioned studies are instances in which an optimal foraging approach has resulted in different, more complete, or better-substantiated conclusions about hunter-gatherer subsistence practices.

Are there dangers in this type of exercise? I see several. It is easy to overextend the purview of optimal foraging models, or to misapply them, individually or collectively. The emaciated expository style of theoretical ecologists often does not make assumptions and constraints accessible to those of us who must be enlightened by the prose between the equations. Collectively the models are bound by the individual-level food acquisition focus and the restriction to a material currency. In their present form, they help to examine food procurement but do not readily extend to supra-individual aspects of economy, such as exchange, wherein social and cultural valuation of goods becomes especially important. And they do not have the character of lawful statements.

For the remainder of this paper I will address two questions mentioned earlier—total foraging effort and risk—while trying to balance among these dangers. This means recognizing limits even while trying to push the models beyond their present limitations. I am interested first in the optimization statement stipulation: "while foraging."

The Opportunity-Cost Foraging Model

The diet-breadth model identifies the prey set giving the maximum net rate of energy intake while foraging. It does not indicate how long the organism should forage, nor how much energy it should harvest. Establishing the latter requires that foraging be evaluated relative to other behaviors. Foraging takes time away from those activities; it also provides the energy needed to engage in them.

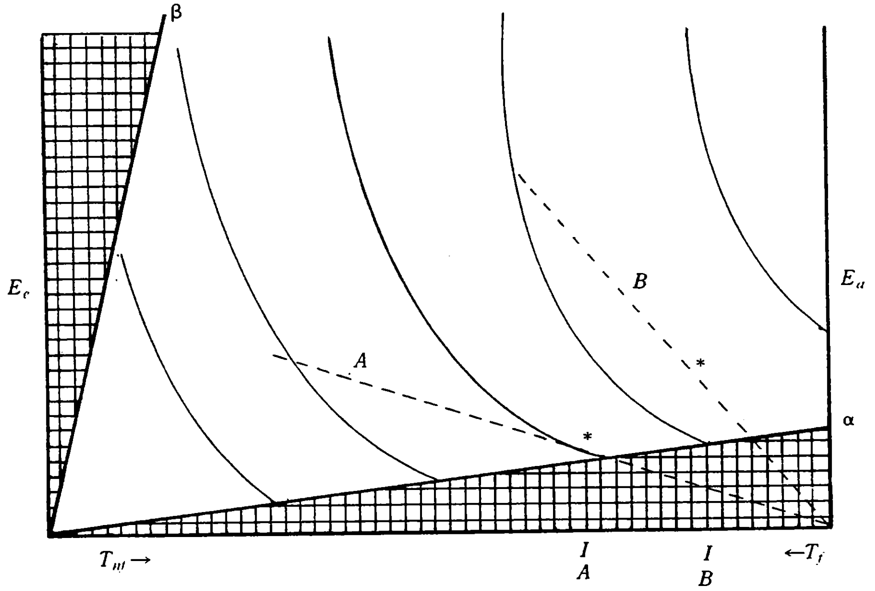
I have been working on a model that addresses the question of how long to forage (see Winterhalder 1983c). It begins with several definitions. The *opportunity cost* of an activity (X) is the value of some alternative activity forgone because resources were invested in X rather than the alternative. This concept assumes that resources are limited relative to potential uses, that different courses of action are evaluated relative to one another, and that one activity among all the foregone activities can be identified as providing the relevant substitute measure. *Marginal value* recognizes that the value (or cost) of an activity can change as a function of its duration. An economic decision to cease or continue will focus on the value (or cost) of the next, the marginal, unit of that behavior (see Charnov 1976). Finally, an *indifference curve* connects points of equal utility or preference; a *value isocline* points of equal sociocultural valuation; and a *fitness isocline* points of equal fitness.

Foraging is represented in the right-hand portion of this model (Figure 12.4); all non-foraging activities are aggregated in the left-hand portion. The right-hand vertical axis measures the net acquisition of energy (E_a) while foraging; the left-hand vertical axis measures the total energy expenditure (E_e) in non-foraging activities. For the interval considered, acquisition must balance expenditure $(E_a = E_e)$. The horizontal axis extending from the right shows the time spent foraging (T_f); that extending from the left shows the time spent in non-foraging activities (T_{nf}). Note that increasing foraging times are read from right to left, and increasing non-foraging times from left to right, subject to the constraint that $T_f + T_{nf} = T_t$, where T_t represents an appropriate interval for analysis.

Combinations of time and energy consumption in non-foraging activities that have the same utility are connected by the indifference curves. Initially, take the configuration of the curves to be consistent with the standard conventions of micro-economic theory (e.g., Stonier and Hague 1972):

- They are convex to the origin, implying that the scarcer of two jointly used resources is likely to be the more valuable. The marginal value of activity X increases (or its relative rate of substitution for Y decreases) as the quantity of Y grows. Thus, an organism with much non-foraging time but relatively little expendable energy will probably value an additional unit of energy more than one of time.
- The indifference (or isocline) map is independent of foraging intake.
- Indifference curves or isoclines more distant from the origin have higher value. In principle, the capacity for increased utility is insatiable.
- And the forager is knowledgeable, has stable preferences, and acts rationally by attempting to obtain the greatest possible utility.

FIGURE 12.4. The Opportunity-Cost Foraging Model for a Time-Minimizer



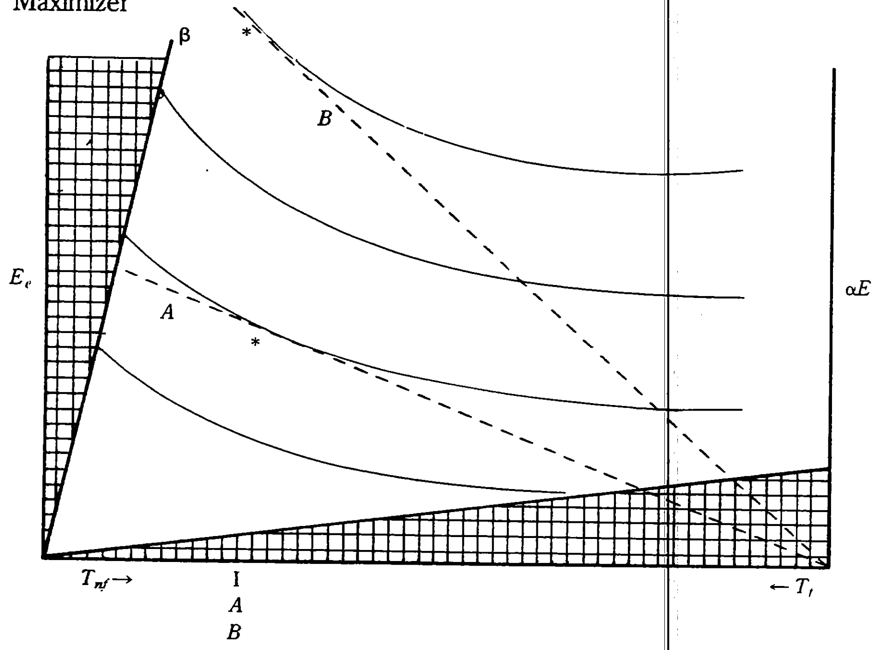
NOTE: The asterisk (*) shows the optimal foraging time allocation (T_f) and energy acquisition (E_a) for two foraging constraint lines, *A* and *B*. The vertical bars below the X-axis show how time is partitioned between non-foraging activities (T_{nf}) and foraging (T_f) in each case.

The 0-to-α line shows the minimum survivable rate of energy expenditure; the 0-to-β line shows the maximum rate attainable in non-foraging activities.

A set of indifference curves can be very sensitive to a forager's circumstances. The model offers distinctions that pass continuously from the strictly time-limited to the strictly energy-limited cases. If the marginal gain in utility from a unit of time freed from foraging is greater than that attached to an additional unit of energy gained by foraging, then the organism is time-limited and will act as a "time-minimizer" (Schoener 1971). The indifference curves will tend toward the vertical (Figure 12.4). Conversely, if the marginal gain associated with a unit of energy is larger, the organism is energy-limited (i.e., it will act as an "energy-maximizer") and has a indifference map that tends toward the horizontal (Figure 12.5). A forager may act as an energy-maximizer in one portion of its indifference map and as a time-minimizer in another. It may switch from one to the other with seasonal or other temporal factors.

The left and right portions of this model are linked in the following way. Each foraging option is associated with a net gain of energy (E_a) for each unit of foraging time (T_f). This is represented by a *foraging-constraint line* on the indifference map. The optimal time investment (and thus the optimal energy

FIGURE 12.5. The Opportunity-Cost Foraging Model for an Energy-Maximizer



NOTE: The asterisk (*) shows the optimal foraging time allocation (T_f) and energy acquisition (E_a) for two foraging constraint lines, *A* and *B*. The vertical bar below the X-axis shows how time is partitioned between non-foraging activities (T) and foraging (T_f) in each case.

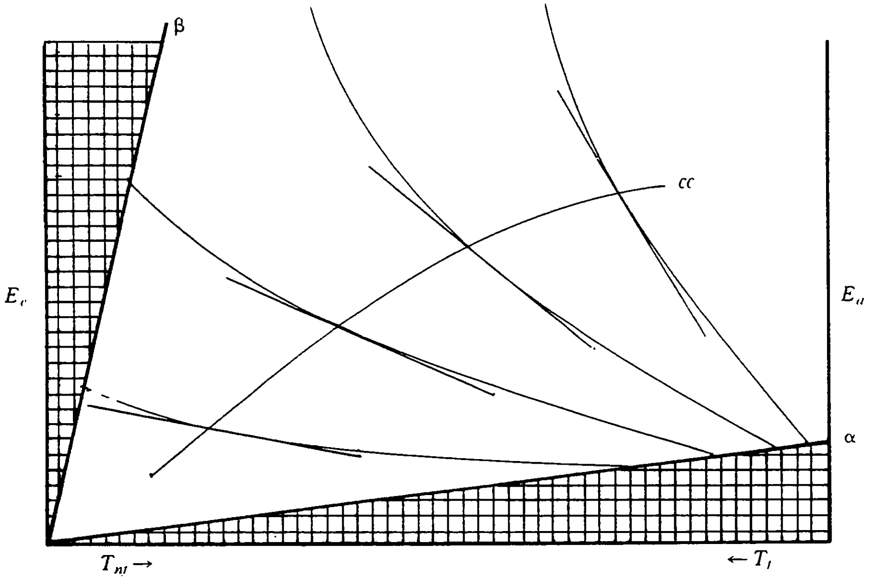
acquisition) is determined by the point on the foraging-constraint line that is tangent to the highest indifference curve (or value/fitness isocline). This linkage establishes the opportunity costs (time) and benefits (energy) of foraging by evaluating them relative to alternative uses in other activities.

If foraging conditions vary, so will the diet choice and efficiency of the optimal hunter-gatherer. This change will alter the slope of the foraging-constraint line. Rotating that line over the indifference map (Figure 12.6) generates a *consumption curve* (*cc*) that characterizes the forager's effort and harvest for all ecological circumstances.

An Opportunity-Cost Currency

The opportunity-cost approach directs attention beyond the diet-breadth model to some related and here exploratory lines of inquiry. What is the relevant currency for the opportunity costs experienced by a human forager? Is there an

FIGURE 12.6. An Opportunity-Cost Model that Depicts the Forager's Consumption Curve (cc)



expected form for a hunter-gatherer opportunity-cost map? What determines that configuration?

Some anthropologists using foraging models (Hawkes et al. n.d.) state flatly that fitness is the sole appropriate currency. I do not find that position compelling. First, fitness has a special, limited, theoretical meaning: differential reproductive success of phenotypic traits expressed variably among the individuals of a population, for those phenotypes tied more or less directly to a corresponding inter-individual genotypic variance. Given our ignorance about mechanisms of biocultural evolution, appeals to fitness outside this biological setting are analogies carrying heavy loads of ambiguity. Second, it is nearly impossible to make a quantitative assessment of the incremental contribution of a particular phenotype-genotype linkage to relative fitness. For those seeking a rigorous, operational measure of segments of human behavior, fitness is a poor candidate. Fitness in the abstract, even the fitness of individuals, will not help, because the analysis actually considers fitnesses associated with a restricted set of activities extracted from the totality of behavior. Finally, Mayr (1974) argues that resource-acquisition behavior has evolved toward "open" behavioral programs based on generalized abilities to accumulate and interpret experience, to learn, and to make choices. It is based in the "cultural retention of individually adaptive behavior" and "cognitive evaluation and retention of beneficial customs" (Pulliam 1981:62). We should expect, then, that forating decisions are heavily influenced by sociocultural information that may be independent of fitness considerations.

In a context in which it cannot be defined or measured, and in which even its relevance is at issue, invocations of fitness must entail some other kind of adaptive judgment, usually related to material utility. The alternative, however, is not particularly attractive. Biologists discomforted by ambiguities in a central concept (e.g., Stearns 1976:4) will find company with the economists and anthropologists when it comes to preference and utility. Despite this, I propose that the appropriate currency for this opportunity-cost map is utility.

In economics utility theory has a convoluted history (Page 1968). Bentham, in his own words, "planted the tree of utility . . . deep, and spread it wide" (quoted in Stigler 1965:66) in the late 18th century, a calculus for an introspective but measurable quantity that could be used for designing efficacious moral legislation. Over the next hundred years the concept changed profoundly. Bernoulli and others formalized the idea of marginal utility. Edgeworth introduced the convention of indifference curves, here adapted to ecological analyses. Marshall got the curves firmly linked to a theory of consumer demand. Pareto showed that utility was not measurable—that, in effect, utility maps represented only ordinal relationships of preference. Hicks and Allen argued that introspective ideas like utility were unnecessary if one replaced marginal utility with marginal rate of substitution. And Samuelson completed the program by showing that behaviorist analysis of "revealed preference" freed the theory of all unscientific notions, like utility. The utility in utility theory extinguished itself. From a social theory it has been transformed into an idea strictly tied to price-demand theory, ordinal, thoroughly behaviorist, and therefore presumably free of any base sociocultural content or psychological assumptions. Despite the Nobel Prize attached to the end of this sequence, I am most comfortable with the utility of the pre-Samuelson period (see Sen 1977; Wong 1978).

I define utility as the worth people attribute to things or actions, either because they are useful, in an adaptive or fitness-enhancing sense, or because they have status within sociocultural systems of meaning or exchange. Preference is the expression of such rankings, revealed in choice or evident in action.

Fitness draws on the deductive power of evolutionary theory; sociocultural valuation on the surety that learned beliefs and experience exert a strong and more or less independent influence on the variability in the specific forms of human foraging choices. Both are necessary for human adaptation research, but neither in the abstract is very helpful. To interpret them (as isocline maps) or evaluate their combined action (in the form of utility), we are forced to consider empirical understandings of behavior and environment, to generalize from facts about the meaning of our deductive postulates, to inquire about, observe, and, if need be, assume preferences. This is necessary to translate those abstract currencies into an indifference map that will produce interesting, testable hypotheses. Utility and preference are messy concepts, but until we have sound theories of biocultural evolution, their use is unavoidable.

An Idealized Hunter-Gatherer Indifference Map

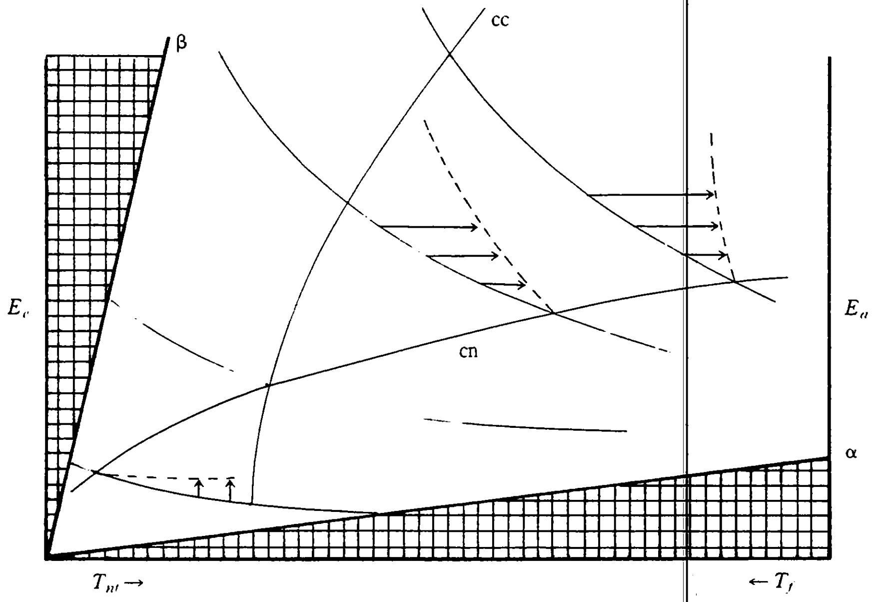
I will also propose a normative or idealized form for the indifference map of a hunter-gatherer. Consider the following question: How would we represent the case in which there is a social stigma or material disadvantage associated with too much or too little success in the harvesting of food? Note that this allows social phenomena an explicit influence on individual preference. Note also that this map will portray long-term averages or behavioral tendencies, ignoring day-to-day vagaries of motivation and success in the food quest.

Social controls come into effect when a person exceeds or falls short of a consumption norm. Controls might have three effects. First, they might cause the person to reevaluate his or her preferences toward greater conformity with the norm. Second, if the person adamantly holds to certain preferences, the group, by withdrawing assistance or otherwise impeding the performance of non-foraging tasks, could reduce that individual's ability to derive utility from various time and energy combinations. Finally, they might reduce the foraging efficiency of the recalcitrant, perhaps by withholding information, thus depressing his or her foraging-constraint line and reducing energy intake (if not the commitment to consumption).

Graphically, a social consumption norm will take the form of a line intermediate between minimum and maximum non-foraging expenditure rates. It can be derived as follows. Begin with a garden-variety indifference map (Figure 12.7), with an individual consumption curve different from the social consumption norm. Social pressures (the second alternative above) can be represented by arrows transforming the indifference map. Above the consumption norm these cause the indifference curves to pivot upward and to the right because the utility that the person can derive from various time-energy combinations is lowered. Below the consumption norm, disapproval of insufficient harvest will also lower the utility of various time-energy combinations, again pivoting the indifference curves upward and to the right. Whether this individual begins as a time-minimizer or an energy-maximizer, his or her individual consumption curve will approach the accepted norm.

The indifference map generated by this exercise is an intuitively reasonable hypothesis about individual preferences as such. If energy shortfalls approach sustenance levels, tactics will tend toward energy maximization and longer foraging. If intake grows to or above a comfortable level, people will tend to adopt time-minimizing strategies and engage in less foraging. This hypothesis also recognizes that the coercive powers of fitness and sociocultural factors over human behavior are not evenly distributed over the indifference map. In the lower and left-hand portions, for instance, sufficient food assumes more importance. Health and survival (and perhaps, but not necessarily, fitness) may be at stake. In the upper and right-hand portion, basic needs have been satisfied, and historically specific, sociocultural determinants of needs and wants may prevail. People are guided sometimes by the belly and sometimes, quite independently, by the head.

FIGURE 12.7. Generation of a Consumption Norm (cn) by Group Pressure on an Individual's Preferences (Indifference Map)



This idealized indifference map should be viewed as a baseline hypothesis. The actual map of any particular forager or foraging group may be different in ways that must be given a situational explanation. Deviations will be a function of various factors, including the following:

1. The number and value of the non-foraging activities performed, including the support of dependents, and their collective demands on energy and time
2. The potential for satiety with respect to energy and time, and their use in non-foraging activities
3. Differences in age, sex, and individual competence in non-foraging tasks

4. Physical hazards and perceived comforts or discomforts of foraging, relative to those for non-foraging activities
5. Uses of resources aside from immediate consumption by foragers or their dependents (perhaps in exchange or for storage)
6. Temporal and situational factors that influence the opportunity costs of behaviors through scheduling constraints on alternative activities

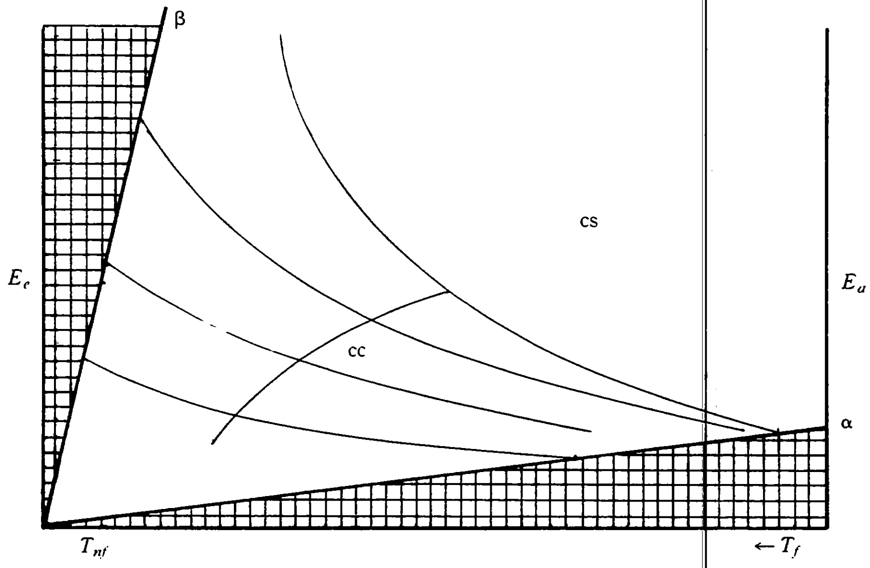
This last point is quite important. The "cost" of an activity is not necessarily the actual time or energy expended on it. For instance, tool manufacture in the secure warmth of one's hut, after the evening's reproductive fitness has been secured and while hunting and gathering are on hold until the following day, has no cost except the increment of energy expenditure above the resting metabolic rate.

Satiety

Economists have no qualms about the assumption that human wants for goods are unlimited, that ever greater amounts of utility can be gained from ever larger baskets containing, for instance, potatoes and grapes (Stonier and Hague 1973:53). The notion of surfeit is absent from the workings of microeconomics, which has formalized the ignorance of excess. But even if we accept insatiability for combinations of goods in a market economy, the combination of time and energy represented in a hunter-gatherer indifference map is a different matter. The time of the model refers to a finite interval, and the metabolic use of energy has a limit at the point of exhaustion. The foraging mode may itself place structural constraints on the use of energy (Lee 1981). Thus, for foragers, consumption of energy is tied to physiological and socioeconomic constraints quite unlike those affecting the consumption of goods in a market economy (where the object is not acquisition of potatoes and grapes to eat but competitive transformation of commodities to sustain a profit or retain a wage).

This brings us to Sahlins's (1972) proposition that hunter-gatherers are in business for their health (a not un-Darwinian statement), and a new question: How would satiation affect the model? It is possible and perhaps likely that foragers have, and readily attain, an upper bound for energy/time utility, and express it in their preferences. If non-foraging leads to boredom, which impels the forager to hunt or gather, or if the social constraints on material acquisition or aggrandizement through accomplishments cause an unusually successful forager to forgo the food quest temporarily (R. B. Lee, pers. comm.), then maximum utility may actually be a curved ridge, or it may reach a plateau (Figure 12.8). More time foraging and greater energy harvest may reach a point of *disutility* or an indeterminant zone of like utility. A ridge would cause the consumption curve to bifurcate into two optimal harvest options; a plateau would generate a set of equivalent options, a *consumption space*. There is no longer a single equilibrium, but a set of alternatives among which pressures for adaptive optimization carry no determinancy.

FIGURE 12.8. An Indifference Map with a Utility/Fitness Plateau, Generating a Consumption Space (cs)



These latter two indifference maps (Figures 12.7 and 12.8) are important because they provide a link between optimal foraging theory and some more traditional analyses of foragers, including the "original affluence" and "limited needs" proposals of Sahlins (1972) and Lee (1979; cf. Hawkes and O'Connell 1981). It is a revealing link because some (Hawkes et al. 1985) have claimed, incorrectly I believe, that an evolutionary ecology approach is theoretically incompatible with this earlier work. Sahlins and Lee inquire principally about the political economy of foraging, raising questions that cannot be answered by foraging theory per se. "Original affluence" and "limited needs" are mainly concepts of sociocultural valuation. They enter an opportunity-cost foraging analysis through their effect on the shape of the individual's indifference map. To have limited needs with respect to foraging is to be, in effect, a time-minimizer. A forager may seek to be optimal in the choice of a foraging strategy in order to be a time-minimizer and energy satisfier in the food quest. There are no theoretical impediments to this possibility, nor does it seem unlikely, given the ethnographic record of hunter-gatherer preferences and foraging efficiencies. The proposition that there is always more utility to be gained from hard productive work is more aptly ascribed to Calvin than to Darwin.

Risk-Sensitive Foraging Models

A second body of recent work focuses on the effects of stochasticity in foraging decision variables (e.g., encounter rate). Most existing models, including those discussed above, are deterministic, based on the simplifying assumption that expected (or average) values adequately characterize the important factors in foraging decisions. But, in fact, foragers may respond to the mean *and* variance in the rewards associated with each diet choice. They may be "risk-sensitive," depending on their preference for variance or certainty in combination with differing mean food reward expectations. A simple result of this work is the prediction that a forager will make choices that avoid variance if its current energy budget is positive, but seek variance if that budget is negative. Figure 12.9 is a simplified depiction of this prediction. There are four possible foraging decisions (*A* through *D*), each with a different mean/variance combination in the associated food reward. For positive mean expected intakes (u_t), those above the net minimum survivable requirement (R_{net}), minimizing variance (var_t) is optimal (*A* is preferable to *B*); for u_t below R_{net}, maximizing variance will result in at least some positive outcomes (*D* is preferable to *C*).

Stephens and Charnov (1982) have derived a model that generalizes the results depicted in Figure 12.9. The probability of starvation (Z') may be given as follows (in a form that avoids mathematical details to the extent possible):

$$Z' = (R_{net} - u_t)/(var_t)$$

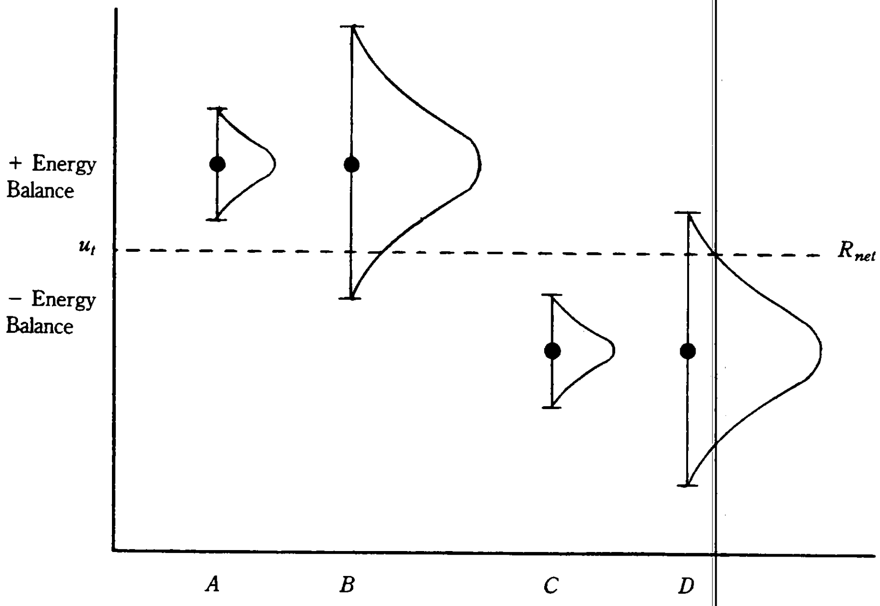
Risk diminishes as Z' decreases, with the troublesome mathematical quirk that the organism is in positive energy balance when Z' is negative. Reference to the equation will show that for positive values of Z'

$$R_{net} - u_t > 0$$

That is, there is a negative energy balance; increasing variance decreases risk. For negative values of Z'

$$R_{net} - u_t < 0$$

FIGURE 12.9. The Extreme Variance Rule for Risk-Sensitive Foraging Decisions in a Stochastic Environment



NOTE: Each of the foraging choices (*A* through *D*) has associated with it a distribution of food rewards, characterized by a mean and a variance.

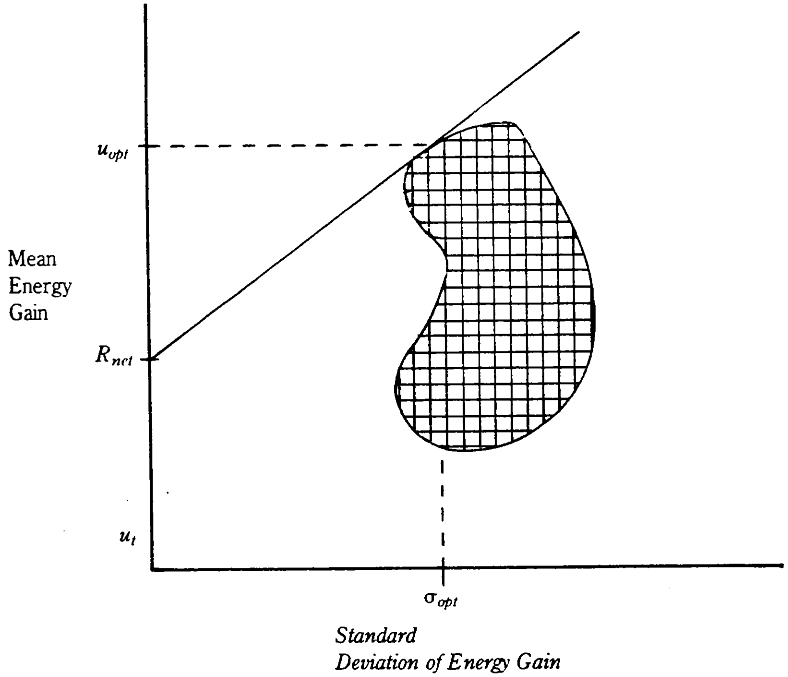
There is a positive energy balance; decreasing variance decreases risk. Large expected values relative to minimum requirements ($R_{net} - u_t \ll 0$; Z' is a large negative number) also reduce risk. The equation can be reorganized as:

$$u_t = R_{net} - Z'(var_t),$$

the standard slope-intercept equation, and then depicted graphically as in Figure 12.10. The full set of mean/variance combinations associated with the available foraging choices can be represented by points (var_t, u_t) on this plane. The optimal diet is that combination intersected by the line extending from R_{net} with the greatest slope. (This is because the greater the slope ($-Z'$), the lower the value of Z, which we want to minimize.)

Stephens and Charnov derive the mean/variance combinations for the marginal-value theorem that result from stochastic variance in the time required to locate a patch. They get an oblong curve with these properties: (1) the

FIGURE 12.10. Generalized Stephens/Charnov (1982) Model for Foraging Decisions with Stochastic Elements



NOTE: The greatest slope $(-Z')$ of the line that intersects one of the available mean/variance pairs (shaded area) minimizes Z' and hence risk.

stochastic result will usually approximate the deterministic outcome; but (2) if minimum requirements are less than the expected maximal intake predicted by the deterministic model, then the forager should remain in patches somewhat longer than predicted by the deterministic model. That the complicated stochastic outcome approximates the simple deterministic one is encouraging, but the unusual set of mean/variance combinations that gives rise to this consequence suggests caution in extrapolating to other situations.

Conclusions on the Process of Stalking

To summarize, optimal foraging models may provide one answer to Bettinger's (1980) "impending crisis" in hunter-gatherer studies—the need for new "predictive/explanatory" models to guide research and interpretation. They may provide a "consequence law"—in the restricted sense of Cohen (1978)—and hence a method for mitigating some shortcomings of functionalism (see Smith and Winterhalder 1981).

By attention to the history of the logistic equation and by carefully listing the assumptions of optimal foraging theory, I hope to have conveyed a particular and somewhat cautious attitude toward models. Partial skepticism is the best favor one can do a favorite theory. The fieldwork examples were meant to demonstrate that this is a heuristically rewarding type of inquiry. The section on opportunity costs and risk was meant to further develop the theory, and to define its boundaries. Extensions of opportunity-cost models may allow us to use formalist approaches in hunter-gatherer foraging and diet studies even while clinging to substantivist insights on forager goals. The initial results of risk-sensitive analyses suggest that we may be able to retain the simplicity of some deterministic models even while acknowledging the presence of stochasticity. In combination with fieldwork, these and other developments using evolutionary ecology theory may eventually generate a rigorous understanding of the ecological component of the foraging mode of production.

References Cited

Bettinger, R. L.
1980 Explanatory/Predictive Models of Hunter-Gatherer Adaptation. *Advances in Archaeological Method and Theory* 3:189–255.

Charnov, E. L.
1976 Optimal foraging: The Marginal Value Theorem. *Theoretical Population Biology* 9:129–36.

Charnov, E. L.; G. Orians; and K. Hyatt
1976 Ecological Implications of Resource Depression. *American Naturalist* 110:247–59.

Cody, M. L.
1974 Optimization in Ecology. *Science* 183:1156–64.

Cohen, G. A.
1978 *Karl Marx's Theory of History: A Defence.* Princeton, N.J.: Princeton University Press.

Connell, J. H.
1975 Some Mechanisms Producing Structure in Natural Communities: A Model and Evidence from Field Experiments. In *Ecology and the Evolution of Communities,* M. L. Cody and J. M. Diamond, eds., pp. 460–90. Cambridge: Harvard University Press.

Durham, W. H.
1976 The Adaptive Significance of Cultural Behavior. *Human Ecology* 4:89–121.

Gause, G. F.
1934 *The Struggle for Existence.* Baltimore: Williams and Wilkins.
Gould, S. J., and R. C. Lewontin
1979 The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme. *Proceedings of the Royal Society of London* B 205:581–98.
Hames, R. B., and W. T. Vickers
1982 Optimal Diet Breadth Theory as a Model to Explain Variability in Amazonian Hunting. *American Ethnologist* 9:358–78.
Hawkes, K.; K. Hill; and J. F. O'Connell
1982 Why Hunters Gather: Optimal Foraging and the Aché of Eastern Paraguay. *American Ethnologist* 9:379–98.
Hawkes, K., and J. F. O'Connell
1981 Affluent Hunters? Some Comments in Light of the Alyawara Case. *American Anthropologist* 83:622–26.
Hawkes, K.; J. F. O'Connell; K. Hill; and E. Charnov
1985 How Much Is Enough: Hunters and "Limited Needs. *Ethology and Sociobiology* 6:3–15.
n.d. Why Reduce It to Fitness? Optimal Foraging and Hunter-Gatherers. Manuscript.
Hutchinson, G. E.
1978 *An Introduction to Population Ecology.* New Haven: Yale University Press.
Jacob, F.
1977 Evolution and Tinkering. *Science* 196:1161–66.
Jochim, M.
1982 Optimization and Risk. Manuscript.
Johnson, A., and C. A. Behrens
1982 Nutritional Criteria in Machiguenga Food Production Decisions: A Linear-Programming Analysis. *Human Ecology* 10:167–89.
Keene, A. S.
1979 Economic Optimization Models and the Study of Hunter-Gatherer Subsistence Settlement Systems. In *Transformations: Mathematical Approaches to Culture Change,* C. Renfrew and K. Cooke, eds., pp. 369–404. New York: Academic Press.
1981 Optimal Foraging in a Nonmarginal Environment: A Model of Prehistoric Subsistence Strategies in Michigan. In *Hunter-Gatherer Foraging Strategies: Ethnographic and Archaeological Analyses,* B. Winterhalder and E. A. Smith, eds., pp. 171–93. Chicago: University of Chicago Press.
Kingsland, S.
1982 The Refractory Model: The Logistic Curve and the History of Population Ecology. *Quarterly Review of Biology* 57:29–52.
Krebs, J. R., and R. J. Cowie
1976 Foraging Strategies in Birds. *Ardea* 64:98–116.

Lee, R. B.
1979 *The !Kung San: Men, Women and Work in a Foraging Society.* Cambridge: Cambridge University Press.
1981 Is There a Foraging Mode of Production? *Canadian Journal of Anthropology* 2:13–19.
Levins, R.
1966 The Strategy of Model Building in Population Biology. *American Scientist* 54:421–31.
Lewontin, R. C.
1978 Fitness, Survival and Optimality. In *Analysis of Ecological Systems,* D. J. Horn, G. R. Stairs, and R. D. Mitchell, eds., pp. 3–21. Columbus: Ohio State University Press.
MacArthur, R. H., and E. R. Pianka
1966 On Optimal Use of a Patchy Environment. *American Naturalist* 100:603–9.
McCay, B.
1981 Optimal Foragers or Political Actors? Ecological Analysis of a New Jersey Fishery. *American Ethnologist* 8:356–82.
Maynard Smith, J.
1978 Optimization Theory in Evolution. *Annual Review of Ecology and Systematics* 9:31–56.
Mayr, E.
1974 Behavior Programs and Evolutionary Strategies. *American Scientist* 62:650–59.
Orians, G. H., and N. E. Pearson
1978 On the Theory of Central Place Foraging. In *Analysis of Ecological Systems,* D. J. Horn, G. R. Stairs, and R. D. Mitchell, eds., pp. 155–77. Columbus: Ohio State University Press.
Orlove, B. S.
1980 Ecological Anthropology. *Annual Review of Anthropology* 9:235–73.
Page, A. N.
1968 *Utility Theory: A Book of Readings.* New York: John Wiley.
Pulliam, H. R.
1981 On Predicting Human Diets. *Journal of Ethnobiology* 1:61–68.
Pyke, G. H.; H. R. Pulliam; and E. L. Charnov
1977 Optimal Foraging: A Selective Review of Theory and Tests. *Quarterly Review of Biology* 52:137–54.
Rapport, D. J.
1980 Optimal Foraging for Complementary Resources. *American Naturalist* 116:324–46.
Reidhead, V. A.
1979 Linear Programming Models in Archaeology. *Annual Review of Anthropology* 8:543–78.
1980 The Economics of Subsistence Change: Test of an Optimization Model.

In *Modeling Change in Prehistoric Subsistence Economies,* T. K. Earle and A. L. Christenson, eds., pp. 141–86. New York: Academic Press.

Richerson, P. J.
1977 Ecology and Human Ecology: A Comparison of Theories in the Biological and Social Sciences. *American Ethnologist* 4:1–26.

Ross, E. B.; J. B. Ross; N. A. Chagnon; and R. B. Hames
1980 Amazonian Warfare (Letter). *Science* 207:590–93.

Sahlins, M.
1972 *Stone Age Economics.* Chicago: Aldine.

Schoener, T. W.
1971 Theory of Feeding Strategies. *Annual Review of Ecology and Systematics* 2:369–404.
1974 The Compression Hypothesis and Temporal Resource Partitioning. *Proceedings of the National Academy of Sciences, USA* 71:4169–72.
1982 The Controversy Over interspecific Competition. *American Scientist* 70:586–95.

Sen, A. K.
1977 Rational Fools: A Critique of the Behavioral Foundations of Economic Theory. *Philosophy and Public Affairs* 6:317–44.

Smith, E. A.
1979 Human Adaptation and Energetic Efficiency. *Human Ecology* 7:53–74.
1981 The Application of Optimal Foraging Theory to the Analysis of Hunter-Gatherer Group Size. In *Hunter-Gatherer Foraging Strategies,* B. Winterhalder and E. A. Smith, eds., pp. 36–65. Chicago: University of Chicago Press.
1983 Optimal Foraging Theory and Hunter-Gatherer Societies. *Current Anthropology* 24:625–51.

Smith, E. A., and B. Winterhalder
1981 New Perspectives on Hunter-Gatherer Socio-Ecology. In *Hunter-Gatherer Foraging Strategies: Ethnographic and Archaeological Analyses,* B. Winterhalder and E. A. Smith, eds., pp. 1–12. Chicago: University of Chicago Press.

Speth, J. D., and K. A. Spielmann
1983 Energy Source, Protein Metabolism, and Hunter-Gatherer Subsistence Strategies. *Journal of Anthropological Archaeology* 2:1–31.

Stearns, S. C.
1976 Life History Tactics: A Review of the Ideas. *Quarterly Review of Biology* 51:3–47.

Stephens, D. W., and E. L. Charnov
1982 Optimal Foraging: Some Simple Stochastic Models. *Behavioral Ecology and Sociobiology* 10:251–63.

Stigler, G. J.
1965 The Development of Utility Theory. In *Essays in the History of Economics,* G. J. Stigler, ed., pp. 66–155. Chicago: University of Chicago Press.

Stonier, A. W., and D. C. Hague
1973 *A Textbook of Economic Theory.* New York: Wiley.

Webster, D.
1981 Late Pleistocene Extinction and Human Predation: A Critical Overview. In *Omnivorous Primates: Gathering and Hunting in Human Evolution,* R. S. O. Harding and G. Teleki, eds., pp. 556–94. New York: Columbia University Press.

Westoby, M.
1978 What Are the Biological Bases of Varied Diets? *American Naturalist* 112:627–31.

Wiens, J.
1977 On Competition and Variable Environments. *American Scientist* 65:590–97.

Winterhalder, B.
1981a Optimal Foraging Strategies and Hunter-Gatherer Research in Anthropology: Theory and Models. In *Hunter-Gatherer Foraging Strategies: Ethnographic and Archeological Analyses,* B. Winterhalder and E. A. Smith, eds., pp. 13–35. Chicago: University of Chicago Press.
1981b Foraging Strategies in the Boreal Forest: An Analysis of Cree Hunting and Gathering. In *Hunter-Gatherer Foraging Strategies.* B. Winterhalder and E. A. Smith, eds., pp. 66–98. Chicago: University of Chicago Press.
1981c Competitive Exclusion and Hominid Paleoecology: Limits to Similarity, Niche Differentiation and the Effects of Cultural Behavior. *Yearbook of Physical Anthropology* 24:101–21.
1983a History and Ecology of the Boreal Zone in Ontario. In *Boreal Forest Adaptation: The Algonkians of Northern Ontario,* A. T. Steegmann, Jr., ed., pp. 9–54. New York: Plenum Press.
1983b Boreal Foraging Strategies. In *Boreal Forest Adaptations: The Algonkians of Northern Ontario,* A. T. Steegmann, Jr.. ed., pp. 201–41. New York: Plenum Press.
1983c Opportunity Cost Foraging Models for Stationary and Mobile Predators. *American Naturalist* 122:73–84.

Wong, S.
1978 *The Foundations of Paul Samuelson's Revealed Preference Theory.* London: Routledge and Kegan Paul.