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The Evolutionary Ecology of Food Acquisition

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6.1. INTRODUCTION

Evolution is competitive. Variants that can more efficiently harvest resources for reproduction should become more prevalent through time. The nature and distribution of resources are thus primary conditioning factors that determine adaptations. Any comprehensive theory of hominid evolution and contemporary human social behavior will rest heavily upon a theory of resource acquisition.

This chapter will present evolutionary models of food acquisition and discuss examples of the associated empirical research among humans. The principal focus will be upon hunter-gatherers and forager-horticulturalists with little or no market involvement. We will examine subsistence decisions, given the technology and resource acquisition abilities of the people in question. We will not address the question of how much time individuals should spend in subsistence activities (see Chapter 7) but instead we consider what people do with the time they devote to food acquisition. We also will assess progress toward the complementary goals of (1) explaining observed variation in diet and food acquisition strategies among and within human groups and (2) developing general models of behavioral decision-making.

Section 6.2 will review the application of optimization theory to dietary decisions and the most general foraging models: prey choice, patch choice, and combined prey and patch choice models. This discussion and the associated mathematical formalisms are drawn mainly from Stephens and Krebs (1986). This will be followed by a selective review of empirical research applying those models to subsistence-level human groups. Section 6.4 will discuss ways in which traditional human economies are likely to violate the assumptions of most existing foraging models, and some areas in

which studies of humans are likely to contribute to a general understanding of subsistence behavior in all organisms. We consider central-place foraging, planning and scheduling of activities, incomplete knowledge and information-gathering, the implications of human communication and information exchange, and individual variation in foraging behavior. Section 6.5 treats what we consider to be the two most important unsolved problems in the evolutionary ecology of food acquisition among humans: nutrient complementarity and within-group specialization in subsistence behavior.

6.2. SIMPLE MODELS

6.2.1. *The Theory of Optimal Behavior and Its Application to Foraging*

Underlying all the models discussed in this chapter is the assumption that organisms will behave as if they are optimizing some fitness-related currency or set of currencies. The logic of cost-benefit analysis is used to justify this assumption. The fitness effects of behavior are multiple and always include some cost. For example, in the act of stalking and firing an arrow at a deer, energy is expended in stalking and shooting, the arrow may be lost or broken and have to be replaced, and if the animal is killed it will have to be butchered and cooked. The hunting attempt also involves *opportunity* costs such as not hunting other animals, clearing gardens, or caring for children.

Natural selection should favor organisms that maximize the *net* (i.e., benefits minus costs) fitness results of their possible behavioral options (e.g., food gains as a function of time and energy spent foraging). This will be true if at least one of the following conditions is met: (1) more food would lead to increased fertility or survivorship; (2) more time spent in one or more nonforaging activities would lead to increased fertility or survivorship; (3) time spent foraging exposes the individual to dangerous predators, pathogens, or environmental conditions that lower fertility or survivorship. Optimization logic does not imply that natural selection will favor the best possible foraging strategy conceivable, but rather that selection will favor the optimal strategy among the *feasible* existing strategies. As long as foragers have valuable ways to spend their time or there are some risks associated with the food quest, efficient foraging will be favored, even when food is not scarce.

6.2.2. *The Construction of Foraging Models*

Foraging models contain three components: decisions, currencies, and constraints. The decision component is the foraging problem to be an-

alyzed, that is, the phenomenon the model is designed to explain. For example, the prey choice model is designed to explain which of several food resources the forager will eat. The currency component defines the measurement scale for evaluating the effects of alternative decisions. Examples of currencies are energy (e.g., net energy acquired per unit time), protein, survivorship, and fertility. These currencies are intervening variables through which the behavior or morphology under investigation affects fitness. The use of intervening currencies has several advantages. Fitness itself is very difficult to measure and, in long-lived organisms, can require more time than the lifespan of a single investigator. Fitness is also affected by many nonforaging factors. A currency such as energy is directly affected by foraging decisions. Furthermore, determining the pathway through which a decision affects fitness generates a more complete understanding of the phenomenon than would a simple correlation between decisions and fitness.

Constraints are all the other terms in the model. They specify options available to the forager and their effects. Examples of constraints are the density and distribution of potential food resources in the environment, the dangers associated with exploiting different resources, and the forager's technology, ability to exploit those resources, mobility pattern, and knowledge of the environment. The initial selection of currencies and constraints in a model may be incorrect. Failure to confirm the model's predictions often leads to the search for more appropriate constraints. Indeed, most elaborations of the simple foraging models in recent years have involved changes in either currencies or constraints (see Stephens and Krebs 1986).

6.2.3. *Modeling Prey Choice*

We begin by outlining the simplest and most general model, presented in various forms by MacArthur and Planka (1966), Charnov and Orians (1973), Schoener (1971), Emlen (1966, 1973), Maynard Smith (1974b), Pulliam (1974), and Stephens and Krebs (1986).

Model Components. The model is designed to predict the food items the forager will attempt to exploit ("handle") and those it will ignore in favor of continued search for more preferred foods. Thus, the decision component of the model is to search or handle. Search is time spent looking for prey whether actively moving through the environment or waiting for food items to pass by. Handling prey includes all time devoted to pursuing, capturing, processing (e.g., transporting, butchering, cooking), and eating the prey, once it is encountered.

The currency component in the simplest model is energy. The model assumes that the forager is designed to maximize the *long-term net rate* at which energy is acquired during foraging.

There are several important constraint components to the model. Searching for and handling prey are *mutually exclusive* activities; they cannot be done simultaneously. Prey are encountered sequentially and randomly, but in proportion to their abundance in the environment. Prey types are not *systematically* clumped into patches or evenly dispersed. The model also assumes that foragers have no impact on resource abundance and distribution. It assumes that encounters without pursuit involve no handling time and do not subtract from search time. Finally, the forager is assumed to know, through past experience, the mean encounter rate, average energy returns, and handling costs associated with each prey type.

Solving for Optimal Prey Choice. Total foraging time (T_f) may be divided into time spent searching for resources (T_s) and time spent handling resources (T_h). T_h includes time spent in failed pursuits, such as chasing animals that escape, as well as successful ones. The total net energetic returns obtained from resources (E) can be thought of as the food energy acquired (E_a) minus the energy spent searching for (E_s) and handling (E_h) resources. The model then solves for the maximal rate (R_{max}) of net energy acquisition:

$$R_{max} = (E/T_f)_{max} \quad (6.1)$$

In order to solve for R_{max} one must know three characteristics of every resource i : (1) the average net energy acquired from each encounter (e_i); (2) the expected or average handling time per encounter (h_i); and (3) the abundance of the resource, measured by the rate at which it is encountered (λ_i). The return rate on encounter for a resource (e_i/h_i) is termed its *profitability*. In addition, the model includes a term describing the probability that a resource will be pursued if it is encountered (p_i).

Net energy acquired during foraging (E) is equal to net energy acquired from resource pursuits (the sum of all encounters with all prey types ($T_i \lambda_i$), times the probability that they will be pursued (p_i), times the expected net energy returns from encounters with each prey type (e_i)), minus the energy expended in search (the energy costs of search multiplied by time spent searching (sT_s)). Time spent foraging (T_f) is equal to time spent handling resources (the sum of all encounters with all prey types ($T_i \lambda_i$) times the probability that they will be pursued (p_i), times the mean handling time per encounter (h_i)), plus time spent searching for resources (T_s). Thus, the rate (R) of energy gain for the total set of resources handled by a forager is found in the following expression:

$$R = \frac{\sum_{i=1}^n T_i \lambda_i p_i e_i - sT_s}{\sum_{i=1}^n T_i \lambda_i p_i h_i + T_s} \quad (6.2)$$

An algorithm allows one quickly to determine which prey items should be pursued. First, all resources are ranked in descending order of their prof-

itability. The prey type that yields the highest return rate upon encounter ($(e_i/h_i)_{max}$) should always be pursued. Other lower-ranked resources should be included sequentially in the set to be pursued until the next most profitable resource yields a lower rate of return upon encounter than could be obtained by continuing to search for and pursue the more profitable items. None of the resources that are ranked lower in profitability should be pursued when encountered.

The set of resources that result in R_{max} are referred to as the *optimal set* or the *optimal diet*. The total number of resources in the diet, counting from the top of the ranked list, is referred to as *diet breadth*. All resources included in the optimal diet must be characterized by higher return rates on encounter than the average foraging return rate for the forager, including all search time.

To see how this works, consider the following example. There are three resources in the environment. The first resource (r_1) is encountered once in every 5 hours of search ($\lambda_1 = 0.2$ items/hr), yields a net return of 1200 cal, and requires 1 hour to handle ($e_1/h_1 = 1200$ cal/hr). The second resource (r_2) is encountered twice in 5 hours of search ($\lambda_2 = 0.4$ items/hr), yields 450 cal, and requires a half hour to handle ($e_2/h_2 = 900$ cal/hr). The third (r_3) is encountered once an hour ($\lambda_3 = 1$ item/hr), yields 200 cal, and requires 1 hour to handle ($e_3/h_3 = 200$ cal/hr). We begin by considering the most profitable resource (r_1). If the forager only exploits r_1 , he or she will on average acquire 1200 cal for every 6 hours spent foraging (5 hours of search plus 1 hour of handling) or a total of 200 cal per hour foraging. Since the second-ranked resource (r_2) will on average result in 900 cal per hour on encounter, the forager will increase his or her return rate by pursuing it on encounter. With both items in the optimal set he will make three encounters in 5 hours of search. He or she will spend 1 hour handling r_1 and 1 hour handling r_2 (twice for a half hour each time). Thus, in 7 total hours of foraging (including search), he will acquire 2100 cal (1200 from r_1 and 900 from r_2) or 300 cal/hr, a higher rate than can be obtained by pursuing r_1 alone. Since the foraging return rate of 300 cal/hr is now higher than the expected returns from r_3 after encounter ($e_3/h_3 = 200$ cal/hr), it does not pay to pursue r_3 . To prove this, consider what happens if all three resources are taken. In 5 hours of search, the forager will handle r_3 five times for 1 hour each in addition to the 2 hours he will handle r_1 and r_2 . Each time he or she handles r_3 he spends on average 1 hour that cannot be used in search. Therefore, in 12 total hours of foraging, he will acquire 3100 cal or 258 cal/hr, less than the 300 cal/hr that could be obtained from exploiting only r_1 and r_2 .

Implications. This model has three important implications. First, each individual prey type will always be ignored or always be exploited ($p_i = 0$ or $p_i = 1$), depending upon whether it is in the optimal set. If exploiting a

food type will increase the average foraging return rate, there is no reason ever to ignore it. If, on the other hand, exploiting it would decrease the average return rate, it should always be ignored. Second, the food value of a resource type alone is not sufficient to determine whether a forager will pursue it; the costs must be considered as well. Thus, foods are ranked by their profitability (net energy gains divided by handling time) not by their food value. Third, the decision to exploit a food type does not depend on its abundance, but rather on the abundance of the more profitable alternative food types. As the abundance of those more profitable resource types decreases, more time will be spent searching and the overall return rate will decrease. Resources of lower profitability may then be added to the optimal diet.

While the prey choice model is extremely useful, it is unlikely that its predictions will match perfectly the patterns of real foragers, even if they do forage optimally. This is because it is afflicted with a series of restrictive assumptions. For example, the rule that resources should always or never be pursued on encounter will be violated if foragers seek information about resources or if test populations include a mix of individuals with different abilities (Stephens 1985). The ranking of resources may be inappropriate if search and handling time are not mutually exclusive (Hill et al. 1987). Despite these limitations, the optimal-diet model is useful because of its clarity, simplicity, and generality.

6.2.4. Methodological Considerations

In order to perform the strongest test of the prey choice model, it is necessary to measure the values of e , h , and λ for every potential resource encountered by a forager. This often is quite difficult. Even when all variables can be adequately estimated in field studies, the use of observational sampling of naturalistic behavior limits the measurements of profitability to those resources that are actually handled by the forager. This is unfortunate since strong tests of the model require a demonstration that resource types that are ignored yield lower returns upon encounter than the expected foraging returns from exploiting the optimal set.

6.2.5. Anthropological and Archaeological Applications of Prey Choice Models

Prey choice models have been employed in analyzing ethnographic data among the Aché of subtropical Paraguayan forests (Hawkes et al. 1982; Hill and Hawkes 1983; Hill et al. 1987; Kaplan et al. 1990), the Alyawara in the central Australian desert (O'Connell and Hawkes 1981, 1984), the Cree in the boreal forests of central Canada (Winterhalder 1977, 1981), the Ma-

chiguenga of tropical eastern Peru (Keegan 1986), the Yanomamo, the Yekwana, and the Stona Secoya in Venezuela and Ecuador (Hames and Vickers 1982), Inuit in the Canadian Eastern Arctic (Smith 1991), and the Senaq Beri of Malaysia (Kuchikura 1988).

Most studies have tested the qualitative predictions of the prey choice model. Qualitative tests predict *directional* tendencies in prey choice or diet breadth in relation to directional changes in parameters such as return rate or abundance, but do not precisely specify the suite of resources to be exploited. *Quantitative* tests require demonstration that every resource exploited increases overall return rate. Ideally, such tests should also demonstrate that every resource ignored would decrease overall return rate if it were exploited.

Qualitative Tests. A qualitative prediction of the prey choice model is that low-ranked resources will drop out of the diet when search costs decrease and hence overall return rate increases. Winterhalder (1977, 1981) compared the early historical period when Cree hunters searched for food on foot and paddled canoe with his observational period when they used motorized canoes and snowmobiles. He estimates that snowmobiles for instance cut search time costs by about 75%. Cree hunters pursued more species of animals (especially smaller ones) in the past than in the present, supporting the model's qualitative prediction. A second application of the prey choice model is Hames and Vickers's (1982) analysis of hunting strategies in three Amazonian societies. They test the prediction that diet breadth increases with a decrease in the density of highly profitable prey items by comparing zones of heavy hunting pressure and putatively low animal densities (the areas around older settlements) with zones of lower hunting pressure (areas around new settlements or distant from current settlements). Based on the assumption that large game are more profitable than small, they suggest that: (1) in zones of high hunting pressure, men shoot large animals when they are found but prey on the more abundant smaller game; and (2) in zones of low hunting pressure large game are more abundant and men often ignore small game. In all three cases, the proportion of large game to small game hunted decreased with increased hunting pressure. Among the Yekwana and Yanomamo, significantly fewer kills of small game (pacas and armadillos) occurred in distant zones than would be expected given the probabilities derived from binomial distribution theory.

Quantitative Tests. O'Connell and Hawkes (1981) use the optimal-diet model to predict the resources Alyawara women gather when they are in patches of collectable foods. They estimated the profitabilities of 10 subsistence foods in resource-abundant sandhill patches and found that women only gathered the three most profitable. Many species of ripe seeds, the most abundant food available, were ignored. Collecting experiments indicated

that the returns on encounter for the ignored seeds were lower than the average foraging return rate, for the three most profitable items. These results are consistent with the prey choice model, but should be interpreted cautiously since the test is based on the assumption that foragers should maximize their return rates while foraging within a patch. Combined prey and patch models (see below) suggest that maximizing the rate of net energy acquisition per unit time within a patch may not maximize overall foraging return rates. In the resource-poor mulga woodland, Atywara women also ignored ripe seeds. This was true even though their foraging return rate in that patch was so low that they could have increased their energetic return rate by collecting the seeds. Their behavior did not fit the model, perhaps because the handling times for seeds was underestimated or that some other assumption built into the model was faulty. We discuss this result again in a later section.

Research with Aché foragers of Paraguay (Hawkes et al. 1982; Hill and Hawkes 1983; Hill et al. 1987) was conducted to determine if all resources exploited by the Aché increased overall return rates. Experience is that most resources were distributed in ways that were not easily predictable by the foragers and that encounters were approximately random during search. Individuals were followed to determine how much time they spent searching for food items, the rates at which they encountered different resource types, and how much time they spent in pursuit and processing after each resource encounter. The food acquired from these encounters was weighed and converted into caloric equivalents. No attempt was made to measure the caloric costs associated with handling different food items; thus profitabilities were calculated without subtracting energy expended in pursuit and processing. Observed encounter rates by foragers rather than prey census data were used to measure λ .

Initial results based upon 4 months of field data (Hawkes et al. 1982; Hill and Hawkes 1983) were consistent with the quantitative predictions of the prey choice model. Aché exploited only those resources whose returns on encounter were greater than the average foraging return rate. No test was carried out to determine whether resources that were ignored when encountered would have increased overall return rates, had they been exploited.

The initial analyses of Aché data aggregated all foragers and activity types. However, since men and women have different skills, abilities, and tools, and exploit different foods, they were considered separately in subsequent studies. Male foraging behavior, when hunting alone is considered, is quite consistent with the quantitative predictions of the prey choice model (Hill and Hawkes 1983; Hill et al. 1987). All 9 meat resources hunted by Aché men increased overall hunting return rate (see Figure 6. 1). Sometimes men hunted with shotguns and at other times with bow and arrows. For shotgun hunters, the overall return rate was higher than the return rate on encounter for monkeys and small birds. For bow hunters, however, the on-encounter

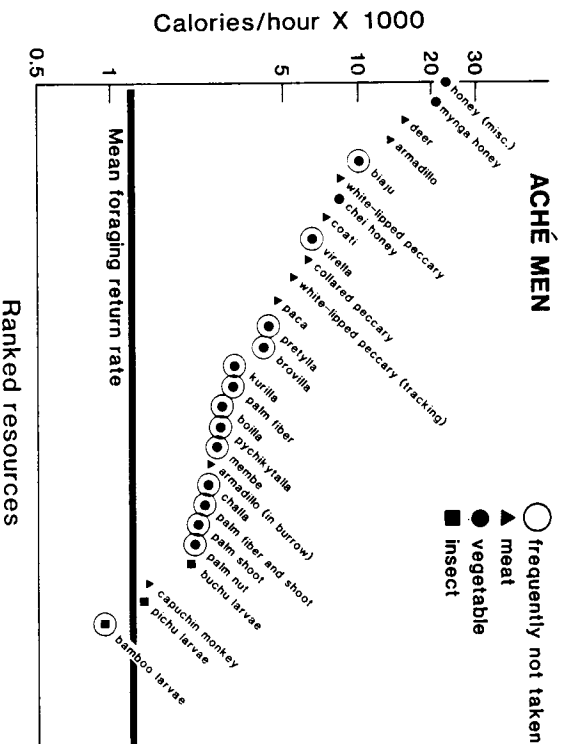


Figure 6. 1. Return rates expected from resources exploited by Aché men in order of descending profitability from left to right. The y axis shows the return rate expected on encounter with each resource type (e./h.). Circled resources are sometimes ignored when encountered (see Hill et al. 1987 for probabilities of pursuit) whereas other resources are always pursued when encountered. Note that 27 of 28 resources handled by Aché men are characterized by higher return rates on encounter than can be expected from overall foraging, as would be expected from Equation (6.2).

profitability for monkeys and small birds was higher than the average hunting return rate, including search. As predicted by the prey choice model, monkeys and small birds almost always were ignored by shotgun hunters but were pursued by bow hunters (Hill and Hawkes 1983). Estimates of return rates for different species of birds led to the calculation that shotgun hunters should take all birds of 1 kg or more and that bow and arrow hunters should take all birds weighing more than 0.4 kg. In fact, the smallest bird shot by shotgun and bow hunters, respectively, was 1.4 kg and 0.4 kg.

Seasonal changes in the pattern of armadillo hunting provide another interesting test of the prey choice model. Aché men always pursued armadillos when they were encountered above ground, but only dug armadillos from their burrows during the late warm-wet and early dry-cold season (Hill et al. 1987). Digging out armadillos greatly increased handling time; however, during the season when armadillos were pursued in their burrows, they were also very fat. They yielded about 3900 cal/hr on encounter. This is much higher than average hunting return rate of 1340 cal/hr. On the other hand, when armadillos were lean in the early wet season, the caloric return rate from digging was about 1220 cal/hr. By ignoring armadillos in burrows

when they are lean and pursuing them when they are fat, Aché men appear to have been maximizing their average hunting return rate.

Although these quantitative results are impressive, Aché men's behavior systematically deviated from predictions of the simple prey choice model because men frequently ignored plant foods that would increase their average caloric foraging return rate (Figure 6.1). Although men maximized meat calories obtained per hunting time, they did not choose the option that maximized total caloric production, which would have consisted mostly of palm fiber. We estimate that Aché foragers encountered an exploitable palm (*Arrecatum romanzoffianum*) about once every 8 minutes on average. Since each palm can be pounded for fiber for 1–2 hours, Aché men would have spent very little time searching and the vast majority of their foraging day extracting palm fiber, if they always exploited palms upon encounter. The overall energetic return rate from this foraging pattern would be approximately 2600–2700 cal/hr, much higher than the observed male foraging return rate of 1100–1340 cal/hr.

Women's foraging patterns show the opposite trend. They avoided pursuing highly profitable game resources, except under special circumstances (Figure 6.2). Generally, women carried no weapons and directed men to kill the animals they happened to encounter. They sometimes pursued burrowing animals, when no men were present and the kill could be made easily. Women also occasionally participated in group hand-hunts of coats, pursuing babies and juveniles but leaving the larger, dangerous animals to the men. Thus, the data on women's foraging patterns show that they could hunt, but avoided doing so. We believe that this is probably because of the reproductive costs associated with pursuing dangerous, mobile prey (see Hurtado 1985 and Hurtado et al. 1985 for the evidence and a detailed discussion).

The data on both men's and women's foraging behavior suggest that plant foods sometimes are ignored when they would increase overall caloric return rates and foods high in fat and protein are exploited even when they decrease foraging return rates. Within each major food class, however, Aché appear to maximize their overall return rate. We might tentatively draw this conclusion: *Existing optimal foraging models are quite useful for predicting food choice among resources composed of similar macronutrients but may need to be modified to account for sensitivity to the nutrient constituents of foods. The assumption that energy is the sole measure of food value may be inadequate.*

Archaeological Applications of Prey Choice Models. One major goal of archaeological research on diet is to explain long-term shifts in subsistence patterns (for reviews, see Earle and Christensen 1980; Smith 1983; Bettinger 1987). There is an increasing trend toward experimental tests of theories about the archaeological record based on prey choice models. For example,

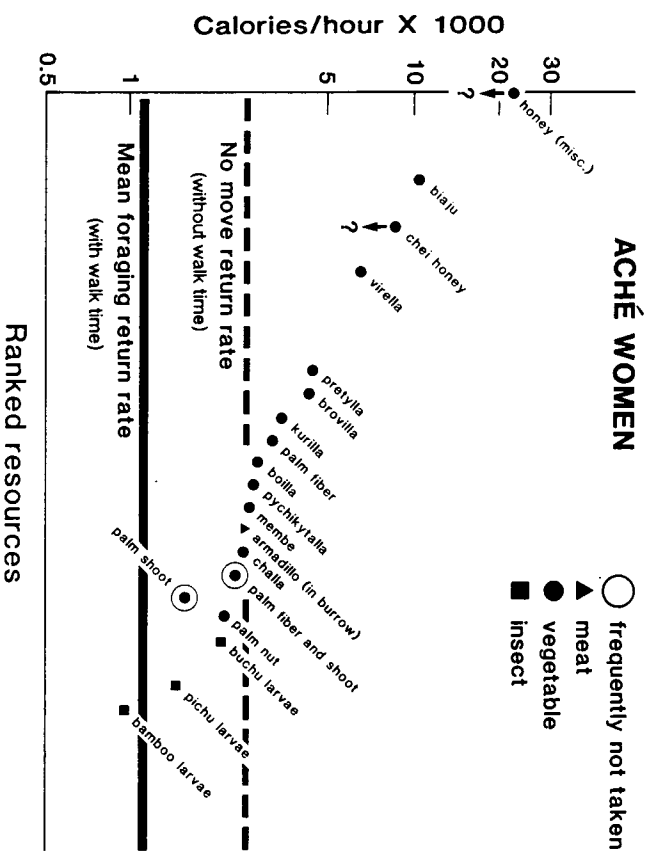


Figure 6.2. Return rates expected from resources exploited by Aché women (as in Figure 6.1). Note that women do not exploit most game resources taken by Aché men (compare ranked resources to those in Figure 6.1). The two estimates for the profitability of encounters with honey are based on return rates observed for men, since the sample size of encounters with honey extraction rates by women is small. The solid line shows the foraging return rate for women if time traveling between campsites is counted as search time. The dotted line shows the return rate for women when they do not move camp and all foraging time is spent in search or handling of resources.

using aboriginal techniques, Simms (1984) experimentally measured return rates from most species of edible seeds in the Great Basin in an attempt to model prehistoric changes in Great Basin foraging patterns. Archaeological data indicated that seeds were ignored by early Holocene foragers but were exploited heavily by later peoples. Simms's data suggested that most species of seeds yield low returns upon encounter because of their high processing time. He used the seed data to predict the threshold at which animal densities would be low enough that prehistoric foragers would have begun to exploit seeds. Such a prediction could be tested using paleoecological and paleontological data. Similarly, O'Connell and Hawkes (1981) used experimentally derived profitabilities from seed exploitation in Australia to postulate that only after the onset of arid conditions in Australia around 17,000 B.P. did Australian foragers begin to use seeds, and eventually populate the central desert regions of the continent.

6.3. PATCH CHOICE

When resource types are clumped together they are said to constitute patches. If foragers are able to perceive resource clumping, they are expected to use it to maximize their average foraging return rates. For example, foragers may face the decision of whether to enter a patch or continue searching other portions of the habitat, and if they choose to enter the patch they must decide how long to stay before looking for another patch.

Patch choice models use the same choice principle (mean rate maximization) and many of the same constraints as simple prey choice models, but they differ in their assumptions about prey distributions and net energy gain as a function of handling time. The prey choice model is based upon the assumption that search time is shared among all potential prey because they are encountered at random as a function of their abundance. However, if environments are sufficiently patchy, foragers may alter their return rate by spending more time searching specific portions of a habitat. Most patch models to date are primarily designed to predict how long a forager should remain in a patch once he or she has chosen to exploit it.

6.3.1. Modeling Patch Exploitation Time

Model Components. When a forager enters a patch and begins to exploit it, the rate at which he or she gains energy from the patch may change as a function of time spent there. It is useful to distinguish between three possibilities. First, energy acquired from a patch may increase linearly with patch residence time over a long time span (Figure 6.3a). This would be the case if the forager does not measurably deplete the resources in the patch as he or she forages. For example, spear fishing in the ocean by Australian aborigines may not deplete fish densities significantly. Under these conditions the forager should spend all his or her time in the most profitable patch because any movement entails travel costs and even the next best alternative would be to find another patch of the same type.

Alternatively, energy gain per unit time may remain constant until the patch is completely depleted, and then abruptly fall to zero (Figure 6.3b). For example, if fruits are evenly dispersed on the ground around a fruiting tree and the forager can easily see all of them, he or she may obtain a constant rate of return until the last fruit is collected. Under these conditions, the forager is expected to exploit only those patches whose initial profitability is greater than expected average foraging return rates for the environment as a whole, including travel between patches. He or she should then move to the next patch only after all food items are exploited. A third relationship between patch residence time and energetic return rate is nonlinear and decelerating (Figure 6.3c). Diminishing return rates

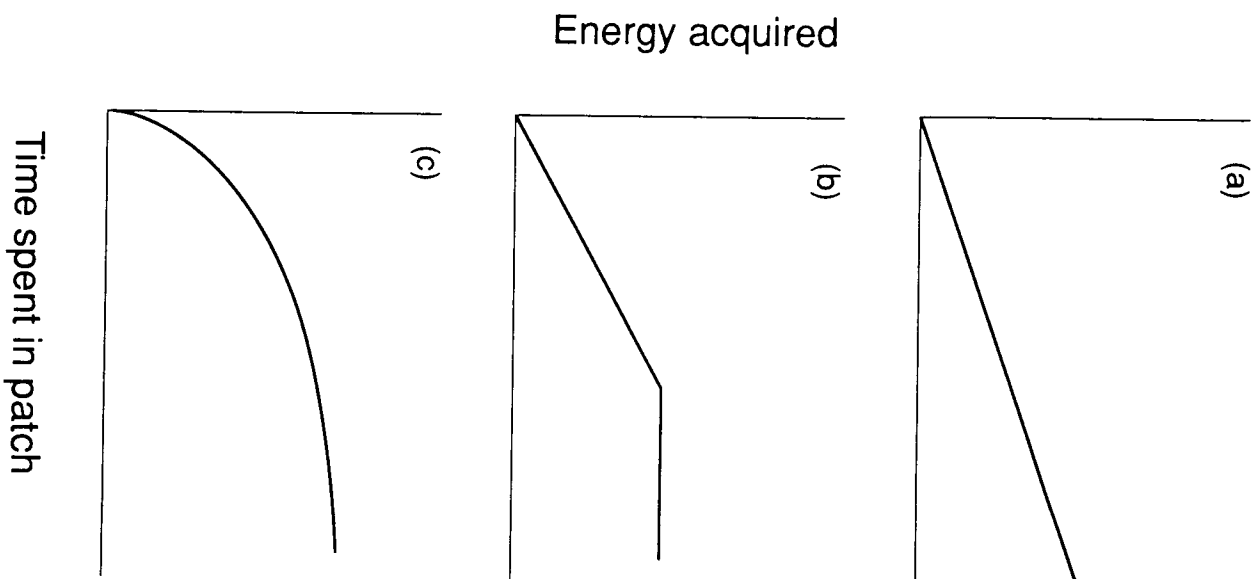


Figure 6.3. Food acquired as a function of time spent foraging in a patch that (a) does not become depleted; (b) provides a constant return rate until the last item is exploited; (c) becomes progressively depleted, or prey items become more difficult to find through time.

- will occur if the forager depletes resources while foraging and obtains a lower return rate in a patch after exploiting it for some time, or if prey become increasingly evasive as they are exploited.

Solving for the Optimal Patch Exploitation Time. The marginal-value theorem (Charnov and Orans 1973; Charnov 1976) was developed to determine the point at which the rate-maximizing forager should leave a depleting patch to search for another one. The patch gain function is assumed to be decelerating, and patches are encountered sequentially. The model predicts that a forager should remain in a patch as long as the expected returns from the next unit of foraging time in the patch are higher than expected returns from searching for and exploiting other patches (see Figure 6.4a). Optimal patch residence time will be a function of both how fast in-patch returns diminish and the overall density of patches in environment. As patches become more abundant and the expected search time between patches decreases, the overall foraging return rate will be maximized by shorter residence times (Figure 6.4b). Two important implications of the patch model are: (1) all patches should be exploited until they deplete to the same return rate; and (2) optimal patch residence time will increase as a function of expected search time between patches.

When prey are distributed patchily but in an unsystematic manner within patches, and when some prey are encountered between recognized patches, a combined prey and patch model is appropriate. These models are the most realistic and probably applicable in many human foraging societies, but unfortunately they are mathematically cumbersome and generally require computer simulation rather than algebra to obtain the optimal solution. Stephens and Krebs (1986) have developed a simple combined prey and patch model to predict both patch choice and patch residence time, to which the reader is referred.

6.3.2. Anthropological Case Studies Using Patch Models

To our knowledge no anthropological studies of patch residence time have been conducted that rigorously meet the assumptions of the marginal-value theorem (or the combined prey and patch model). Most studies attempt to predict which patch types a forager will exploit, given the average return rates associated with each patch in the environment. In these applications, the forager does not sequentially encounter patches but instead chooses which patch to visit each day. For such decisions the patch models described so far are *inappropriate* and may lead to erroneous predictions (Stephens and Krebs 1986:38–45). Choosing the patch with the highest average profitability will not necessarily maximize the overall foraging

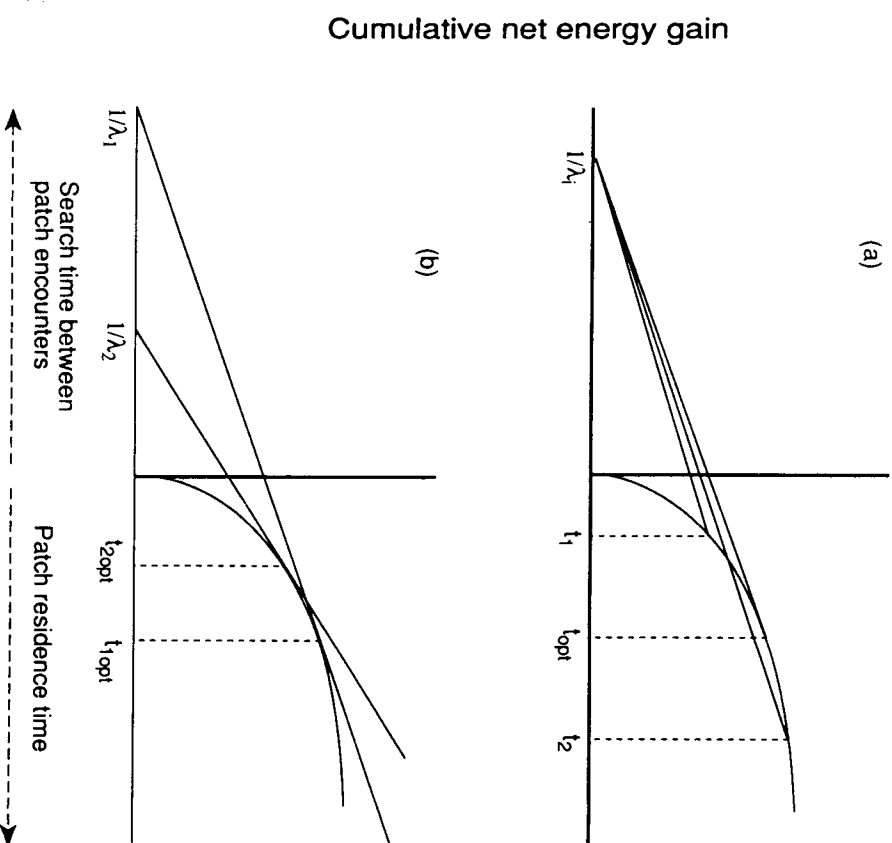


Figure 6.4. Graphical solutions to the problem of optimal patch residence time: (a) Energy acquired as a function of time spent in the patch (the gain function) is defined by the thin curved line. Overall foraging return rate is defined by the slope of the bold lines [$E/T_{\text{search}} + T_{\text{residence}}$]. Overall return rate is maximized when the slope of the bold line is maximized. Given the expected search time to encounter another patch ($1/A_2$) the forager maximizes the average long-term return rate (slope of bold line) at the patch exploitation time (t_{opt}), which forms an end point to the line tangent to the gain function. Patch exploitation times t_1 and t_2 are too short or too long, respectively, thus decreasing E/T. (b) The marginal-value theorem predicts that patch residence time will increase as the search time ($1/A_2$) for new patches increases. Thus, as it takes more time to find a new patch ($1/A_2$), it pays to stay longer in a depleting patch (t_{opt}).

return rate. Hill et al.'s (1987) analyses of why Aché hunters choose to exploit lower-ranked peccary patches rather than higher-ranked armadillo patches when both are encountered simultaneously is the only anthropological study that we are aware of that explicitly analyzes this situation. Several examples of patch choice studies among humans are given below.

Smith's (1991) research on Inuit examined time spent hunting in terrestrial and marine habitats as a function of seasonal variability in the return rates obtained from the two habitats. He attempted to determine whether foragers adjusted foraging time spent in each habitat according to their relative profitabilities. Marine habitat profitability peaked in summer (3030 cal/hr) and decreased steadily from fall (2310 cal/hr) to spring (2140 cal/hr). Terrestrial habitats yielded fairly similar returns in spring (1700 cal/hr), summer (1660 cal/hr), and fall (1570 cal/hr), and then peaked in winter (3810 cal/hr). There was no evidence of short-term depletion in either patch; thus return rate is maximized by always selecting the single patch with the highest rate. While it was observed that in each season Inuit hunters spent more time in the more profitable habitat, they did not choose the most profitable patch exclusively. Why might the Inuit sometimes exploit the patches with lower average profitability? Is it possible that patches exploited for several days or weeks in a row yield returns lower than the seasonal average, but recover after some period of nonexploitation? Are there conditions (e.g., weather and recent signs of prey) that reverse rankings of patch profitability on particular days? Investigating these issues should provide a good deal of new information about human subsistence decisions.

Beckerman (1983) examined patch choice among the Bari of Colombia. He measured return rates from fishing and hunting. The findings did not appear to support the prediction that the Bari would choose only the patch that yielded highest average return rate. Specifically, Beckerman showed that for each of 5 time periods sampled, fishing resulted in a higher rate of capture (kilograms of meat/man hour) than hunting, yet in 4 of the 5 time periods men spent more time hunting. Time spent fishing, however, did increase during the months when the ratio of fishing to hunting return rates was higher.

As in the Inuit example, the use of long-term averages limits the test of the patch choice model. First, as Beckerman pointed out, daily changes in environmental conditions may account for the observed pattern. Bari may have chosen to hunt on days when they expected fishing returns to be poor. Second, the gain function of each activity type is unknown. If the number of fishing patches within range was limited, temporary depletion (or changes in prey behavior) might have made hunting the best alternative for several days following fishing expeditions. Third, fishing is associated with a constrained time investment due to preparation and the fact that only one patch can be exploited per day. Conversely, time spent hunting is open-ended for the Bari. It may result in more total food per foraging day than fishing, even though the food is acquired at a less efficient rate. In the Bari case, it may be useful to complement observation naturalistic of foraging behavior with experiments designed to test these alternative hypotheses. For example, it might be possible to ask Bari to fish on some rainy days and just after

successful fishing expeditions to determine whether rates are depressed on those days.

O'Connell and Hawkes (1981, 1984) combined prey and patch models in their analysis of Alyawara hunting and gathering. Alyawara men, traveling in O'Connell's vehicle, engaged in two types of hunts, "discretionary" and "embedded." In the former, a decision was made to visit a specific patch in order to hunt there. In the latter, firearms were carried on trips whose primary purpose was other than hunting, such as station work. On those trips, the route taken was determined by the primary purpose and hunts were conducted opportunistically when game was sighted. The embedded hunts allowed the investigator to monitor returns from patches that hunters would not have chosen to visit if the primary purpose of the trip was hunting. Since the returns from embedded and discretionary hunts in the same patches were not significantly different, the data from the two hunt types was comparable. They found that of 11 patches sampled, hunters chose the most profitable patch type most frequently on discretionary hunts. Again, however, the same questions remain unanswered: Why did men spend any time in less productive patches? Were the high-return patches being depleted by hunting? O'Connell and Hawkes attempted to determine if there was temporal variability in patch quality that predicted patch switching. On days when hunting in the grassland was productive (i.e., a kill being made in the first half hour of search), hunters remained in the grassland. On days when it was cool and windy, preventing close approach to kangaroos, kills were not made on the grassland and hunters switched to the hills and ridges. Hunters were apparently acquiring information while hunting.

O'Connell and Hawkes (1981) also examined women's collecting trips. In this case, sandhill patches were characterized by an average return rate 6 times higher than in the mulga woodland. However, on 4 of 9 occasions when women were offered a jeep ride to the patch of their choice, they chose the mulga patches. Exploiting the mulga woodlands results in a much lower energetic return rate but a greater amount of animal flesh in the diet, especially in the hot-wet season. This may be another case of foraging biases on the basis of the macronutrient composition of foods.

Keegan (1986) reanalyzed Johnson and Behrens's (1982) data on Machiguenga forager-horticulturalists combining prey and patch models. He shows that caloric returns per hour of labor investment are about 15 times higher for gardening than they are for fishing or hunting. Yet the Machiguenga were observed to spend only 54% of their food acquisition and production time gardening and the remainder fishing and hunting. Keegan concluded that the simple patch choice model needs to be modified to include the differential nutrient composition of foods. In this case, the vast majority of the calories in Machiguenga gardens were derived from manioc, which is almost pure carbohydrate.

6.3.3. Summary

Simple prey choice models have proven extremely useful in predicting the foods foragers exploit. The tests conducted so far with humans suggest that foragers maximize return rates within classes of foods composed of similar macronutrients but bias resource choice away from calorie maximization in favor of increased protein and lipid consumption. Virtually all applications of patch choice models to human cases have addressed the proportion of time people spend exploiting different food patches when encounters are simultaneous (known locations). Such studies incorrectly assume that foragers should choose the patch characterized by highest returns, but foraging theory clearly specifies that this is *not* the case. Optimal patch choice under conditions of simultaneous encounter is dependent on a number of characteristics (Stephens and Krebs 1986:38–45) that have never been measured in any human study thus far. The gain functions of the patches have not been measured and the reliance on naturalistic observations have limited tests on temporal variation in returns from patches. Foragers sometimes appear to be scheduling short-term patch use in relation to changing return rates, but often there is little information to assess this possibility. At least two applications of the patch model suggest that nutrient differences may be an important criterion affecting optimal patch exploitation time.

6.4. RELAXING AND CHANGING ASSUMPTIONS

6.4.1. Central-Place Foraging

Theory. Humans frequently return to a central place when they forage. Central-place foraging can vary along a continuum from a random search and encounter to targeted search and pursuit. At one end of the continuum, the forager leaves camp, searches the environment for the entire suite of resources that he will exploit upon encounter, and returns to a camp with food (usually but not always, where he began). The Aché and perhaps !Kung hunters exemplify this pattern. At the other end of the continuum, the forager leaves the central place with a specific resource target determined in advance. Binford (1978) suggests that Nunamut Eskimo men leave camp seeking a specific target, often a specific animal, such as a hibernating bear, whose location is known. !Kung women (Lee 1979) visit known mongongo trees and Hiwi foragers visit named resource patches whose characteristics are known in considerable detail (K. Hill, personal observation). Many foraging situations lie somewhere in the middle of this continuum. Machinguenga and Bari men travel to known fishing sites but carry bows and arrows in order to exploit opportunistically encountered game en route (H. Kaplan, personal observation; Beckerman 1983). Cree hunters may leave

with moose as their reported prey target, but are prepared to shoot fowl if they are encountered (Winterhalter 1981). These situations present specific problems, each of which require extensions of the simple foraging models.

Central-place foraging imposes special travel costs. Sometimes this is just the cost of returning to a sleeping or activity site. However, if food is brought to another place to be eaten the costs of carrying the food item to the central place must also be considered (Jones and Madsen 1989; Metcalfe and Barlow 1991). In addition, carrying food items can sometimes decrease the forager's ability to capture new food items while he/she searches. Thus, carrying time can be partially or entirely exclusive of search and handling of additional foods. Two questions arise concerning deferment of consumption and transport: (1) Why is consumption deferred? (2) How does central-place foraging affect prey choice and prey handling? We are aware of no explicit models in the human literature that address the first question.

The effects of central-place foraging on prey choice and handling have received formal treatment in Schoener's (1979) encounters-at-a-distance model and Orians and Pearson's (1979) single- and multiple-prey-loader models. Schoener's model imagines a predator that waits at a central place from which it can scan for food items until it observes a prey pass by. The model shows that as distance from the central place to the site of encounter decreases, diet breadth increases and includes items of both high and low profitability. Longer distances narrow the diet to include fewer items of high profitability.

The single-prey-loader model (Orians and Pearson 1979) makes a similar prediction but is designed for choices about which prey to handle when resources are sequentially encountered in patches at some distance from the central place. Again, as distance increases, the model shows that foragers should return only with higher-ranked resources, passing by low-ranked items. Hames and Vickers's (1982) demonstration that Yanomamo hunters bring back larger prey when hunting in more distant zones is consistent with this prediction.

The multiple-prey-loader model considers a forager who travels to a patch and captures prey items until it returns with those items to a central place. The forager must carry all items it has already captured while it searches for and handles additional items (i.e., until it drops them off at the central place). The efficiency of search and capture within the patch is assumed to decrease as the load increases (e.g., a full beak may inhibit a bird's ability to capture additional prey). Thus the patch shows a negatively accelerated gain function and the forager faces a trade-off between in-patch foraging efficiency and travel time back to the central place. The forager must choose between more trips of smaller loads acquired at a higher return rate, and fewer trips of larger, less efficiently acquired loads. This trade-off can be modeled with the marginal-value theorem and makes a similar prediction: optimal load size increases with distance to the central place.

Anthropological Applications. Although no field tests of central-place foraging models have been carried out with human populations, some interesting archaeological models have been developed to look at the implications of central-place travel costs. Jones and Madsen (1989) considered the way in which maximum load will affect the ranking of resources located at a distance from a residential site. They conclude that when travel time is high relative to handling time for each resource, and when basket size limits the maximum load that can be carried back, a rate-maximizing forager will exploit resources that provide highest net caloric value per basketload rather than those of highest profitability. Metcalfe and Barlow (1991) have modeled optimal processing times for resources that are acquired at some distance from a residential camp where they will ultimately be consumed. Their model suggests that when transport costs are high, rate-maximizing foragers will often do better to remove low-utility parts in the field rather than transport them to a central place, even if the parts removed have some utility. Both of these archaeological models have important implications for the types of refuse likely to be found in archaeological sites distant from resource sources.

6.4.2. *Acquiring Information*

Theory. The foraging models discussed so far assume that the forager has complete information about resource distributions and yields. This assumption is frequently tenable even though foragers are never fully informed. Often, however, foragers appear to engage in behaviors that reduce short-term return rates but provide information that increases long-term gain. Information acquisition and the effects of incomplete information are important issues particularly relevant to human foragers, who rely extensively on learning and communication to assess resource distribution, abundance, and profitability.

Foraging models focused on information assume that information acquisition has some cost but provides a benefit. The costs might include time dedicated to sampling and travel to patches in order to determine their productivity. Rate maximization models can be modified to ask: How much effort should a forager expend in information acquisition? Some human foragers such as those in the Great Basin (Steward 1938) and Australia (L. R. Binford, personal communication) apparently travel very long distances to obtain information about food patches. Can we determine if such forays are worth the effort?

To offset its cost, information must increase the foraging return rate. There must be some environmental variability that affects the success of alternative behaviors. Suppose that caribou hunting is more effective in passes and canyons when many animals migrate through and that there is annual

variability in the passes and canyons chosen. Knowing the route of the caribou could have a major effect on return rates, but acquiring that information will entail a cost.

These problems can be addressed by models that make interesting qualitative predictions (Stephens and Krebs 1986). If environments change so rapidly that knowing the state at time t provides little information about time $t + 1$, information may be of little value. Knowing that there was a deer in a given location yesterday may not affect return rates today because it will have moved to another unknown location. On the other hand, if the environment does not change at all there is no reason to update knowledge about it. It is in cases of intermediate rates of change that information is most useful. A second factor is the range or scale of variability. Aché data suggest that meat returns do not vary greatly from place to place through the seasons. Knowing which animals inhabit a given area may be unimportant if similar returns are found in all areas. On the other hand, the difference in yield between the passes that do or do not contain caribou may be enormous. This suggests that patchy environments that vary temporally at an intermediate rate but in large scale should be those in which foragers expend the greatest effort in information acquisition.

Information acquisition may pay off in currencies other than calories. Steward (1938) reports that young adult males in the Great Basin frequently traveled great distances to visit and share information about food distributions with their hosts. For their hosts the value of the information may have been increased food yields. The value of the information for the young men might have been to obtain welcome in groups containing marriageable women.

Anthropological Applications. No anthropological tests of information models have been carried out to date. The Alyawara (O'Connell and Hawkes 1981) and Bari (Beckerman 1983) studies, reviewed above, did invoke information acquisition as an explanation for the exploitation of low-return patches. In neither case, however, were the relevant parameters measured to test those suggestions. Beckerman (1989) presented a model of the value of information to Bari foragers, but concluded based on new data that environmental sampling was an unlikely explanation for the foraging patterns he had described earlier.

6.4.3. *Sensitivity to Variability in Rates of Consumption*

Theory. All the models discussed so far have been based upon the premise that long-term rate maximization is the goal of human foraging. According to these models, foragers are insensitive to short-term temporal

variation in the food supply. This assumption, of course, is not necessarily in accordance with the real world. If food intake is highly variable, there may be a chance of starvation. Variation in the amount of food eaten during some time period may also affect fertility and mortality even though the likelihood of starving is low. Under some conditions, foragers will be sensitive to *variability* in foraging returns as well as to *mean rate* of capture. This possibility has been considered for both animals (Stephens and Krebs 1986:Chapter 6) and humans (see Smith 1983; Kaplan et al. 1990; Winterhalder 1986).

When foragers alter their behavior in response to expected variation in rewards, they are said to be *risk-sensitive*. If they adjust their behavior so as to reduce the expected variation in rewards, they are said to be *risk-averse*; and if they act to increase the variation, they are said to be *risk-prone*. Stephens and Krebs (1986) show how the mean and variance in gain rate can be modeled so that risk-aversion and risk-prone behavior can be predicted. Most models of risk-sensitivity among humans have focused on risk-aversion (e.g., Kaplan et al. 1990; Winterhalder 1986), although Hawkes (1990) provides an interesting example of potential payoffs to risk-prone behavior.

Humans can reduce temporal variation in the food supply in at least four ways. First, they can alter diet choice to emphasize less variable resources. Such changes in diet choice may often lower long-term average rate of food acquisition, however. A second method of reducing intake variance is to store foods, which also may involve costs. Processing foods for storage requires time, food value may be lost in processing or later due to spoilage or pests, and storage entails protection and opportunity costs in terms of reduced mobility. A third method of variance reduction is information sharing about food sources. Finally, direct food sharing is another method of reducing expected variation in the food supply. Winterhalder (1986) explored optimal prey choice and risk with a computer simulation. His results suggested that under many conditions, (1) the rate-maximizing and risk-minimizing diets will be the same; (2) food sharing is more effective than changes in diet breadth for reducing risk; and (3) most of the risk reduction obtained from sharing requires only a very small number of participants.

Anthropological Applications. As far as we know, no direct field tests of risk-sensitive models have been carried out, although Aché research (Kaplan and Hill 1985b) showed that variability in the acquisition of resource types positively correlated with the extent to which they were shared, and that sharing can be an effective method of reducing daily variance in food intake. One simple model showed that food sharing would result in an 80% increase in nutritional status. Given that the Aché never ignore the resources in their environment that are characterized by the highest acquisition vari-

ance (tapirs and peccaries), we speculated that food sharing alone eliminates the need for any other variance reduction strategies (Hill et al. 1987).

6.5. HUMAN SUBSISTENCE PATTERNS: SPECIAL CONSIDERATIONS

6.5.1. Omnivory

Many authors have been skeptical of human foraging models that reduce the biological value of alternative resource types to energy (e.g., Keene 1981, 1983; Jochim 1983; Sih and Milton 1985). In section 6.2.5.B, we suggested that Aché foragers bias diets away from energy maximization in favor of foods containing high proportions of lipids and protein. During the dry season, Yaminahua foragers of Peru exploited three major food types (wild bananas, caiman, and several species of fish), but would have maximized energy return rates if they only exploited bananas and caiman (Hill and Kaplan 1989; Hill 1988). Including fish in their diet decreased overall return rate. Similarly, among the Hiwi foragers of Venezuela, men pass by roots that yield 8500 cal/hr on encounter in favor of hunting, which yields an average of 3070 cal/hr (Hill 1988). Virtually all South American horticulturalists obtain much higher caloric return rates from farming than they do from hunting or fishing (Beckerman 1989; Hames 1988), yet most spend considerably more time hunting and fishing than farming (Hames 1988). In even more extreme cases net energetic return rates from hunting may be negative, and yet horticulturalists still chose to hunt rather than farm exclusively (e.g., Dwyer 1974; Johnson and Behrens 1982). This bias in favor of exploiting resources of relatively low energetic profitability but high in protein-lipid content is found in many other human groups and among nonhuman primates (e.g., McGrew 1978; Terborgh 1983).

Some nutritional requirements are absolute and inflexible; other nutrient requirements apparently can be met partially or completely by substituting sufficient quantities of an alternative nutrient. This introduces complexities that have yet to receive substantial theoretical or empirical treatment in foraging research. In fact, with the exception of a few studies (e.g., Belovsky 1988 and Rapport 1981), most foraging research on nonhuman animals has not been conducted with omnivores. However, several different approaches have been used to model sensitivity to the nutrient composition of foods.

Linear Programming. Linear programming is a method of solving for behavioral optima under specified constraints. Belovsky's recent (1987) application of linear programming to predict !Kung diets illustrates nicely the advantages and disadvantages of this approach. The model assumes that hunting and gathering are mutually exclusive activities and attempts to solve

for the optimal allocation of the !Kung foragers' time hunting and gathering. Four constraints (boundary conditions, defining lower or upper bounds of a currency requirement that either must be met or cannot be exceeded) are defined: protein, energy, stomach capacity, and time. Protein and energy are lower-bound constraints (i.e., minimum requirements); stomach capacity and time are upper-bound constraints (i.e., maximum tolerable). Two possible objectives are considered: energy maximization and time minimization. If energy is the goal currency, time is a constraint, and if time is the goal currency, energy is a constraint. When a modified version of this model is developed, taking into account the constraints for an entire family rather than a single adult, the energy-maximizing point predicted by the model matches almost exactly the !Kung diet observed by Lee during July 1964. This success, however, depends heavily on the assumptions underlying the time and stomach upper bounds. For example, the time constraints are based upon a calculation suggesting that longer amounts of time spent foraging would have resulted in net heat loss during the winter months. However, this calculation does not allow !Kung foragers to compensate for heat loss through extra caloric expenditure or through warming themselves by the fire after foraging. As Belovsky notes (1987:41) !Kung foragers frequently violate the time constraint over short time periods. The stomach capacity constraint is also problematic since the maximum food intake that Belovsky allows is much lower than observed consumption rates of modern foragers (K. Hill, personal observation). The success of the model is therefore somewhat problematic, since the predicted diet is quite sensitive to the values of both maximum constraints.

In general, linear programming models may be useful for modeling decisions in which constraint and objective functions are linear and all currencies except one may be characterized as constraints. Linear constraint functions are not expected when search costs are shared among resources (the assumption of the prey choice model discussed above) or when costs of acquisition vary nonlinearly as a function of amount produced of each resource (a common gain function in patch models). Modifications and nonlinear programming models are being developed to deal with both problems (Belovsky et al. 1989). Perhaps more problematic is the assumption of linear programming models that the benefits associated with constraint currencies are essentially single step-functions. This means that acquiring more than the minimum of the lower-bound currencies (or utilizing less than the upper bound) is not a better solution for the organism than achieving the constraint boundary. For example, once the protein requirement is satisfied, additional protein is assumed to have no further positive effect. This assumption may not be biologically realistic for many currencies.

Indifference Curves and Nutrient Complementarity Models. One approach to modeling diet choice with multiple goal currencies is the use of indifference curves to model trade-offs in investment among alternative resources. Such models assume that humans make choices that maximize utility gained from investment. Utility generally is defined as the level of satisfaction derived from the consumption of resources and is determined inductively by measuring what people maximize. Biologists who employ the indifference curve approach assume that fitness or some correlate of fitness is the ultimate utility. An additional assumption of indifference curve modeling is that for any two desirable resources, an infinite number of combinations of the two resources would yield equal utility (or fitness). For example, 3 kg of meat and 4 kg of plant food might be equal in utility to 1 kg of meat and 8 kg of plant food. All combinations that yield equal utility define a line (or curve) to which the consumer should presumably be indifferent (hence the name indifference curves). Other combinations yielding higher or lower utilities exist on different indifference curves, and there are an infinite number of indifference lines associated with higher and lower utilities (see Figure 6.5.). Thus, indifference curves are isoclines (analogous to thermoclines or contour lines).

The indifference curve approach assumes that the forager will adopt the strategy that yields the highest utility. Three factors must be specified in order to predict the optimal mix of resources: (1) the total foraging time available, (2) the time cost of each resource or patch (the reciprocal of the return rate for a resource, patch, or foraging strategy), and (3) the shape of the indifference curve set. The first two factors allow for construction of a "budget constraint" function, which defines all the possible combinations of resources that can be acquired given the time available and time costs of resources. For example, if time spent acquiring plant foods is mutually exclusive with time spent obtaining animal foods (i.e., no shared search time) then total time spent foraging is equal to time spent hunting plus time spent collecting: $T = T_h + T_c$. The mix of time spent hunting and time spent collecting is the decision variable in the model (precisely analogous to the linear programming models above). If we know the hunting return rate (R_h) and the collecting return rate (R_c), it is possible to determine all possible combinations of meat and plant foods that can be acquired in time T throughout the range from $T_h = 0$ to $T_h = T$ (or, alternatively, from $T_c = 0$ to $T_c = T$). These values describe the *budget constraint line*. The model predicts that the forager will choose the mix of hunting and collecting times that yields the combination of meat and plant foods with the highest utility. This is the point on the budget constraint line that is tangent to the highest indifference curve (Figure 6.5).

Using data from three South American foragers, the Aché, Yaminahua,

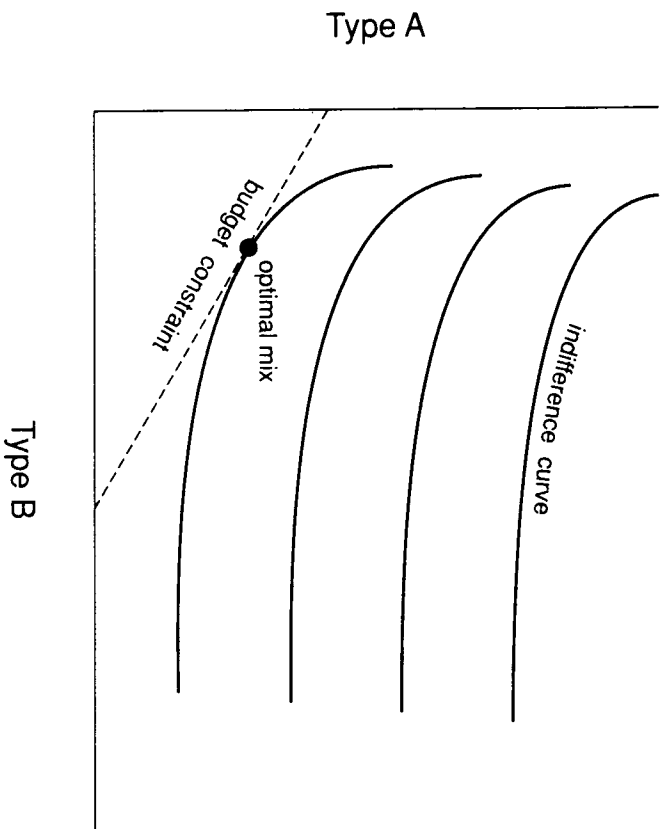


Figure 6.5. Indifference curves for two resource types that are partially substitutable and complementary. A budget line can be defined by the amounts of each type of resource that can be acquired given the foraging time available and the time costs of acquiring each. The point at which the budget constraint is tangent to the highest indifference curve is the optimal mix of resources that should be acquired in order to maximize utility gain.

and Cuiva, Hill (1988) derived a composite indifference curve (Figure 6.6) by calculating a series of restriction angles from measured return rates and dietary mixes chosen, and then superimposing each graph on the next. A single indifference curve shape fit all data points. As a test of the generality of this particular model, he then used the derived indifference curve set from the South American data to predict the dietary mix of Pygmy foragers who trade meat for agricultural products with neighboring horticulturalists. Since, according to Hart (1978), Mbuti Pygmies receive, on average, 4.6 calories of carbohydrate for every calorie of meat, the slope of the budget constraint line is known. Using this budget constraint and the South American indifference curves, Hill's model predicted a Pygmy diet of 25% meat and 75% carbohydrate, whereas the observed diet is about 30% meat and 70% carbohydrate (Figure 6.6).

The close match between the model derived from the South American data and the observed Mbuti pattern seems encouraging. Nevertheless, the indifference curve approach as applied so far suffers from serious limita-

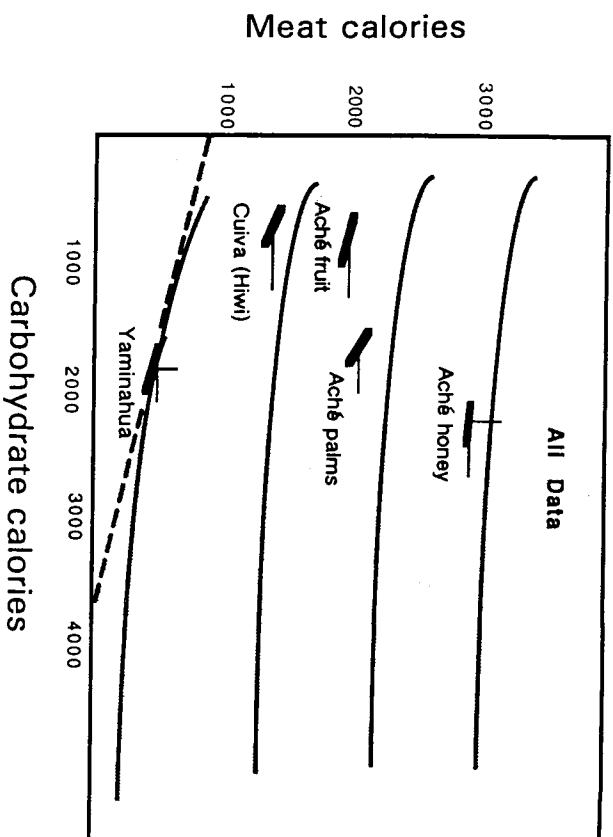


Figure 6.6. The measured slope of the budget constraint and the observed choice point define and angle that restricts the possible slope of the indifference curve to the left and right of the choice point. The indifference curve must have a slope between the budget slope and horizontal right of the choice point, and between the budget slope and vertical to the left of the choice point. Restriction angles derived from observed foraging choices of Aché, Cuiva, and Yaminahua foragers can be used to create a composite of the indifference curve shape. Applying the Pygmy budget line (dashed) with a slope of $-1/4.6$ allows one to predict the Pygmy diet (point tangent to the indifference function) which will maximize dietary utility if Pygmies show the same preferences as South American natives. The predicted diet is about 75% carbohydrate, whereas the observed diet is about 30% carbohydrate.

tions. First, the model Hill developed its two-dimensional and thus can only be used to model trade-offs between two food types. This limits its generality to food types that are either protein/lipid rich or carbohydrate rich. However, many mixes of the three macronutrients are possible. For example, some insect foods that are important in human diets are very lipid rich but not protein rich. Many plant foods contain significant amounts of protein and some fat as well as carbohydrates. Multidimensional models can be developed but they must be solved with differential equations. Second, Hill's application assumes that time costs of hunting and collecting are always exclusive. More likely, however, some time spent looking for hunted resources will also result in encounters with collected resources and vice versa. When search and acquisition costs of different resource types can be partially shared, the budget constraint is not a straight line, but instead bows upward in the middle. Shared search is so common in human foraging that it

may turn out that the shape of the budget constraint is more important for determining the diet mix than is the shape of the indifference curves.

Finally, the inductive determination of indifference curves on a case-by-case basis is not satisfying. Using preference curves from one group to predict dietary preferences in another group begs the question of the functional significance of the observed preferences. And it is notoriously easy to generate multiple inductive models a posteriori that are consistent with a set of data. Although these models can later be tested on independent data sets, such models can be empirically adequate for the wrong reasons.

Summary. Each of the models discussed thus far has strengths and weaknesses, and each is designed to explain patterns in a different decision variable. The combined prey and patch model provides the most well developed mathematical tool for measuring the trade-offs in benefits expected from handling or continued search. The model can treat both shared and unshared search and handling costs. It is equipped to deal with both continuous and discontinuous gain functions. The principal problem encountered in applying "handle-or-search" models to human foraging, however, is that the use of calories as a currency in the measurement of gain functions does not generate empirically adequate predictions. Linear programming models are well suited for considering multiple currencies. The major problems with linear programming models are that they assume step-function effects (satisfaction or death) of all constraint currencies and become mathematically complex with multiple resources and shared search or production costs. Indifference curve approaches are well suited to combining distinct objective currencies (e.g., protein and carbohydrate) into a single currency (e.g., utility, nutritional status, or fitness) so that trade-offs between resources can be measured. They are not limited to the step-function assumption, nor do they require linearity of effects. However, they are limited by the fact that the models also become complicated with shared search and many different resource types. Additionally, the shapes of indifference curves are difficult to measure, and the models are inductively derived rather than theoretically based.

6.5.2. Food Sharing and Sex-Dependent Foraging Models

The facts that people share food and that the producers and consumers of food items are frequently different individuals can complicate foraging models. If foragers can expect to exchange food with other individuals, their foraging strategies are likely to be sensitive to those expectations, especially if nutrient complementarity is important. Food sharing is also likely to affect the time individuals allocate to foraging (see Chapter 7). These considera-

tions represent a largely unexplored area of foraging theory (but, see Hawkes 1990; Chapter 9). In addition, the fitness costs and benefits of alternative foraging strategies appear to differ between men and women. Although there are exceptions, women generally avoid activities that involve danger, prolonged high-speed movement, and high mobility (Brown 1970a; Hurtado et al. 1985). Trade-offs between food acquisition, child care, and fertility have been proposed to explain both variation in time allocated to foraging and prey choice by women (e.g., Hurtado 1985; Hurtado and Hill in press).

Factors other than gender may be important as well. For example, Hurtado et al. (1985) found that, among the Aché, nursing women forage less and produce less food than nonnursing women, and that the woman's number of older children is positively correlated with productivity and time allocated to foraging. This pattern was also found among Hiwi foragers, but with additional effects of seasonality (Hurtado and Hill in press). Kaplan and Hill (1985b) showed that there are long-term differences between men in hunting return rates. Children also produce varying amounts of food across societies (Burton Jones et al. 1989). Their return rate is likely to vary across ecological contexts as a function of the nature and distribution of food resources they can exploit and is probably age and sex specific. Thus, the time that children allocate to foraging and their expected gains is likely to affect parental decisions about what foods to acquire and how much they should provision their children.

It appears that food sharing combined with age-sex differences in goals and constraints leads to a variety of complications when considering the fitness payoff of different foraging patterns. For example, the differences between men and women in prey choice will affect macronutrient-sensitive models of prey and patch choice. In the case of the Aché, the female return rate was approximately 2600 cal/carbohydrate, and almost no protein or lipid per hour spent foraging. For men, the return rate was approximately 600 cal protein, 300 cal lipid, and 400 cal carbohydrate for every hour spent foraging. Since men spend 6.9 hr/day and women about 1.9 hr/day in direct food acquisition, the combined daily diet produced by a man and a woman is 4140 cal protein, 2070 cal fat, and 7770 cal carbohydrate per day. This diet could be easily adjusted if either sex changed their prey selection or time spent foraging. In fact, the observed Aché diet contained even more fat and protein than these numbers suggest because of the high adult sex ratio in observed residential groups.

These types of problems may require the techniques of game theory and frequency-dependent models that solve for equilibria rather than maxima, particularly if the reproductive interests of men and women differ or conflict. Foraging and food production, sharing, and sex differences in behavior are closely related in humans. Eventually these must be incorporated into any comprehensive theory of human food acquisition.

6.5.3. Symbolic Communication

Humans rely heavily upon symbolic communication in the food quest. Symbolic communication can be used to increase the information available to foragers in at least two ways: (1) by increasing their sample size of resource distributions and characteristics; and (2) by providing information on prey or patches that the foragers have never exploited. In fact, effective communication among foragers greatly increases their knowledge of their environment relative to what is known or measured by researchers attempting to test foraging models.

The foragers we have observed use both types of information. First, they listen daily to accounts of other foragers. These accounts commonly include details of resource encounter rates (λ_i) and profitability (e_i/h_i), so that the forager is able accurately to assess short-term changes in the environment relevant to prey and patch decisions. The forager's sample of these parameters is a function of how many other individuals in the social group forage independently. Aché men, for example, live in social groups consisting of about 10 hunters, and at the end of day, each man usually reports to the others in considerable detail concerning every game item that he encountered that day, and the outcome of the encounter. At minimal cost, each man gains 10 times as much information about encounter rates as he actually experiences.

Second, foragers learn from older individuals who report on a lifetime of foraging experiences. Most children have detailed knowledge of resource characteristics and capture techniques before ever foraging themselves. In some cases, the knowledge of older individuals has been gained through communication as well, rather than through direct experience. This means that the body of information available covers long time spans and the experiences of hundreds of individuals. Extremely rare events unlikely ever to be experienced by a single forager can be sampled indirectly through information access. Some food taboos may have their origins in long-term information transfer about the low profitability of rarely encountered prey. Whether foragers should pay attention to food taboos and how often they should break them can be addressed in models about the value of information for behavioral decisions (e.g., Stephens and Krebs 1986:Chapter 4) and the conditions that lead to copying others with or without sampling other alternative behaviors (Boyd and Richerson 1985; see Chapter 3, this volume).

The fact that human foragers possess more information than can be gained through personal experience has implications for tests of foraging models on humans. Foragers may adjust their foraging pattern in ways that the researcher is unlikely to understand. The completely informed forager may be sensitive to long-term average conditions, whereas the scientist generally can only measure current conditions. Alternatively, the forager may behave according to knowledge about the specific characteristics of the immediate

situation, whereas the researcher must average out the parameter values of his or her model over a much longer period. For example, Inuit foragers may choose terrestrial hunting over marine hunting depending on wind conditions (Smith 1991:Chapter 7), or Bari men may hunt when rainfall patterns suggest that fishing will not be profitable (Beckerman 1989).

A second implication of the information available to human foragers leads to greater optimism. Most foraging models assume complete information on the part of the forager. This assumption may be more correct for human foragers than for any other species. Communication systems allow humans rapidly to track changes in their environment, and they actually may be more likely to adhere to the predictions of optimization models than are most other animals, which may instead develop foraging "rules of thumb." Human behavior, in general, is more likely to be adaptive in changing environments than can be expected for other organisms.

6.5.4. Proximate Mechanisms of Change

We have not yet discussed the question of how humans come to adapt their food acquisition practices. We know virtually nothing about the specific nature of the cognitive processes governing foraging decisions nor about the developmental processes by which children become adult foragers. Although most observers of human foragers are impressed by the seeming importance of observational learning in the development of foraging skills, the specific nature of these learning processes remains unstudied. We also do not know the extent to which processes of cultural evolution (cf. Boyd and Richerson 1985; Chapter 3) affect human foraging practices and diets. For example, the Aché kill coats (*Nasua nasua*) and pacas (*Cuniculus paca*) with their hands, using techniques not practiced by other South American foragers. When these techniques are explained to other South American foragers and forager-horticulturalists, they can imagine how they are done but comment on their danger. Were those techniques invented by the cultural ancestors of the Aché and simply not invented by other groups? Could it be that such techniques will only be invented when the costs of injury are outweighed by the benefits of more meat? In general, optimal foraging theories treat capture techniques and the proximate mechanisms that underlie them as givens. Treating them as variables to be explained is an important area for future theory development and research.

6.6. LINKING MODELS OF INDIVIDUAL BEHAVIOR WITH LARGE-SCALE EXPLANATION

All the models discussed so far have focused on the decision processes of individuals, given a set of assumptions about their abilities and attributes of the environment. How can we account for evolutionary change in foragers'

abilities? What factors determine cross-cultural variability in tools, techniques, and the composition of the diet? Perhaps the first and certainly the second set of questions can be productively studied using modifications of current foraging models.

6.6.1. Long-Term Change

Even though prey and patch models treat the abilities, techniques, and technology of the forager as givens, their underlying logic can be used to ask questions about long-term change in those constraints. For example, the domestication of plants and animals is a problem that seems quite tractable using simple modifications of foraging theory.

If we follow the optimal prey and patch choice models we would expect foragers to spend time manipulating the reproductive, growth, or behavioral patterns of protodomestic plants and animals as soon as such practices would have increased return rate. The decision variable for a protodomestic would be: How much time should be spent manipulating growth and reproduction of a protodomestic so that it can be harvested at a greater rate? The increase in return rate for the protodomestic conferred by the manipulation time would be compared to overall return rate for foraging. This is analogous to the decision to add a new prey or patch type to the diet, or to change patch residence time when encounters are simultaneous. Setting the problem up in this manner suggests that investigators search for factors that might have lowered overall foraging return rate in the areas and times of domestication, or that might have raised the rewards associated with manipulation practices. Some possible factors are the terminal Pleistocene extinctions of megafauna and increases in human population density that, in turn, lowered encounter rates with profitable resources.

In order to test these hypotheses, it would be necessary to measure both foraging return rate and the returns from the earliest attempts at domestication. Optimal foraging theory provides the mathematical framework for comparing those return rates, but rigorous tests of hypotheses require data at a degree of precision that archaeologists have not yet been able to obtain. For some kinds of resources (such as fruit collection and seed collection), it may be fairly simple to conduct experiments that will provide robust estimates of return rates (e.g., Simms 1984). For other resources (such as small-game hunting returns for *Homo habilis*), developing adequate estimates of return rates may prove to be a difficult challenge.

6.6.2. Cross-Cultural Variability in Subsistence Patterns

So far, there has been very little work within optimal foraging theory on large-scale ecological trends in the composition of human diets. What kinds of ecological communities are associated with different proportions of meat,

plant foods, and insects in the diet, different ratios of male, female, and child labor, and different kinds of foraging practices (ambush hunting, random search, specific-resource-targeting, home base, storage, food sharing, etc.)? What features of the abiotic environment such as rainfall, temperature, and drainage affect human diets? Since humans are part of their own environment, how do demographic processes such as increasing and decreasing population density affect plant and animal communities and human foraging patterns?

Winterhalter et al. (1988) have addressed this last problem in an optimal foraging model that allows the forager to affect the encounter rate of prey types through his or her own prey choice. Surprisingly, the model indicated that population densities were dependent on subsistence work effort, and that both human and prey densities cycled dramatically under a variety of conditions. Both results strongly challenge the utility of the concept of "carrying capacity" that is so common in the anthropological literature. Large-scale subsistence trends in hunter-gatherers have also been modeled by Belovsky (1987) with a linear programming approach. Using an empirically derived relationship between hunting and gathering cropping rates (return rates) and primary productivity, Belovsky develops a model to predict reliance on hunting and gathering as well as the contribution of each sex to the total diet. Binford (1990a) has used a measure (effective temperature) developed by Bailey (1960), which incorporates rainfall, temperature, and drainage to account for both plant and animal productivity in environments and the proportion of meat and plant foods in human diets. Both these models seem to fit well with reported large-scale patterns, although many of the estimates of the relevant dependent and independent variables are very rough.

The development and testing of ecological theories of human dietary variation using the cross-cultural record deserves more emphasis. We are slowly building the quantitative database necessary for conducting those tests. However, more attention needs to be paid to quantitative descriptions of environments, in addition to measuring return rates and foraging decisions.

6.7. CONCLUSIONS

The utility of the optimization approach to subsistence problems must be evaluated in light of what we can learn from it. The models have been better at predicting qualitative patterns in human subsistence than any other current approach. However, many of the predictions drawn from optimal foraging theory have not closely matched the empirical record. To some extent this is inevitable, since the models are explicit simplifications of complex decisions. Why else might the models fail?

One reason is that the empirical data are not suited for testing the foraging model in question. At this stage in the development of human behavioral ecology, it is important to confront squarely the limitations of most tests of foraging models carried out on humans. In many cases, restrictive assumptions of the foraging model under test have been overlooked. Some "tests" have chosen inappropriate models for the decisions being examined. Future research must carefully consider the particulars of each study. What is the decision variable? Are the types to be chosen prey or patches? Has the gain function for different patches been measured? Have encounter rates with types been adequately measured? Are encounters sequential or simultaneous? Is the currency employed adequate for the problem? Careful examination of the character of each foraging model relative to the character of the problem addressed is likely to improve greatly the quality of empirical tests.

Some foraging studies, however, have deliberately violated the assumptions of the model as a means of learning whether those assumptions are important. For example, many early critiques of foraging models (e.g., Keene 1981; Jochim 1983; Sih and Milton 1985) suggested that energy is not the appropriate currency for analyzing human diet choice. Aware of these critiques, we applied the simple prey choice model to Aché foraging to see how it performed in spite of its restrictive assumptions. Our results showed that the Aché *did* bias diet choice away from energy maximization in favor of increased meat and insect consumption. We now know that nutrient-sensitive models are required for many human foraging problems. In this sense, the violations of the predictions of foraging models help us learn about the important constraints on human subsistence decisions.

For those who accept the utility of the approach and wish to apply it to specific problems, the future is indeed exciting. Appropriate modifications of foraging models should allow us to address a broad range of problems in human subsistence practices. The process of discovering the necessary modifications is likely to provide an enormous amount of information about our species. This, then, is the real value of optimization modeling of human behavior. It is a systematic process for learning about ourselves.

6.7.1. Chapter Summary

This chapter has reviewed the basic principles of optimal foraging theory, and their application to human food acquisition. The central points made are these:

1. Behavioral ecologists study food acquisition using an optimization approach. This approach assumes that individuals maximize some currency (usually food energy acquired per unit foraging time), and employs models consisting of decisions, currencies, and constraints (6.2).

2. The classical prey choice model assumes random encounters, a single rank of all prey types, mutually exclusive search and handling costs, and complete information. Tests of the model with human foragers indicate that they generally follow its predictions within choice sets composed of similar macronutrients, but bias resource choice in the direction of protein-lipid maximization in mixed sets (6.2).

3. Optimal patch choice and time allocation depend very much on the shape of the depletion curve, as well as the information available to the forager. The marginal-value theorem (6.3.1) assumes diminishing returns, but existing studies of human patch choice do not adequately demonstrate that this assumption applies to the data analyzed (6.3.2).

4. The classic prey and patch models can be modified in several ways, or incorporated into a combined prey and patch choice model. When food choice involves central-place foraging (6.4.1), acquisition of information (6.4.2), or sensitivity to risk (variance in consumption, 6.4.3), existing theory allows interesting predictions to be made about choice behavior and social interactions (6.4). Little work has yet been done to test such models.

5. The problem of omnivory and multiple components of food value can be addressed in several ways, including linear programming and indifference analysis (6.5). Each approach has strengths and weaknesses, and both suffer from being inductive and succumbing to mathematical intrac-
tability when realistic constraints are included.

6. Many possibilities for elaborating simple foraging models to deal with behavioral complexity exist, including food sharing and gender division of labor (6.5.2), symbolic communication (6.5.3), long-term subsistence change (6.6.1), and large-scale cross-cultural variation in subsistence practices (6.6.2).