

why hunters gather: optimal foraging and the Aché of eastern Paraguay

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In the recent literature, there are some differences of opinion about the determinants of hunter-gatherer subsistence patterns. Richard Lee (1968, 1979), among others, has observed that plant resources are often the dominant element in the diets of mid- to low-latitude hunter-gatherers. He argues that this is because plant resources are more dependable than animal foods and, in most cases, more efficiently exploited. He suggests that meat will provide the bulk of hunter-gatherer diets only where plant foods are unavailable. Marvin Harris (1977, 1979) implicitly rejects this position by maintaining that animal foods are the more efficiently exploited resources. He attributes the predominance of plant foods in the diets of many modern hunters to the depletion of large mammal populations through a combination of late-Pleistocene climatic change and overhunting. In Harris's view, modern hunters take plants *in spite of* the fact that they "cost" more than meat, primarily because meat is scarce. Yet a third line of argument has been offered by Marshall Sahlins (1976) and others, who reject economic and ecological factors as the principal determinants of subsistence patterns.

In our view, Harris is essentially correct, though for reasons that remain inadequately appreciated. We argue here that hunter-gatherer subsistence patterns can be explained largely, if not entirely, in cost/benefit terms, specifically as these are expressed in models derived from the theory of optimal foraging (Pyke, Pulliam, and Charnov 1977). We support this argument by an analysis of foraging among the Aché of eastern Paraguay, who are notable for the very high proportion of meat in their diet. We also briefly consider how the same principles may be used to explain the rather different mix of plant and animal foods taken by the !Kung. We conclude with some comments on the general implications for our approach.

The determinants of food choices made by hunter-gatherers have long been a topic of speculation and controversy. In this paper, we analyze the foraging behavior of the Aché of eastern Paraguay and conclude that it is consistent with predictions derived from optimal foraging models. We infer that these very general models will continue to prove useful in explaining variation in hunter-gatherer subsistence patterns throughout time and space. [Aché, hunter-gatherers, optimal foraging theory, South America, tropical forest]

the problem

The array of resources taken by hunter-gatherers and the determinants of that array have long been matters of concern to anthropologists, particularly because of their implications for the form and evolution of other aspects of human behavior (e.g., Dart 1953; Steward 1936, 1955; Lee and DeVore 1968). Several somewhat contradictory approaches to this problem are represented in the recent literature. One, pursued initially by Lee (1968, 1969, 1979), is based on the observation that plant foods are often the dominant element in modern hunter-gatherer diets. Lee argues that plant foods are favored because they are abundant, reliable, and readily located, and therefore more efficiently exploited than are animal foods. Plants are said to be low-risk/high-return resources, while animals are high-risk/low-return resources. Animals are taken in spite of the inefficiencies involved because of the taste appeal of meat and the prestige that accrues to successful hunters. Still, Lee contends, given a choice, hunter-gatherers will always rely more heavily on plants. Only when this option is unavailable (e.g., at high latitudes) will animals make up the bulk of hunter-gatherer diets (for similar views, see Gould 1969, 1980; Meehan 1977; R. Jones 1980; Flannery 1968; see Bettinger 1980 and Hayden 1981 for comprehensive reviews of opinion).

Harris (1977, 1979) also appeals to cost/benefit relationships in explaining hunter-gatherer subsistence patterns, but sees them in a different way. He contends that meat is the favored (if not dominant) element in hunter-gatherer diets because of its nutritional value and because heavy reliance on meat is the more efficient strategy where meat resources are abundant. Only when these have been depleted (e.g., through long-term climatic change or overexploitation) does it become more efficient to add a greater proportion of plant foods to the diet.

Yet a third line of argument identifies cultural preference as the principal determinant of subsistence. In referring to a particular ethnographic case, Sahlins (1976:171) makes an observation he evidently takes to be generally true: "Specific valuations of edibility and inedibility [are] themselves qualitative and in no way justifiable by biological, ecological, or economic advantage." While this is an extreme position, the idea that traditional preferences frequently nullify biological or economic costs and benefits is widely held by anthropologists of very different theoretical persuasions (e.g., Douglas 1975; Jochim 1981).

We reject this third argument because of the archaeological record of near-synchronous changes in hunter-gatherer diets in many parts of the world over the past 30,000 years. These changes occur independently in at least some areas, yet are similar in that they involve significant increases in the relative proportions of plant foods and other sessile resources (such as shellfish) in local diets (e.g., Flannery 1969; MacNeish 1967; Allen 1974). They are often closely correlated with periods of major climatic change. In light of this, it seems quite likely that "biological, ecological and economic" factors are critical determinants of subsistence strategy, even if the details of this relationship remain unclear. Moreover, appeals to cultural preference or systems of meaning beg precisely the question with which we are concerned, namely, the explanation of the preferences themselves.

By contrast, it seems to us that in spite of the inconsistencies that separate their positions, Lee, Harris, and others who treat this problem in terms of ecological costs and benefits are on the right track. Still, some important problems remain to be resolved. Lee's argument may be faulted in that it involves a miscalculation of the relative costs of plant and animal foods (Hawkes and O'Connell 1981) and is inconsistent with the archaeological record. If Lee were right, plants should always have been the dominant element in hunter-gatherer diets, at least at low latitudes. Harris's argument seems much closer to the mark but needs a conceptual framework to account for the mix of resources exploited in any particular setting.

We propose that variation in hunter-gatherer subsistence patterns can be explained largely in terms of models derived from the theory of optimal foraging (Pyke et al. 1977). These models are designed to describe and explain foraging behavior in nonhuman organisms and are based on the assumption that, all else being equal, foraging strategies that are more efficient will be favored by natural selection and will spread at the expense of those that are less efficient. Examples of the use of such models with reference to human (especially hunter-gatherer) behavior are found in Winterhalder and Smith (1981), Hames and Vickers (in press), and Earle and Christenson (1980). We are concerned here with two models that seem particularly useful: the *optimal diet model*, which describes prey selection in a uniform or "fine-grained" environment, where resources are encountered at random; and the *patch choice model*, which describes the movement of predators where resources display a nonrandom or "coarse-grained" distribution. We apply these models in the analysis of foraging practices observed among the Aché of eastern Paraguay. This case is of some interest because of the surprising success the Aché enjoy as hunters and because the research reported here was designed specifically to assess the utility of optimal foraging models in analyzing hunter-gatherer subsistence. We begin with a descriptive account of Aché foraging and then turn to the analysis of diet and patch choice.

background

The Aché (or "Guayaki") speak a language of the Guaraní family and have lived as hunters in the forests of eastern Paraguay since before the arrival of the Spanish. They divide themselves into three groups on the basis of differences in dialect, customs, and geographical range. Two of these groups have been described ethnographically by Clastres (1968, 1972). Earlier descriptions are in Vellard (1939) and in the references in Metraux and Baldus (1946). Our experience has been with the third group, the Northern Aché, who have come into unarmed contact with outsiders only within the past decade (Hill 1979).

The traditional range of the Northern Aché covers some 5000 km² between the Río Paraná and the Río Paraguay, about 240 km northeast of Asunción. This area is characterized by gently rolling hills covered with broadleaf evergreen forest and by flat-floored valleys filled with tall broadblade grasses. The climate is marked by hot summers (October–February) and cool winters (March–September). Average daily temperatures in July are about 17°C, with minima as low as –3°C; temperatures in January average about 27°C, with maxima as high as 41°C. Annual rainfall averages about 1600 mm but varies greatly from year to year in both total amount and seasonal distribution. The Aché divide the year broadly into "hot time" and "cold time" and mark finer divisions by reference to the particular resources then in season.

The fauna and flora of this region are poorly described (but see Hill and Hawkes in press). We have identified 33 mammals hunted by the Aché and have Aché names for several others. The Aché also eat at least 10 species of reptiles and amphibians, more than 15 species of fish, and a seemingly endless list of birds. They take the adult forms of more than 5 insects, at least 10 types of larvae (notably cerambicid larvae), and at least 14 kinds of honey, most commonly that of *Apis mellifera*. In addition, they collect the edible products of more than 40 species of plants, the most important of which is the palm (*Cocos romanazoffiana*).

More than 130 Aché now live at a Catholic mission established in 1978 as an agricultural colony. Under the supervision of the mission staff of five, they grow manioc, sugarcane, corn, and sweet potatoes, and they keep a few pigs, goats, chickens, and burros. The mission provides additional resources in the form of milk, sugar, rice, flour, noodles, and salt,

as well as cast-off clothing, tools, and agricultural implements. Some Aché reside full time at the mission, but others spend more than half their time in the jungle on long-range foraging trips, sometimes of several weeks' duration.

Two of us accompanied the Aché on seven such trips and recorded all subsistence-related activity (Table 1). Hawkes stayed with the women, noting time spent in travel, search, and collecting and processing resources, weighing the latter whenever possible. Hill made comparable observations of the men's activities. The complete record covers 61 gathering days and 58 hunting days, for a total of 457 woman-gathering days, 794 man-gathering days, 674 man-hunting days, and 1570 consumer days.¹ Each day's report includes information on all game animals taken (species, number, and weight of individuals), the composition of the hunting party (including identities of those who made kills) and the time spent in a sample of pursuits, a partial tally of insect and plant resources taken, and a record of time spent collecting and processing them. Because groups commonly disperse throughout most of the day, these tallies represent a minimum count of resources taken.

Table 1. Quantitative data on seven Aché foraging trips.

TRIP NUMBER	1 ^a	2 ^b	3 ^c	4	5 ^d	6 ^e	7 ^f
TRIP DATES	Mar 31 -Apr 3	Apr 5 -Apr 16	Apr 25 -May 3	May 15 -May 20	May 30 -Jun 13	Jun 21 -Jun 29	Jul 5 -Jul 16
STARTING COMPOSITIONS							
Men	8	18	27	20	5	19	11
Women	4	10 ^g	15	8 ^g	5	9 ^g	8 ^g
Children	1	4	14	2	2	3	7
Infants	2	8	8	3	3	3	2
RESOURCES COUNTED							
Number of individuals							
white-lipped peccary (avg. 30 kg)	4	3	2	2	2	4	—
armadillo (avg. 4.3 kg)	4	9	12	5	20	23	17
monkey (avg. 2.5 kg)	4	20	53	20	24	67	33
paca (avg. 7.5 kg)	2	4	13	8	1	8	5
coati (avg. 3.5 kg)	1	19	18	19	11	21	2
collared peccary (avg. 20 kg)	1	9	2	—	—	1	—
deer (avg. 30 kg)	1	7	1	1	—	1	—
fish	—	—	200+	—	—	—	—
bird (avg. 1 kg)	—	11	2	4	6	5	3
snake (avg. 1.4 kg)	3	3	—	1	—	—	—
In kilograms							
palm fiber	28	191	213	177	220	280	270
oranges (avg. 0.18 kg)	68	188	192	54	254	323	205
honey	5.6	25.0	7.4	2.3	9.2	5.5	1.6
palm larvae (small:avg. 0.003 kg; large:avg. 0.01 kg)	8.0	4.8	4.6	1.3	15.0	4.2	4.5
palm heart (avg. 0.33 kg)	5	44	30	11	19	31	30
palm fruit (avg. 0.005 kg)	92	57	125	11	18	10	15

^a Shotgun used.

^b Shotgun used; some palm nuts taken.

^c The initial target was fish on April 28; 14 adults left the foraging band after this.

^d On June 13 one man left the foraging band.

^e On June 25 the group split; it reunited on June 28.

^f On July 11 the group split.

^g One man taking a woman's role is included here.

This qualification applies most strongly to gathered resources, because the Aché eat as they travel. Since game animals come in tidy packages that require processing before they can be consumed, we are fairly confident that our tally includes almost all those taken. In addition to the animals listed in Table 1, several baby monkeys (*Cebus apella*), a few coatis (*Nasua nasua*), a tamandua (*Tamandua tetradactyla*), and a fawn (*Mazama americana*) were taken as pets.

resources and subsistence techniques

The list of plant foods exploited by the Aché during the study period is a short one. The most important are oranges and palm products. Oranges occur in groves of varying size and are taken by climbing trees and shaking the fruit loose. Branches or entire trees may be cut down if climbing is difficult and the fruit is out of reach. Both men and women are adept climbers, but usually it is the men who do the climbing and the women who gather the fallen fruit.

Palm products (usually *Cocos romanazoffiana*) include the moist, starchy fiber of the trunk, the terminal bud (or "heart"), and the fruit. The fiber is taken by felling the tree, cutting a section from the trunk, and beating loose the exposed inner fiber with the butt of an ax. The fiber may be picked out by the handful, sucked dry, and discarded, or else bound in palm leaves and carried to camp, where its moisture is squeezed out and the fiber is cooked separately or with meat. Some kinds of fiber are sifted to separate the flour, which may be eaten alone, mixed with meat, and/or roasted in balls in the fire. The terminal bud of a palm is cut from the fallen tree with an ax and removed from its inedible outer husk. The palm heart is large, the edible portion averaging about 0.33 kg. It is usually eaten immediately but may be carried to camp and cooked in palm broth, sometimes with larvae or meat. The apricotlike fruit of *Cocos romanazoffiana* grows in huge clusters and is sometimes taken in larger quantities, then mashed and mixed with water. Ripe fruit is often collected from the ground and eaten, almost without pause, while walking.

Insect products taken by the Aché include larvae and several kinds of honey. The Aché harvest cerambycid larvae, which grow in rotting palm trunks, by cutting chunks of the logs free with an ax, then breaking the soft wood further by hand, sometimes using a twig to dislodge larvae from their burrows. Some of the larvae are always eaten immediately; others are either lightly toasted in hot ashes or boiled in palm broth. Honey is taken by men with fire and axes. The honey tree is usually cut down, the bees quieted with smoke, and the comb extracted. Honey produced by other insects is also collected, although less frequently.

Aché hunting techniques are varied. Collared peccaries (*Pecari tajacu*), white-lipped peccaries (*Tayassu pecari*), red brocket deer (*Mazama americana*), capuchin monkeys (*Cebus apella*), tapir (*Tapirus terrestris*), and birds of many species are always hunted with bows and arrows or shotguns. Of these animals, the white-lipped peccary and capuchin monkey are pursued by groups of men, the others by solitary hunters.

Armadillos (usually *Dasybus novemcintus*), pacas (*Cuniculus paca*), and coatimundis (*Nasua nasua*) are taken without bows and arrows. Armadillos are dug from their burrows with machetes, with bows, or by hand, often by solitary hunters. Pacas are always hunted by groups of men. The several entrances of an occupied paca burrow are located and each is guarded by a hunter. A log is then pushed into one of these to send the animal running out. The nearest hunter falls on the large rodent and smothers it. Troops of coatis in the forest canopy are surrounded on the ground below by groups of hunters. When all hunters are in place, arrows are shot until the animals try to escape by leaping out of the trees. The

hunters grab the fleeing animals and slam them against the ground. Snakes are killed quickly with a bow or machete. Often this is a matter of self-defense, for snake bite is one of the most frequent causes of death mentioned in Aché folklore. Fishing is done in large groups. Tree branches are piled across a lagoon to form a dam, which is then rolled or pushed down from one end of the lagoon to the other, trapping fish behind it. The cornered fish jump with increasing frequency as the space is constricted, and as they do, they are grabbed and tossed onto the bank.

Most food processing is done after camp is made for the night. While women tend to process the plant food they collect, it is unusual for a hunter to butcher, cook, or distribute his own game. Although this varies with different kinds of animals, one person rarely carries out all the processing steps. Men perform these tasks more often than women, especially the distribution of cooked meat. In accordance with an explicit prohibition, a hunter almost never eats an animal he has killed with an arrow, but everyone else is likely to get some. Cooked meat is cut into pieces and these are distributed to all the men, who pass them on to their wives and children.

Aché foraging trips

Trips reported here began at about 8:00 A.M. when men left the settlement carrying only bows and arrows and machetes (on the first two trips some took shotguns). The direction of departure was usually guided by expectations about peccary hunting. Women (usually wives) and children followed, the women carrying infants and children up to age four, as well as axes, carrying baskets, and sometimes a pet (usually a monkey or coati). Each basket held all the household gear brought by a single family, including one or more knives and pots, a plate or cup, matches, a sewing kit, extra clothing, and a mat or blanket. Most women began these trips with several kilos of manioc or corn, and someone always brought sugar and salt.

After about an hour's walk, the group stopped for a brief rest and some discussion about the direction of the hunt. Serious foraging seemed to begin only after this stop. When the party moved again, men set the pace as they walked ahead looking for signs of game. Women followed at some distance, tracking the men through the jungle. When men were in active pursuit of animals, women stopped to await the result. They might eat a bit from their baskets or scout the area nearby for palms, often taking hearts or fiber and eating them on the spot. When a hunting episode was finished, women packed the game in their baskets while the men took off in search of other prey.

Women were sometimes more actively involved in the hunt. If monkeys or coatis were the target, women might act as spotters and noisemakers, keeping track of the animals and trying to direct their movement through the canopy. When pacas were hunted, women might guard a burrow exit.

Oranges and honey typically brought men and women together. Orange groves provided an occasion for all to eat and for women to fill their baskets with fruit. When honey was found, all waited while one or two men extracted it. Most of it was generally eaten immediately, but often some was carried away, later to be mixed with water and drunk. Women took insect larvae whenever they encountered them. Men also stopped for this resource, although it did not produce the group aggregation that formed for oranges and honey.

An hour or so before dark, a camp was established by the women, who collected huge fire logs. On arriving at a camp, a man might take an ax and go off to cut palms and take palm hearts; on his return he would report the location of those with good fiber to the

women. On rainy days when there was little or no hunting, or after an early stop, husbands and wives might exploit palms as a team, the husband cutting them and testing the fiber, the wife then pounding the fiber in the good ones and/or collecting ripe palm fruit.

Throughout the day, plant and insect food was eaten as it was collected, although some larvae or honey might remain to be finished in the evening. Only rarely was game not cooked on the day it was killed. Most of the meat would be consumed that evening, with some remaining for the next day's breakfast. The Aché do not store or preserve anything. Seldom did any food remain two days after it was acquired.

Nuclear families slept at the same fire, women pillowing their husbands and children, sometimes more than one couple to a hearth. The extra men scattered among these fires to sleep, men laying against each other.

The next morning, people awakened just before first light. Meat and perhaps palm broth or oranges not finished the night before were eaten. Men sharpened their arrows. People talked about the prospects for the day, where to go, what they were hungry for. Unless it was raining or very cold, the men were off within two hours, usually together in a sudden, quiet exodus. The only days that the men did no hunting (two) and the only days (with two exceptions) that we did not move camp were days of heavy rain. After the men departed, the women finished packing their baskets and followed.

This pattern was repeated each day as the Aché walked through the jungle in search of food and other necessities, including material for their bows, arrows, baskets, and mats. When they finally returned to the colony, they almost always brought meat, oranges, and sometimes honey taken on the last day or two of the trip to share with those who had remained behind.

foraging returns

Our sample of seven foraging trips represents about 1570 consumer-days, counting all the Aché who took part in each trip (except infants) and including Hawkes and Hill as equivalent consumers. Over this period, the average daily per capita intake from foraging was about 3600 Cal (Table 2). Eighty percent of this total (ca. 150 g per day) came from game animals. Both the high Calorie total and the large proportion of meat are quite surprising in view of recent generalizations about lowland South America and low-latitude hunters in general.

It is often said that hunting returns in lowland South America are poor by comparison with other parts of the world (Meggers 1971). Lathrap (1968:29) has remarked that the "hunting cultures of the tropical forest zone of South America offer highly explicit examples of the cultural and demographic effects of a dependence on hunting in an area where hunting is neither profitable nor easy." Harris (1974, 1977), Gross (1975), and Ross (1978) have held that the limited availability of animal protein places serious constraints on human population density, community size, and organizational complexity throughout this region. These views are widely disputed (Chagnon 1975, 1977; Lizot 1977; Beckerman 1979; Chagnon and Hames 1979; Hames 1980). The unexpected richness of the Aché diet represents another exception to the generalization that lowland South America is a poor place to hunt.²

The Aché figures are also exceptional for mid- to low-latitude hunter-gatherers in general. Lee (1969:72) reports that the Dobe !Kung take in approximately 2140 Cal per consumer-day, only about 60 percent of the total available to the Aché, who are about the same height (158 cm for a sample of ten adult men, 150 cm for a sample of nine adult women) as the !Kung (Howell 1979). Meehan (1977) calculates a figure of 2150 Cal for the Anbara of coastal Arnhem Land, who, by her reckoning, are relatively well fed in com-

Table 2. Total caloric return, total time invested, and average caloric return per consumer-day.

AVERAGE CALORIES PER CONSUMER-DAY (N = 1570 consumer-days)			
Animal Resources		Plant Resources	
white-lipped peccary	568	oranges	290
armadillo	479	honey	109
monkey	441	palm fiber	105
coati	436	palm larvae	86
paca	381	palm heart	65
collared peccary	288	palm fruit	55
deer	156	Subtotal	710
fish	117		
bird	28		
snake	6		
Subtotal	2900		
Grand total		3610 Cal per consumer-day	

TOTAL CALORIES	
Animal Resources	4,555,625
Plant resources	1,113,041
Total	5,668,666

TOTAL FORAGING HOURS	
Animal resources	4086
Plant resources	1405
Carrying	1024
Total	6515

Notes: Caloric values for plant food and larvae are from the Ford Chemical Laboratory, Salt Lake City, Utah, analysis of samples we collected in the field. Since standard drying procedures were impossible, we preserved our collections by adding 25 ml methanol to each 100 g of food.

The Aché eat every edible bit of an animal. We have estimated this to be 65 percent of the live weight for mammals and birds, 70 percent for reptiles and fish. Caloric values for most mammals are estimated at 300 Cal/100 g edible portion (Meehan 1977; Lee 1979). Deer and monkey are estimated at 125 Cal/100 g and 200 Cal/100 g edible portion, respectively; birds at 190 Cal/100 g; reptiles and fish at 150 Cal/100 g and 137 Cal/100 g. All of these estimates are derived from the USDA Agricultural Handbook No. 456, or Meehan (1977); the former is also the source of our caloric figure for honey. The caloric content of palm fiber may be inaccurately estimated—we have used the result from an analysis of the nutritional constituents of the liquid squeezed by hand (sucking may extract more from the fiber).

parison with other Australian Aborigines. Certainly, the high proportion of meat in the Aché diet is quite inconsistent with Lee's (1968) widely cited generalization that hunting dominates hunter-gatherer subsistence only at latitudes higher than about 60 degrees above the equator.

Circumstances that might have altered Aché hunting success in this area during these four months of 1980, making the results unrepresentative of traditional returns, should be considered. One factor is the use of firearms. On the first two trips, some Aché hunters carried shotguns, but at our request they used only bows and arrows on all succeeding trips. (Hill always carried a .22 caliber rifle.) On the 43 hunting days when shotguns were not used, the return rate from hunting fell from 2755 to 2657 Cal per consumer-day, a drop of less than four percent. Guns *do* make a difference in hunting efficiency (Hill and Hawkes in press), but shotgun hunting is so small a component of this data set that the difference in meat per consumer is insignificant.

The second factor that may increase hunting success is the reduced dependence on foraging due to the mission's agricultural and provisioning activities. Since the Aché are not

entirely dependent on hunting and gathering as they were in the past, each individual takes less from the jungle. While in one sense this reduces pressure on resources, the effect is countered by the size and permanence of the mission colony. More hunters cover less area, thereby increasing the pressure on local resources (Hill and Hawkes in press). There is also a growing Paraguayan population in this region, which has the twin effect of raising the number of competing hunters and decreasing the size of the game habitat. We cannot sum these effects in any precise way, but it seems unlikely that they could combine to increase current hunting success very much.

The extremely high Calorie totals remain to be explained. Two things should be noted here. First, foraging parties almost always brought food back to share with those remaining at the mission colony. Thus the returns of the last day or two were spread over more consumers (although mission provisions carried into the jungle balance this to some extent). Second, the bias in the population profile of these groups is in a direction that raises average dietary requirements as well as food totals. The very high sex ratio and the small number of children in these foraging groups elevate the Calories per consumer figures by inflating the proportion of hunters and reducing the proportion of dependents (Table 1).

is gathering a supplementary practice?

Since the Aché do so well hunting, why do they gather? The notion that plants are a low-risk/high-return food source while game is a high-risk/low-return resource (Lee 1968) suggests that gathering provides insurance against hunger if hunting fails. If, as Lee generalizes from the Dobe !Kung, "people eat as much vegetable food as they need, and as much meat as they can" (1968:41, original italics), we might expect a significant inverse correlation between the amount of meat and the amount of gathered food in each day's menu, especially in the Aché case, where the pattern of movement allows men and women to exchange information during the day, so that the success of the hunters is usually known by all as the day proceeds. A supplementing pattern would be obscured by storage where daily acquisition did not provide daily fare, success rates being averaged out over longer periods. But since the Aché do not store, they provide a particularly good test of this expectation.

The correlation coefficient for total Calories from plant and insect food to total Calories from meat over 61 foraging days ($r = -.04$) shows *no* correlation between the two. The view of plant and insect resources as supplements to cover failures in high-risk hunting is not supported. Why then do the Aché gather? An answer to this question is provided by optimal foraging theory.

the optimal diet model

Optimal foraging models predict certain features of the set of resources foragers will exploit so as to maximize the returns they get for their work. The underlying assumption is simple: people will continue to use or adopt foods and techniques that give them greater returns (measured conventionally as Calories) to cost (measured conventionally as time); and they will stop using, or fail to copy the use of, foods and techniques that decrease their returns to cost. A series of nonintuitive propositions flow from models built on this assumption.

Consider the optimal diet model (Charnov and Orians 1973; MacArthur and Pianka 1966; MacArthur 1972; Pulliam 1974; Pyke et al. 1977; Emlen 1966; Schoener 1971; Charnov 1976a). Resources may be ranked according to the ratio of returns they provide (Calories) to the cost (handling time) of acquiring and processing the resources once they have been en-

countered.³ The model shows that returns will be maximized if foragers take those resources for which this ratio is equal to or higher than the average returns they get for foraging in general *and* if they ignore all potential resources for which this ratio is lower than their average returns. Thus, whether or not a potential resource is in the optimal diet does not depend on its abundance: an item that is out of the optimal diet is out no matter how abundant it becomes; an item that is in the optimal diet is not excluded no matter how rare it becomes.⁴

We can state this more formally, following Charnov and Orians (1973), given the simplifying assumption that the energetic costs per unit of time do not differ significantly for exploiting different resource types:

Define: E = total Calories acquired foraging
 T = foraging time
 E_i = Calories available in a unit of resource i
 $T = T_s + \sum h_i$
 T_s = search time
 h_i = handling time per unit of resource i
 λ_i = the number of units of resource i encountered in a unit of search time (T_s)

An optimal forager will maximize: $E/T = \frac{\sum \lambda_i \cdot E_i \cdot T_s}{T_s + \sum \lambda_i \cdot h_i \cdot T_s} = \frac{\sum \lambda_i E_i}{1 + \sum \lambda_i h_i}$

Thus, an item j will be included in the diet only if: $E/T \leq \frac{E_j}{h_j}$

since, for some item a *not* in the optimal set, the following inequality must hold:

$$\frac{\sum \lambda_i E_i}{1 + \sum \lambda_i h_i} > \frac{\sum \lambda_i E_i + \lambda_a E_a}{1 + \sum \lambda_i h_i + \lambda_a h_a}$$

which implies that

$$E/T > \frac{\lambda_a E_a}{\lambda_a h_a} \text{ or } E/T > \frac{E_a}{h_a}$$

In the following application we treat carrying time as a fixed cost, like search time. This would be reflected in the preceding algebra if T_s were defined as the sum of search time *plus* carrying time.

Note that the resource rankings of this model say nothing about the quantitative importance of a resource to optimal foragers. High-ranked items may be so rarely encountered that they represent only a very small proportion of the diet; low-ranked items in the optimal set may be encountered with sufficient frequency to contribute the bulk. The ranking shows instead which resources are more likely to enter or leave the diet and in what order. If the encounter rate with high-ranked resources fluctuates widely, the optimal diet will fluctuate, with the very highest ranked resources being the only ones that never go out.

Table 3 shows the resources taken by the Aché ranked in order by the ratio of caloric returns to handling time (E_i/h_i). Average returns per forager-hour (E/T) include time spent searching for resources. These are calculated as total Calories (5,668,666) divided by the sum of total hunting hours (4086) plus gathering hours (1405) plus carrying hours (1024), or 870 Cal per foraging hour.

Figure 1 shows the ratio of Calories returned to handling time (E_i/h_i) for each of the resources ordered by rank and the average returns for foraging in general (E/T) that result

Table 3. Costs and benefits of Aché resources.

Resource	Total kg	Cal/kg ^a	No. of measured pursuits	Pursuit hr/kg	Processing hr/kg ^b	Handling hr/kg ^c	Calc. total handling time	E _h ^d	Rank
Collared peccary	232	1950	none ^e	-.01	.02	.03	7.0	65,000	1
Deer	300	819	none ^e	-.01	.02	.03	9.0	27,300	1
Paca	307	1950	33	.24	.04	.28	86.0	6,964	2
Coati	351	1950	20	.22	.06	.28	98.3	6,964	2
Armadillo	386	1950	20	.27	.06	.33	127.4	5,909	3
Snake	10	1000	none ^e	-.01	.16	.17	1.7	5,882	3
Oranges	1283	355	34			.07	89.8	5,071	4
Bird	35	1240	none ^e	-.01	.25	.26	8.75	4,769	5
Honey	57	3037	48			.93	52.5	3,266	6
White-lipped peccary	457	1950	13	.69	.02	.71	324.5	2,746	7
Palm larvae	43	3124	41			1.32	56.8	2,367	8
Fish	189	975	3	.45	.01	.46	86.9	2,120	9
Palm heart	171	595	13			.39	66.7	1,526	10
Monkey	533	1300	37	.97	.10	1.07	570.3	1,215	11
Palm fiber	1377	120	83			.10	137.7	1,200	11
Palm fruit	249	350	31			.37	94.6	946	12

^a We assume the edible portion to be 65 percent of the live weight.

^b We assume 0.5 hr for large and 0.25 hr for small animals.

^c This is average pursuit time plus processing time per kg.

^d This is Calories per handling hour.

^e These animals are shot immediately upon encounter: a miss or a near miss means the target escapes; a good hit ends the pursuit in a few seconds.

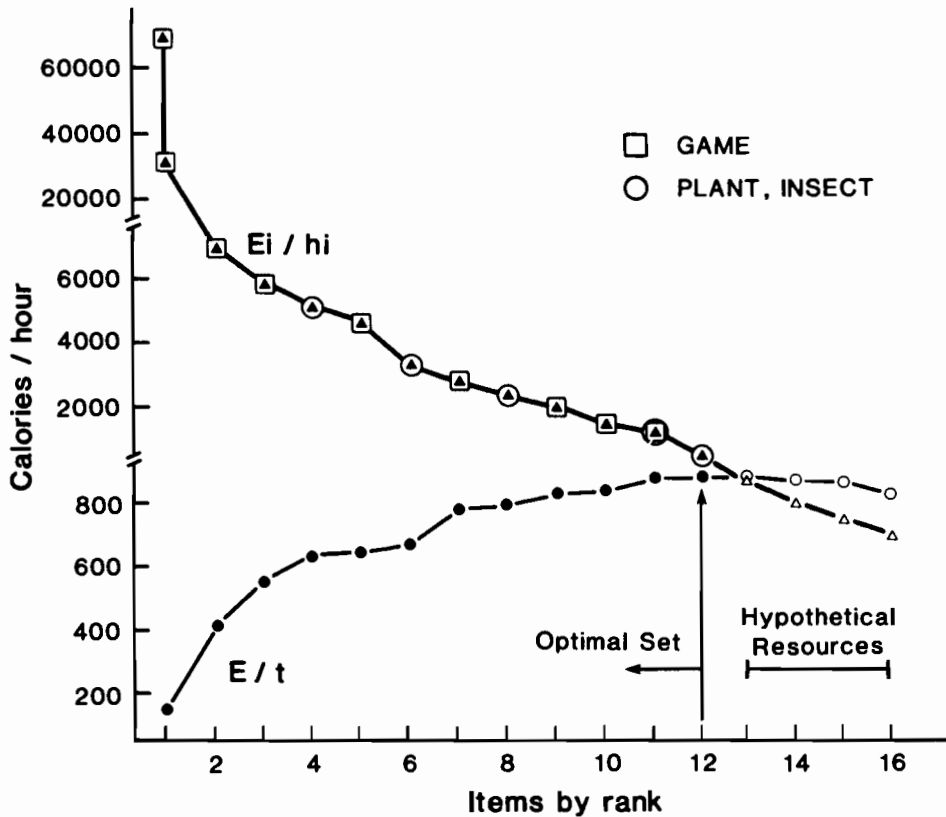


Figure 1. An optimal foraging model of Aché resources.

from the addition of each of these resources. The latter numbers are derived as follows: 3673 forager-hours were spent searching during the 61 foraging days (this is the total 5491 hunting and gathering hours minus 1818 total resource handling hours—column 8, Table 3). If only the top-ranked resources (i.e., collared peccaries and deer) were taken, average returns would be 148 Cal/hr (452,400 Cal plus 245,700 Cal for these resources, respectively, divided by 3673 hours of search plus 1024 hours of carrying plus 16 hours of handling peccaries and deer). Adding the second-ranked resources changes the average, as the total Calories for pacas and coatis are added to the numerator, the handling time for these animals added to the denominator. The result is 405 Cal/hr. The foraging returns gained after the addition of resources of each rank are as follows: 1st-ranked resources only—collared peccaries and deer = 148 Cal/hr; add 2nd-ranked—paca and coati = 405 Cal/hr; add 3rd-ranked—armadillo and snake = 546 Cal/hr; add 4th-ranked—oranges = 625 Cal/hr; add 5th-ranked—bird = 632 Cal/hr; add 6th-ranked—honey = 660 Cal/hr; add 7th-ranked—white-lipped peccary = 783 Cal/hr; add 8th-ranked—palm larvae = 799 Cal/hr; add 9th-ranked—fish = 821 Cal/hr; add 10th-ranked—palm hearts = 829 Cal/hr; add 11th-ranked—monkeys and palm fiber = 871 Cal/hr; add 12th-ranked—palm fruit = 872 Cal/hr. Four hypothetical resources with E_i/h_i ratios of 850, 800, 750, and 700, respectively, would reduce rather than increase average foraging returns. Assuming that each was encountered at a rate to constitute 1,000,000 Cal during this foraging period, the cumulative addition of these items would result in averages of 868, 859, 845, and 828 Cal/hr.

As the figure illustrates, the inclusion of the plant and insect resources that the Aché

take *increases* their ratio of Calories returned for time invested. Changes in the encounter rate with higher-ranked resources alter the position of the E/T curve. If encounter rates increase, search time is reduced and this curve shifts up, intersecting the descending E_i/h_i line at a higher point; and conversely if encounter rates are depressed. Thus, low-ranked resources move in and out of the optimal diet.

It is interesting to note that on several occasions, reports of nearby palm fruit (ranked 12) were ignored, something that did not happen with oranges. On several other occasions people discussed the relative merits of hunting monkeys (ranked 11), reaching consensus that monkeys should not be pursued "because they are not fat." While we observed that monkeys once encountered were actually ignored only twice, this ambivalence was not expressed toward any other game animal. This suggests an alternative to the idea that monkeys are often excluded as game because they are so "like humans." Such an alternative would have the virtue of accounting for the differential treatment of monkeys from one region to another. The Aché, after all, find monkeys to be humanlike, but they hunt them all the same.⁵

Note that size is not the only factor that affects return ratios. Differences in the habits of the animals and in hunting techniques are very important. The white-lipped peccary is the larger of the two peccaries in this area, but its return ratio is lower than that of the collared peccary by more than an order of magnitude. White-lipped peccaries travel in larger groups. Usually several men track them over long distances, investing a relatively large amount of time in pursuit. The smaller peccaries, by contrast, travel quickly in smaller groups. Hunters, alone or in pairs, try to take them immediately upon encounter, only pursuing animals they judge to be mortally wounded. Although the suggestion will not be explored here, the optimal foraging perspective suggests that differences in hunting techniques, for example, group or solitary hunting, the use of bows and arrows, or hunting by hand—which the Aché practice in hunting pacas, coatis, and armadillos—may themselves be accounted for by optimality criteria.

hunting, gathering, and optimal patch choice

The optimal diet model just considered assumes a "fine-grained" environment, that is, one in which resources are randomly distributed. If this array of Aché resources were encountered at random, optimal foragers would take any of the items in the optimal set whenever they came upon them. For example, anyone finding a palm tree that looked likely to have good fiber would cut down the tree, take the palm heart, and pound out the fiber. Yet as hunters search for game, they pass by innumerable palm trees and ignore them, turning to this resource only in late afternoon after camp has been established.

The distribution of tools suggests itself as an explanation for this. To take palm fiber, palm larvae, palm hearts, and honey, the Aché use axes. When they are hunting the men usually carry only bows and arrows. Still, the availability of the tool does not account satisfactorily for the hunters' treatment of nonmeat resources, since they pass palms throughout the day but almost always stop and call for an ax to take honey. Why stop hunting for oranges and for honey but not for palm hearts and palm fiber? Optimal foraging models that deal with the use of patchy environments, that is, those in which resources are clumped, are relevant here.

The patch choice model predicts that where resources are differentially distributed in kind and quantity, foragers will operate on that spatial set or patch which produces the best energy return for time spent traveling to the patch, searching it, and gathering and processing the resources found there (Charnov and Orians 1973; MacArthur and Pianka 1966; Pyke

et al. 1977; Schoener 1971; Charnov 1976b). Note that while the ranking of diet items *excludes* the cost of search, the return figures for a patch *include* the cost of searching it. Among other things, this means that high-ranked resources may be avoided by a forager if they occur in patches with high search costs and low return rates.

The patch choice model can be applied to the Aché as follows. The average energy return for hunting, including search, pursuit, and processing of animals, is 4,555,625 total Cal divided by 4086 total hunting and processing hours, or about 1115 Cal per hunter-hour. If game animals are conceptualized as a patch, optimal foragers will exploit that patch in preference to patches with lower average returns and leave it for patches with higher average returns.

Consider oranges as a patch. When an orange grove is encountered, search time within it is effectively zero. The time required to exploit the patch is almost entirely time required to scale trees, shake the fruit loose, and gather the fallen oranges. Once in a grove, average returns are 355 Cal/kg divided by the sum of ~ 0.01 hr/kg in patch search time plus 0.07 hr/kg handling time, or 4438 Cal per forager-hour. Since returns for the orange patch are higher than the hunting patch, foragers should leave the hunting patch for the orange patch.

Honey, considered as a patch, has similar characteristics. When a honey tree is located, the patch and its resources are encountered at the same time. Occasions on which trees were cut but produced only dry combs have been included in the calculations of average handling costs as "failed pursuits": 3037 Cal/kg divided by the sum of ~ 0.01 hr/kg in patch search plus 0.93 hr/kg handling yields 3231 Cal/hr. Foragers should leave the hunting patch for honey.

Palm larvae patches are rotting palm logs that usually occur in clumps. These clumps may be conceptualized as patches. Some search time is required within patches of logs because they may be meters apart in dense jungle and because not every one contains larvae. On one occasion a husband and wife spent 64 minutes each, or 2.14 foraging hours, exploiting several clusters of logs from which they took 1.26 kg of larvae. Included here is the time (1.69 hr) spent finding and checking new logs after they had started exploiting the patch. This means that the return for the patch was about 1849 Cal per forager-hour. Hunters should stop for larvae.

The palm patch contains palm hearts, palm fiber, and palm fruit. As with palm larvae and honey, encountering the palm patch is not the same as encountering its resources; some investment in search is necessary. Trees must be cut and the fiber tested before one can be certain whether this resource is "good." No doubt the Aché can often judge fiber quality on standing trees, but it is still frequently the case that fiber is found unacceptable after a tree has been felled. Similarly, palm hearts are not available on every tree cut. On one occasion one of us requested the heart from a palm being pounded for fiber. Remark- ing that it would be no good, one of the women eating the fiber cut the terminal bud, which proved to be less than half the average size of those usually taken.

We can make a very tentative approximation of the return rate for the palm patch in the following way.⁶ On the basis of 25 observed events in which fiber was taken from several trees and time spent searching (including evaluation of the trees) estimated, an average return in fiber for this patch type is 74.63 hr/379 kg, or 0.20 hr search and handling per kilogram. Subtracting from this the 0.10 hr/kg handling cost for fiber (Table 3) gives 0.10 hr/kg average search cost. Using this figure we can estimate $1377 \text{ kg} \times 0.10 \text{ hr/kg} = 137.7$ total search hours in the palm patch during the foraging period under study.

Viewing the *patch* as a fine-grained environment, the optimal diet model may be applied. If only palm hearts were taken, returns in the patch would be $(171 \text{ kg} \times 595 \text{ Cal/kg}) \div (137.7 \text{ hr search} + 66.7 \text{ hr processing}) = 498 \text{ Cal per forager-hour}$. Adding fiber raises hour-

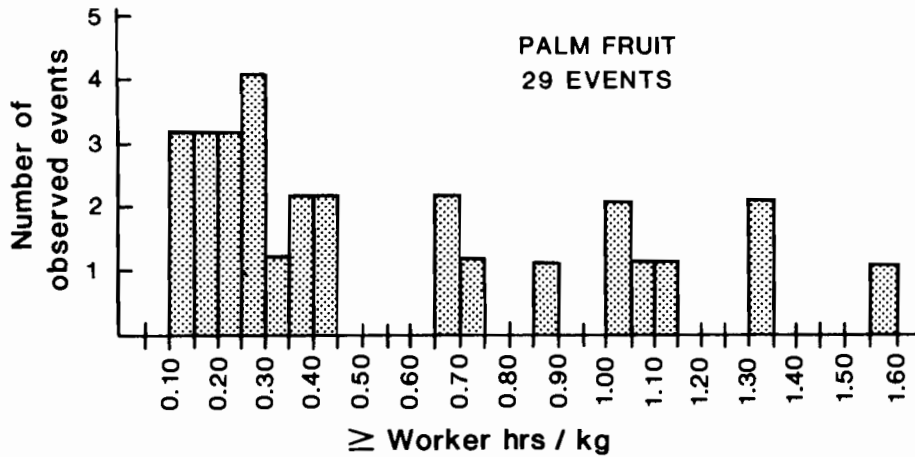


Figure 2. Variation in costs and benefits of exploiting palm fruit.

ly returns to $(171 \text{ kg} \times 595 \text{ Cal/kg} + 1377 \text{ kg} \times 120 \text{ Cal/kg}) \div (137.7 \text{ hr search} + 66.7 \text{ hr processing} + 137.7 \text{ hr processing}) = 780 \text{ Cal per forager-hour}$. Finally, adding palm fruit raises returns to 810 Cal per forager-hour.

It is important to note that the returns for patches and resources vary considerably. This is illustrated by the returns for palm fruit presented as event averages in Figure 2. We expect that such fluctuations will affect both patch choice and resource exploitation within patches. Individual foraging practices may be expected to differ depending on features of particular context—including differences in skill. It will be of interest to determine which averages, long-term or short-term, individual or group, are the best predictors of various sorts of foraging behavior.

The average value for the palm patch shows that optimal foragers should not stop hunting for that patch unless hunting returns had fallen to about 800 Cal per forager-hour. It may be that hunting returns decline as the day wanes so that the palm patch enters the optimal set. This possibility remains to be investigated. Still, this tentative treatment suggests that hunters may well be maximizing their foraging efficiency in bypassing palms.

One patch is still to be considered: the fishing patch. On the two days of the third trip in which fishing was the main activity, 85 forager-hours fishing and about 2 forager-hours processing were spent for 189 kg of fish. The group fishing technique of the Aché includes no search. The return ratio for the fishing patch is equivalent to the returns to handling time for the resource. Since this is over 2000 Cal per forager-hour, markedly higher than the average returns for the hunting patch, why don't the Aché fish more often?

Two events may shed some light on this. On April 11, during the second trip, five women spent 2.25 hr each fishing a small lagoon and stream. Their returns were negligible: less than 2 kg of fish. This seemed to be viewed more as play than foraging. On April 20, at the mission colony, 38 adults spent 5 hr each fishing the lagoon and took about 25 kg of fish. The addition of these two incidents to the figures for April 26 and 27 (trip 3) results in a total of 288 forager-hours for 216 kg of fish, which is 1.3 hr/kg or about 733 Cal per forager-hour. These figures suggest that the Aché fish infrequently because they do better hunting. We suspect that in a larger data set returns in the fishing patch will be lower on average than those in the hunting patch.

Where the patches exploited by optimal foragers are randomly encountered, they may be treated as formally equivalent to the set of individual resources in the optimal diet.

Patches for which the ratio of energy gained to time invested equals or exceeds the average ratio for foraging in the environment as a whole should be included in the set of exploited patches. Patches with ratios that fall below this average should be excluded. Low-ranked patches move in and out of the optimal set as average foraging returns fluctuate with the depletion and renewal of high-ranked patches. High-ranked patches always stay in the optimal set. Applying this model⁷ to the Aché exploitation of oranges, honey, palm larvae, game animals, palm trees, and fish does two things. First, it accounts for some general features of the patterns, including the tendency for hunters to stop for oranges, honey, and (usually) larvae, but not palms or (provisionally) fish. Second, it raises questions and poses hypotheses for further research: Why do the Aché take palms when they do? Why do they fish when they do?

what about the !Kung?

Aché hunting and gathering appears to be consistent with predictions derived from optimal foraging theory. If these predictions are truly general in character, then they should enable us to explain the mix of resources taken by other hunter-gatherers. In particular, they might be expected to resolve what now seems an anomaly: Lee's (1968, 1969, 1979) influential conclusion that the !Kung devote substantial time to hunting in spite of the fact that it is less rewarding in terms of energy yield than is gathering. If Lee is right, optimal foraging predictions are violated by the !Kung.

Lee's data allow a brief exploration of this. The returns for gathering suggested by his figures are about 670 Cal per forager-hour (as recalculated by Hawkes and O'Connell [1981] to include processing time). Each man-day of hunting produces about 7230 Cal (Lee 1979:262). The cost in time is about 8 hr hunting plus 1.12 hr processing the kill (Lee 1979:278), or about 9.12 hr, which indicates a return rate of about 793 Cal per hunter-hour. This makes hunting the optimal choice for anyone doing as well as the average hunter. Thus, the foraging models that fit the Aché may also account for the hunting and gathering behavior of the !Kung.

conclusions

The question raised initially was why hunter-gatherers take the set of resources they do from among the available array. Our answer is that such choices are determined largely by cost/benefit considerations as expressed in optimal foraging theory. We have supported this argument by showing that Aché foraging behavior is consistent with predictions derived from the optimal diet and patch choice models.

The result has important implications. We suspect that game animals, especially large game animals, will often be high ranked in optimal diet terms and because of this will frequently be identified by hunter-gatherers as preferred foods, regardless of their local abundance or quantitative contribution to the total diet. Conversely, plant foods, especially those that require extensive processing (e.g., roasting, grinding, or leaching), will often be relatively low ranked. Indeed, they may move in and out of local diets depending on the abundance of higher-ranked foods relative to the number of potential consumers but regardless of their own abundance or nutritional quality. We do not mean to imply here that *all* animals are high ranked and *all* plants are low ranked. Still, the available data indicate that many large and medium-sized mammals are high ranked and many seeds and nuts are low ranked (Keene 1981; Earle and Christenson 1980; Winterhalder and Smith 1981; K. T. Jones 1981; Simms 1981).

If we are correct in this, then optimal foraging models may account for the broad spatial and temporal patterns in hunter-gatherer diet noted by Lee, Harris, and others. We note, for example, that present-day mid- and low-latitude hunters often compete with pastoralists and agriculturalists in situations where large-mammal populations have been depleted (e.g., Schrire 1980). In such circumstances, it should be not surprising that they often rely heavily on high-cost plant resources in spite of an expressed preference for meat. It is interesting (and consistent with optimal foraging theory) that such resources may be among the first to be dropped from the diet when higher-ranked items become more abundant (O'Connell and Hawkes 1981).

It also seems likely that the same processes account for broad patterns of dietary change widely noted from the late Paleolithic through the development of agriculture. Certainly, the coincidence between the disappearance of large mammals and other fauna at or near the end of the Pleistocene and the emergence of "broad spectrum" or mesolithic subsistence economies is consistent with this idea.

We conclude with the caution that optimal foraging theory need not necessarily explain all the variation in hunter-gatherer subsistence. Nevertheless, its value lies in its capacity to provide testable hypotheses about foraging behavior and about the changes that behavior is likely to sustain under different circumstances. Whatever the outcome of any particular test, our knowledge of hunter-gatherer subsistence will have been enhanced by the use of such theory.

notes

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¹ Data collection techniques are further described in Hill and Hawkes (in press).

² Since they do so well as hunters, it is not surprising that the Aché have persisted as such in a neighborhood of farmers. The material presented here in no way contradicts the historical observation that refugee populations often remain nomadic because the depredations of stronger enemies make the cost of resettling too high. They may thus take great cuts in "standard of living" and suffer by comparison with their stronger neighbors. Nevertheless, the Aché data dispute the view that all South American hunters have been pushed into environments where they must pursue a demanding food quest.

³ Some anthropologists (e.g., Reidhead 1980; Keene 1981) have constructed optimal foraging models based on assumptions about nutritional requirements. We recognize that such requirements may constrain foraging behavior in some circumstances (see Belovsky 1978 for an example), but prefer to use Calories as a currency, primarily because this simplifies analysis and facilitates cross-cultural comparisons. The addition of other nutritional parameters to these models inevitably increases analytical complexity. The more variables included in an analysis, the more difficult it becomes to perform; yet, conversely, any attempt to keep the list within manageable limits requires difficult, often arbitrary, decisions about which variables to include and which to omit. This also puts the general utility of the models at risk in that different investigators may often use quite different parameters, thereby inhibiting comparison with other cases. Finally, incorporating more than a very few nutritional parameters may reduce accuracy by requiring precise estimates of intake requirements for which data are at best equivocal (Dubos 1980; Wing and Brown 1979:25-26). The power of optimal foraging models lies in their simplicity and generality. It seems appropriate to take advantage of these attributes by using simple, general currencies, at least initially.

⁴ These generalizations are modified to the extent that abundance or scarcity alters handling cost. But it is the change in handling cost, not abundance, that has the effect.

⁵ Further analysis by Hill and Hawkes (in press) shows that monkeys are excluded from the optimal diet of shotgun hunters.

⁶ We use this estimate because it gives results that fit the model. The problem of distinguishing search time from other activities remains far short of solution.

⁷ More knowledge about the background ecology and more detailed analysis of the foraging data should allow a fuller application of the patch choice models. Like plant and insect resources, animals are patchily distributed; for example, pacas tend to live along rivers.

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