Foraging Decisions Among Aché Hunter–Gatherers: New Data and Implications for Optimal Foraging Models

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This article summarizes 5 years of research on resource choice and foraging strategy among Ache foragers in eastern Paraguay. Successes and failures of simple models from optimal foraging theory (OFT) are discussed and revisions are suggested in order to bring the models in line with empirical evidence from the Ache. The following conclusions emerge: (1) Energetic returns from various alternative resources and foraging strategies is probably the best single predictor of foraging patterns. (2) Nutrient constraints should be added only when they significantly improve the predictive power of the model. Importance of meat versus vegetable resources may be one important modification based on nutrients that enhances the ability of OFT models to account for empirical reality in human foragers. (3) Men's and women's abilities and foraging patterns differ enough that they should be treated separately in all OFT analyses. (4) Opportunity costs associated with resources that are processed when foraging is not possible may be sufficiently low to predict that high processing time resources will be included in the optimal diet even when their associated return rates (including processing) are lower than mean foraging returns. (5) When food sharing is extensive and foraging bands include several adult males and females, foragers may not need to modify foraging strategies in other ways in order to reduce the risk of not eating on some days.

KEY WORDS: Hunter–gatherers; Foraging models; South America.

INTRODUCTION

The study of the determinants of resource choice and diet for humans is important for many reasons. First, there is good evidence of a direct link between nutrition, health, fertility, and child mortality in many different societies (e.g., Butz and Habicht 1976;

Received April 12, 1985; revised June 23, 1986.

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Ethology and Sociobiology 8: 1–36 (1987)

0162-3095/87/$03.50
52 Vanderbilt Ave., New York, New York 10017

Mosley and Chen 1984). Since a good deal of time is spent in food acquisition and since the outcome of foraging choices can have important effects on survival and reproduction, understanding resource choice should be important to understanding the general adaptive patterns of humans.

Second, many models of hominid–pongid divergence consider dietary patterns of principal importance in understanding the morphological and behavioral evolution of the hominid lineage (e.g., Dart 1953; Washburn and Lancaster 1968; Jolly 1970; Winterhalder 1981; Hill 1982; Kurland and Beckerman 1985). We may be able to reach a better understanding of the evolutionary trajectory of hominids if we can reconstruct hominid diets and feeding strategies during different periods of time in the past.

Third, ever since Steward (1936, 1938) some anthropologists have seen the food quest as a very important determinant of social structure and settlement pattern, especially among band level human societies (e.g. Birdsell 1953; Damas 1969; Yellen and Harpending 1972; Wilmsen 1973; Wobst 1974; Smith 1981). Indeed, specific hypotheses proposing that resource exploitation patterns account for group size, territoriality, movement patterns, and other aspects of social behavior are common in anthropological literature (e.g., Lee 1972; Jochim 1976; King 1976; Winterhalder 1977; Birdsell 1978; Dyson-Hudson and Smith 1978; Durham 1981; Smith 1981; Cashdan 1983; Hill and Hawkes 1983).

There is a similar recognition of the importance of understanding foraging decisions in studies of nonhuman organisms. A direct link between nutrition and fitness is suggested by the data on a wide variety of organisms (Gaulin and Konner 1977). Biologists have hypothesized that the character of exploited resources (e.g., low or high quality, large or small packages, low or high processing time required) and their distribution in space and time (evenly distributed or patchy, abundant or scarce, predictable or nonpredictable, seasonal or nonseasonal) can be used to predict a wide variety of social behaviors from group size and territoriality to movement patterns and reproductive strategies among nonhuman organisms. These hypothesized causal relationships have led to a number of predictions that are partially supported by data on food resources and social organization of a number of different animals (e.g., Caraco and Wolf 1975; Clutton-Brock and Harvey 1977; Bekoff and Wells 1980; MacDonald 1983; Terborgh 1984).

In order to understand human resource choice, diet breadth models derived from optimal foraging theory (OFT) have been increasingly employed by anthropologists (Smith 1983). Optimal foraging theory is an attempt to discover rules that predict decisions about which resources to exploit and how to exploit them. These decisions, via the neural mechanisms (shaped by natural selection) that produce them, are assumed to result in the tendency for living organisms to acquire nutrients as efficiently as possible. This is likely to be whenever more food could increase fitness, foraging exposes the organisms to greater risks than nonforaging, or more time spent in alternative activities could increase fitness. Models derived from OFT make specific behavioral predictions about how an organism can be most efficient. These predictions are compared with behavioral data in an attempt to falsify the models or the assumptions built into them. Although it is impossible to demonstrate that any organism is not foraging optimally, because many assumptions are built into OFT models, specific models can be falsified (Krebs et al. 1983).

Optimal foraging theory diet breadth models are based on the premise that the ratio of costs to benefits resultant from exploiting each potential resource will determine whether it is exploited when it is encountered in the environment. The important independent variables in these models are the return rate defined as the benefits per unit time that can be obtained from resources in question, and the amount of time necessary to search for alternative resources. Most models are purposely simplified to consider the benefits in energy alone (calories) and thus ignore the importance of other nutrients. This simplification is based on the probable correlation between energy acquisition rates and fitness for most organisms. Such a simplification, however, leads to several potential problems (see Pyke et al. 1977, or Smith 1983 for discussion). Nevertheless, models based on maximizing energy return rates have been widely applied and tested because they have been shown to explain a good deal of the observed variance in foraging patterns for different organisms (see Krebs et al. 1983 for review of tests on nonhumans, and Smith 1983 for review of anthropological applications).

This article summarizes many of the results from the past 5 years of foraging studies with Ache hunter–gatherers in Paraguay. It emphasizes both the successes and difficulties of using OFT models, and discusses some potentially useful modifications. We collected and analyzed data on Ache foraging patterns, specifically with the intention of assessing the utility of OFT diet breadth models. Although the Ache represent only a single ethnographic case, we have tried to emphasize the generality of the models used with the hope that other researchers will also attempt to test and modify them, or propose explicit alternative explanations for observed foraging patterns.

In previous publications on the Ache, we tested some predictions derived from models of OFT (e.g., Hawkes et al. 1982; Hill and Hawkes 1983). In particular, we concentrated on gathering data to test predictions from models concerning resource choice. We demonstrated, for example, that all 16 resources exploited by Ache foragers during a 4-month field period were characterized by returns after encounter (in calories per person hour) higher than overall Ache foraging returns, including search time (Hawkes et al. 1982). This agrees with the prediction of the optimal diet model (McArthur and Pianka 1966; Emlen 1966; Schoener 1971; Charnov 1973, 1976a; Charnov and Orians 1973) that no resource will be exploited that reduces overall foraging returns. The finding we reported would be improbable if energy returns were not constraining Ache foraging decisions. If we assume that there are at least as many unexploited but potentially edible resources in the forest of Paraguay as the number we saw exploited, and assume that the median return rate for all resources is equivalent to the Ache mean foraging return rate,[1] the probability of obtaining the observed result is 2×10 [illegible] (0.5^{16}) if resources are exploited without regard to energy returns.

Also in agreement with predictions from the optimal diet model was the finding that low-ranked resources (monkeys and small birds) were not exploited when men hunted with shotguns rather than with bow and arrows (Hill and Hawkes 1983). Shotguns raised overall foraging returns sufficiently that the pursuit of monkeys and birds would have actually lowered their foraging returns. Despite these encouraging results, many questions remained. It has correctly been pointed out that these studies did not demonstrate that some other alternative foraging pattern would not produce higher calories per hour than the one we observed. If this were true, some of the resources exploited by the Ache might actually lower their foraging returns, and thus the same data set might *not* agree with predictions from the optimal diet model. For example, if some high-return resources were ignored by Ache foragers, this would result in a lower mean foraging return rate. The lower mean foraging return rate would then lead one to predict the inclusion of low-ranked resources in the optimal diet when they should actually be excluded if the higher ranked resources were not ignored. This means that we cannot unequivocally conclude, based on available data, that the Ache forage in such a way as to maximize their foraging return rate.

We also made several observations that did not fit the prediction from the optimal diet model that resources should either always be taken upon encounter, or never taken. Although some sampling of nonoptimal resources is expected (Oaten 1977) we could not easily explain why resources in the optimal set were sometimes passed by. The possibility that resources were patchily distributed and should be abandoned before patches were completely depleted (Charnov 1976b) was considered but did not seem to account for many of the observations. These and other questions led to a follow-up study of Ache resource choice that is presented here.

BACKGROUND

There are several references to the Ache (also called Guayaki) in historical accounts before the 1960s (see Metraux and Baldus 1963; O'Leary 1963), but the first modern ethnographic reports that became widely available are those of Clastres (1968, 1972), who studied two of the four living Ache groups. The data reported here pertain to the northern Ache, who have only come into unarmed contact with outsiders during the past decade (Hill 1983).

The traditional range of the northern Ache is an area about 12,000 km^2

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[1] Both of these assumptions are probably quite conservative. There actually appear to be several hundred edible fruits, birds, and insects the Ache foragers ignore. Most are very small and dispersed and could be expected to give very poor returns per time spent to acquire them.

between 54–56 degrees west and 24–25 degrees south. During the 10 years prior to their first peaceful contact with outsiders (1960–70) they probably numbered between 600 and 800 persons (Hill 1983). Tropical broadleaf evergreen forest, which the Ache prefer to open grassland, covers much of the area. Rainfall is quite unpredictable from month to month and year to year, although there is a statistically significant wet and dry season. Annual average precipitation is approximately 1600 mm. Fluctuations in temperature are much more regular, with an annual January maximum around 40°C and a July minimum of about −3°C. Ecology and climate are more fully described in Hill et al. (1984).

The northern Ache, who were full-time hunter–gatherers until the mid-1970s, currently live primarily at an agricultural settlement (Chupa pou) sponsored by a Catholic mission, but continue to forage frequently in the nearby forest (approximately 25% of all days, Hawkes et al. 1985). Although the shift to part-time residence at an agricultural colony has undoubtedly affected some Ache behaviors, there is no a priori reason why foraging decisions on extended forest trips should not be made using the same criteria that were used by the Ache as full-time foragers (Hill 1983; Hill et al. 1984).

The study presented here is designed to determine whether *current* foraging patterns can be predicted from *current* ecological parameters. It is likely to represent past Ache foraging patterns before contact only to the extent that the character and values of relevant variables in resource choice have not changed.

On observed foraging trips the Ache take a wide variety of animal species, among which the most important quantitatively are peccaries (*Tajassu tajacu* and *Tajassu pecari*), pacas (*Cuniculus paca*), coatis (*Nasua nasua*), armadillos (*Dasypus novemcintus*), and capuchin monkeys (*Cebus apella*). They also exploit numerous plant products, especially of the palm *Arecastrum romanzolfianum,* from which they take the fruit, the heart, and the starch from the trunk. Fruits and honey are also major resources, with insects providing a small but consistent component of the diet.

We have previously described Ache foraging trips, reporting on diet choice (Hawkes et al. 1982; Hill and Hawkes 1983), the seasonal pattern of food acquisition (Hill et al. 1984), the sharing of food resources (Kaplan et al. 1984; Kaplan and Hill 1985a), and men's and women's time allocation to activities (Hill 1983; Hill et al. 1985; Hurtado et al. 1985; Hurtado 1985). In addition, Jones (1983, 1984) has published ethnoarcheological analyses of Ache camps and faunal refuse. Recent analyses have concentrated on Ache reproductive strategies (Hill and Kaplan 1986), child development (Kaplan and Dove 1986), and the relationship between hunting ability and reproductive success (Kaplan and Hill 1985b).

Because we are particularly concerned with the mix of resources in the Ache diet, as well as the strategies employed to obtain that mix, two points should be clarified. First, no resources acquired on any foraging trip were brought back to the mission colony for sale or trade. Virtually all resources exploited were consumed by men, women, and children of the foraging party. Second, although the Ache diet at the mission colony is characterized by more carbohydrate, less meat, and fewer calories than are consumed in the forest, diet compares favorably with most tribal or peasant peoples in South America, and daily per capital meat consumption among the Ache at the mission settlement appears to be higher than that reported for many populations of native South Americans (Hawkes et al. 1985).

METHODS

Data on Ache foraging patterns were collected in two separate field sessions in 1980 and 1981–82. Methods of data collection and analysis for the 1980 field session have been previously reported (Hawkes et al. 1982; Hill and Hawkes 1983). New data on foraging behavior were collected on nine foraging trips out of the Chupa pou mission between October 1981 and April 1982. Foraging groups included men, women, and children and have been described in detail elsewhere (Hill 1983; Kaplan 1983; Hurtado et al. 1984). All resources acquired were weighed with Homs hanging spring scales and calibration after the field session showed less than 1% error. Caloric equivalents were determined from published tables or direct laboratory analysis of food samples (see Hill et al. 1984b for details). Edible portion by weight of each resource was determined from between two and ten measurements in the field. Time spent in food procurement and processing was recorded to the nearest minute with an electronic digital stopwatch. Men's foraging time was determined by clocking them out of camp in the morning and back to camp in the evening. We have previously demonstrated, based on focal individual observations, that 87% of such time is indeed devoted to food getting activities (Hill et al. 1984a). Women's foraging time was measured directly. Definitions of foraging activities (i.e., pursuit time, processing time, search, etc.) and other relevant methodological details have been previously published (Hawkes et al. 1982; Hill and Hawkes 1983; Hill et al. 1984).

Return rates for all men and a randomly picked subset of women were calculated for this period. This was done by dividing total calories acquired by each individual by the total number of hours spent in food acquisition and processing activities. The time component of this calculation consists of three parts: (a) time spent searching for resources; (b) time spent pursuing or extracting the resources; and (c) time spent processing, butchering, or cooking the resources. These three components of foraging time are referred to as search time, pursuit time, and processing time. Monitoring the daily behavior of individuals using focal person or instantaneous scan sampling techniques led to approximately 611 man foraging days, and 61 woman foraging days of return rate data. Although the ethnographer's presence might conceivably alter the return rates of focal subjects, a one-way ANOVA revealed no significant differences between focal men's return rates and those for other men not accompanied by an ethnographer on the same day ($F = 0.966, p = 0.41$).

The procedure for calculating overall foraging return rates along with return rates for specific resources has also previously been described (Hawkes et al. 1982; Hill and Hawkes 1983). Overall mean foraging returns were calculated by dividing all calories acquired by the members of the group in question by the sum of all time they spent in food acquisition and processing. Return-rates upon encounter with individual resources were calculated by dividing the total of all calories acquired of each resource by all time spent pursuing (whether successful or not) and processing it.

RESULTS

The overall mean foraging return rates for adults during the 1981–82 sample period are presented in Table 1. The rates are slightly higher than those presented earlier (Hawkes et al. 1982; Hill and Hawkes 1983) and should supersede the earlier results, as they are based on a larger sample and more accurate monitoring. We have divided foragers and foraging conditions into several categories in order to examine differences in return rates that may lead to different foraging strategies.

Men and women differ in their overall return rates and also show different rates depending upon specific conditions during the time they were monitored (Table 1). Men's foraging produces a mean of 1339 calories per hour before processing the food that they acquire. Women's foraging produces a mean of 1221 calories per hour before processing. Adding in processing time changes calculated return rates only slightly (see discussion below) in the Ache case. The above results agree well with those we calculated in previous studies (Hawkes et al. 1982; Hill and Hawkes 1983). Although the data suggest that men's foraging is characterized by a higher

Table 1. Mean Foraging Returns in Calories per Hour (Person Days Sampled[a])

	Oct–Dec	Jan–July	In Forest[b]	Near settlement[c]	"No Move Days"[d]	In Forest with Process
Men	1619 (247)	1118 (364)	1339 (503)	1018 (108)	1344 (80)	1253 (50)
Women	826 (30)	1233 (31)	1221 (50)	302 (11)	2804 (12)	1087 (50)

Daily returns for males as a function of age:

Males, 14–20 years	1545 (215) calories per day
Males, 21–59 years	9240 (503) calories per day
Males, 60–75 years	797 (42) calories per day

[a] All but first and last days of foraging trips.

[b] First and last days of foraging trips.

[c] Days on which Ache remain in the same camp site for two or more consecutive nights.

[d] These scores are pooled across subjects but no single individuals contribute inordinately to the data set (see Kaplan and Hill 1985b)

return rate than women's foraging, one observation suggests that this is not the case.

Return rates for women on days that camp does not move are more than twice as high as women's return rates on the days when camp does move. This is important to note because we believe that women, unlike men, do not always search for resources when they are walking to a new campsite (Hurtado et al. 1984). We have observed women to pass numerous resources without exploiting them when they walk, and estimates of palm densities indicate that they must pass dozens each day and yet only exploit some of them. If women's time spent walking is not actually search time, then women's foraging return rates have been underestimated. On "no move days" all walk time is unambiguously spent searching for resources. The women's return rate on "no move days" is therefore probably a better estimate of their true *foraging* return rate. The fact that women's true foraging return rate seems to be higher than that for men presents a problem that is discussed in the next section.

In addition to the differences between the sexes in foraging return rate we find differences between individuals and across age classes. For the 25 adult men for whom we have more than 10 sample days of foraging data, the mean returns per man range from 446 to 2124 calories per hour. Although some of this variance is undoubtedly due to hunting luck on the days monitored, we have discovered positive and significant correlations between return rates measured for individual men in 1980 and 1982 (Kaplan 1983, p. 100). These differences also correlate with amount of time spent foraging daily (Hill et al. 1985) and reproductive success (Kaplan and Hill 1985b). This implies that there are long-term stable differences in the hunting abilities of different men. In addition, male adolescents and old men have foraging returns that are almost an order of magnitude lower than adult men (see Table 1). Such differences are likely to affect individual foraging strategies.

Women's return rates also vary from individual to individual. Most importantly, Ache data suggest that women who were nursing infants during our sample period are characterized by significantly lower foraging return rates (Hurtado 1985). It is also our impression that there is some variance in foraging returns between individual women based on age, size, and personality characteristics.

Several conditional factors can be shown to affect the return rates of Ache foragers. Men's rates appear to be higher during the first half of the warm-wet season when honey is abundant (see Hill et al., 1984 for description of seasonal dietary variance). Women's rates on the other hand appear higher in the late warm-wet season when some important fruits are abundant. These differences, however, are not significant (warm-wet daily mean of hourly return vs. cold-dry, *t*-test $p > 0.05$ for both). Both sexes have significantly higher return rates when they are more than one day distant from the mission, indicating resources depletion[2] near the permanent settlement (t-test, $p < 0.05$ for both).

The overall foraging return rate including *all* food processing time is presented in Table 1 under the column entitled "with process." Although processing time barely affects men's overall returns, adding it in causes women's returns to decrease by about 11%. This is because vegetable resources exploited by the Ache require relatively more processing per unit of food value than do game items. In fact, compared to the amount of time spent in pursuit of animal prey, processing time is almost a negligible component of their total cost. For example, the largest game animal, white-lipped peccaries, require almost 7.5 man hours of pursuit for one successful kill. Singeing off the hair, gutting the animal, and butchering the animal into suitable for pieces cooking takes just under 15 minutes. Although the meat requires several hours to cook, the actual time spent tending it is only a few more minutes, thus the total processing time is just under 20 minutes, or about 4% of the total time cost of a white-lipped peccary. For palm fiber, on the other hand, approximately 30% of the total time cost is processing time.

Now, let us examine how well these foraging patterns conform to predictions of optimal diet models. As mentioned above, the optimal diet model (McArthur and Pianka 1966; Emlen 1966; Schoener 1971; Charnov 1973, 1976a; Charnov and Orians 1973) predicts that none of the resources exploited by the Ache should give returns after encounter (in calories per hour) that are lower than overall foraging returns. This prediction is met for all but one of the 26 resources whose returns we were able to measure. That resource is bamboo larvae, which is taken primarily by women but occasionally by men. Since the test reported here is based on an entirely new data set, it represents a partially independent (the same people were monitored in both studies) replication of findings reported eariler (Hawkes et al. 1982).

The original OFT models were kept as simple as possible in order to ensure their generality. When considering modification of these models one faces a tradeoff between maintaining that generality and increasing the precision of the models with respect to their explanatory power in specific cases. The piecemeal approach described by Krebs (1983) allows for both generality and increasing specificity of models. One begins with the simplest model possible and then adds modifying factors one at a time if they significantly reduce the unexplained residual variance that is of concern to the researcher. Using this approach, the first and most important lesson to be learned from the Ache case is that the energy costs and benefits of exploiting alternative resources allow for reasonably accurate predictions concerning which re-

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[2] This difference could also be partially due to differences in foraging strategies on the first day of trips vs. other days. Ache walk for more hours and appear to be less involved in active search for resources on the first day of trips.

sources will be exploited in an area. There appear to be hundreds (if not thousands) of edible resources in the Paraguayan forest as judged by what is eaten by peccaries, rodents, monkeys, and birds. Many of these items (such as insects, small fruits, and small birds) would be expected to give very low returns if pursued, and are, in fact, never taken. The finding that all but one of the resources we saw taken by the Ache gave caloric returns higher than the mean return rate for the age–sex category of Ache foragers who exploit it is therefore quite impressive. Nevertheless, some intriguing difficulties remain.

ACHE FORAGING STUDIES: INSIGHTS AND PROBLEMS

Results from the previous section, along with the difficulties that we encountered in attempting to operationalize OFT models and analyze the data that we collected, have led us to some simple insights about studying resource choice and some modifications of the basic OFT models that may help in predicting human resource use. Most of these modifications were clearly anticipated by the proponents of the original OFT models (e.g., Pyke et al. 1977), all have been discussed in the abstract by recent theoretical works on foraging theory (e.g., Stephens and Krebs 1986), and many have been recognized as general problems with applying OFT to the human case (Smith 1983).

At this point it is important to clarify that many of the ideas in the following discussion should be regarded as hypotheses that require further evaluation. Explanations consistent with evolutionary theory and OFT are offered for observations that seem, at least initially, to contradict OFT models. Particularly we were bothered by the observation that the caloric returns from adult male hunting seem to be considerably lower than the caloric return rate that characterizes women's palm collecting activities. This implies that men were choosing a low-return foraging strategy when a higher-return alternative strategy was possible. This observation forced us to deal directly with nutrient constraints in the analysis of data even though we had not anticipated this problem in the data collection phase. Because the observations on Ache foraging patterns were used to derive some of the explanations we propose, the same data cannot be used to support our ideas. Most of the discussion below is an example of the constant interplay between theoretically derived initial expectations, empirical observations, and new interpretations of theory with new expectations. We offer these interpretations with the hope of stimulating the collection of new field data among other human foragers.

Nutrient Preferences

Although the above results are consistent with the basic predictions of the optimal diet model, there is good reason to believe that an alternative foraging strategy would result in a higher *caloric* return rate. According to the data, women achieved higher return rates than men on days when camp was not moved. Not only did they obtain higher caloric returns than did men on those days, but they obtained higher returns on "no move" days than men do on average over the entire sample period. Since Ache men are capable of all foraging activities that women engage in, it appears that the men choose a foraging strategy that gives fewer calories per hour than they could potentially acquire.

Data on palm densities also suggest that men opt for a "lower return" strategy day after day. Results from aerial surveys and ground transects indicate that the area in which the Ache forage has about 300 palms per square kilometer. Foragers pass within 15 meters of a palm at an average rate of about one every 2 minutes. Since we estimate and informants report that about one in four has good palm fiber, we can calculate, using data on the time necessary to acquire palm fiber and growing shoots, that Ache men could obtain approximately 2630 calories per hour if they did nothing but exploit palms all day. Instead they hunt 7 hours per day with mean caloric returns of only 1340 calories per hour. Because Ache men and women are acquiring resources of greatly different nutrient composition, the simplification of food value to energy appears to result in an important loss of predictive power.

If Ache foragers are indeed trying to maximize the efficiency of food acquisition, the Ache data suggest that meat and plant resources are probably not equivalent in value; 1340 calories derived from meat (men's hourly hunting rate) may be worth more than 2630 calories of palm products.

Observations of the exchange rate between other foragers and their agricultural neighbors indicate that meat is worth much more than carbohydrate calories (e.g., Hart 1978; Peterson 1981). Hart, in his study of exchanges of meat and casava between Pygmy foragers and neighboring agriculturalists, found that approximately four and one half times as many calories of casava were exchanged for each calorie of meat given.[3] In addition, it appears that almost everywhere in the world meat calories from domestic animals are probably expensive to produce relative to plant calories, and yet subsistence farmers continue to use at least some of their "cheap" plant calories to produce "expensive" animal calories (see Harris 1985 for discussion). Quantitative data on returns from hunting and other activities show that hunting returns sometimes result in an overall energy loss (Dwyer 1974; Johnson and Behrens 1982) and frequently are much lower than the returns that could be achieved from plant collecting or agriculture (e.g., Eder 1978; Hames 1984).

Humans are not the only organisms for which calories derived from

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[3] According to Hart (1979, Table VIII), 387 kg of meat were traded for 805 kg of manioc flour and rice. Calculating meat at 1460 cal/kg and the starch at 3300 cal/kg meat appears to be worth 4.7 times as much as starch.

animal products may be more important than an equivalent number of plant calories. Primates in general have often been reported to forage long hours for insects, which appears to result in much lower caloric return rates than foraging for vegetable resources (McGrew 1979; Terborgh 1984). Chimpanzees appear to greatly relish game items that they spend hours to completely consume (Teleki 1973). If consumption time is counted as processing, the caloric returns of such episodes are extremely low. Nevertheless, meat acquisition appears to be an important part of the chimpanzee foraging repertoire (Wrangham and Bergmann Riss, 1984).

Something about animal prey appears important enough to require modifications of calorie maximization models. Two macronutrient components of animal tissue are obvious candidates: protein and fat (lipids).[4]

Protein has long been recognized as an important macronutrient in the diets of most organisms. Experimental data have shown that organisms who are allowed to select their own diets are quite capable of avoiding nutrient deficiencies, even when nutrients are administered intravenously (see Blundell 1983 or Gaulin and Konner 1977 for review). Whether this is due to specific hungers or delayed monitoring of physiological states is an interesting question but is probably not relevant to the issue of the importance of nutrients to feeding strategies. This is because either mechanism would be expected to lead to the same diet. In any case, the final result may be nutrient preferences. Studies with humans have conclusively demonstrated that extremely low levels of protein in the diet can have serious consequences (see Nowak and Munro 1977 for review). Whether low but "sufficient" levels of protein result in adequate health is still debatable. Evolutionary theory, however, would suggest that other things being equal, the best possible state of health, rather than merely an adequate state of health, is likely to be the nutritional goal of living organisms.

The Ache eat substantial amounts of meat and are certainly not concerned with meeting minimum protein requirements (Hill et al. 1984). How-

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[4] Other alternative explanations for why men hunt rather than gather are also possible. Of particular interest in the Ache case is the fact that the daily variance in calories acquired is much higher for hunting than it is for gathering (Kaplan 1983). It is possible therefore that hunting may be a strategy to intentionally increase the probability of very high production on some days even if, in general, it lowers average caloric return rate. If fitness payoffs from foraging (e.g., increased mating opportunities) are most important only when men are clearly well above average, this type of high risk strategy might be adaptive. Although this is a possibility that should be further investigated, it may not be a good explanation for Ache male foraging behavior. Although daily variance in men's hunting returns is quite high, the returns over longer periods of time are quite consistent for individual men (Kaplan 1983). Most possible advantages conferred to men with high foraging success (i.e., nutritional, better treatment of their children, incrased mating opportunities) are most likely to be a result of success rate on a time scale much longer than a single day; thus increasing daily variance in returns at the expense of a higher long term mean return rate is unlikely to be adaptive. On the other hand, if women rewarded hunters with increased mating opportunities as a function of short-term hunting success, all men might be expected to hunt more each day. Even those men who could not expect to be the best hunters over a monthlong period might be expected to have the highest daily returns occasionally. This might be enough incentive to stimulate men into hunting frequently as a form of mate competition.

ever, there are indications that even in amounts well above "minimum protein requirements," most animals show positive effects from increasing levels of protein in the diet. Studies with isocaloric diets show that higher protein levels usually produce higher growth rates and body weights (e.g., Gloria 1981; Burkhardt et al. 1982; Burns et al. 1982; Grimbergen et al. 1982; Yoshimura et al. 1982). Growth rate and body weight are generally correlated with reproductive success for both males and females (e.g. Gaulin and Konner 1977; Whitten 1983). The same appears to be true of the Ache as well. Data suggest that body weight is positively associated with fertility among Ache females (Hill and Kaplan 1987). Low but "sufficient" protein intake is associated with lower reproductive success in white-tailed deer relative to higher protein intake levels (Murphy and Coates 1966). Protein intake has also been shown to affect reproductive function in various other organisms (Sadleir 1969). In this light, the fact that the Ache males choose a foraging strategy (like hunting) that yields lower caloric returns than alternatives (i.e., palm fiber exploitation) may be accounted for by the compensation effect of increased protein complexes.

There is an equally good reason to believe that lipids are the most important nutritive component of animal tissue. Some fatty acids are clearly essential in human diets (Holman 1981). Crawford (1975) and Crawford et al. (1981) have pointed out that even when protein "requirements" are met from plant foods, animal products are indispensible because of their lipid content. Based on nutritional and brain lipid studies, Crawford concluded "The current enthusiasm for substituting knitted vegetable protein and oil for real meat may be biologically undesirable: to suggest that it may be eaten instead of meat is fraudulent" (Crawford 1975, p. 33). Since 50–60% of the brain solids are structural lipids, high lipid intakes are extremely important for pregnant and lactating women and young children, and since the human brain is so large relative to body size, the value of increased lipid consumption may be greater in humans than almost any other organism. Although a direct connection to reproductive success has not yet been demonstrated, rats fed high-fat diets reach sexual maturity earlier than rats fed low-fat diets (Frisch et al. 1975).

Anecdotal support for the importance of lipids can be found in statements about the desirability of fat game animals among most hunter–gatherers. In modern societies where nutritional desires are more easily met it is the fat component of the diet, not the protein component, that is much higher than in primitive societies (Whiting 1958; Gaulin and Konner 1977). It is interesting that bamboo larva, the single Ache resource that was included in the diet even though its energy returns are lower than overall foraging returns, is high in fat (26%) and protein (9%) relative to most vegetable resources. Hill and Kaplan (1983) also observed Mashco–Piro women in southeastern Peru taking palm nut larvae that should have been excluded from the diet on energy considerations alone. These observations lend further support to the hypothesis that protein and fat are of greater nutritional value than an equivalent amount of carbohydrate.

The question of how to incorporate nutrient constraints in OFT models is very important (Pulliam 1975; Altman and Wagner 1978; Greenstone 1980; Rapport 1980). Nutrient constraints may sometimes be more important to herbivores than are energy constraints (e.g., Owen-Smith and Novellie 1982; Moss et al. 1972; Belovsky 1978, 1984; Milton 1979). Since the original OFT models predicted that energy should be maximized *when all else is equal*, these results do not negate the models. Other researchers have also shown that when alternative strategies differ on other parameters important to fitness, animals may not maximize caloric rates from foraging. For example, when one strategy exposes the organism to a higher risk of predation, it may be avoided even if it would give higher energy returns (Milinski and Heller 1978; Sih 1980; Werner and Mittelbach 1981). Strategies that allow for monitoring territorial boundaries or potential competitors may also be favored even if they slightly lower the foraging return rates (Kacelnik et al. 1981; Davies and Houston 1981; Martindale 1982). In the Ache case, hunting and gathering may not be equal strategies, because meat products appear to be of higher nutritional value than plant products.

Although meat products may be more valuable than most plant foods, several Ache observations suggest that neither meat nor carbohydrate is more valuable under all conditions. Orange groves are frequently exploited for a period of time and then abandoned before the returns from the grove appear to diminish. The same resources are then exploited again later that day or in following days. By leaving the groves the group moves further and men are allowed more time to hunt and cover a greater distance. Thus it would seem that initially the value of exploiting oranges is greater than continuing to search for game, but once the oranges have been consumed in quantity, the value of searching for game is greater than continuing to exploit the fruit groves.

If Ache foragers are trying to maximize the nutritional returns they derive from time spent foraging, these observations suggest that the relationship between the amount of each resource-type acquired and the nutritional benefits derived is not linear. As more of each nutrient is consumed, the nutritional value begins to decrease for additional increments of consumption (see Figs. 1a, 1b). The value of meat or carbohydrate is probably very high initially since some amount of each may be necessary each day for optimal body growth and maintenance. When different foraging strategies are likely to produce different nutrients, the optimal nutrient mix becomes a problem of optimal amounts of time spent in each strategy (or patch). The relationship between fitness and the amount of *time* spent in acquiring a resource is also likely to be characterized by diminishing returns.

Consider a hypothetical example (Fig. 1). Given the *nutritional* value of an amount, x, of each resource type, the *fitness* value for *time* spent acquiring that resource is calculated by subtracting the costs of acquiring

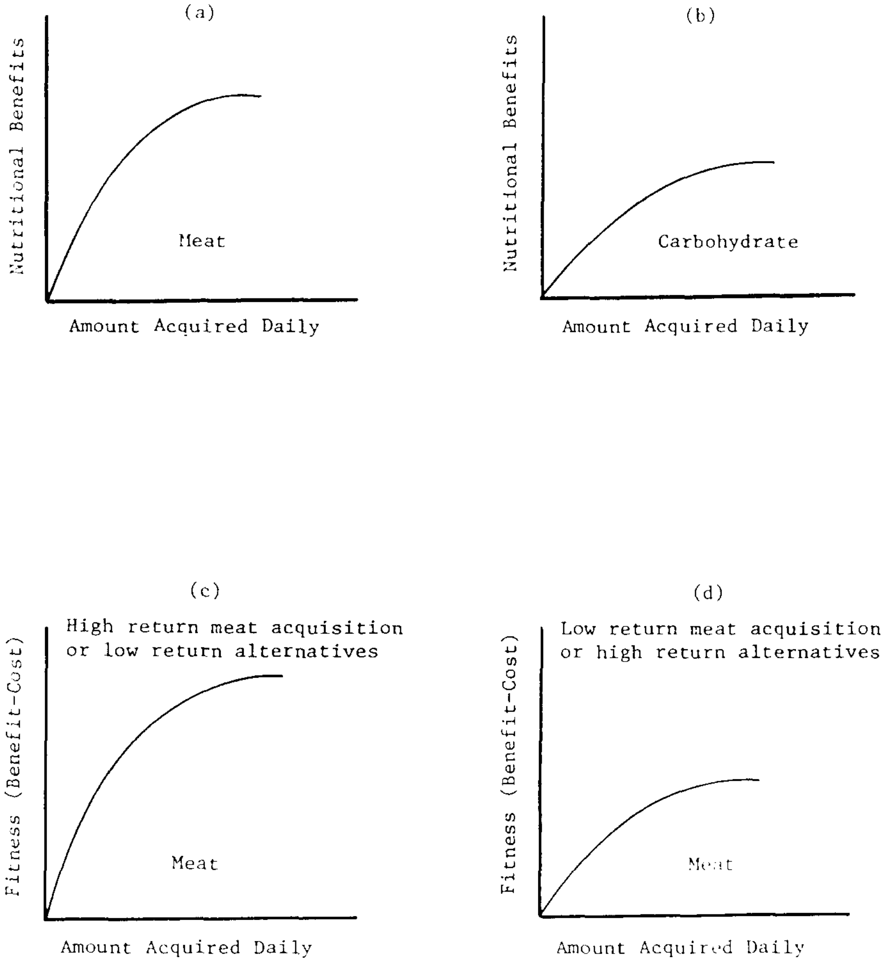

FIGURE 1. Relationship between benefits derived and amount acquired daily for different food types.

amount x (in time, energy, and lost opportunities) from the nutritional benefits gained from amount x. In order to derive maximum fitness benefits a forager should allocate time to extracting each resource according to their fitness value given the projected amounts of each resource that will be acquired through the day (see Hill 1983 for similar model of time allocation to activities). If the value of each resource diminishes with the amount acquired, foragers should switch from the exploitation of one resource to an alternative one at the point when additional increments in the first resource yield lower fitness payoffs than would time spent in the acquisition of alternative resources. It should be noted that this is essentially a model of nutrient complimentation rather than one of nutrient constraints (see Stephens and Krebs 1986).

For Ache men, the cost of obtaining meat may be quite low or the returns may be very high (Fig. 1c); thus the fitness–benefit curve is steep and they should spend a good deal of time foraging for meat. For some other foraging people (or agriculturalists) the cost of obtaining meat may be much higher and, as illustrated in Figure 1d, the fitness–benefit curve from meat would be lower. This could be due either to greater difficulty of acquiring meat, or greater value of other fitness-enhancing activities (including easier carbohydrate caloric production) that would compete with time spent hunting. Thus, the relative amounts of various resources that should be exploited vary with the precise shape of the fitness curves associated with different amounts of time spent to acquire resources and the fitness value of time spent in alternative activities.

Simple adjustments in classical OFT models may be able to correct for the apparently higher value of animal products over plant resources. If one were to propose, for example, that resources high in protein and fat (i.e., mammals, fish, birds, insects, nuts) are worth about four times as much as carbohydrate resources (the exchange rate between meat and carbohydrate reported by Hart 1979 for the Pygmies), the optimal diet model would still be very simple and easy to test. This modification would still result in all observations made on Ache foragers, both men and women, meeting predictions of the optimal diet model. All 26 resources taken (including bamboo larvae) would be predicted to be in the diet given men's and women's respective return rates. The modification would also help to explain why men almost never stop to take any nongame resource except for honey. The nutritionally adjusted return rate for meat would be over 5000 carbohydrate calorie equivalents per hour and few nonmeat resources give returns that high. On the other hand, honey, which is very frequently taken by men, is characterized by returns of over 20,000 calories per hour. This line of reasoning, however, raises the question of why women do not hunt. This is briefly discussed in a later section.

We do not wish to suggest that the actual difference in value between meat and carbohydrate is a factor of four, but only to point out the potential simplicity of a single factor modification (rescaling of resource values). It should be noted that if the relative values of meat and carbohydrate are negatively accelerated functions, and each changes as a function of the amount of the other complimentary resource that has already been acquired, resource tradeoff modeling is even more complicated. At least one experimental study suggests that this is the case. Yoshimura et al. (1984) present data demonstrating that the increase in growth rate of rats as a function of either more protein or energy depends on the amount of the other that is available. This means there is an interaction effect between the value of protein and carbohydrate. In this case, a two-factor mathematical programing model for maximizing the amount of both resource classes according to their weighted values as a function of how much of each has already been taken would probably be the most accurate predictor of resource exploitation patterns. Such models, however, may quickly become more complex than is necessary for making general and accurate predictions about human resource choice in a wide variety of circumstances. On the other hand, they may be necessary for understanding the tradeoff between time spent in farming vs. hunting, for example.

In any case, the Ache data indicate that some additional factor must be added into even the simplest models in order to appropriately weight the value of animal products more heavily. Only additional empirical data from other foragers and other primates will allow us to determine its exact nature.

Preferences Due to Differences in Opportunity Costs

In addition to the direct energetic cost of procuring resources, it is important to consider the cost equivalent of what could be gained by spending time in an alternative activity (opportunity cost). Opportunity costs, other than those associated with the tradeoff between pursuit time and search time, have often been considered in models of time allocation to foraging, but are less frequently considered when applying diet breadth models. Classical OFT models assume that each component of foraging time (i.e., search, pursuit, and processing) is a mutually exclusive activity. The value of spending time in pursuit or processing is traded off against the advantage of spending more time searching for resources. However, there are clear cases among many organisms for which this assumption does not hold, and the human case may be the most problematic. This is primarily due to two common characteristics of human foraging. First, human hunting often includes much longer pursuits (in both duration and distance) than is the case for most other organisms. Second, among human foragers, a good deal of food processing takes place when other foraging activities are not possible or would be more costly and less effective (e.g., after dark, when it is very hot, when it is very cold, and so on). These two observations lead to both qualitative and quantitative adjustments in OFT predictions.

Long-distance pursuits of game animals seem fairly common among human hunters. The Ache are no exception. Although many animals are either acquired immediately after encounter or they escape, some such as white-lipped peccaries may be tracked for several hours. Tracking and continuing to search are not mutually exclusive activities since other resources are sometimes encountered and acquired. But, as Ache men track peccaries, they pay close attention to ground surfaces immediately in front of them and move at much higher rates of speed than they do while searching in general. This probably means that they miss many opportunities to kill other game that might be encountered as the distance is covered.

In the Ache case, measuring the opportunity cost for tracking peccaries is relatively simple. One need only compare the return rate of hunters during various phases of pursuit to the mean foraging return rate. During the 31 hours of peccary tracking we observed, hunters acquired 318 calories per hour. Since the mean foraging return rate is about 1340 calories per hour, Ache hunters pay an opportunity cost of just over 1000 calories per hour while tracking peccaries. During the 62 hours of pursuit time after which peccaries were heard or seen, the return rate from other resources is 0 calories per hour. This indicates that "hot pursuit" of peccaries is absolute and mutually exclusive of searching for other resources. The opportunity cost of this "hot pursuit" is 1340 calories per hour and all time spent in this phase of the hunt is exclusive of other activities.

Any decrease in opportunity cost from that of the mean foraging return rate (100% mutually exclusive with search for other resources) should be taken into account when determining if a resource should be taken upon encounter. If pursuit of a resource is very compatible with continuing to search effectively for other resources, the resource in question should be taken even if return rate upon encounter is low. As long as the combined return of all resources taken during a pursuit (including the principal target) is higher than the overall foraging return rate, the resource should be included in the diet. This is the case for white-lipped peccaries since 556,175 calories per peccary plus 56,653 calories of other resources were taken during 111 man hours of peccary pursuits (including tracking time), yielding a return rate of 5323 calories per hour. This means that the question of whether resources characterized by long pursuits should be included in the optimal diet is essentially a "patch choice" model (e.g., McArthur and Pianka 1966).

Another example of opportunity costs involves items that are usually in the diet, but are occasionally passed by. We mentioned above that women appear to pass by palms in order to keep the band moving so that men can hunt greater distances (women also follow them and carry all game so that men do not have to return a long distance to the camp with game before continuing to hunt unencumbered). This may indicate that the opportunity costs of stopping for palms (i.e., possibly lower hunting returns) when the band is on the move are higher than the expected benefits.

Monkey encounters also illustrate the effect of high opportunity costs on foraging decisions. We recorded 18 cases where monkeys were not hunted after their location was known. Monkeys are the lowest-ranked game item, so it is not surprising that they should be occasionally ignored. However, since returns from monkeys are higher than men's overall mean foraging returns, it is important to determine why they are sometimes ignored. In 10 of the 18 cases, hunting conditions at the time were poor (e.g., almost dark, wet forest, baby monkeys, thorny forest, or few arrows) and the expected return rate was probably much lower than the average that we measured for monkey encounters. In seven of the remaining eight cases, monkeys were ignored because they were found in the middle of a peccary pursuit. Since returns from peccaries are almost five times higher than for monkeys, the opportunity costs of stopping a peccary hunt in order to chase monkeys may be very high. This is especially true since the average monkey hunt uses about 6 man hours of time. If six men stopped their peccary pursuit for 1 hour in order to hunt monkeys, their probability of finding the peccaries later may be very low. Since peccary pursuits are a much more efficient way to get meat, the opportunity costs incurred by a monkey hunt offset their food value. Monkeys should therefore be ignored when chasing peccaries even though monkey hunts are characterized by higher returns than men's overall foraging return rate.

The opportunity costs of processing food during times when foraging opportunities are poor are much harder to calculate. Much of Ache plant processing and almost all game butchering, cooking and eating take place after dark.[5] Time after dark seems relatively cheap for the Ache. Foraging after dusk would be difficult and risky. On the other hand, having to process food at night does imply some cost since there is always some other alternative activity that might be preferred (e.g., flirting, sleeping, grooming, fixing a hut or bed). In the Ache case, processing times are not generally major components of total foraging time, so the problem is minor. In other situations, however, where strong seasonal factors make foraging impossible for some period of the day or year, resources that require much processing might be included in the diet even if their characteristic returns including processing time are lower than mean foraging return rates. However, if *all* foods are processed equivalently during cheap time, predictions from the optimal diet model will still hold, since the calculation of their relative ranks will remain unchanged. On the other hand, if one food requires a long period of pursuit and little processing whereas another requires short pursuit but long processing, the latter food may actually be higher ranked even if its relative rank when processing time is included as a cost is lower than the former.

Resource Consumption Preferences

When asked about their favorite foods, Ache informants often ranked resources in a way that did not match the resource ranking in Table 2. This might suggest that the resource rankings generated in OFT analyses are not useful, but such a conclusion is unwarranted. Food preferences and return rate ranking are very different measures of resource quality.

The order of ranking of resources from highest to lowest returns may predict which foods are first dropped from the diet as conditions change, but that ranking is not expected to match preferences in taste. Taste preferences (i.e., which resource an informant would most like to eat) are a function of the food value of the resource and ignore costs of acquisition and processing. Thus, while most Americans, for example, may prefer the taste of lobster to that of rice, it is not necessarily the resource that they would most often choose to buy given the cost. Similarly, foragers may enjoy the taste of a resource, yet not exploit it because the time or energy costs

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[5] Although this problem is not usually confronted in animal studies on optimal foraging, some animal behaviors are analogous. The squirrel that gathers nuts during good weather but waits to crack and eat them until a later time when foraging is not a possibility is a good example.

Table 2. Returns in Calories per Hour After Encounter with Various Ache Resources

Description	Number of Pursuits Sampled	Scientific Name	Calories/ per Hour[a]
Palm growing shoot	(17) (15)	*Arecastrum romanzolfianum*	2.356, 1,584[b]
Palm fiber starch	(30)	*Arecastrum romanzolfianum*	3.219, 2,246[c]
Palm fiber and shoot	(43)	*Arecastrum romanzolfianum*	2,436
Palm nut	(4)	*Acromia totai*	2.243
Brovilla fruit	(16)	*Casimiroa sinesis*	4,181
Membe fruit	(9)	*Philodendron sellam* (unripe)	2,708
Biaju fruit	(10)	*Philodendron sellam* (ripe)	10,078
Challa fruit	(6)	*Jacaratia* sp.	2,549
Virella fruit	(14)	*Campomanesia zanthocarpa*	6,417
Pychikytalla fruit	(1)	*Annona* sp.	2,835
Kurilla fruit	(20)	*Rheedia brasilense*	3,245
Pretylla fruit	(2)	*Ficus* sp.	4,414
Boilla fruit	(2)	*Chrysophyllum gonocarpum*	2,884
Large palm larva	(17)	*Calandra plamarum*	2.133
Small palm larva	(22)	*Rhynophorus palmarum*	1,331
Bamboo larva	(10)	Unknown	936
Mynga honey	(73)	*Apis melifera*	20,609
Chei'i honey	(31)	Unknown	8,666
Other honey	(6)	Various unknown	22,411
White-tipped peccary	(21)	*Tajassu pecari*	5,323, 8,755[d]
Deer	(12)	*Mazama americana*	15,398
Collared peccary	(5)	*Tajassu tajacu*	6.120
Paca	(53)	*Cuniculus paca*	4,705
9-banded Armadillo	(26) (31)	*Dasypus novemcinctus*	13,782, 2,662[e]
Coati	(11)	*Nasua nasua*	7,547
Capuchin monkey	(59)	*Cebus apella*	1,370

[a] Includes time spent in acquisition attempts plus all relevant processing.

[b] Significant difference between men's and women's return rate. Men's rate listed first.

[c] Second number includes optional processing time.

[d] First number includes time spent following tracks. Second number only includes time after animal is heard or seen.

[e] First number is for animals encountered on the surface. Second number is for animals dug up.

are too high. This is probably often true for small dispersed fruits and seeds. Food preference lists alone, while interesting, are not useful for predicting dietary change across time or space. (However, see discussion of nutrient constraints above.)

Resource Encounter Preference

It may be somewhat surprising to discover that informants do not necessarily prefer to encounter the largest or most calorie-dense resources in their area. In fact, some such resources may be ignored altogether, even when they are encountered. OFT leads one to expect that informants should prefer to encounter the highest *ranked* resources at any point in time. This will generally lead to the highest foraging return rate. However, which resources will be the highest ranked is not easily predicted from theory, and is primarily an empirical question.

Return rates for specific resources are a function of both the intrinsic food value of resource and the costs associated with acquiring and processing those resources. Because of this, it is not surprising that size or resource type alone is not a good predictor of return rates.

The lack of a relationship between package size and return rate can be clearly seen in Table 2. For each category, fruits, honey types, and game animals, resources are listed in Table 2 in descending order of their average weights. Some require long pursuit or processing times whereas others are easily acquired and can be eaten with little or no processing. The differences within size classes overwhelm any possible correlation of size with return rate. Similarly, the costs of acquiring resources in each category such as fruits, honey, game, etc. vary so much that there are very high and low ranked resources in each class. In eastern Paraguay the returns from honey are generally higher than for other resource classes but this may not be true elsewhere (or with stone technology in the same environment). Game returns are slightly higher than the most commonly encountered vegetable resources, but this would not necessaarily be true in all environments. Although large game clearly have the potential of being very high ranked resources, they may in fact give medium or low returns (e.g., peccaries in Table 2) if long and unsuccessful pursuits are common. This may explain food taboos on what appear to be very attractive resources. On the other hand, small game resources may be very high ranked if they can be acquired quickly and consistently and require little processing (e.g., armadillos in Table 2).

Time Scale Preferences

We found that the Ache consistently expressed a wish to encounter white-lipped peccaries above all other resources. This is surprising because white-lipped peccaries are not one of the highest ranked resources (Table 2). Armadillos, when encountered above ground for example, are characterized by much higher immediate returns than are white-lipped peccaries. Nevertheless, Ache men prefer to search for areas which show signs of peccaries rather than looking for areas of the forest with signs of armadillos. When one examines foraging returns on a daily basis, however, this preference is not surprising. Occasionally, a hunting strategy that will give high immediate returns also results in lower overall daily returns (e.g., shooting small game with shotguns may provide a high immediate return but may lower overall returns if larger game are nearby and scared away). The decision concerning the time frame over which the return rate should be maximized is crucial to OFT models. If the important time frame is an hour, a day, a month, or a year, the optimal strategy may be very different in each case. Because the Ache primarily consume game animals at the end of each day, and because we find no evidence that hunting behavior on one day affects returns on subsequent days, we might expect Ache hunters to be primarily concerned with daily returns. Let us reexamine the preference for peccary encounters in this light.

Peccary hunts on the average require 316 man minutes of foraging time and yield an average of 29,040 calories (5514 cal/hr). Above-ground armadillo hunts which give much higher return rates for *their duration* (17,520 cal/hr) require an average of only 12 man minutes and on average produce only 3504 total calories. Although armadillo hunts give higher return *rates* than do peccary hunts during the first 12 minutes of the hunt, peccary hunts give much higher returns over the duration of several hours than does the combination of armadillo hunting for a few minutes and then searching for and pursuing other resources at the average rate. For example the return rate from hunting peccaries over 400 man minutes of time is 29,040 calories per 316 minutes (average peccary returns) + 1868 calories per 84 minutes (average foraging returns), or 4637 cal/hr. The return rate for the next 400 minutes after encountering an armadillo above ground is 3504 calories per 12 minutes (average armadillo returns) + 8665 calories per 388 minutes (average foraging returns), or 1825 cal/hr. Not surprisingly, men would rather encounter peccaries than an armadillo. Higher *daily* returns can be expected from an encounter with peccaries.

The time frame problem points out the utility of considering many hunting strategies as patch choice decisions (see MacArthur and Pianka 1966; Charnov and Orians 1973; Hawkes et al. 1982, for example). The peccary "patch" is better than the armadillo "patch" even though peccaries are lower ranked. This is because the peccary patch allows for a much longer period of exploitation before it is depleted, and the increase in future expected return rates is worth the slightly lower return rate obtained during the first few minutes of pursuit. We suspect that in some cases the time frame over which foraging decisions are made may be much longer (e.g., when food patches are widely dispersed in space, as may be the case with Australian Aborigines).

Preferences Due to Energy Costs

The energy costs of foraging are usually measured as time spent in food acquisition. This is based on the assumption that the energy expended per unit time while pursuing and processing various resources is approximately equivalent. This asumption is often not true, but its effect on optimal diet predictions has rarely been calculated. For Ache foragers there is little doubt that hunting requires higher expenditures of energy than does gathering, and both are probably more strenuous than food processing. Montgomery and Johnson (1977) measured Machiguenga energy expenditure in a number of activities and their numbers suggest that the ratios of energy expenditure for hunting, gathering, and food processing are 2.8 to 2.3 to 1, respectively. If these levels of energy expenditure applied to the Ache, predictions from the optimal diet model would not change from those we made using return rates in calories per hour. All resources seen taken would still be in the optimal diet, but the adjustment would indicate that meat is even more expensive relative to carbohydrate, and that resources that require much processing are actually cheaper than our data indicate.

Preferences Due to Risk Sensitivity

It has been pointed out that there are many situations in which the need to avoid the risk of falling short of some critical food level can be expected to be more important than maximizing the rate of food acquisition (Caraco 1980; Stephens 1981; Stephens and Charnov 1982; Stephens and Krebs 1986). Indeed many anthropologists have suggested that the need to minimize risk rather than maximize efficiency is the major constraint on human foraging (Durham 1981; Keene 1981; Cashdan 1982; Gould 1982; Jochim 1982; Wiessner 1982). Usually risk aversion is considered to be most important when considering overall foraging strategy (i.e., patch choice and time allocation to patches). Its implications for diet breadth or resource choice have been less studied.

The optimal diet model proposes that all resources should be included in the diet if the returns upon encounter are higher than overall mean foraging returns. On the other hand, humans are likely to suffer severe consequences if they go without food for more than a few days. This is especially true for pregnant and lactating women and small children. If a potential resource is large, it may be characterized by high average returns upon encounter even if many man hours or days are generally expended before a single successful kill is made. For example, in order to kill a whale, dozens of man days of pursuit (counting all failed pursuits) may be required, and yet the mean returns in calories per hour spent might still be tremendously high. Should small groups of human foragers really be expected to pursue whales, if these pursuits entail, on the average, 20 days without food before a successful kill is made?

Ethnographers have long suspected that food sharing may serve to reduce risk of food shortage for human foragers. We have also hypothesized that reduction in the variation of daily food acquisition may have important fitness consequences that favor sharing (Kaplan and Hill 1985a). Because food sharing may be a strategy to reduce risk of failure as well as reduce variation in daily food intake, while foraging on a set of resources, we have considered the study of sharing patterns among the Ache as an extension of OFT. Earlier analyses (Kaplan 1983; Kaplan and Hill 1985a) demonstrated a high correlation between the daily variance in amount of a resource acquired, and the extent to which it is shared among the Ache. We were able to show that sharing does in fact reduce both variance in daily consumption and the risk of going without any food for several days. Reduction in the daily variation of food consumption should increase the fitness of those who share when large packages are frequently acquired asynchronously (Kaplan

1983). Others have detailed the conditions under which such "reciprocal altruism" might arise (e.g., Trivers 1971; Axelrod and Hamilton 1981). Although the data are consistent with the proposition that food sharing *is designed* to reduce variation in daily consumption and/or avoid a critical shortfall, they are not conclusive. Indeed other explanations for food sharing that do not see it as a mechanism designed to reduce variance have also been proposed (e.g., Kaplan 1983; Blurton Jones 1984), and Ache data suggest that those who share food fain other advantages independent of their own nutrition (Kaplan and Hill 1985b).

Regardless of the *motivation* for food sharing in hunting and gathering bands, one of the *effects*, in almost all cases, is that the risk of getting no food on a single day is reduced. For the Ache, if the sharing pattern and band size are taken as a givens, there appears to be no reason to adjust foraging strategy toward risk reduction with respect to the array of resources taken. The resources whose pursuit entails the highest risk of acquiring nothing are peccaries and tapir, and neither were ever ignored. Only about one third of all peccary hunts are successful, but they usually require only about half a day, and usually only about half the hunters in a band are involved, while the others continue to hunt elsewhere. We have calculated elsewhere (Hill and Hawkes 1983) from the distribution of daily return rates for individual men and the observed Ache sharing pattern, that the risk of going more than 1 day without food is extremely low for Ache bands that contain more than three hunters. Kaplan (1983) has also noted that food sharing effectively eliminates variation in daily consumption for all but the smallest band sizes. It is possible, therefore, that among human foragers risk will have little effect on the suite of resources pursued and a much greater effect on the handling of the food once acquired.

Preferences Due to Individual and Context Specific Variation in Foraging Returns

Original diet breadth models derived from OFT suggested that decisions about foraging are made by comparing the average returns obtained from a specific resource to the mean foraging returns that can be obtained if the forager continues to search for other resources. The mean return rates that characterize a resource or foraging in general are used as an estimate of what the forager can expect from either exploiting the resource in question or continuing to search. However, mean return rates that are measured over a long period of time and a wide variety of circumstances may be irrelevant to the current decision facing a forager. To the extent that a forager can perceive relevant variables that make the current situation a subset of the general situation, he should take those factors into account and compare only the means of the relevant subset situations (e.g., Getty 1985).

If average overall foraging returns are 50 percent lower on rainy days, the decision to pursue a resource on rainy days should be made based on the mean foraging returns *for rainy days*. The forager should not make his decision by comparing the returns from the resource in question to the overall mean foraging return rate from all days.

Although it is quite difficult for an anthropologist to learn all of the relevant criteria that are involved in a decision about whether to pursue a specific resource in a specific situation, some of the data that we collected allowed us to discover inductively what some of those criteria must be. Different age–sex categories of foragers have different return rates (Table 1). Since these rates were stable over at least a 2-year period, the data suggest that members of each forager class are likely to make foraging decisions according to their own expected mean foraging return rate. As noted above, these different age–sex classes do have different foraging strategies, as indicated by the amount of time they spend trying to acquire vegetable or meat resources. Men's returns from extracting palm growing shoots (a very strenuous but short-term activity) are one and a half times higher than women's returns (Table 2). Importantly, women's returns from palm shoots are actually lower than our best estimate of their overall mean foraging rate (returns on "no move" days). We observed that whereas men frequently take palm shoots, women very rarely do. Indeed the data show that men acquired 78% of all palm shoots taken during the sample period. This is especially notable since Ache men acquired less than 2% of all other palm products (fruits and fiber).

In addition, differences in individual return rates among adult men are also considerable and statistically significant. Since their mean foraging returns differ, each should pursue a slightly different set of resources upon encounter. Informant reports suggest that this is the case. Several Ache men have developed reputations for specializing in different animal species and it is our impression that they adjust their search strategy to increase encounter rates with those animals.

Situation specific strategies may also be observed. As noted above, in peccary hunts much higher returns can be expected once the animals are seen or heard than are expected during tracking. Although we observed men stop tracking peccaries on 5 out of 11 events in order to pursue another resource, they never stopped a peccary pursuit (20 events) *after hearing or seeing the game* in order to pursue another resource. Likewise, if returns from monkey hunts are much lower when monkeys are encountered in tangled thorny jungle, this should be taken into account. As noted above, monkeys *are* frequently ignored if something about the encounter situation indicates that returns will be exceptionally low.

The most impressive example of the importance of the foraging context was discovered when tabulating returns from armadillo hunts. We found that the returns upon encounter varied more than fourfold depending on whether the animal was discovered above ground or already in its burrow (Table 2). Further investigation into the Ache strategy of hunting armadillos led to particularly revealing findings. Ache informants claimed that they do not dig

Table 3. Mean Weight of Adult Armadillos (*Dasypus novemcintus*) Captured 1980–82

Date	*N*	× kg
2–8 October	9	4.40
17–23 October	4	4.60
11–14 November	8	4.69
10–16 December	2	4.65
7–14 January	12	4.90
6–16 February	3	4.88
25 February–11 March	17	4.79
28 March–7 April	12	4.79
18–27 April	26	5.00
April 1980	3	5.27
May 1980	7	5.23
June 1980	28	4.94
July 1980	11	4.44

up armadillos during the early wet season (October–December) because the animals are not yet fat enough to make it worthwhile. Behavioral data confirmed that men rarely excavate burrows during the early wet season. Between October and December 1981, we recorded 13 encounters with armadillos in their burrows. Eleven of these were passed by and only two were dug out (Table 3). Between January and April of 1982, 30 armadillos were dug out of their burrows and only five were passed by. Data from 1980–82 on mean adult weight of armadillos through the year shows that adult armadillos increase in weight by 20% from the beginning to the end of the wet season (Table 3). Armadillos have an extremely thick fat layer relative to body size at the end of the wet season and may indeed fluctuate from less than 1% to almost 20% body fat by weight. If this is the case, we can recalculate the returns from armadillos for both seasons. The mean return rate from digging up armadillos is 0.57 armadillos per hour regardless of season. This is 1.88 kg/hr in the early wet and 2.14 kg/hr in the late wet season. At 0.5% body fat by weight, and 75% edible portion, the caloric return rate in the early wet season is 1220 cal/hr. At 20% fat and 75% edible portion, the return rate from digging armadillos in the late wet season is 3948 cal/hr. The results show that men should not dig armadillos in the early wet season because they are lower than the overall mean foraging returns for that period (Table 1).

WHY DO HUNTERS GATHER?

In 1982 we published an article entitled "Why Hunters Gather" (Hawkes et al. 1982). In that paper we noted that the Ache obtain such high returns from hunting that one might ask why they should ever gather. We suggested that the answer to this question was that the returns from the gathered plant foods exploited by the Ache were high enough that they should be included in the optimal diet. In subsequent work we have been forced to revise our understanding of Ache foraging. Specifically, we began to understand that our conception of the problem, as well as our answer, would have to reflect many of the modifications noted above.

All Ache foragers are not equal. Men and women appear to have greatly different capabilities and their foraging patterns are widely divergent. This implies that decisions concerning men's strategies should be made with respect to their abilities, and women's strategies with respect to their own abilities. The question "why do hunters gather" may be better expressed as "why do women gather, and why do men hunt?" Quantitative data indicate that game animals make up less than 1% of the calories that Ache women produce, while men obtain only about 4% of the calories that they acquire from collecting plant foods. If calories alone are to be maximized both sexes should concentrate on plant resources through most of the year. On the other hand, if it is the case that meat calories are worth several times the value of vegetable calories, neither sex should gather vegetable resources if they can hunt. Since we believe there is good evidence that meat is of higher nutrient value than are plant foods, this leaves us with two problems. Why do women not hunt more, and why do men spend any time at all collecting vegetable foods?

The answer to why women do not hunt is beyond the present scope of this article. Although it has often been assumed that women do not hunt because they are unable to do so, we do not believe this to be the case (see, for example, Estioko-Griffin 1985). Ache women sometimes do hunt certain game items when they are encountered and there are no men nearby. Instead, we suggest that the cost in offspring mortality to Ache mothers who hunted would probably outweigh the fitness benefits derived from hunting. In other words, women probably do not hunt because hunting is an activity that is incompatible with high-quality childcare, and, in the Ache environment, such childcare is probably very important to the survival and development of children. Because women are unlikely to hunt as adults, they do not spend the same time that males do training in hunting skills as children, and this along with their smaller physical size, probably also makes the return rate (and thus the value) from their hunting very low. We have presented this argument in more detail (Hurtado et al. 1985; Hurtado 1985) elsewhere, and demonstrated that childcare constraints appear to affect plant gathering strategies as well.

Why Ache men collect plant resources on occasion, if meat is worth many times as much as carbohydrate calories, continues to intrigue us. Although some plant resources are picked up off the ground and eaten while continuing to forage, more than 50% of all vegetable calories that men acquired in 1981–82 were collected after returning to camp, usually in the later afternoon. Several hypotheses were considered based on OFT diet breadth models and the modifications discussed above. The first and simplest explanation was that most plant resources were acquired by those hunters who had the lowest overall hunting returns. Since their overall caloric returns from foraging were quite low (even after being quadrupled to adjust for the value of meat) we expected that they might alter their foraging strategy to include lower ranked resources (i.e., vegetable foods). We found this possibility to be especially likely since we had previously demonstrated that good hunters spend more hours per day hunting than do poor hunters (Hill and Hawkes 1983; Hill et al. 1985).

In order to test whether poor hunters acquire more low ranked vegetable resources than good hunters, we paired good and bad hunters on whom we had focal person data on the same foraging trip. We also paired men according to family size since this variable seems to affect the amount of vegetable foods collected. This procedure resulted in 12 matched pairs of men who differed primarily in hunting return rate. The low return hunters acquired a mean of 624 calories of vegetable foods daily, whereas the high return hunters acquired a mean of only 246 vegetable calories per day. This difference was significant (Wilcoxon Signed-Ranks test, one tailed $p = 0.04$) and confirms that lower return hunters take more lower ranked resources (if meat is several times more valuable) than do higher return hunters, in agreement with the optimal diet model.

Despite the difference between good and poor hunters, all men acquire some plant foods, and most of them were acquired late in the day. Why hunters gather remains problematic. Three hypotheses can be identified and tested with our data. The first is that men took vegetable resources when much meat had already been acquired. Since this would make the value of more meat relatively low (Fig. 1), men might switch to taking vegetable foods. This hypothesis (resource complementation) predicts that there should be a positive correlation between amount of meat taken early in the day and the amount of vegetable calories taken after returning to camp. The second hypothesis is that men took plant resources on days when hunting was unsuccessful, as an insurance against the risk of going hungry on those days. These hypothesis (risk-reduction) leads to the opposite prediction from the first; there should be a negative correlation between amount of meat acquired during the day and the amount of vegetable that men collect after returning to camp. The third hypothesis is that the return rate from hunting was always much lower late in the day so men simply opted to return to camp and take vegetable resources. This hypothesis predicts that no correlation between meat returns during the day and amount of vegetable acquired after men returned to camp should be found. It also requires, however, a demonstration that return rates for hunting decreased significantly late in the day.

The first two hypotheses were tested by comparing the total amount of meat taken before men arrived at camp to the amount of vegetable calories that they acquired after arriving. No correlation, either positive or negative, was found. Hawkes et al. (1982) also found no correlation between amount of meat and vegetable taken per day by Ache foragers. Both the resource complementation and the risk reduction hypotheses appear to be falsified by the data. In order to test the hypothesis that hunting returns are so low that vegetable exploitation becomes profitable, we compared the return rates throughout the day from a sample of 30 focal men. The data showed that the return rates for the last 2 hours of the day before sunset were virtually identical to the return rates for the rest of the day (1532 vs. 1522 cal/hr in this sample). None of the three hypotheses are supported by Ache foraging data.

The negative results from these tests force us to consider other hypotheses about men's vegetable gathering. Over 50% of men's gathering occurs during the last hour or so of the day after men return to camp. Ache men are often not exactly sure where camp is at the end of the day. Camp location changes almost daily, and it is sometimes difficult to determine how far the women and children will walk. Men appear to be very concerned about spending a night in the bush because they carry no fire, and thus may intentionally start back a little early in order to be sure that they find camp before dark. This should result in men often returning earlier than is optimal, in order to minimize the risk of a night alone in the bush without food or fire. Good hunters would probably be willing to take slightly higher risks since the payoff for their foraging time is higher. Once men locate the new camp shortly before dark, they are faced with the dilemma of going back out a short distance to hunt, or staying around camp to obtain plant resources. Our impression is that they do both and that this depends upon the length of time remaining before dark and the probability of encountering game near camp.

The problem of why hunters gather is still not convincingly solved after 5 years of intensive data collection and analysis. Although some critics might suggest that this demonstrates the futility of the OFT approach, we are more optimistic, especially since we have yet to encounter a more productive alternative. We have learned a good deal about Ache foraging that was not immediately evident in our original conception of the problem. Indeed, the entire set of modifications and considerations discussed in previous sections are the result of trying to answer one simple problem, "Why do hunters gather?"

SUMMARY AND CONCLUSION

Many of the modifications of OFT discussed above are illustrated by the Ache case, but are likely to be critical in studying foraging decisions in any human group. There are also other factors particular to the Ache that allow for more precise predictions about foraging behavior over short time periods and under specific conditions. However, at some point, we must confront the issue of when it is appropriate to consider more complex models. This can only be answered by considering the goal of the study in question. If a study examines dietary changes over long time periods, day-to-day precision in predicting foraging decisions may be unnecessary. For example, explanations of why seed usage became common in the Great Basin (Simms 1984) or Australia (O'Connell and Hawkes 1981) do not require knowledge of what a forager will do in specific circumstances (e.g., on rainy days when camp is not moved). A simple application of the optimal diet model with few or no modifications is likely to be extremely helpful for explaining these problems. Likewise, changes in foraging strategies around the time of worldwide extinctions of Pleistocene megafauna, or the origin of agriculture and pastoralism in a variety of ecological settings, may be explained by the simplest versions of cost–benefit OFT models.

On the other hand, many anthropologists are concerned with understanding day-to-day behavior and decision making. Many of these issues can be tackled using the OFT approach, but each may require consideration of particular details not specified in the simplest models. The critical point to consider with each application of OFT is: What is the question of interest? As specific decisions rather than general patterns become the topic of study, so too must the OFT models be more specific.

Data from the past 5 years of intensive study on foraging patterns of Ache hunter–gatherers suggest the following:

1. Analyzing energetic return rates from different alternative foraging strategies is probably the best single predictor of foraging patterns. Specifically, resources that give higher caloric returns upon encounter than can be expected from general foraging will be included in the diet. Their contribution to the diet will therefore be determined by their frequency of encounter. Resources that give lower caloric returns upon encounter than would be expected from a given increment of foraging time if they are ignored, will not be taken.
2. Nutrient constraints should only be added into models if they are shown to significantly improve the predictive power of the model. The importance of animal matter vs. vegetable (carbohydrate) calories appears to be one such example. How to adjust for this will have to be determined empirically from many human and primate studies. Other nutrient constraints may be unimportant for foragers because they generally exploit a wide variety of resources and acquire other nutrients as a side effect of trying to maximize energy returns.
3. Specific conditions often lead to very different return rates even in the same environment. For example, men's and women's abilities and return rates are often different enough that they should be considered independently. Or again, the time scale over which returns are maximized is important for predicting the best strategy.
4. Opportunity costs associated with other activities are important when deciding what to do and how long to do it. Strategies that postpone some of the cost of food processing until a time when foraging is not possible

are likely to be common as long as the activities that they compete with are not more important to fitness than is foraging time.

5. The primary form of risk reduction among human foragers may be food sharing. If sharing is extensive, no other risk reducing strategy may be necessary.

The Ache data suggest that diets are primarily a function of only two variables—encounter rate and return rate. This knowledge may be useful for understanding many current human subsistence strategies, but should also be especially useful for predicting the diets of our ancestors in a wide variety of ecological circumstances.

This research was supported by NSF Grant #BNS-8309834 and NIH Grant #1 R01 HD16221-01A2, as well as two grants from the L.S.B. Leakey Foundation. We are especially grateful for the hospitality of Wayne Robbins of Divine Word Missions in Paraguay and Graciela O'Cariz of the Instituto Paraguayo del Indigena. Useful comments were provided by Nicholas Blurton Jones, Kevin Jones, Eric Smith, Dave Stephens, William McGrew and two anonymous reviewers.

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