

ON PREDICTING HUMAN DIETS

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ABSTRACT.—Optimal Foraging Theory (OFT) has helped animal ecologists understand the dietary preferences of animals. This paper addresses the question "Can OFT shed light on the food choices of humans?" In its simplest form, OFT predicts the diet which maximizes net energy gain to the forager. In the harshest of human environments, humans may be forced to maximize their energy intake; however, in most environments, humans are probably more concerned about a nutritionally balanced diet than about an energy-rich one, OFT theory can predict nutrient-constrained diets but the theory becomes more complicated and the required information on the nutrient contents of wild foods is usually lacking. Nonetheless, some evidence does suggest that humans often choose food so as to meet their nutrient requirements.

The area of OFT known as Central Place Foraging Theory may be directly applicable to stationary, hunter-gatherer societies. The theory predicts that people should be food generalist when hunting and gathering near home but should become progressively more specialized in foods they choose to bring home when they forage farther and farther afield. The evidence for and against this prediction is discussed.

Finally, the evolutionary mechanisms which might result in optimal human foraging behavior are discussed in some detail.

INTRODUCTION

In recent years, animal ecologists have become increasingly interested in the criteria which animals use to select their diets. Many ecologists believe that animals do not select food at random, but rather select food according to criteria that have evolved by natural selection (Pyke et al. 1977; Schoener 1971). More precisely, ecologists argue that the neural and sensorimotor mechanisms which, in large part, determine food choices, have evolved by natural selection to maximize Darwinian fitness. This viewpoint has led to a body of ideas known collectively as Optimal Foraging Theory. The purpose of this paper is to ask whether or not this theory might be useful to human ecologists studying human diets.

The usefulness of Optimal Foraging Theory to animal ecologists has largely been that it has allowed them to organize their thoughts and to ask new questions. Ecologists have long argued that food selection is, in some ill-defined way, adaptive. Optimal Foraging Theory has focused the adaptation picture by forcing investigators to state precisely what they mean by adaptive behavior. The result is that, for the first time, ecologists are formulating testable hypotheses about food selection. These hypotheses are being tested in laboratory and field experiments. As some hypotheses are accepted and others rejected, ecologists are coming closer to an understanding of the actual criteria of food selection.

In this paper, I address 2 questions. First, I ask "How might human food habits become adapted to local conditions?" This is fundamentally a question of evolutionary mechanisms and inevitably leads to the nature-nurture problem. Second, I ask "What patterns of human food selection are predicted by Optimal Foraging Theory?" As an animal ecologist with very little training in anthropology, I can only point out what the predictions are; fortunately, a number of qualified anthropologists are now attempting to test them (e.g., see Winterhalder 1977).

DISCUSSION

Mechanisms of Evolution

Even in the case of non-human behavior, ecologists have usually avoided the difficult questions of mechanisms. Ecologists have argued that adaptive foraging behavior results from natural selection working on heritable variation, but they have avoided the questions

of how, in learning animals, behaviors are transmitted from generation to generation.

Pyke et al. (1977) state, without further elaboration, that "the selection that has so far been considered, either implicitly or explicitly, is Darwinian natural selection coupled with genetic inheritance, but the evolution could also be cultural and yet governed by selection." In the present paper, I consider 3 possible mechanisms of evolutionary change. These are:

- 1) Genetical evolution of learning mechanisms,
- 2) Cultural retention of individually adaptive behavior, and
- 3) Cognitive evaluation and retention of beneficial customs.

The first 2 mechanisms are variations on the old theme of natural selection. The third requires no differential fitness yet produces adaptive behavior. I shall present my personal view of the relative importance of each of these mechanisms to the evolution of human diets.

Genetical selection is the change in gene frequencies accompanying the differential survival and reproduction of individuals. A coherent viewpoint of the genetical evolution of behavior has been developed by ethologists and, more recently, by sociobiologists (see Wilson 1975 and Tinbergen 1951). This viewpoint, in my opinion, reveals little about the behavior of learning organisms, particularly humans. A basic tenet of sociobiology has been that genes may cause animals to behave in certain ways which propagate those genes in future generations. Human genes do not *cause* humans to behave; however, genes do influence how humans learn. No doubt, some ways of learning are more adaptive than others. The real problem is to specify *how genes influence learning* (see Pulliam and Dunford 1980).

The likelihood that an animal repeats a particular behavior depends, in part, on the reinforcement it experiences. The sensory and neural mechanisms of reinforcement may have evolved by genetical selection in 2 ways (Pulliam and Dunford 1980). First, genes specify certain *primary reinforcers* which guide early learning. Second, genes specify certain *learning programs* which control how experience with reinforcers is integrated.

For example, the taste of mother's milk is a *positive* primary reinforcer. That is, the genes specify certain connections between the sensory elements which detect this taste and the central nervous system mechanisms which evaluate experiences as positive. A child learns that certain behaviors increase its likelihood of access to this reinforcer, and that the other behaviors decrease this likelihood. Furthermore, the child's learning program specifies that stimuli consistently associated with the primary reinforcers shall become *secondary reinforcers*. Thus, the visual image of the child's mother become a secondary reinforcer by association with mother's milk. Once this association is perceived, the child will work for the *reward* of access to secondary reinforcers just as it will work for access to primary reinforcers.

The relevance of primary reinforcers to food selection is that primary reinforcers guide the learning of food habits. Certain tastes, such as from low concentrations of salt and intermediate concentrations of sugar, positively reinforce the eating of certain foods. Similarly, the taste of toxic compounds negatively reinforces eating other foods. Circumstantial evidence for the importance of primary reinforcers as adaptive guides to food selection comes from a variety of studies. For example, C.M. Davis (1928, 1939) found that human infants grew normally and maintained good health on a diet they selected for themselves. More carefully controlled experiments with naive rats have shown similar results. (For a review, see Nachman and Cole 1971).

If the mechanisms of reinforcement have evolved by natural selection to produce adaptive learning, then the reinforcing properties of food should change as the nutritive needs of the individuals change. The best evidence in favor of this view of the development of food habits comes from studies of *specific hunger* in laboratory animals. Numerous animal studies support the idea that animals with a particular nutritional need "learn to develop a preference or aversion to a particular food as a result of the beneficial or toxic consequences" (Nachman and Cole 1971: 340). For example, rats given a diet deficient in thiamine develop a preference for any food containing thiamine. Similarly, after several days of salt

deprivation, sheep accept previously rejected, salt-rich foods.

The evidence for the role of specific hungers in humans is circumstantial. For example, a 3.5 year old boy with a severe adrenal deficiency maintained himself by eating salt by the handful (Nachman and Cole 1971). The child died shortly after his salt intake was restricted by physicians who thought that such high salt intake could not be good for the child. The specific cravings of pregnant women have also been interpreted as specific hungers for required nutrients. All in all, very little is known about the role of specific hungers in human food selection.

Although taste and specific hungers are surely important to human food selection, their importance is probably far outweighed by social learning. Parents not only can control what foods their children have available to eat, but they also use many forms of persuasion to influence their children's eating habits. Parents mold the food habits of their children by the selective presentation of reinforcers. This process of strong parental influence leads to a second mechanism of evolutionary change: selective retention of adaptive behavior.

Darwin recognized the importance of social learning to human behavior when he wrote that facial expressions "serve as the first means of communication between mother and her infant; she smiles approval and this encourages her child on the right path, or frowns disapproval" (Darwin 1896: 364). Darwin's viewpoint is echoed by the modern theory of social exchange. According to George Homans, an eminent sociologist, human values are "learned by being linked with an action that is successful in obtaining a more primordial value" (Homans 1974: 27). Homans (Ibid:27) goes on to say:

Suppose a mother often hugs her child and getting hugged is probably an innate value - in circumstances in which the child has behaved differently from other children, and, as the mother says, 'better.' The 'behaving better' than others is a means to a rewarding end and is apt to become, as we say, 'rewarding' in itself. By such a processes of linking, men may learn and maintain long chains of behavior leading to some ultimate reward.

The important point that I wish to draw from Homans is that parents can control what their children learn by manipulating their social experience. Some of the 'values' acquired by social learning are what I call 'ideas' about behavior. An idea about behavior is what a person *perceives* as the relationship between behavior and access to rewards. Children learn ideas about behavior during the socialization process because adults, particularly their parents, control their access to positive and negative reinforcers.

What does social learning have to do with the *evolution* of behavior? Parents tend to teach their children the same ideas that they once learned from their own parents. Thus, acquired ideas may be passed from generation to generation. Since ideas are perceptions about the relationships between behavior and rewards, ideas *motivate* behaviors (Pulliam and Dunford 1980). Some behaviors affect individual fitness, i.e., they affect an individual's chances to survive and reproduce. Ideas that motivate behaviors which affect individual fitness also affect the likelihood that those same ideas will be acquired by the next generation.

As previously stated, a basic tenet of sociobiology has been that genes can cause people to behave in ways that increase or decrease the likelihood that those genes are replicated in future generations (Dawkins 1976). I argue that ideas can motivate people to behave in ways that affect the likelihood that those ideas are replicated in subsequent generations. Furthermore, I argue that such cultural selection of ideas has been far more important to the evolution of human behavior during the past million years than has genetic selection.

Humans have many ideas about what to eat and what not to eat. Decisions to avoid eating certain mushrooms or to eat beans with rice, or to eat insects when mammals are scarce are all decisions which potentially affect survivorship and reproduction. The ideas which motivate these behavioral decisions are perceptions of the relationship between feeding behavior and individual (or group) welfare. Some ideas about food selection have no doubt been "weeded out" of human cultures because they motivated maladaptive behavior. Other ideas have been selectively retained, i.e., replicated in subsequent generations, because they motivated adaptive behavior (see Durham 1976 and Ruyle 1973).

Interestingly enough, even though ideas which evolve by selective retention are perceptions of relationships between behavior and welfare, they may be *misconceptions* and yet lead to adaptive behavior. For example, an herb may have been added to the pot to appease the gods. The idea to do this may have been retained from generation to generation because the herb contained a rare vitamin which increased infant survivorship. Parents who defied the gods were unlikely to have children who survived long enough to learn their parents' non-orthodox beliefs. The point is that cultural retention of an adaptive behavior may be based on misconceptions about physical reality.

In the above example, selective retention was the result of selective deaths of the children of parents who had maladaptive ideas. Cultural evolution need not be such a blind process. If people correctly perceive the relationships between their behavior and their own welfare, adaptive behavior may evolve without any selective deaths. This is what I refer to as the cognitive evaluation and retention of beneficial customs.

Cognitive evaluation and retention of new ideas (i.e., of the relationships between new behaviors and welfare) depends on both individual perception of the welfare of others who have already evaluated the new ideas *and* individual perception of the consistency of new ideas with those already personally evaluated. The way in which these 2 factors influence food habits can be better understood by briefly considering the sociological theory of cognitive balance.

How does an individual decide to accept or reject a new kind of food? The evaluation of the new food can be analyzed using the P - O - X cycle of balance theory (Davis, C.M. 1939 and Heider 1958). *P* is the person making the evaluation and *X* is the new food being evaluated (more precisely, *X* is the idea that eating the new food is beneficial). *O* is a significant other used in making the evaluation. In this case, *O* is another person, institution or idea. The evaluation of the new food (*X*) depends on the person's previous evaluation of *O* and the person's perception of the relationship between *O* and *X*. For example, if a person's respected friend accepts a new food, then the person *P* is more likely to try it too. On the other hand, if a new food is sanctioned by the church *O*, then the person will try it if the person evaluates the church positively, and may reject it otherwise.

The purpose of bringing up a cognitive balance theory is that I think it sheds some new light on the question of when human behavior will be adaptive. I have argued that humans have genetically-inherited learning mechanisms which also play a role in the evaluation of new foods. If cognitive balance leads a person to try a new food, the food may be reevaluated according to its taste. A person will only accept a new food that "tastes bad" if the person's evaluation of the significant other (e.g., church or friend) outweighs the negative reinforcement of the taste. For example, the behavior of eating a noxious-tasting medicine when ill, because the doctor recommends it, will only persist if evaluations of doctors are very positive. Furthermore, the positive evaluation of "doing what the doctor says is best" will be culturally retained from generation to generation only if the idea leads, on average, to an increase in individual fitness, or, at least, to a perception of increased welfare.

I am proposing that the initial evaluation of new ideas depends on their own consistency with older, more established ideas, but that new ideas must also eventually pass the tests of individual reinforcement and cultural retention. Primary reinforcers are genetically-inherited guides to behavior that slow down the acceptance of potentially dangerous new ideas even if the new ideas are consistent with established ideas. Furthermore, ideas, even once totally accepted, may be selectively removed from societies if they motivate maladaptive behaviors. This is because individuals who have learned maladaptive ideas are less likely to pass their ideas on to children of the next generation. As a result, many more or less neutral ideas may be retained from generation to generation but those which truly lower the Darwinian fitness of the idea bearers will be gradually "weeded out" (Durham 1976).

The selective sieve of cultural retention can only be expected to operate efficiently over long periods of cultural and environmental stability, yet if a society's values become adapted to local conditions, cognitive evaluation of new ideas will be more and more likely to result

in the rejection of those that motivate maladaptive behavior. A society whose ideology is well adapted can quickly adapt to minor changes in conditions. Nonetheless, if conditions change too rapidly, maladaptive ideas and behaviors are bound to accumulate. Furthermore, maladaptation breeds more maladaptation because previously accepted ideas are the basis of selecting yet other ideas. For these reasons, adaptive foraging behavior is only to be expected in stable cultures of people that have inhabited the same region for many generations. Optimal Foraging Theory may help human ecologists predict what foraging behavior is adaptive in a particular environment. The question of how well behavior is adapted to an environment can then be resolved empirically.

Optimal Foraging Theory

Optimal Foraging Theory consists of a set of reasonable propositions which can be made precise and which are, therefore, testable. For example, it seems reasonable that energy-stressed animals might make foraging decisions so as to maximize their net rate of energy intake while foraging. An optimization model turns this general supposition into a set of precise predictions which can be rejected or confirmed by comparison to real data.

Energy maximization does *not* mean that animals eat as much as they can, whenever they can. As applied to humans, the theory states that when energy-stressed,

1) people choose food so as to harvest as much energy as possible during the time they devote to hunting or gathering, or

2) people hunt and gather in such a manner as to minimize the time required to meet their energetic requirements.

Of course, minimizing foraging time also maximizes the time available for other activities (Smith 1979).

The theory makes both quantitative and qualitative predictions. I expect that, in general, the quantitative predictions will only be verified for human societies during periods of extreme food shortage. Nonetheless, the qualitative predictions of Optimal Foraging Theory are likely to predict trends in the foraging behavior of all hunters and gatherers.

No doubt, during some periods food is abundant and people are not so much energy-limited as they are nutrient-limited. During such periods, models of protein maximization or energy maximization with nutrient constraints (Pulliam 1975) might be more appropriate. Of course, the theory is only as good as its assumptions, and the assumptions for any particular study must be based on detailed field studies. Actually, most of the qualitative predictions are the same for energy maximization models and nutrient maximization models. It is these robust, qualitative predictions that are most likely to predict trends in human foraging behavior.

In the case of energy-maximization, the *value* to a forager of a particular prey item is defined as the ratio of its energy content to its handling time. Handling time is the average total time required to pursue and capture a food item after it has been encountered. In the case of human foragers, handling time would consist mostly of stalking and capturing time for a hunter, and digging and picking time for a gatherer.

A forager that maximizes net rate of energy intake, pursues prey with the highest value every time they are encountered. The decisions to pursue or ignore prey of lower value depend only on how frequently the higher-value prey are encountered. One of the most robust predictions of the theory is that when high-value prey are rare, the diet expands to include more low-value prey, and, conversely, when high-value prey are common the diet contracts.

A number of animal studies have tested qualitative and quantitative predictions of Optimal Foraging Theory. For example, Werner and Hall (1974) offered bluegill sunfish a choice of prey of 3 different sizes. They manipulated the abundance of the highest-value prey available in the aquarium and predicted when the fish should eat and when they should ignore the 2 kinds of lower-value prey. They found that not only did the fish diets expand

when the highest-value prey were rare, but also that the fish began to eat the lower-value prey at the abundance of highest-value prey that was predicted by the theory.

Krebs et al. (1974) presented Great Tits with a choice between large and small mealworms. They varied the prey abundance by putting the mealworms on a conveyor belt which passed prey by the birds at different speeds. They found, as predicted, that the decision to eat or ignore the small mealworms was independent of the abundance of small prey and dependent *only* on the abundance of large prey. As expected, when mealworms were common, the tits ate only large ones, but when mealworms were rare, they ate both large and small ones. However, the theory predicted a specific abundance of large prey at which the tits should quite suddenly change their behavior and eat every mealworm presented. Instead, Krebs et al. (1974) found that the small prey were only gradually added to the diet. The results of this experiment support the qualitative predictions of the theory but not the quantitative predictions.

A few investigators have tried to test Optimal Foraging Theory under more or less natural conditions in the field. For example, Goss-Custard (1977) studied Redshanks foraging on invertebrates on a natural beach. He found that whether or not these birds accepted small prey depended only on the abundance of large prey and not on the abundance of the small prey themselves.

In a study of Chipping Sparrows in a natural oak woodland (Pulliam 1980), I found that these sparrows preferred seeds of high energy value and expanded their diets when high-energy prey were less abundant. However, I also found that the prey were not eaten in the same frequencies as predicted by theory. So again, the qualitative but not the quantitative predictions of the theory were supported.

How close animals come to matching the quantitative predictions of the theory seems to depend on how energy-stressed they are. This is shown dramatically by the experiments of Caraco et al. (1980) on *risk aversion* by Yellow-eyed Juncos. The theory of risk aversion is an extension of classical optimization problems to the situation where an animal must choose between food of high-value and high-risk and food of lower-value and lower-risk. The theory predicts that animals will be more likely to maximize energy intake even if a risk is involved when they are energetically stressed.

Caraco and his coworkers gave Yellow-eyed Juncos a choice of walking down one side of a Y-maze to receive 3 seeds or walking down the other side to receive 7 seeds half of the time, but no seeds the other half. The *expected* reward was then 3 seeds on the "low reward low value" side and 3.5 seeds on the "high reward, high risk" side. As predicted, the birds adopted high-risk strategies when energetically stressed and low-risk strategies when *not* energetically stressed. I expect this is a very robust prediction which will apply to many animals including humans.

A final robust prediction which may also apply to human food choices comes from what is known to ecologists as Central Place Foraging Theory. Many foragers start from a central place such as a nest, a den, or a village to which they return with food. The theory predicts how prey choices will vary as a function of prey abundance and how far the foragers will go from the central place.

Optimization models of central place foraging predict that as prey abundance declines and foragers go farther from the central place, they will be more selective about the prey they choose to bring back. This is because once the forager has travelled far from a central place, any extra time required to select a better prey may be small compared to transit time to and from the central place. This prediction holds regardless of whether the foragers are energy-maximizers or nutrient-maximizers.

CONCLUSION

During much of the history of mankind, people have survived by hunting and gathering. During periods of food shortage, individual survivorship has, no doubt, often depended critically on individual decisions about which foods to hunt and gather. These decisions

have been made, in part, by reference to traditional knowledge about hunting and gathering techniques, favored hunting grounds, alternative foods, etc.

Traditional knowledge about hunting and gathering consists of culturally-inherited ideas about the relationship between foraging behavior and individual welfare. If ideas leading to adaptive behavior have been more likely to be culturally retained as part of traditional knowledge, then general trends of foraging behavior should be predictable by Optimal Foraging Theory.

Among the more robust qualitative predictions of Optimal Foraging Theory as applied to stationary human hunters and gatherers who have inhabited the same region for many generations are the following:

- 1) Human foragers should become more selective in their prey choices as the abundance of preferred prey increases;
- 2) Decisions to specialize or generalize the diet should be independent of the abundance of less preferred prey;
- 3) During times of food shortage, prey preferences should roughly be ordered according to the ratios of energy content to handling time;
- 4) Human foragers should be more willing to take risks for high energy gains during periods of food shortage;
- 5) People should be food generalists when hunting and gathering near home (a central place) and become progressively more selective about foods they choose to bring home when they forage farther afield.

Probably, human foragers never exactly maximize their rate of energy gain while foraging. Nonetheless, their behavior is probably much closer to this ideal than it is to random foraging. Optimal Foraging Theory should be a useful yardstick for measuring how well the behavior of hunters and gatherers is adapted to their energetic requirements. If the qualitative predictions listed above are supported, the quantitative predictions should also be tested.

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