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Foraging Theory and Hypothesis Testing in Archaeology: An Exploration of Methodological Problems and Solutions

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Archaeological tests of hypotheses drawn from foraging theory face a unique set of challenges. Simple foraging models, such as the diet breadth model, rely on assumptions that are clearly violated in the human case. Testing is complicated by the indirect nature of the observations used to reconstruct environment and behavior and by the cumulative nature of the archaeological record. However, the negative impact of these issues on understanding can be ameliorated by adding and valuing research strategies that go beyond those those designed to test hypotheses derived from the model against archaeological evidence. One such strategy is to probe the model's failures by manipulating constraints and variables. The model's performance under varying environmental conditions constitutes a partial test of alternative explanations of behavior. The value of such an approach is illustrated by a case study involving plant use by early food producers who lived in the rugged hill country of eastern Kentucky during the early 3rd millennium B.P. Archaeobotanical data suggest changes in the dietary contributions of different mast-producing tree species during the transition to food production. Possible explanations for these changes were evaluated using linear programming. Running the model under varying conditions of resource availability showed that the broad-based mast diet inferred from nutshell assemblages was probably not energetically optimal. Although chestnut is profitable to exploit when hickory is limited, acorns are too costly to use under most environmental conditions unless efficent processing techniques are used. The substitution of starchy seeds for nuts with similar nutritional characteristics would have been inefficient, although seed crops are potentially important sources of macronutrients and energy when mast supplies are depleted. These findings point out vulnerabilities in economic efficiency-based explanations for the origins of agriculture in eastern North America.

The theory of evolution by means of natural selection is the most powerful tool available for explaining diversity in the organic world. Because humans are part of this world, evolutionary processes are essential to any complete explanation of human behavior (Winterhalder and Smith 1992:4). Behavioral ecology has inspired many who study subsistence change because of its emphasis on adaptation in ecological context and its employment of simple models as heuristic tools for understanding relationships between environmental variables and behavioral evolution (Bettinger 1987; Gremillion 1996; Kelly 1995; O'Connell and Hawkes 1994; Piperno and Pearsall 1998; Winterhalder and Goland 1997). This approach has been particularly appealing to prehistoric archaeologists, who are often called upon to explain historical patterns of land and resource use. The application of aspects of neo-Darwinian evolutionary theory to archaeological problems has met with varying success as researchers attempt to strike a balance between preserving the essential theoretical strengths of the approach while at the same time tailoring methods, assumptions, and standards of verification to the archaeological record (Barlow and Metcalfe 1996; Broughton and O'Connell 1999; Gardner 1992; Grayson and Cannon 1999; Grayson and Delpech 1998; Keene 1981; Metcalfe and Barlow 1992; Reidhead 1976; Reidhead 1980; Rhode 1990).

The potential of such an approach for the explanation of long-term subsistence

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change seems clear enough viewed in general terms. However, putting this approach into practice is another matter, as many researchers have discovered while wrestling with particulars. My goal in this article is to identify some of the problems confronted in the process of applying foraging models to archaeological problems. I am especially interested in the issue of testing, which is the crucial point at which general theory is brought to bear on real-world observations—the empirical link in the cyclical chain of scientific method. Testing of hypotheses derived from foraging models against archaeological data faces a unique set of problems. First I review these problems and approaches to solving them. I then illustrate how such a strategy might work by using an example from my research on changing use of plant foods among early forager-farmers of eastern North America.

FORAGING THEORY AND HYPOTHESIS TESTING IN ARCHAEOLOGY

Problems

Foraging models predict optimal behavior in specific environmental contexts, subject to certain constraints and assumptions. The use of such models to better understand adaptive aspects of subsistence behavior holds many advantages: it forces explicit recognition of assumptions; simplifies complex problems; clarifies relationships between causal variables and between behavior and fitness; and provides a rigorous methodology for explaining subsistence change as an evolutionary process (Bettinger 1991; Krebs and McCleery 1984; Levins 1966; Maynard Smith 1978; O'Connell and Hawkes 1994; Pyke et al. 1977; Smith 1983; Smith and Winterhalder 1992; Winterhalder and Smith 1992). Foraging models posit relationships between key variables (such as resource density and diet breadth) given a goal of optimization (usually defined in economic terms) that is assumed to be correlated with fitness (conceived broadly to encompass cultural as well as genetic modes of inheritance).

Foraging models advance knowledge primarily through the generation and testing of hypotheses. In archaeology, the models are most often assumed to accurately capture essential relationships between key variables. They are enlisted to help explain patterning in the archaeological record that indicates behavioral change (Grayson and Delpech 1998). This is done by formulating hypotheses that predict how the general relationships outlined by the model will be played out in a particular real-world situation and then comparing these predictions with empirical observations (Lloyd 1987). It is possible to learn much from the failure of models (Seger and Stubblefield 1996), but in order to best take advantage of the modeling approach it is important to understand accurately the reasons for the mismatch between modeled predictions and reality (Kitcher 1985:242; Loehle 1987). Success at this stage of the research process is essential for guiding model refinement in the direction of improved understanding of how the world actually works, whereas "without certainty as to the source of errors, parameter adjustment by any algorithm can yield arbitrary results" (Loehle 1987:298).

This is where archaeology presents unique challenges for the use of foraging models. It is important to be able to identify the specific sources of error that cause the model to fail, whether these arise from inappropriate content, flawed methods of empirical evaluation or incorrect inference (Loehle 1987). In archaeology, achieving this goal is unusually problematic because of the indirect nature of the observations used to reconstruct both environment and behavior. Observational error is always possible; but compare the situation of the archaeologist to that of the biologist studying the foraging behavior of cave crickets

(Helf and Poulson 1996). These crickets actually have transparent exoskeletons, so that one can observe the stratified contents of the gut, revealing not only what was eaten but the temporal sequence of consumption. The clear crickets metaphorically highlight the comparative murkiness of the archaeological and paleoenvironmental records. The biologist knows exactly what the cricket ate and when and what was available to it in its circumscribed world; it is a *relatively* simple matter to determine whether the model went wrong. But with archaeology, when the predicted results fail to materialize, it might be the model (due to either general inapplicability or inaccurate input) or it might not. Perhaps incorrect environmental data have produced spurious predictions or maybe the behavioral response has been inaccurately reconstructed. The correct answer is difficult, sometimes impossible, to identify.

Solutions and Remedies

Solutions to problems of optimal resource use depend on the estimation of environmental and behavioral phenomena that must be reconstructed because they cannot be directly observed. If these reconstructions are initially inaccurate, the model's performance should improve as we refine methods of data analysis and interpretation. There are preservation biases to consider which can be addressed through skillful manipulation of data so as to reduce this kind of noise (Grayson and Delpech 1998). Field processing can significantly affect the composition of refuse assemblages that accumulate at a central place (Bettinger and Malhi 1997; Bird 1997; Jones and Madsen 1989). It is essential to filter out or at least take into consideration the effects of such factors as differential preservation and fragmentation and the relationship between inedible remains and food actually consumed. Although these issues are not unique to applications of foraging theory (see for example more general discussions in Grayson 1984; Hastorf 1988; and Pearsall 1989), they are tightly focused by its concern with specific decisions about food choice. Foraging theory also places special demands on the analysis of long-term change in subsistence patterns. Foraging models are designed to address individual decisions, but archaeological deposits represent the accumulated traces of many such individual decisions (Grayson and Delpech 1998).

We need not restrict ourselves to developing more accurate tests using archaeological data. A model's performance may be difficult to assess because it exceeds the degree of resolution offered by the data. We might address this problem by scaling back the level of precision at which we expect the model to produce accurate predictions. Even where a model fails to predict all relevant details of a phenomenon, it may adequately capture its more general features (Maynard Smith 1978). For example, although the optimal resource sets generated by the diet breadth model in a given case are unlikely to match the archaeological record of behavior in all particulars, if the model is able consistently to predict the *direction* of change (say an increase in diet breadth), it has identified a relationship likely to provide fertile ground for hypothesis testing.

Probing the model systematically is also likely to yield insights into its performance. This type of analysis allows us to identify situations in which the chosen model is simply inappropriate for the case at hand and to discover alternatives or modifications that might have more explanatory power (Krebs and Kacelnik 1991; Seger and Stubblefield 1996). We might, for example, increase the precision of predictions to gain a better understanding of how the model performs under different environmental conditions (Caswell 1988; Krebs and McCleery 1984). The clarification of relationships between variables narrows the field of plausible explanations for the model's failure to predict behavior.

I, and others, have discussed elsewhere the reconstruction of subsistence behavior from archaeological data for comparison with foraging models (Grayson and Cannon 1999; Grayson and Delpech 1998; Gremillion 1998) and the development of general predictions using simple heuristic tools (Gremillion 1996). However, in this article I emphasize the third strategy, that of evaluating alternative explanations for behavior by manipulating the models directly.

Application: Harvesting of Mast Resources at the Cold Oak Shelter

This example is drawn from investigations into plant use by early food producers who lived in the rugged hill country of eastern Kentucky during the early 3rd millennium B.P. Several sites from rockshelters in the area have produced evidence of cultivation and domestication of native plants [including *Cucurbita* gourds, sunflower (*Helianthus annuus*), sumpweed (*Iva annua*), and goosefoot (*Chenopodium berlandieri*)] as early as 3500 B.P. (Cowan 1985a; Cowan 1985b; Cowan et al. 1981; Gremillion 1993; Gremillion and Sobolik 1996). Two sites, Cloudsplitter and Cold Oak, present strong evidence for a shift at about 3000 B.P. to more intensive use of cultivated plants, some of which were stored. The record of mast exploitation (as reflected in the remains of hickory nuts, *Carya* spp.; acorns, *Quercus* spp.; chestnuts, *Castanea dentata*; and walnuts, *Juglans nigra*) is more variable between rockshelters in eastern Kentucky and it is difficult to compare these data sets adequately because of differences in analysis, reporting, and preservation conditions. However, at Cold Oak there appears to be a change in the deposition of different types of nutshell after 3000 B.P. Acorn shows a significant decline as percentage of total nut remains, and hickory a corresponding increase. The drop in acorn is relative not only to other types of mast but also to the total quantity of plant remains deposited. Chestnut shows a moderate decline, and walnut appears not to have been important at any time during the occupation of the site (Gremillion 1998). I assume that deposition of processing refuse reflects the frequency of decisions to harvest the resource as well as the quantities that are harvested once that decision has been made (Kelly 1995:87; Winterhalder and Goland 1997). Paralleling these changes in mast use is an increase in quantities of starchy seed crops such as maygrass (*Phalaris caroliniana*), goosefoot, and knotweed (*Polygonum erectum*).

The regional pollen record provides support for the acceleration of anthropogenic disturbance of vegetation that has been inferred from macrobotanical remains. Sharp increases in the pollen of *Ambrosia* and other disturbance-loving herbs after ca. 3000 B.P. have been recorded in cores from Cliff Palace Pond, located approximately 20 km to the southeast of Cold Oak on the western margin of the Cumberland Plateau (Delcourt et al. 1998; Delcourt and Delcourt 1997). Environmental conditions after 3000 B.P. increasingly favored favored fire-tolerant species (including oaks and chestnut) at the expense of fire-intolerant ones. Increases in charcoal deposition also indicate the growing ecological influence of human management of the environment as plant cultivation became more frequent and widespread.

METHODS FOR GENERATING OPTIMAL DIETS

The assumption that lies at the heart of all optimal foraging analyses is that natural selection plays a key role in shaping food acquisition behavior in humans as well as other animal species (Pyke et al. 1977; Smith and Winterhalder 1992). It does so by shaping the genetic basis of phenotypic response, which in humans is highly plastic and contingent on individual and social learning (Flinn 1997). Learned behavior can also be transmitted in Lamarckian fashion in a system that some researchers argue is one of cultural inheritance (Boyd and Richerson 1985; Durham 1991). Whatever the mode of transmission, selective sorting of options results in the differential persistence of behavioral variants that improve the organism's adjustment to its environment.

Because energy capture plays a critical role in survival, development, and reproduction, it makes sense to look to evolutionary processes to explain subsistence patterns. However, the relationship between subsistence behavior and factors such as abundance, distribution, and yield is not intuitively obvious, partly due to the existence of many dimensions of environmental variability and the complexity of human decision making. However, this situation can be better understood by focusing on a single fitness-related variable that can be estimated for different behavioral options. In many foraging models, the variable (or currency) chosen to play this role is energetic efficiency, following the logic that efficiency can be translated into fitness benefits either by increasing energy acquisition or making more time available for other fitness-enhancing activities (Smith 1979). The validity of this approach is also supported by evidence for the effects of cost–benefit relationships on human foraging patterns (Borgerhoff Mulder 1993).

The Diet Breadth Model

The diet breadth model (hereafter the DBM) has been widely used to explore the energetic (and therefore evolutionary) implications of food choice (Bettinger 1991; Kaplan and Hill 1992; Stephens and Krebs 1986). The DBM employs a simplified version of the real-world situation to predict which combination of food items maximizes overall energetic efficiency in a given environmental setting. The core of the model is the trade-off between the costs of searching for prey (which decline along with selectivity) and the costs of pursuing prey (which simultaneously increase because time is being spent on resources that offer comparatively low yields) (MacArthur and Pianka 1966:604). An important implication of the DBM is that an increase in the abundance of the most profitable resources favors a narrow diet, whereas a decrease in the same variable favors expansion of the diet to include a wider range of foods (simply put, abundance encourages specialization) (Pyke et al. 1977:141). Related models of patch choice are driven by the trade-off between search costs within a patch and travel between patches (Charnov 1976; MacArthur and Pianka 1966; Wiens 1976) or between transportation costs and pursuit costs (Orians and Pearson 1979).

There are many justifications for using the diet breadth model as a framework for understanding variation between archaeological assemblages of plant, and especially animal, remains (Grayson and Delpech 1998; O'Connell et al. 1988). First, the DBM has been shown to have predictive power in ethnographic cases (Hawkes et al. 1982; Hill et al. 1987; O'Connell and Hawkes 1981). Second, this model is robust enough to withstand violations of its assumptions and still come up with successful predictions (Sih and Christensen 2001). Third, it is a general model that has broad applicability to many types of foraging situations.

However, there is reason to believe that the DBM is not the best tool for gaining insight into the subsistence record of the Cold Oak shelter. Its application in this case places considerable strain on the robusticity of the model by violating two key assumptions, those of random search and fine-grained distribution of prey (MacArthur and Pianka 1966). These assumptions are critical because without them search costs do not predictably increase as prey density declines. Second, previous analyses (Gremillion 1998) have shown that hickory has by far the highest return rate of locally available mast and according to the diet breadth model should be exploited exclusively unless in very short supply. A shortage of hickory is, however, only one possible explanation for the varied mast diet represented at the Cold Oak shelter. Several alternatives have been suggested, for example, the influence of nutrient composition on food choice and the effects of technological innovation on handling costs. To test these hypotheses, it is necessary to look beyond the DBM.

The Advantages of Linear Programming

The technique of linear programming is an alternative approach to modeling optimality that permits the various explanatory hypotheses described above to be more closely evaluated. Linear programming is a mathematical method for manipulating multiple variables in order to satisfy a goal subject to certain constraints. It has been used often in microeconomic research to search for optimal solutions to complex problems of resource allocation. Linear programming has also proved useful as a tool for solving ecological optimization problems. In archaeology, the method enjoyed a brief period of popularity as an application of optimal foraging theory to prehistoric diets (Gardner 1992; Keene 1981; Reidhead 1976, 1980). These studies introduced elements (such as nutritional constraints) that better reflected the likely decision criteria used by human foragers than did the simple efficiency maximization currency used by the DBM. Another great strength of the linear programming method is ability to manipulate many variables in order to better understand how they influence each other. However, linear programming has its own drawbacks, including the assumption of linearity and the omission of search costs from return rates. In addition, the effort involved in constructing a linear programming model represents major investment of energy in an outcome that may have fairly limited applicability (say, to a particular site or environment). Partly as a consequence of these costs, optimal foraging approaches in archaeology have moved away from linear programming, instead favoring application of relatively simple models such as the DBM or central place foraging.

Although this trend is in many ways well founded, I propose that linear programming has a useful, if more limited, role to play in the analysis of prehistoric subsistence behavior. I suggest that, rather than forming the basis for an analysis of the diet as a whole (including plant and animal resources across all seasons)(Gardner 1992; Keene 1981; Reidhead 1976), researchers can employ it on a smaller scale to test the feasability of alternative hypotheses. For this task, linear programming is a more suitable tool than the DBM. First, by predicting the relative contribution of different resources to the optimal diet (not just their number and ranking), linear programming results take advantage of the availability of quantified archaeobotanical data. Second, linear programming allows us to manipulate variables in sequence to test their potential effects on the structure of optimal diets. For example, we can use linear programming to introduce nutritional constraints that might explain the drop in acorn consumption in favor of starchy crops.

PUTTING THE MODEL TO WORK

Estimation of Resource Characteristics

In the present case, I assume that optimal behavior will take the form of acquiring a certain amount of energy (measured in kilocalories) while minimizing costs (measured in units of time spent). This assumption lays the groundwork for running the linear programming model, which requires estimation of resource characteristics (in this case, mast and crops) and the costs entailed by exploiting them. In addition, it is also necessary to determine a set of fairly realistic constraints that can be placed on the solution in order to see how resource use will change under different conditions. Such constraints include the available quantities of each resource, the energy and nutrient needs of a hypothetical prehistoric population, and the amount of time available for the food quest.

Thanks to previous archaeological and archaeobotanical work in the Red River Gorge, vegetation surveys have been conducted in the area with particular emphasis on economic plants. Survey plots for this study are located about 20 km to the north of the Cold Oak shelter, but local topography and vegetation are similar. Botanical survey data collected presented in Cowan (1985a:130–146) give counts of individual stems of all four of the mast producers in a variety of habitats. These figures were used to estimate numbers of stems per hectave in four topographic settings (ridgetop, upper slopes, lower slopes, and river valley) and then multiplied by the total area represented by each setting within a 1-km radius of the site. The resulting figures were divided in half as a rough estimate of the number of trees producing in a given year, following Gardner (1992:52–62). Nut and crop yields were culled from several sources (Table 1). I make the simplifying assumption that all resources were available simultaneously, which would have been the case during at least part of the autumn harvest season.

These and other sources were consulted by Gardner (1992:52–62) and used to estimate handling costs (the time required to travel to, harvest, and process each item) (Table 2). Costs of collecting have been experimentally determined for sumpweed, chenopod, acorns, hickory nuts, and walnuts; for chestnut, I used the figures available for acorn. I assume that because the trees are not significantly clumped, that travel and transport costs consist of the time required to make a 1-km round trip to and from the shelter at the rate of 2.5 km / h (this would represent a maximum travel time for purposes of the model). I then adjusted these costs to take into account the differing amount of waste (shell) included in loads of the four nut types, assuming that no field processing took place. This assumption is a reasonable one given the tendency for field processing to be inefficient when short travel distances are involved (Metcalfe and Barlow 1992), although if violated it can result in significantly flawed estimates of subsistence importance based on relative quantities of midden refuse (Bird 1997).

I also calculated processing costs, which often have significant effects on overall return rates. Experimental data are available for acorn, walnut, and hickory using alternative methods of separating food from waste. In the case of acorn, the costs of leaching to remove bitter tannins are potentially quite high, depending on which techniques are used. Similarly, there are efficient and inefficient methods of processing hickory. Processing costs for these resources therefore represent a range of options that can be substituted within the model to see how they affect the optimal solution. Chestnut processing costs (which do not include leaching) were estimated by making a modest downward adjustment in processing costs for acorn. Table 3 summarizes net return rates (average energy obtained per unit handling time) for all resources under different processing regimes.

Population Size and Caloric Needs

The model also needs a goal in the form of the nutritional needs of a hypothetical human population. I created such a population to be consistent with the space limitations of the Cold Oak shelter and to reflect a plausible age and sex composition. The

TABLE 1
Resource Characteristics

Reference no.		Hickory	Acorn	Black walnut	Chestnut	Chenopod	Sumpweed
1	No. of stems, 1-km radius (all zones)	4734	26476	1376	2210		
2	No. of productive stems	2367	13238	688	1105		
3	Yield per tree (kg whole nuts)	4.50	1.50	2.40	2.50		
4	Losses due to predation, etc. (kg whole nuts)	0.0	1.1	1.2	1.8		
5	Refuse (kg shell)	2.9	0.2	0.9	0.1		
	Yield of edible meats per stem (kg)	1.6	0.3	0.3	0.6		
	Total yield, 1-km radius (kg)	3728.3	3693.5	181.6	671.2		
6	Yield, whole fruits (kg/ha)					1300.0	1125.0
7	Adjusted yield (kg clean seed)					910.0	787.5
8	Energy (kcal/kg)	6570	3870	6070	2240	3200	5350
9	Macronutrients (g/kg)						
	Carbohydrates	183	408	121	491	459	110
	Protein	127	62	244	42	133	323
	Lipids	644	24	566	11	56	45

Reference no.	Source	Comments
1	Cowan (1985a:130–145)	
2		Assume 50% of stems productive (Gardner 1992)
3	Cowan (1985a:138)	Hickory
	Gardner (1992:59)	Acorn
	Cowan (1985a:146)	Black walnut
	Purdue (2000)	Average production figures from wild trees in Indiana
4	Talalay (1984)	Hickory
	Cowan (1985a:136)	Acorn (70% predation loss, adjusted from Cowan's 90%)
	Purdue (2000)	Walnut (estimated 50% abortion rate; reported rate = 95%)
	Cowan (1985a:136)	Chestnut (based on acorn)
5	Watt and Merrill (1975)	Hickory (based on 65% waste)
	Gardner (1992)	Acorn (based on 38% waste)
5	Watt and Merrill (1975)	Black walnut (based on 78% waste)
	Watt and Merrill (1975)	Chestnut (based on 19% waste)
6	Smith (1987)	Goosefoot
	Smith (1992a)	Sumpweed
7	Smith (1987)	Chenopod; assume seed coat is 30% of harvested weight; field 1 ha in size
	Smith (1992a)	Sumpweed; achene coat is 30% of harvested weight; field of 1 ha in size
8	USDA (2000b)	Hickory, black walnut: dried. Raw values unavailable; both are ≤ 5% water Oak acorn: raw Chestnut: Chinese chestnut (*C. mollissima*), raw
8	Asch and Asch (1978)	Goosefoot
	Asch and Asch (1978)	Sumpweed
9	USDA (2000b)	Hickory, acorn, walnut, chestnut
	Asch and Asch (1978)	Goosefoot, sumpweed

population consists of two males, ages 19–24 years; one female, 19–24 years; one male and one female, 25–50 years; one infant, .5–1 year; one child 4–6 years; one child 7–10 years; one female 51+ years; and one lactating female. I based calorie and protein re-

TABLE 2
Resource Costs

		Collecting and processing costs (hr / kg)					
Reference no.	Method	Hickory	Acorn	Black walnut	Chestnut	Chenopod	Sumpweed
	Collect and clean						
1	Crack / pick with hammerstone	40.00					
1	Crush / boil with stone	3.00					
1	Crush / boil with wooden mortar	2.00					
2	Collect and shell		1.40	10.50	1.40		
3	Soak		0.00				
4	Boil in skin or basket		6.00				
5	Boil in pot	2.00					
6	Parch			1.00	1.00		
7	Grind / pound	0.00	0.25	0.00	0.25		
8	Winnow, thresh, cook					2.00	2.00
9	Harvest					0.67	0.76
10	Transport	0.11	0.06	0.18	0.05	0.05	0.05
11	Clear, maintain					0.02	0.02
Total (by method)							
	Crack / pick with hammerstone	40.11					
	Crush / boil with stone	3.11					
	Crush / boil with wooden mortar	2.11					
	Collect and shell		1.31				
	Soak		8.71				
	Boil in skin or basket		4.71				
	Boil in pot						
	General collect / process			10.68	2.45	2.74	2.83

Reference no.	Reference	Comments
1	Talalay et al. (1984)	
2	Petruso and Wickens (1984)	Acorn; chestnut is based on acorn
3		Assumed to be virtually zero
4	Gardner (1992)	Estimate based on a container that holds 10 l (1.09 kg shelled meats), constantly supervised and reheated
5	Gardner (1992)	Estimate based on 10 l container, limited supervision
6		Estimated; assumes sequential parching of small quantities in baskets
7		Estimated; assumes that acorn and chestnut converted to flour
8		Estimated; assumes removal of chaff and brief cooking
9	Smith (1987)	Goosefoot
	Smith (1992a)	Sumpweed
10		Assumes 1 load = 18.2 kg (Gardner 1992); adjusted for amount of waste per load; assumes a 15-min walk to the garden; for nuts, assume 2-km round trip per load at 2.5 km / h (Gardner 1992)
11		Estimate; assumes cost of garden preparation spread over entire crop

quirements for this population on recommended daily allowances. These values do not represent minima required for survival, but rather “safe and adequate” intake levels for Americans as determined by nutritional scientists (National Academy of Sciences 1989). There are no established minima for lipids (except for the essential linoleic acid) or carbohydrates (although a carbohydrate-free diet may result in starvation ketosis).

TABLE 3
Net Return Rates for Mast and Crop Resources Included in the Model (in Kilocalories per Hour Handling Time)

Processing method	Hickory	Acorn	Walnut	Chestnut	Chenopod	Sumpweed
Crack / pick with hammerstone	164					
Crush / boil with stone	2112					
Crush / boil with wooden mortar	3114					
Soak		2954				
Boil in skin or basket		444				
Boil in pot		821				
General collect / process			568	914	1169	1891

Instead, requirements for these macronutrients were based on standard dietary guidelines for Americans (Anderson et al. 1999; Merrill and Shireman 1999; United States Department of Agriculture 2000a). Because only a segment of the diet is considered, I also made assumptions about what percentage of these required amounts must be provided by the mast (or mast plus crop) component of the diet. These percentages vary depending on the seasonal scenario being examined.

Basics of Linear Programming

There are several detailed discussions of linear programming that describe its rationale and assumptions in the context of archaeological problem analysis (Gardner 1992; Keene 1981; Reidhead 1976, 1980). Here I summarize aspects of the method that are directly pertinent to the present case.

Linear programming is a mathematical method that manipulates a set of variables in order to meet a predetermined goal, subject to certain constraints. To handle the mathematical manipulations, I used a commercially available program called Solver that is included with the spreadsheet program Microsoft Excel (Frontline Systems 1999). After the data are entered, the computer program is allowed to make changes in the amount of each resource to be used in order to meet the goal under the specified constraints. I ran the program under different conditions of resource availability, nutrient requirements, and food preparation technology. Each run of the model was subjected to a sensitivity analysis that determines the percentage change that would be needed in constraints and in costs in order to modify the optimal solution. This analysis is important for indicating which variables are most sensitive to uncertain data input and for isolating the effects that constraints have on the optimal solution. Each table lists the amount of each resource that would have to be collected by the hypothetical population to satisfy all constraints while minimizing total time costs; the cost of handling each resource; and the minimum percentage increase and decrease in costs and constraints that would modify the optimal solution. High values suggests robust results, whereas low values indicate that the outcome is vulnerable to errors in estimating parameters.

Model Results

Model 1: Energy only. The model was first directed to construct an optimal combination of mast types that would meet the basic energy needs of the population at the lowest possible cost. Constraints included those used in all the models: that all values in the solution be nonnegative, that quantities to be harvested not exceed available yields, and that time costs be limited to

1440 h (the time spent by 5 adults working 5 h / day for 30 days). The minimum number of calories required (for a period of 30 days during peak nut production in the autumn and assuming that mast had to provide 50% of total food energy) was set at ≥ 322,500 kcal.

The optimal solution, not surprisingly, is to harvest only hickory (Table 4). The sensitivity analysis shows that the results would be the same even with substantial reductions in the costs of the other types of nuts (of roughly 60–70%) or as much as a 131% increase in the cost of exploiting hickory. This result indicates that the highly specialized solution recommended by the model on the basis of energetic efficiency is fairly robust. To explain the varied mast diet represented at the Cold Oak shelter, then, it is necessary to consider scenarios that either (1) make a case for significant revision of return rates or (2) explore the consequences of constraining the model to account for variables other than energetic efficiency that influence subsistence decisions.

Model 2: Shortfalls of one or more mast types. The estimated return rates used in the model are likely to have poor predictive value if the actual availability of resources fluctuated widely. Such variation is not accounted for in the model, which assumes constant conditions of tree density and yield. The yield figures I have used as model input represent averages over several species and various habitats that together present a very broad range of values. Such inevitable simplification of heterogeneity within ecosystems is a major problem encountered in constructing models (Loehle 1987). Although average figures may offer a fairly good approximation of conditions at some point in time, they are very unlikely to come close to capturing the complexity of the real environment faced by prehistoric forager-farmers in their search for food.

The basic version of the model predicts that hickory, which has a very high net return rate (Table 5), will be used exclusively until it is no longer available. Costs can only be minimized by depleting each resource in rank order, much as the DBM predicts the addition of prey types as search costs for high-ranked prey increase (although the linear programming model does not make return rates directly dependent upon prey density). For example, limiting the amount of hickory results in the addition of chestnut to make up the remainder of required energy (Table 5). The insight that arises from this aspect of the model's logic is that a broad mast diet is likely when one or more resources is limited in quantity. This situation probably occurred often and somewhat

TABLE 4
Model 1 Results

Resource (kg to be used)	Final value	Resource cost (h / kg)	Allowable increase (%)	Allowable decrease(%)
Hickory	49.09	3.11	131	100
Acorn	0.00	4.71	*	61
Black walnut	0.00	10.68	*	73
Chestnut	0.00	2.45	*	57

Constraints	Final value	Constraint	Allowable increase (%)	Allowable decrease (%)
Total cost (hours) ≤	152.66	1440	*	89
Total energy (kcal) ≥	322500	322500	843	100

*No limit.

TABLE 5
Model 2 Results

Resource (kg to be used)	Final value	Resource cost (h / kg)	Allowable increase (%)	Allowable decrease(%)
Hickory	1.00	3.11	131	*
Acorn	0.00	4.71	*	10
Black walnut	0.00	10.68	*	38
Chestnut	141.04	2.45	11	57

Constraints	Final value	Constraint	Allowable increase (%)	Allowable decrease (%)
Total cost (hours) ≤	348.66	1440	*	76
Total energy (kcal) ≥	322500	322500	309	98

*No limit.

unpredictably, as yields of oaks, walnuts, and hickories are notoriously variable, both interannually and between individual trees (Gardner 1997). However, it would take a very unproductive year for hickory to fail to meet the modest needs of the model's small population (49 kg of nutmeat). This quantity could easily be provided within a 1-km radius of Cold Oak, even assuming a nutmeat yield of only 1.2 kg / ha (10% of estimated yields from the historic forest). This hypothetical yield falls well below the 5 kg / ha that is the lowest annual value from one study site in southeastern Ohio (Gardner 1997). Even under pre-3000 B.P. conditions, when chestnut and perhaps also hickories were less numerous in local forests than in recent historic times, a small population of efficiency-maximizing foragers is unlikely to have resorted to harvesting acorns.

Model 3: Processing costs. Techniques used to process a food can result in considerable variability in the return rates obtainable from it (Kelly 1995:80; Winterhalder and Goland 1997:148). For example, experiments have shown that hickory can be efficiently processed by crushing the whole nuts, shell and all, and then boiling them to separate the nutrients (which float) from refuse (the heavy shell, which sinks) (Talalay et al. 1984). A wooden mortar is somewhat more cost effective for this purpose than a stone mortar. This method of processing was and still is used by Native American groups in the Eastern Woodlands (Gardner 1997). In constrast, crushing the nuts individually and extracting the meats is prohibitively time-consuming.

For acorns, the question of processing is even more problematic because of the many possible stages involved and their widely varying costs. The tannin content of acorns generally requires some sort of leaching to render them edible or at least palatable. The costs associated with chemical processing have the potential to greatly reduce the return rates available from acorns, which otherwise would have a fairly high nutritional payoff. As a result, human groups seem to resort to intensive acorn exploitation primarily under conditions of resource depression or in the wake of innovations in food processing technology (Basgall 1987; Broughton 1994). However, leaching methods vary from the relatively time-consuming (e.g., crushing and burying or boiling the meats in repeated changes of water) to the nearly cost-free (soaking the pulverized meats in cold water) (Basgall 1987; Petruso and Wickens 1984). Furthermore, tannin content varies considerably between species of oak and some acorns may be eaten without leaching.

Models 1 and 2 assume for hickory and acorn the processing method of intermediate cost: for acorns, boiling in a pot (rather than in a basket or skin container), and for hickory, crushing and boiling with a stone mortar (Talalay et al. 1984) (Table 2). These choices represent reasonable assumptions, but they are not based on direct archaeological evidence. We do know that nuts, probably hickory, were opened by pounding against sandstone bedrock at the Cold Oak shelter, that baskets and pots were used there, and that pits were excavated in the sediments for storage and other purposes (Gremillion 1993, 1995). Hickory nutshell sometimes occurs in very small fragments, often burned, suggesting that the nuts were finely crushed and then separated, perhaps by boiling. Acorn shell is also fragmented, but it is inherently more fragile and vulnerable to natural attrition than is hickory shell. We can assume on the basis of experimentation and ethnographic data that separation of the acorn meats was done by hand. The techniques used to detoxify them are unknown, although there are several possibilities (Table 2). The method of intermediate expense is to boil the acorn meats in a ceramic pot. This method should be less time consuming than boiling in a skin or basket, which requires frequent replenishing of the hot rocks used as fuel and must be checked frequently. I assume that a ceramic pot could be left unattended for longer periods. In both cases, I assume that a container holds 10 L whole acorns or 1.09 kg shelled meats. Costs for processing acorns, including shelling, leaching, and pounding into flour, range from 1.31 to 8.71 h / kg (Table 2).

We know that the basic solution to the optimal diet problem (Model 1) will change if the cost of acorn is lowered by 61% (2.9 h). If the lowest cost estimate for acorn is used (Model 3), that based on soaking rather than heating to remove tannins, the population's caloric needs are met at lowest cost by harvesting *only* acorn (Table 6). Efficient processing of acorn may therefore make an enormous difference in its food potential, one sufficient to transform it from a marginal resource to a staple.

Model 4: Nutrient constraints. Inclusion of nutrient constraints can be expected to increase greatly the realism of any model of optimal diet (Krebs and McCleery 1984). In the present case, there are marked differences in nutritional content between the four mast resources, with chestnut and acorn being rich in carbohydrates and hickory and walnut high in lipids. Clearly, acorn and hickory provide different types of energy: carbohydrates are efficient fuel and the basis of most human diets, whereas

TABLE 6
Model 3 Results

Resource (kg to be used)	Final value	Resource cost (h / kg)	Allowable increase (%)	Allowable decrease(%)
Hickory	0.00	3.11	*	28
Acorn	83.33	1.31	40	100
Black walnut	0.00	10.68	*	81
Chestnut	0.00	2.45	*	69

Constraints	Final value	Constraint	Allowable increase (%)	Allowable decrease (%)
Total cost (hours) ≤	109.17	1440	*	92
Total energy (kcal) ≥	322500	322500	1219	100

*No limit.

TABLE 7
Model 4a Results

Resource (kg to be used)	Final value	Resource cost (h / kg)	Allowable increase (%)	Allowable decrease(%)
Hickory	2.36	3.11	131	71
Acorn	0.00	4.71	*	40
Black walnut	0.00	10.68	*	75
Chestnut	137.05	2.45	111	57
Constraints	**Final value**	**Constraint**	**Allowable increase (%)**	**Allowable decrease (%)**
Total cost (hours) ≤	343.12	1440	*	76
Total energy (kcal) ≥	322500	322500	654	4
Total carbohydrates (g) ≥	67725	67725	4	87

*No limit.

lipids are readily stored and quickly converted for rapid use by the body (Lieberman 1987; Speth and Spielmann 1983).

To test the hypothesis that macronutrient constraints can explain the broad-based mast diet indicated at Cold Oak, I added to the model population requirements for lipids, protein, and carbohydrate. I assume that during the autumn, when mast was harvested, game would have been plentiful, providing ample supplies of protein and lipids, and that mast had to provide 70% of total carbohydrates (the remainder being covered by various fleshy fruits). With the constraint on carbohydrates (Model 4a), the optimal diet changes to one dominated by chestnut with minor amounts of hickory (Table 7). During the spring, protein and lipid needs would have been much harder to meet because of the scarcity and leanness of game. To model this situation, I assumed that stored mast had to provide 80% of lipids and 50% of required protein as well as 70% of carbohydrate needs (Model 4b). The result is restricted to the same two resources, hickory

TABLE 8
Model 4b Results

Resource	Final value	Resource cost (h / kg)	Allowable increase (%)	Allowable decrease(%)
Hickory	21.80	3.11	169	71
Acorn	0.00	4.71	*	40
Black walnut	0.00	10.68	*	76
Chestnut	129.81	2.45	110	98
Constraints	**Final value**	**Constraint**	**Allowable increase (%)**	**Allowable decrease (%)**
Total cost (hours) ≤	385.83	1440	*	73
Total energy (kcal) ≥	433995	322500	35	*
Total carbohydrates ≥	67725	67725	317	29
Total protein (g) ≥	8220	6630	24	*
Total lipids (g) ≥	15480	15480	1440	59

*No limit.

TABLE 9
Model 5a Results

Resource (kg to be used)	Final value	Resource cost (h / kg)	Allowable increase (%)	Allowable decrease(%)
Hickory	49.09	3.11	12	100
Acorn	0.00	4.71	*	61
Black walnut	0.00	10.68	*	73
Chestnut	0.00	2.45	*	57
Goosefoot	0.00	2.74	*	45
Sumpweed	0.00	2.83	*	10

Constraints	Final value	Constraint	Allowable increase (%)	Allowable decrease (%)
Total cost (hours) ≤	153	1440	*	89
Total energy (kcal) ≤	322500	322500	843	100

*No limit.

and chestnut, but in greater quantities (Table 8). This result indicates that the macronutrient content of the different mast types has the potential to explain the broad-based nature of this component of the diet, but only up to a point. Even under fairly severe constraints on availability of protein and lipids, hickory and chestnut alone suffice; it would take a substantial decrease in the cost of acorn (40%) or walnut (76%) to modify the optimal solution. Macronutrient needs alone do not seem to explain the presence of either walnut or acorn in the diet.

Model 5: Availability of seed crops. The final manipulation of the model addresses the question of the impact of the availability of cultivated seed crops on the mast component of the diet. To do this, I calculated yield estimates for two crop plants: sumpweed (*Iva annua*) and chenopod (*Chenopodium berlandieri*). These were chosen because they represent contrasting nutritional profiles (high lipid and high

TABLE 10
Model 5b Results

Resource (kg to be used)	Final value	Resource cost (h / kg)	Allowable increase (%)	Allowable decrease(%)
Hickory	2.36	3.11	4	71
Acorn	0.00	4.71	*	40
Black walnut	0.00	10.68	*	75
Chestnut	137.05	2.45	1	57
Goosefoot	0.00	2.74	*	1
Sumpweed	0.00	2.83	*	15

Constraints	Final value	Constraint	Allowable increase (%)	Allowable decrease (%)
Total cost (hours) ≤	343.12	1440	*	76
Total energy (kcal) ≥	322500	322500	654	4
Total carbohydrates ≥	67725	67725	4	87

*No limit.

carbohydrate, respectively) and because detailed harvest data are available (Smith 1987, 1992a). The basic version of the model, without any nutrient constraints, produces the same result as it does when crops are not available (i.e., all hickory) (Model 5a; Table 9). Although acorns are absent from all the optimal solutions produced so far, they seem to have been used, and the replacement of acorns by starchy seed crops remains a possibility. If such a replacement pattern is valid, it should also be reflected in the use of chestnut (which, like acorn, is high in carbohydrates). To test this hypothesis, the model was run with the two crops, the four nuts, and with the carbodydrate constraints (the autumn scenario) (Model 5b). However, the solution remains the same as it was without the availability of the two crops (Table 10). If chestnut availability is limited under the carbohydrate constraint, goosefoot fills the gap rather than acorn (Model 5c; Table 11). The spring scenario, with constraints on lipids, protein, and carbohydrates (Model 5d), turns to hickory and chestnut while ignoring the seed crops (Table 12). Limiting availability of hickory or chestnut under these conditions yields an optimal diet of sumpweed and chestnut or chenopod and hickory, respectively (Tables 13 and 14). In light of this analysis, it is difficult to argue that cultivation of small seeds would have been efficient in an environment in which mast, especially chestnut and hickory, was abundant and available. However, during times of food shortage seed crops would have been potentially valuable sources of macronutrients.

DISCUSSION

The application of foraging theory to the prehistoric past presents several unique challenges for the researcher. The most prominent of these challenges arise from the difficulty of measuring behavior and environmental features using archaeological data. I have demonstrated in this article one strategy that addresses this problem by shifting attention from archaeological tests to examination of the model itself. The model's performance under varying environmental conditions can indicate which explanations of archaeological patterning are worth pursuing and which can be safely discarded. Linear programming works well

TABLE 11
Model 5c Results

Resource (kg to be used)	Final value	Resource cost (h / kg)	Allowable increase (%)	Allowable decrease(%)
Hickory	0.00	3.11	*	65
Acorn	0.00	4.71	*	48
Black walnut	0.00	10.68	*	93
Chestnut	1.00	2.45	19	*
Goosefoot	146.48	2.74	94	16
Sumpweed	0.00	2.83	*	77

Constraints	Final value	Constraint	Allowable increase (%)	Allowable decrease (%)
Total cost (hours) ≤	403.29	1440	*	72
Total energy (kcal) ≥	470973.77	322500	46	*
Carbohydrate (g) ≥	67725	67725	257	31

*No limit.

TABLE 12
Model 5d Results

Resource (kg to be used)	Final value	Resource cost (h / kg)	Allowable increase (%)	Allowable decrease(%)
Hickory	21.80	3.11	36	71
Acorn	0.00	4.71	*	40
Black walnut	0.00	10.68	*	76
Chestnut	129.81	2.45	13	98
Goosefoot	0.00	2.74	*	11
Sumpweed	0.00	2.83	*	27
Constraints	**Final value**	**Constraint**	**Allowable increase (%)**	**Allowable decrease (%)**
Total cost (hours) ≤	385.83	1440	*	73
Total energy (kcal) ≥	433994.74	322500	35	*
Total carbohydrates (g) ≥	67725	27000	317	29
Total protein (g) ≥	8220.51	6630	24	*
Total lipids (g) ≥	15480	15480	1440	59

*No limit.

for this purpose because it facilitates the introduction and modification of constraints and parameters. I illustrated this approach by using linear programming to test alternative explanations for the poor fit between the predictions of the diet breadth model and the archaeological record of mast exploitation at the Cold Oak Shelter.

This analysis highlights some of the chief benefits of the modeling approach in general and linear programming in particular.

1. Optimization modeling forces us to think in terms of environmental characteristics that have immediate impacts on the organism—those that express intensive rather than extensive variables (Winter-

TABLE 13
Model 5e Results

Resource (kg to be used)	Final value	Resource cost (h / kg)	Allowable increase (%)	Allowable decrease(%)
Hickory	11.69	3.11	36	65
Acorn	0.00	4.71	*	35
Black walnut	0.00	10.68	*	76
Chestnut	1.00	2.45	13	*
Goosefoot	141.82	2.74	79	11
Sumpweed	0.00	2.83	*	27
Constraints	**Final value**	**Constraint**	**Allowable increase (%)**	**Allowable decrease (%)**
Total cost (hours) ≤	426.89	1440	*	70
Total energy (kcal) ≥	532851.69	322500	65	*
Total carbohydrates (g) ≥	67725	67725	88	52
Total protein (g) ≥	20388	6630	208	*
Total lipids (g) ≥	15480	15480	1429	47

*No limit.

TABLE 14
Model 5f Results

Resource (kg to be used)	Final value	Resource cost (h / kg)	Allowable increase (%)	Allowable decrease(%)
Hickory	1.00	3.11	36	*
Acorn	0.00	4.71	*	32
Black walnut	0.00	10.68	*	67
Chestnut	130.84	2.45	9	97
Goosefoot	0.00	2.74	*	8
Sumpweed	30.10	2.83	72	27

Constraints	Final value	Constraint	Allowable increase (%)	Allowable decrease (%)
Total cost (hours) ≤	408.82	1440	*	72
Total energy (kcal) ≥	460669.51	322500	43	*
Total carbohydrates (g) ≥	67725	67725	312	47
Total protein (g) ≥	15328	6630	131	*
Total lipids (g) ≥	15480	15480	1291	79

*No limit.

halder and Goland 1997). Model building therefore helps to guard against the tendency to treat unexamined concepts such as “ecological stress” or “environmental degradation” as if they had the status of causal factors.

2. Calculation of return rates from a variety of data sources (experimental, archaeological, and nutritional) helps to refine understanding of the relative benefits of the different resources used by prehistoric people. Doing so makes it possible to partition the concept of resource quality into separate components (such as nutrient composition, processing costs, and yields).

3. Linear programming allows these components to be manipulated independently in order to reveal their effects on the optimal diet. In the present case, performance of the model under different conditions played the role of a partial test of specific hypotheses about changing resource use. For example, in the model high caloric returns and modest processing costs make specialization on hickory the best option as long as it is available. However, although the archaeobotanical record from Cold Oak indicates that hickory had a strong and central subsistence role throughout the site’s occupation, it was not used to the exclusion of other, less profitable, types of mast. One possible explanation for this discrepancy is that there were periodic shortages of hickory. However, estimates of mast yields in the vicinity of the shelter suggest that nut resources in general were abundant enough to supply a small population with sufficient calories and that hickory should have been plentiful enough under most conditions to play that role. Interannual variability in yields alone, although sometimes considerable, probably does not explain the broad-based mast diet.

The use of acorns at Cold Oak is especially puzzling given that processing costs nearly always exclude them from the optimal diet. By changing those costs in plausible ways, I was able to show that the technology used to prepare acorns for consumption can potentially transform them into a first-line resource. However, if detoxification is time-consuming, it is difficult to explain the use of acorn except in situations of severe resource shortage. This question can only be fully resolved empirically, but the construction and manipulation of the linear programming model indicates that this goal is worth pursuing.

The addition of macronutrient constraints to the model yielded some important insights into the origins of food production. These analyses suggest that starchy crops such as goosefoot were not necessarily economical substitutes for starchy nuts such as chestnut (although if chestnut were not available, they would have been useful for meeting carbohydrate needs). In similar fashion, sumpweed is a potentially important source of lipids when hickory intake is limited. However, except in the context of mast failure, these results do not give strong support to the hypothesis that significant nutritional advantages account for the incorporation of crop plants into the diet. Instead, as others have suggested (Cowan 1985b; Smith 1992b), it seems increasingly likely that the chief benefit of crop cultivation in this environment was the predictability of yields in the context of seasonal food shortage. Risk minimization rather than efficiency maximization may be the appropriate currency in this case.

CONCLUSIONS

The use of formal ecological models to better understand the evolutionary implications of subsistence behavior also holds the advantage of producing insights independently of empirical test results. Optimization models have heuristic value (Krebs and McCleery 1984; Seger and Stubblefield 1996) that is not dependent on the verification of the model's details in any particular case (Caswell 1988). The lessons learned from the linear programming analysis of the Cold Oak archaeobotanical record have been helpful in ways that advance the project of understanding historical patterns of subsistence change in evolutionary terms. They have assisted in constructing a framework for research design (Krebs and Kacelnik 1991), generated previously unasked questions (Why is there such great diversity in mast use? What factors account for the dietary role of acorn?), revealed interactions between variables (such as nutrient needs, processing technology, and return rates) (Seger and Stubblefield 1996), and forced the explicit statement of assumptions (Kitcher 1985:169).

Given the typically ambiguous results of many archaeological tests, it may be useful to adopt a model of scientific progress that has as its primary goal improved understanding of natural phenomena (Pickett et al. 1994). This is a realistic objective that preserves the distinctive value of scientific knowledge while recognizing the limitations of empirical testing. These limitations are well understood by evolutionary ecologists, who must cultivate a tolerance for "some ambiguity and partial resolution" (Winterhalder and Smith 1992:17; see also Kitcher 1985). Simple models are unlikely to produce more than partial agreement (Maynard Smith 1978). Sometimes we must be satisfied with "how possibly" as opposed to "how actually" kinds of explanations, as long as they have testable consequences (Brandon 1990). If we expect to conclusively demonstrate the truth of our theories, we are bound to be perpetually disappointed; however, the more modest goal of improving our understanding of the determinants of behavior is always reachable.

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