Chapter 13
Human Behavioral Ecology and Plant Resources in Archaeological Research

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Once associated primarily with simple foraging models that analyze food choice using economic efficiency as a proxy for fitness, human behavioral ecology (HBE) in archaeology has expanded well beyond its original parameters. However, applications of optimal foraging theory (whose models often figure prominently in HBE) to understand the archaeobotanical record of plant use remain outnumbered by those that target hunting behavior and zooarchaeology (Jones and Hurley 2017). The reasons for this pattern are partly historical but also signal some specific methodological challenges that are peculiar to plant resources. Despite these challenges, HBE models have been used successfully to gain insights into changes in plant foraging, including the labor inputs involved in modifying plant communities to increase production. While simple models remain useful because of their generality, modifications to make them more realistic have been successful in advancing knowledge of how and why subsistence changes. These efforts have spawned fruitful examinations of the economic consequences of central place foraging and food storage (Bettinger et al. 1997; Gremillion 2002a; Price 2016; Rhode 1990; Barlow and Metcalfe 1996), gendered division of labor (Zeanah 2004; Elston and Zeanah 2002; Elston et al. 2014), colonization of landscapes (Winterhalder et al. 2010), and the costs of agricultural production (Barlow 2006).

The results obtained have encouraged more complex modeling efforts, some of which take the principle of economic optimization that is central to many HBE models and apply it to predict the behavior of virtual agents tasked with achieving multiple goals at once (Kohler et al. 2012). Increasing attention is being given to the dynamic relationship between human populations and the plant populations that sustain them. Although the current fashion for niche construction theory has brought this issue into the limelight, human behavioral ecologists have long recognized that population interactions of predators and prey influence resource abundance and shift economic preferences. The most vocal critics of optimal foraging theory tend to ignore this literature, as well as more recent efforts to incorporate anthropogenic effects into traditional optimal foraging approaches. Far from being the excessively reductionistic, mechanistic, and dehumanizing discipline characterized by critics, HBE is becoming increasingly holistic. In archaeology, HBE provides a theoretical framework that relates the general process of natural selection (and parallel cultural mechanisms) to human behavior in specific ecological settings. HBE's formal models further structure inquiry by specifying assumptions and systematically comparing the archaeological record with predictions based on natural

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selection theory. In recognizing that humans as well as plants and other animals are the products of evolutionary processes, HBE is well positioned to contribute to the ongoing effort to explain the origins of agriculture.

This chapter reviews the application of HBE to the study of plant foraging and domestication through archaeology. I first outline the initial appearance of HBE and its models in archaeological subsistence studies. Then I discuss some of the methodological issues that relate specifically to plant resources, particularly the difficulties involved in testing model-derived hypotheses against archaeological data. I proceed with a tour through applications of simple HBE models to plant use, including the prey choice model's predictions and the role of resource depression in broad-spectrum foraging; the implications of central place foraging and storage; and the economics of plant domestication and food production. I then discuss efforts within HBE to introduce greater realism into modeling efforts by using techniques such as simulation to examine the interaction of multiple variables across time.

Evolutionary Ecology, Behavioral Ecology, and Models

Evolutionary ecology has been defined as the study of "evolution and adaptive design in ecological context" (Winterhalder and Smith 1992, p. 3). One of its subfields, behavioral ecology, is devoted to behavior and its consequences for fitness under varying environmental conditions. One of the underlying assumptions of HBE is that the human lineage has evolved to rely upon a highly flexible phenotype capable of quickly adjusting to changing conditions (Winterhalder and Smith 1992, 2000; Codding and Bird 2015). The cognitive mechanisms that support this adaptation have been shaped by natural selection in ways that promoted survival in diverse contexts. Using these assumptions, HBE predicts solutions to challenges such as finding food and successfully raising children. Formal models in HBE employ phenotypically measurable proxies for fitness, such as foraging efficiency, to compare the adaptedness of behavioral options under different environmental conditions (Codding and Bird 2015; Bird and O'Connell 2006).

In archaeology, modeled outcomes are generally compared to behavior as inferred from the material record. One of the earliest and most frequently used models, the diet breadth or prey choice model (PCM), still plays an important role in HBE studies of subsistence and diet. However, the PCM emphasizes generality at the expense of realism and precision (Winterhalder 2002) and makes a number of assumptions that fit poorly with human behavior. HBE archaeologists have addressed this issue by constructing more complex models that account for the costs of central place foraging, the discounting effects of delayed returns, and other phenomena that violate the assumptions of simpler models.

The proliferation of terminology in HBE has created some confusion among archaeologists regarding what the approach actually includes. First, HBE is a broad field that encompasses both ethnographic and archaeological methodologies (Codding and Bird 2015). It is not limited to studies of diet breath, or indeed subsistence more generally, but is flexible enough to analyze any behavior set that affects fitness. In archaeology, HBE research is often congruent with the application of formal models, but this ingredient is not essential to the approach. Models do provide a structured format for creating hypotheses through deductive inference, such that if the model's assumptions are true, the hypotheses deduced from it must also be true. Negative tests indicate a mismatch between model and real world. Finding out whether that mismatch is the result of a violated assumption, a poorly estimated environmental parameter, or an inappropriate currency permits ongoing refinement of models to improve their predictive accuracy (Winterhalder 2002). Many models used in HBE are based on optimization—solving the problem of how to meet competing demands at the lowest possible cost. Unlike maximization, optimization recognizes constraints like fixed environmental parameters, limitations on available time, and costs of lost opportunity. The PCM, for instance, predicts the optimal roster of prey items which, if pursued whenever encountered, will maximize energetic efficiency of the food quest under the constraints specified (e.g., prey population size, distance traveled, and the like) (Winterhalder and Smith 1992).

One common misconception about evolutionary approaches to human behavior is that they require that fitness-enhancing behaviors be perpetuated through genetic inheritance. This notion is not only false; it should be easily recognized as inconsistent with the modern understanding of how evolution works. Phenotypic plasticity and epigenetic inheritance are widely recognized in evolutionary biology as processes that mediate gene expression (Piperno 2017). Given this understanding, the notion that HBE endorses genetic determinism is far wide of the mark. Instead, HBE generally remains agnostic about the means of transmission of variant behaviors, which may be primarily cultural and unconstrained by biological relatedness (Winterhalder and Smith 1992). Transmission mechanisms and their dynamics are being investigated theoretically and empirically by other evolutionary researchers (Borgerhoff Mulder et al. 2006; Eerkens and Lipo 2007; Bettinger 2008; Kolodny 2018).

HBE and Archaeological Subsistence Studies

It is not surprising that human behavioral ecology entered the repertoire of archaeologists during the era when processualism was near its peak. At the same time archaeologists were seeking scientific legitimacy by explicitly employing hypothesis testing and empirical rigor, systems ecology was on the rise (Harris 1968). Americanist archaeology in particular became preoccupied with Julian Steward's cultural core, which structures relationships between human groups and the natural environment (Steward 1955). Research took a distinct turn toward analyzing subsistence behavior as one element of larger adaptive cultural systems. Process was in; description, taxonomy, and even history were out. Cultural evolution provided a framework for understanding human adaptations. Processual archaeology found inspiration in the transformational cultural evolution of Leslie White, in which cultural progress tracked the increasing ability to control and capture energy (White 1949, 1959). Subsistence patterns were expected to evolve accordingly, from hunting and gathering to horticulture, to pastoralism and agriculture, in step with transformations in social organization, religious beliefs, and economic exchange.

But in this, processualism had left Darwinian evolution behind. Robert Dunnell (1980) pointed this out in a compelling essay and advocated instead for a revival of natural selection theory and its application to cultural variation (see also Chap. 1, this volume). Dunnell's evolutionary archaeology saw artifacts as fossils whose correct interpretation would reveal differential replication of advantageous variants over time. However, evolutionary archaeology's mission was to identify time-transgressive evolutionary processes such as selection and drift in the artifactual record. In this, it took its methodological cues from paleontology rather than ecology. Some archaeologists sought a more systematic framework for linking behavior to natural selection theory. They found it in the emerging field of behavioral ecology, which enlisted a set of simple formal models that could predict optimal behavior in specific environmental settings (Winterhalder 1981; Bettinger 1980). Many archaeologists were intrigued by the possibilities of formal modeling to identify optimal strategies of food acquisition—that is, strategies that balance trade-offs in the most advantageous way. For example, the prey choice model derives the optimal solution to the contingent choice faced by a hunter: whether to pursue a prey item or continue searching for something better. The trade-off here is that in an environment of scarcity, broad diets are more efficient energetically than narrow ones because the cost of searching for profitable but rare items erodes the benefit of specialization.

Behavioral ecology models were first embraced by zooarchaeologists and applied to the analysis of changing hunting patterns (see also Chap. 12, this volume). The logic of the prey choice model was compelling; it could explain, for example, why depression of preferred game populations would lead to expansion of the diet to include smaller animals and plants with relatively low rates of return. There were some notable successes in understanding the evolutionary logic behind changes in zooarchaeological assemblages (Broughton 1994b; Stiner 2001). However, few researchers attempted similar studies with plant resources (for an exception, see Barlow and Metcalfe (1996)). Some regarded the strategy of modeling suspect, concerned about a loss of empirical rigor. Others rejected such applications of evolutionary theory on grounds of human exceptionalism (Smith 1983). However, even for researchers open to evolutionary explanation and convinced of the usefulness of models, applying them to plant resources presented some unique challenges.

HBE and Plant Resources: Methodological Issues

Because HBE models were initially developed in reference to predators in search of mobile prey, the simplifying assumptions they make are usually more applicable to hunting than to plant foraging (Gremillion 2014). For example, unlike most vertebrate prey, plant foods often require extensive pre-consumption processing. Uncertainty about processing methods complicates the estimation of return rates, which can differ significantly depending on the technology available. Delayed returns related to storage or agricultural production are additional complications that pertain more often to plant than to animal resources. And whereas vertebrate assemblages often provide the opportunity to estimate the amounts of food they represent, macrobotanical remains are often too fragmented to reliably extrapolate from in this way.

Plants and the Prey Choice Model

One of the earliest, simplest, and most widely discussed HBE models is the prey choice model (PCM), which predicts the optimal roster of prey items a forager ought to pursue on encounter (see also Chap. 12, this volume). Optimal in this case is defined as the resource set that provides the best average rate of return while foraging. This average represents an optimum, not a maximum, because of the trade-off that exists between the time spent searching for prey (a function of prey abundance) and time spent handling it (pursuing, capturing, and processing). Under the assumptions of the PCM, handling time increases compared to search time as the most highly ranked resources become less abundant. Foraging efficiency declines in this case because common but low-ranked prey are being passed up as increasing time is spent searching for food. Addition of items to the diet in rank order of their profitability reduces mounting search costs while also lowering the average rate of return, reaching an optimum at which either expansion or contraction of diet breadth would lower rates of return (Bird and O’Connell 2006; Winterhalder and Goland 1997; Bettinger 1991).

The PCM is not complex mathematically, although it requires some work to estimate realistic parameters. It is fairly robust, meaning that is relatively insensitive to violations of its assumptions. Random encounter of prey items might fit some hunting forays, but plants are likely to be sought in known locations. Encounters are therefore more likely to be predicted based on previous knowledge of resource abundance and acted on accordingly, rather than experienced directly by the forager. Other concerns arise in the case of mass resources, animals or plants of small body size that occur in concentrations. Mass resources violate the assumptions of sequential encounter of prey, mutual exclusivity of search and handling, and consistent response to prey types (Madsen and Schmitt 1998). A stand of seed-producing grasses, unlike an individual animal, does not have a consistent profitability ranking because the density of individual plants varies. In a sense, this prey item is more like a patch because it declines in quality under predation (and can rise in rank as a result of labor input) (Winterhalder and Goland 1997).

Estimating Return Rates and Evaluating Archaeological Tests

The nature of archaeological data makes it difficult to complete one of the key tasks that makes models useful: finding out why the model failed to accurately predict behavior (Winterhalder 2002). A poor fit can potentially be traced to violated assumptions, inaccurate estimates of environmental parameters, an inappropriate currency (e.g., energy) or goal (e.g., maximization of efficiency under constraints), or a failure to account for the effects of improved technology on return rates. Discovering the source of the discrepancy is handicapped by the inability to observe behavior directly, or to accurately determine the structure of plant and animal communities using environmental proxies.

Application of HBE to paleoethnobotanical data has lagged behind similar work in zooarchaeology. One reason for this pattern is the difficulty of accurately reconstructing plant use from material remains. In part, this situation reflects the fragmentary nature of the archaeobotanical record and the difficulty of estimating food quantity or subsistence importance from plant remains (Gremillion 2014). For animal resources, especially mammals, body size can in some situations be an appropriate proxy for the return rate of a prey type (although not in the case of mass resources; see discussion above) (Broughton 1994a, b; Grayson and Cannon 1999). This method obviates the need for detailed calculations of energy content and procurement costs for each prey type in order to predict optimal diet breadth. Researchers have also developed ratios of large- to small-bodied prey and of fast-moving to slow-moving animals in order to assess diet optimization (Stiner et al. 2000).

There is no such simple solution for plants in part because the unit of capture is not always congruent with an individual in the biological sense. Compared to vertebrates, there is much more variation between plants in anatomical and chemical characteristics that have nutritional significance. Costs and benefits must be derived experimentally or from ethnographic data for each taxon (Grayson and Cannon 1999), sometimes from published data on related taxa rather than the species in question. Plant foraging often occurs as foraging within a patch (like mass resources more generally), in which the rate of return declines as resources are harvested. Also contributing to the difficulty of estimating return rates of plant resources is that their handling costs may vary widely depending on the technology available for post-harvest processing. A dramatic example is the hickory nut of North America, which is nutrient-rich but requires laborious removal of the inedible mesocarp (shell). With waterproof vessels, bulk crushing and boiling of the nuts is possible, greatly reducing processing effort. Hickory nuts can consequently be near the top of a ranked list of resources or near the bottom, depending on technology (Gremillion 2002).

Production Cycles and Delayed Returns

When food is not consumed immediately on collection, and returns are delayed by caching or storage, there may be some loss over time due to spoilage and predation. For this reason, return rates while foraging may be different than what they are at the point of consumption (Bettinger 2009; Tucker 2002). This departure from simple models like the PCM is more likely to be an issue for plant foods than most animal foods. However, the costs of such losses can be estimated and incorporated into return rates. It is more difficult to account for the risk that a cache will not be needed at all, which may be the case with highly flexible economies with fluid settlement patterns. These situations favor back-loaded resources, which are relatively cheap to collect and store so that the expensive processing required can be deferred until the need is certain. The front-back-loaded model addresses this complication by separating storage costs from culinary costs (Bettinger 2009) (see discussion below).

Delayed returns also characterize agricultural production even when storage is not involved; like foods that are costly to process, crops require the investment of labor "up front," introducing some risk of loss that is not accounted for in the PCM or other simple, general models that assume immediate consumption. The delay between planting and eating and its attendant risks may significantly discount the energetic payoff from foods that are produced rather than collected (Tucker 2002).

Applications of Simple Foraging Models to Plant Resource Use

HBE researchers have taken up the challenge of applying simple models to foraging systems in which both plants and animals play important roles. Much of the pioneering work in the behavioral ecology of plant resource use was done in the context of hunter-gatherer research in the western USA, particularly the Great Basin (Madsen 1993; Jones and Madsen 1989; Grayson 2000; Grayson and Cannon 1999; Elston and Zeanah 2002). Here, plant resources were crucial components of stable long-term subsistence adaptations (Fowler and Rhode 2011). Researchers attended to the energetics of harvesting plant resources such as small seeds, which were dietarily important despite their high processing costs and low returns relative to hunting (Simms 1987; Barlow and Metcalfe 1996).

A similar logic may underlie other archaeological examples of diet diversification, such as the transition that took place in the Near East and elsewhere across the Late Pleistocene-Early Holocene boundary (Stiner 2001). Because this shift preceded the domestication and cultivation of plants, and because grass seeds and other small grains tend to have relatively low return rates, broad-spectrum foraging offers a potential explanation for the initial use of cereal grains and weedy annual seed producers. This is the link between resource depression and initial domestication of plants that some researchers have dismissed as untenable, maintaining instead that the coevolutionary trajectory of plant domestication is an ongoing ecological process that emerges from human niche constructing tendencies (Smith 2009, 2016). While true, this interpretation does not explicitly address the economic logic of the decisions to plant, tend, and replant that must have initiated the process. Beyond the domestication question, HBE researchers have introduced greater realism to the original suite of relatively simple HBE models by modifying some of their assumptions to better accord with observed human behavior. For example, central place foraging models consider the costs of round-trip travel (Gremillion 2002a; Zeanah 2004) and the discounting of delayed returns when consumables are stored for future use (Tucker 2006). Other studies have taken the simple models of HBE and modified them to account for delayed returns and the labor investments that drive food production (Bettinger 2009; Tushingham and Bettinger 2013).

Diet Breadth and Resource Depression

The PCM is particularly useful for helping with explanations for the expansion of diet breadth because it specifies the economic consequences of being a specialist or a generalist under different environmental conditions. The simplicity and elegance of the model have been attractive to researchers attempting to understand the causes of subsistence change, particularly the transition from reliance on a few high-quality resources to a more diversified subsistence base (Gremillion 2014). This so-called broad-spectrum revolution (Flannery 1969) matched the predictions of the prey choice model in intriguing ways (Stiner et al. 2000). It offers a causal mechanism behind the frequently observed shift from focused hunting of large game to the more diversified diets of the Pleistocene. In PCM terms, resource depression (here used to mean a decline in abundance whether caused by human predation or some other factor) made specialization on a limited number of high-value game animals too costly an option. Whether due to population growth and circumscription or climate change, the phenomenon of resource depression (in which declining abundance of top-ranked resources erodes foraging efficiency) predicted by the prey choice model was a potential evolutionary explanation for the broad-spectrum foraging that emerged during the Early Holocene.

Stiner and her colleagues recognized early on the potential of the PCM to help explain the broad-spectrum revolution of the Mediterranean Basin (Stiner 2001; Stiner et al. 2000). She conducted an analysis of zooarchaeological data from multiple components across the region dating to the Late Pleistocene and early Holocene (Stiner et al. 2000). Stiner observed that applications of the PCM were often flawed by reliance on Linnean taxonomic categories to define types of prey, which do not adequately distinguish between small prey that are difficult to catch and those that are easy targets. By making these distinctions, Stiner was able to identify diet breadth expansion to include lower-ranking prey in the zooarchaeological record—in other words, confirmation that the broad-spectrum foraging transition was indeed a real phenomenon and one that seemed to match the predictions of the PCM.

Zeder (2012) dismisses Stiner's findings in this study on the grounds that her interpretations of patterning in the zooarchaeological data were inappropriately "dictated" by the assumption that broad-spectrum foraging is invariably caused by resource depression. More importantly, Zeder refers to numerous examples of broad-spectrum foraging in a context of resource abundance that "defy optimal foraging predictions and call for the consideration of alternative approaches to the explanation of subsistence change in human history" (Zeder 2012, p. 7). This conclusion betrays a fundamental misunderstanding about the use of HBE models: that if its predictions fail, the model itself should be discarded. In fact, the HBE approach offers a systematic way to probe causality by testing model assumptions and reexamining environmental parameters. It forces researchers to quantify "resource abundance" and "resource scarcity" in ways that make hypotheses about resource depression or anything else more amenable to testing.

While many researchers have found that the application of the PCM to cases of expanding diet breadth succeeds in clarifying the link between natural selection theory and subsistence behavior, others remain skeptical on theoretical grounds. Critiques claim that HBE in general, and optimization models in particular, are fundamentally wrong-headed because they ignore human agency and narrowly constrain explanations to conform to the model's assumptions (Zeder 2009, 2012; Smith 2006, 2009, 2011, 2015). Such critics argue that the application of HBE models to initial plant domestication is flawed because they ignore niche construction, the process by which organisms (humans in this case) modify the environment in ways that affect their own fitness and that of their offspring. Archaeologists who work with HBE models have been unimpressed with the critique on theoretical grounds, citing the critics' misunderstanding of the logic of modeling and the stance of HBE with respect to agency and niche construction (Gremillion et al. 2014; Stiner and Kuhn 2016; Codding and Bird 2015). In fact, HBE has no difficulty incorporating niche construction effects into its analyses (see discussion below under Niche Construction and HBE in Origins of Agriculture Research).

Central Place Foraging

One point at which the PCM lacks realism in the human case is the assumption that the optimal forager should maximize the rate of return *while foraging*. In the interests of simplicity, the PCM does not consider the costs that may accrue outside of the search for and capture of prey. In the human case, particularly for groups with high residential stability, foragers typically remain tethered to a central place that is situated near multiple resource patches to which community members must travel to obtain food. Once acquired, the bulk of food collected is generally carried back to the central place for consumption. The costs of round-trip travel are taken into account by the central place foraging (CPF) model, initially formulated by Orians and Pearson (1979). These costs have implications for food choice because travel can significantly alter the ranking of resources. In addition, CPF places constraints on the quantity that can be collected during a foraging trip (Bettinger et al. 1997; Barlow and Metcalfe 1996).

Jones and Madsen (1989) introduced the concept of maximum transport distance (MTD), the maximum distance at which the amount of energy expended and the amount obtained are equal. The constraints of human biology set limits on the weight and volume of material that can be transported using simple carrying tools such as baskets. Because of this constraint, the relevant currency is not the average rate of return while foraging, but rather rate at which energy can be transported to the central place. Jones and Madsen explored the performance of the CPF model and found that plant foods that offer modest return rates but are energy-dense have a greater MTD than alternatives that have higher rates of return but represent poor-quality loads. Thus, resource rankings should vary considerably with distance from the central place, with some dropping out of the diet entirely as their MTDs are exceeded. The effects of the load size constraint are particularly marked in the case of grasshoppers, which are cheap to procure locally and can yield a whopping 272,649 kcal/h, but have an MTD of 301 km. Beyond that distance, the poor quality of a basketload of grasshoppers boosts the relative ranking of small seeds (such as bulrush and tansy mustard) that have much lower return rates. Rhode (1990) observed that the MTDs calculated by Jones and Madsen are in many cases much greater than actually observed ethnographically and archaeologically, suggesting that other constraints are operating, such as the quality of locally available resources. When profitable alternatives are available nearby, the opportunity costs of ignoring them can be high enough to encourage foragers to abandon distant resources well before travel costs exceed caloric returns. While this critique makes an important point about marginal valuation as a decision criterion, the CPF model as applied by Jones and Madsen takes a step toward greater realism as compared to the simple PCM.

Despite its shortcomings, the Jones and Madsen CPF model inspired other researchers to seek further refinements. Metcalfe and Barlow (1992) followed up by asking how processing at the collection site can improve the value of a load by reducing the quantity of inedible material included in it. They analyze the trade-off between the increased utility of the load and the added costs of processing to remove waste. Their analysis shows that greater distances demand a greater investment in processing to maximize the rate at which energy can be delivered. For example, pinyon seeds can be profitably collected as entire cones when very close to camp, but as distance increases, further processing is required to counter the costs of travel and transport. This model of field processing is important because of its implications for the archaeological record, which may contain little evidence of plants that are typically processed far away from the central location where material evidence has accumulated. Recently, Price (2016) further refined the model by recognizing that the costs of labor at home and in the field are not always equivalent because processing at home faces competition from a larger array of alternatives (introducing greater opportunity costs).

Travel costs also are central to David Zeanah's marginal value model (Zeanah 2017). This project takes up the question posed by Gremillion (2004) for eastern Kentucky: given the low return rates from small seeds (precursors to domesticates), why were they incorporated into human diets at all? This outcome diverges from what the PCM predicts for an environment in which higher-quality resources are abundant. Gremillion suggests that seasonal scarcity of food during the cold season calls for reconsideration of resource rankings; stored seeds rise to the top when alternatives are in short supply, and expensive processing can be carried out when opportunity costs are low because other activities are curtailed. Zeanah incorporates travel costs and marginal valuation into his model in order to show that hickory nuts, despite their high rate of return, can be costly to harvest during years of low yields. Low yields occur periodically but unpredictably because hickory produces masts, superabundant but periodic annual crops that exceed the demands of predators (Gardner 1997). In non-masting years, hickory trees are both less productive (thus more quickly exhausted) and more widely scattered than in masting years. Zeanah compares return rates for a nearby patch of goosefoot (also known as chenopod, a weedy annual producing edible seed that was domesticated in the central USA by ca. 4000 BC) with those of hickory nuts at varying distances from a home base. This model more accurately mimics the perspective of a forager, who is more likely to be sensitive to what the next unit of labor will yield, than the PCM, which is based on average rates of return. With these adjustments, it is apparent that despite their nutrient density, in years of low production, the costs of traveling between diminished patches becomes prohibitive. In such situations, harvesting a nearby dense patch of seed crops is more efficient. Zeanah's analysis establishes that a broad diet including small seeds does not necessarily indicate a sacrifice of efficiency in order to extend food availability through storage. It demonstrates how the structure provided by HBE models offers a systematic way to explore alternative hypotheses when models fail to perform as expected.

Storage and Delayed Returns

When foragers return their harvests to a central place, they often do so with the intention of storing them in whole or in part for future use. Collection for storage requires a different economic calculus than collecting for immediate use. Because of the delay, there is a greater likelihood of loss (to predation or spoilage), and where storage practice varies interannually and mobility is high, there is also a chance that the stored food will not be used. If that probability is large, foragers should choose resources that are back-loaded (i.e., their costs of collecting for storage are low relative to culinary costs) (Bettinger 2009). Such resources can be collected cheaply, and culinary costs are not incurred until (and unless) the stored food is needed. In contrast, front-loaded resources (for which storage costs are high relative to culinary costs) are a poor choice when future use is unpredictable or unlikely. Failing to consider this factor can result in puzzling divergences from the predictions of the PCM, like the reliance on acorns in California predating economies based on storage of salmon. Salmon offers better returns overall, but it is too heavily front-loaded to be compatible with high mobility and the absence of permanent storage facilities (Tushingham and Bettinger 2013).

The economics of storage and central place foraging have also informed explorations of gendered division of labor. HBE models as applied in archaeology usually make the simplifying assumption that a generic individual makes decisions based on economic payoff, an assumption that perhaps justified when little is known about the distribution of tasks within past communities. However, the fact that collecting plant foods is usually women's work ethnographically worldwide supports consideration of plant foraging in the context of specifically female constraints. Zeanah (2004) assumed that women and men in the Carson Desert of western Nevada, USA, foraged separately based on ethnographic evidence and the prevalence of female-sourced, seed-rich coprolites in caves that indicate foraging in nearby marshes. However, reconstruction of the local environment indicates that pursuit of these small seeds would have been a poor choice economically when other more productive patches were present. Zeanah explores a number of possible reasons for the mismatch that relate to the concerns and constraints of female foragers that were probably different from those of males. Women's foraging was likely biased by concern for provisioning children and the constraints child care may have placed on long-distance foraging. Women's plant collecting could be relied upon, whereas male hunting had a highly variable success rate. For males, the value of big game hunting was enhanced beyond its caloric value because success in this endeavor conferred prestige. To incorporate these variables, Zeanah employs a central place foraging model that takes into account the contrasting and sometimes conflicting goals of women and men. His argument is too complex to recount here, but it convincingly synthesizes modeled predictions, archaeological evidence, and ethnographic data in an effort to explain settlement patterns as representing a compromise that allowed both women and men access to the patches most productive for them.

Gendered division of labor also means that women and men face different opportunity costs. When deciding what resources to collect for storage, women must consider how these activities preclude attention to child care. Whelan et al. (2013) suggest that women living on the western slopes of the Sierra Nevada mountains in California chose to store acorns rather than gray pine seeds despite their lower rate of return because acorns are strongly back-loaded. Acorns could therefore be collected efficiently and transported for processing at the base camp, easing the conflict between mobility and caring for children.

Plant Domestication and Optimization of Production

It is not surprising that HBE and its models attracted the attention of a number of researchers interested primarily in the transition from foraging to food production. In principle, decisions about what resources to use are agnostic with respect to whether the resources in question are domesticated or not. Handling costs for crops include the labor investments in clearing, planting, soil amendments, and other agricultural tasks. William Keegan (1986) first grappled with the task of adjusting optimization models to better capture the economic costs and benefits of food production. He reasoned that garden preparation costs, like search costs in the PCM, are a characteristic of the diet as a whole and can play a similar in an optimization analysis of production. In this version of the PCM, "garden breadth" (the variety of crops planted) should expand as the costs of labor mount because of declining soil fertility. Although Keegan compared the modeled outcomes to ethnographic rather than archaeological data, archaeologists took up the challenge of including the management of plant resources in studies of subsistence optimization. Early efforts along these lines used linear programming to identify optimal combinations of food resources under specific demographic and environmental conditions (Keene 1981; Reidhead 1976; Gardner 1992). More recently, methods and concepts from HBE have informed attempts to explain the adoption or intensification of food production (Gremillion 1998, 2004; Diehl 1997; Diehl and Waters 2006; Piperno and Pearsall 1998; Piperno et al. 2017; Barlow 2002, 2006). In 2006, an entire book was published (Kennett and Winterhalder 2006) that showcases applications of HBE to the analysis of food production.

The promotion of NCT as an alternative to HBE, and the belief that the two are fundamentally opposed, seems to depend on a failure to recognize that evolutionary questions often require a division of labor (Gremillion 2009). Because HBE is focused on the economic logic of human decisions, it is not well equipped to analyze the selective forces at work across generations during the process of domestication. That process is best understood as a form of mutualistic coevolution, a natural consequence of animals feeding on plants and dispersing their propagules. Rindos (1984) became famous for pointing out that such relationships are not unique to humans and are understandable as an outcome of natural selection. Framed in this way, domestication is not an economic decision, but rather an evolutionary process. While this observation is correct (and ripe for dissemination at the time of its publication), this insight does not imply that the economic logic of human decisions is irrelevant to initial domestication. In fact, the microeconomic models of HBE are extremely useful for understanding this logic as it relates to habitat disturbance, seed saving and planting, residential mobility, and other behaviors that comprise "primary mechanics" (Stiner and Kuhn 2016). They are poorly suited to understanding the "compounding mechanics" of larger-scale emergent phenomena that operate across generations, a task better performed by analyzing feedback between human alteration of the environment and selection in plant and human populations (the framework provided by NCT).

Resource Depression and the Eastern Agricultural Complex

Gremillion (1996, 1998, 2002a, b, 2004) has used the PCM as a platform from which to examine the rise of seed crop cultivation in eastern North America. In the uplands along the western slope of the Appalachians in eastern Kentucky, rock-shelters with excellent conditions for organic preservation have yielded collections of plant remains from the Archaic (8000–1000 BC) and Woodland (1000 BC to AD 400) periods. Paleoethnobotanical research has indicated that storage and consumption of small starchy and oily seeds, many of which show morphological signs of domestication, intensified after ca. 1000 BC. This change seems puzzling in an environment in which hickory, oak, chestnut, butternut, and walnut trees were common and in some cases locally abundant. All produce potentially high yields of edible seeds (nuts), although they do so by masting at irregular intervals. In comparison to these nuts, which can be quite profitable, seeds seem like an inefficient choice for an optimal diet. Analyses of models using realistic environmental and demographic parameters confirmed that cultivation of small seed crops in a habitat with abundant mast would have been inefficient (Gremillion 2002).

Estimates based on average yields of different tree types fail to account for interannual variation, which was high due to the masting adaptation. This pattern required a flexible strategy that could shift between types as conditions changed. It is plausible that only in particularly poor masting years across all species would seed crops have been an appropriate choice, as Zeanah (2017) has noted. Gremillion (2004) also considered the costs of processing plant foods and the impact of technology on their return rates, concluding that whereas some nuts could offer high return rates with improved technology, the profitability of small seeds was consistently constrained by the time-consuming tasks of winnowing, pounding, and cooking. One insight to emerge from this analysis is that stored seeds would have had a much higher rank during the winter, when other foods were scarce, especially in years when mast yields were low. Small seeds are relatively cheap to harvest and need not have interfered with collection of other foods; processing could have been postponed until winter or spring, when energy was scarce and time was freed from many competing activities (Gremillion 2004).

While Gremillion did not see evidence of population density at levels that would suggest resource depression, she did not conduct a formal test. Smith also claims that there is no evidence of "population packing" associated with sites yielding evidence of early domesticated plants, citing the distance between known sites likely to have been contemporaneous (Smith and Yarnell 2009). Weitzel and Codding (2016) test this component of Smith's argument by using archaeological data to estimate demographic trends across time in the midcontinent of the USA. Based primarily upon radiocarbon dates, their reconstruction of the population history of eastern North America shows correlations between periods of relatively high population and the initial appearance of domesticates. This finding challenges Smith's generalization that initial plant domestication is not associated with resource depression in the context of population growth. Additional studies of this kind will be needed to assess whether the historical record of subsistence change supports the resource depression to domestication scenario in particular cases. It does clearly illustrate, however, why claims about resource depression must be evaluated empirically and quantitatively rather than asserted as guesswork or excluded on theoretical grounds.

Fremont Agriculture and Marginal Valuation

A second example of application of optimization models to explain incorporation of domesticates into subsistence is Barlow's study of Fremont maize farming (Barlow 2002, 2006). This research takes into account the diminishing returns over time that are characteristic of agriculture, a factor that is likely to influence decisions about whether to continue investing or switch to an alternative food source. Decision-making "at the margin" thus has potential for explaining the great spatial variability in the economic importance of maize agriculture within a mixed foraging-farming economy. Barlow approaches the question of why the prehistoric Fremont populations of the Great Basin, USA, maintained a flexible and varied strategy of maize production by estimating return rates for different levels of investment. Because maize yields follow a diminishing returns curve over time (i.e., the rate of increase in yield falls off as more labor is invested), after some period of time, farming should be abandoned in favor of more profitable alternatives. Intensive agriculture is so costly due to the heavy investment in labor it requires that it would have paid off only rarely. However, low to moderate investments in maize cultivation would have made economic sense, but only if game and highly ranked wild plant foods became scarce. These results indicate that maize farming is not a single resource type because rates of return vary depending upon labor costs. The combined predictions of the DBM and the diminishing returns curve for agricultural investment help to make sense of the variability in Fremont agriculture. Barlow's use of models in this study argues against the idea that agriculture is either so highly productive that it will outrank foraging for wild foods or so unproductive that it should be adopted only in the most dire shortages. Fremont populations chose a flexible strategy that allowed for casual maize farming as an occasional supplement to reduced availability of preferred wild foods.

Production Strategies

Some HBE-oriented archaeologists have investigated specific aspects of the practice of plant cultivation from an optimization perspective. In fact, the earliest attempt at optimization modeling of food production (Keegan 1986) investigated whether ethnographically documented garden "patches" of the Machiguenga were populated with an optimal set of plant resources. Observing that the return rates available from garden patches greatly exceeded those available from alternatives such as fishing and hunting, he proposes that protein constraints limit the utility of maximizing the rate of overall energy capture. Availability of protein within the energetically optimal diets varies seasonally, requiring adjustments to meet nutritional requirements. Keegan's argument is notable for its conceptualization of the garden as a patch and its efforts to consider multiple relevant variables, including marginal valuation, travel costs, and seasonal variability. Since that time, many researchers have had success in more systematically investigating how models perform under modified assumptions, currencies, and goals.

For example, Gremillion (2002a) compared rates of return available from garden plots with different soil characteristics in eastern Kentucky. This study used a simulation approach to compare energetic returns from alternative garden locations at varying distances from a central place. Her conclusion is that cultivation of alluvial soils at some distance from the storage location could pay off energetically despite the added travel costs because the fertile soils allowed for delivery of higher-quality packages. In comparison, the lower yields available from an upland plot with less fertile soils could be compensated by the reduction or elimination of travel costs. Though it did not settle the question of where garden plots were actually located, this study demonstrated that optimal locations for food production need not be limited to a single option.

Foster (2003, 2010) also used optimization principles in conjunction with simulation as a method for explaining decisions about field location among the Creek (Muskogee) people of southeastern North America during the historic period. His dynamic optimization model of a single historical village's farmland showed that fields were abandoned well before the marginal value theorem predicts they should have been on the basis of diminishing returns over time. Foster concludes that the strategy of field rotation practiced by the villagers of Cussetuh, though not optimal with respect to energy capture, minimized the risk of a serious food shortage. Risk minimization may under some conditions have more profound fitness consequences than energetic efficiency, as when variance in subsistence outcomes and energy requirements are both high (Winterhalder and Goland 1997; Winterhalder et al. 1999).

Dominguez (2002) examined labor inputs into water capture and conservation techniques in the Pueblo IV period of the northern US Southwest. Using hydrologic data, he was able to show that gridded plots were an efficient and reliable technique for increasing moisture. On this basis he argues that the shared technological attributes of Pueblo water management converged on an optimal solution to the problem of producing maize in an arid environment.

Summary

Although the appropriateness of the PCM and other simple HBE models for studying the origins of food production has not gone unchallenged, researchers persist in applying them to this research domain. Models such as the PCM are particularly useful for specifying the economic consequences of different subsistence options (usually measured in terms of efficiency, or kcal per unit time spent). They also provide a justification for using efficiency measures as a proxy for fitness. They were not originally designed with cultural animals in mind, but their simplicity and generality allow for broad application and permit modest adjustments to introduce variables (such as round-trip travel costs) that are likely to have been important to human foragers and farmers. Researchers have also tried to move beyond relatively simple models of optimal food choice to better understand the process of subsistence change. These newer approaches pose questions about how and why plant food production developed and changed over time, often employing dynamic models that can simulate outcomes under different conditions by manipulating multiple variables.

Beyond Optimization: New Directions

The optimization approach and reliance on simple models derived from foraging theory have clearly yielded benefits in the improved understanding of the energetics of plant subsistence (Gremillion 2014; Gremillion and Piperno 2009; Gremillion et al. 2014). However, these simple optimization models are not well suited to address causal questions about the process of plant domestication and long-term trends to agricultural intensification. In the following section, I focus on two elements missing from traditional HBE models: the effects of anthropogenic environmental modification on resource characteristics and future selection pressures (niche construction) and the simultaneous manipulation of multiple variables across time in agent-based models.

Niche Construction and HBE in Origins of Agriculture Research

The application of HBE models to agricultural subsistence has been challenged on the grounds that they do not consider niche construction (see also Chaps. 11 and 17, this volume). Niche construction is the process by which organisms modify their own niches and those of other organisms in ways that affect their fitness and that of their offspring (Odling-Smee et al. 1996; Odling-Smee et al. 2003). However, the claim that NCT is incompatible with HBE (Smith 2014) betrays a misunderstanding of the flexibility of optimal foraging models. These models fail to acknowledge niche construction, not because they require the assumption that humans passively react to environments over which they have no control, but because they were not designed to model the feedback between predator and prey populations. Even before the term “niche construction” had entered the literature, a number of researchers had employed HBE models to better understand the economic implications of interactions between human predators and their prey. Winterhalder and Goland (1993, 1997) explored the PCM as a framework for understanding the adoption of small-seeded annuals in eastern North America and their subsequent domestication. They use it to frame their discussion of the varying economic implications of reliance on plant resources depending on their quality (profitability) and density (abundance). This structured analysis shows how reliance on an abundant but low-ranked plant resource is likely to spur population growth, stimulating attempts to intensify production and thereby fueling domestication.

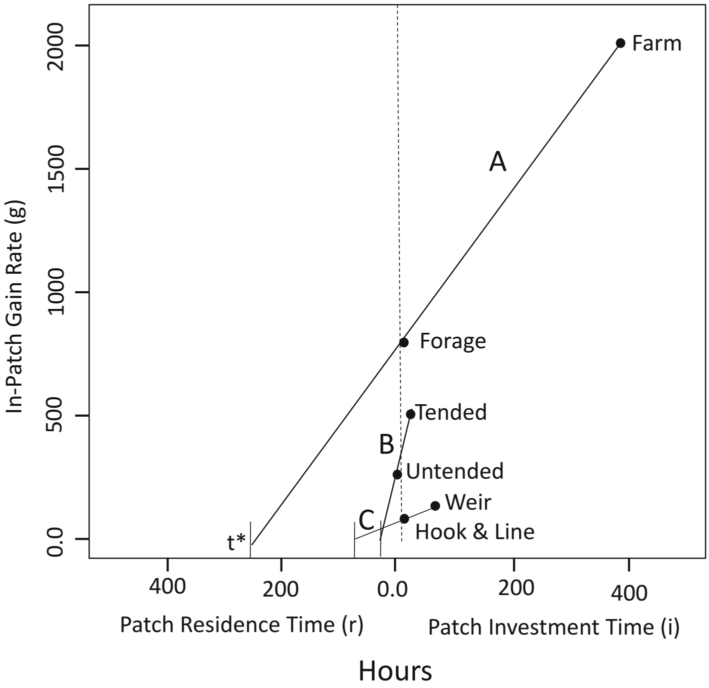

Fig. 13.1 Graphical illustration of the optimal patch investment model applied to three different subsistence activities. Line A shows that investment in maize farming in the Great Basin of western North America would have offered superior return rates compared to foraging, but only after 248 h spent harvesting. This critical threshold for maize farming (t*) is considerably higher than the one for burning acorn groves in California (Line B) or constructing a fishing weir on the Northwest Coast (Line C). Redrawn from Mohlenhoff and Codding (2017, p. 221, Figure 2)

More recently, niche construction was quickly recognized by HBE archaeologists as the process driving resource depression. Broughton et al. (2010) documented a relationship between resource depression and the intensification of agriculture in the Mimbres region of southern New Mexico. Increasing reliance on maize there corresponds to a decline in foraging efficiency documented by zooarchaeological data. Here the application of HBE makes sense of a correlation between bone chemistry, settlement, and technology that might otherwise go unexplained.

Mohlenhoff and Codding (2017) demonstrate one way in which these two important theoretical and methodological tools can be applied together to a problem. They conceptualize incipient food production as a decision to invest labor in a resource patch (by tending, weeding, soil amendments, and possibly planting). Using several case studies, they show how optimal investment in a patch varies with the time spent in it. Investment is only worthwhile when time spent harvesting the patch is sufficient to offset its cost, further discounted by uncertainty about the future yields of the improved patch. For example, controlled burning of acorn groves is a low-cost activity that pays for itself after about an hour of foraging. In contrast, even the most rudimentary type of maize production in the Great Basin Desert would exceed returns from foraging only after 248 h spent harvesting (Fig. 13.1).

Agent-Based Models

The relatively simple models typically employed to investigate foraging decisions (e.g., the PCM and models of central place foraging) are analogous to snapshots; they attempt to identify the key variables driving subsistence choice at a given moment in time. A series of such "snapshots" can help to determine whether change has occurred as well as its magnitude and direction. However, a different approach is required to assess the dynamics of a system over time. One way to effectively model process is by using simulation, which sacrifices generality in favor of greater realism and precision

(Levins 1966). Simulations are time transgressive and able to capture not only the results of static strategies at different points in time but also aspects of the process itself such as rates of change and cycling.

Agent-based models (ABMs) hold particular appeal for researchers studying subsistence transitions because they predict the behavior of decision-makers in the context of the complex system of which they are a part (Cegielski and Rogers 2016). ABMs are based on simulation rather than mathematically derived solutions to optimization problems (Winterhalder and Kennett 2006). Often they use optimization principles to determine how virtual agents make decisions under changing conditions. The computational models employed in ABM, once constructed, can be easily manipulated to assess optimal outcomes under different conditions.

Because of their scale of analysis at the system level, ABMs take into account multiple variables and therefore do not restrict themselves to the plant component of subsistence. They can be very useful for modeling the costs and payoffs of food production under realistic environmental conditions that fluctuate over time. A notable example is the Village Ecodynamics Model used to investigate patterns of population aggregation and dispersal in the Mesa Verde area of the northern US Southwest. Agents representing households were set the virtual task of acquiring sufficient supplies of firewood, game, and maize under different demographic and environmental conditions. The failure of the original model to accurately predict human population sizes led investigators to reevaluate the model inputs. By omitting domestic turkeys as a potential resource, the model had greatly underestimated the ability of the study area to support human communities (Varien et al. 2007; Kohler et al. 2008; Kohler 2010; Kohler et al. 2012).

It is not difficult to envision how HBE models might be embedded within ABMs to address specific decision points within a larger, system-level analysis. Like the agents of the Village Ecodynamics Model, the virtual foragers of the PCM operate under particular decision rules. These rules, predicted from evolutionary theory, can then be integrated into an agent-based model of a larger dynamic system. An example of such an approach appears in Morrison and Allen (2017). This study explores the relationship between life histories of molluscan prey, human foraging efficiency, and resource depression over time using an ABM. Within the model, resource rankings and prey choice are derived in the manner of the PCM but are integrated into a more complex simulation that also includes human and mollusc population dynamics and the life histories and growth patterns of multiple molluscan taxa. Similar efforts might be productively applied to other sessile resources, such as plants.

Conclusions

Archaeologists who specialize in analysis of plant remains and origins of agriculture have been relatively slow to adopt the models of HBE as analytic tools. However, microeconomic models such as the PCM offer a framework for linking behavior to natural selection by using proxy measures (such as efficiency). They encourage researchers to be explicit about their assumptions. Models require metrics such as yields (energy per unit land) and return rates (energy per unit time spent) that may challenge impressionistic assessments of resource values and costs. The structure afforded by HBE also facilitates the research process by directing the evaluation of models that fail to replicate real-world outcomes. Microeconomic models are not well suited to investigating how evolutionary processes, such as plant domestication, unfold over time, but they can help in identifying the decision criteria that initiate and maintain those processes. A broad HBE perspective does not limit itself to modeling as a method, or even to a particular set of models. As the study of adaptive design of human behavior in ecological context, HBE will continue to play a key role in the search for evolutionary explanations of human-plant interaction.

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