

Behavioral Ecology and the Transition from Hunting and Gathering to Agriculture

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THE VOLUME BEFORE YOU is the first systematic, comparative attempt to use the concepts and models of behavioral ecology to address the evolutionary transition from societies relying predominantly on hunting and gathering to those dependent on food production through plant cultivation, animal husbandry, and the use of domesticated species embedded in systems of agriculture. Human behavioral ecology (HBE; Winterhalder and Smith 2000) is not new to prehistoric analysis; there is a two-decade tradition of applying models and concepts from HBE to research on prehistoric hunter-gatherer societies (Bird and O'Connell 2003). Behavioral ecology models also have been applied in the study of adaptation among agricultural (Goland 1993b; Keegan 1986) and pastoral (Mace 1993a) populations. We review below a small literature on the use of these models to think generally about the transition from foraging to farming, while the papers collected here expand on these efforts by taking up the theory in the context of ethnographic or archaeological case studies from eleven sites around the globe.

THE SIGNIFICANCE OF THE TRANSITION

There are older transformations of comparable magnitude in hominid history; bipedalism, encephalization, early stone tool manufacture, and the origins of language come to mind (see Klein 1999). The evolution of food production is on a par with these, and somewhat more accessible because it occurred in near prehistory, the last eight thousand to thirteen thousand years; agriculture also is inescapable for its immense impact on the human and non-human worlds (Dincauze 2000; Redman 1999). Most problems of population and environmental degradation are rooted in agricultural origins. The future of humankind depends on making the agricultural "revolution" sustainable by preserving cultigen diversity and mitigating the environmental impacts of farming. Simple population densities tell much of the story. Hunter-gatherers live at roughly $0.1/\text{km}^2$; rice agriculturists in Java at $1,000/\text{km}^2$, a ten-thousand-fold difference. There were an estimated ten million humans in the world on the eve of food production (Price and Feinman 2001: 194); now over

six billion people live on this planet, an increase of 600% in only ten millennia. Agriculture is the precursor, arguably the *necessary* precursor, for the development of widespread social stratification, state-level societies, market economies, and industrial production (Diamond 1997; Zeder 1991). Social theory (e.g., Trigger 1998) maintains that present-day notions of property, equality and inequality, human relationships to nature, etc., are shaped, at least in part, by the social organization, technology, or food surpluses entailed in our dependence on agriculture.

Domestication today is a self-conscious enterprise of advanced science and global-scale effort, an applied research endeavor comprised of thousands of highly trained and well-supported international specialists. Major research centers like the International Potato Center in Lima, Peru (www.cipotato.org/) support ongoing efforts to further the domestication of useful species; seed banks have been established in many countries to insure the future diversity of the world's key domesticated plants (www.nal.usda.gov/pgdic/germplasm/germplasm.html). The prehistoric beginnings of agriculture though were quite different. The modern world that funds and depends on this continuing process of domestication is, in fact, a creation of the first early humans that pursued, consumed and, in doing so, modified the wild ancestors of the staples that we consider to be important today—wheat, millet, sweet potato, rice, and domesticated animals such as camelids, pigs, sheep, goats, and cows—to name a few. At present it appears as if at least six independent regions of the world were the primary loci of domestication and emergent agriculture: the Near East; sub-Saharan Africa; China/Southeast Asia; Eastern North America; Mesoamerica; and South America (Smith 1998), roughly in the time period from thirteen thousand to eight thousand years ago (Binford 1971; Diamond 2002; Flannery 1973; Henry 1989). The archaeological record suggests that this transformation took place in societies that look much like modern day hunter-gatherers (Kelly 1995; Lee and Daly 1999). Many of the early domesticates

were transmitted broadly through preexisting exchange networks (Hastorf 1999), stimulating the migration of agriculturalists into the territories of hunter-gatherers, who were in turn ultimately replaced or subsumed into agricultural economies (Cavalli-Sforza 1996; Diamond and Bellwood 2003).

Foraging peoples initiated domestication. They did so through the mundane and necessary daily tasks of locating, harvesting, processing, and consuming foodstuffs. The Mass from the 1928 Book of Common Prayer (Protestant Episcopal Church 1945, 81) speaks eloquently of “these thy gifts and creatures of bread and wine . . .” In less poetic non-ecclesiastical terms, but with no less awe at the high importance and, well, the simple gastronomic pleasure of domesticates in our lives, this volume attempts to advance our understanding of why and how this happened. In particular, we hope to demonstrate the utility of a branch of evolutionary ecology, human behavioral ecology.

DEFINITIONS

Clear, standardized terms for the biological and cultural processes involved in the origins of agriculture worldwide remain elusive, despite considerable efforts to define them (Flannery 1973; Ford 1985; Harris 1989; Harris 1996a and b; Higgs 1972; Piperno and Pearsall 1998; Rindos 1984; Smith 1998; Smith 2001a; Zvelebil 1993; Zvelebil 1995; Zvelebil 1996). The reasons for inconsistencies in the treatment of terminology are several and tenacious because they are ultimately rooted in the nature of the problem itself. These include, but are not necessarily limited to the following: (1) research on domestication and agricultural origins is inherently a multi-disciplinary activity, and as such, a wide-ranging set of specialists have worked on the problem, each emphasizing definitions that are somewhat parochial; (2) historical change in each research tradition of archaeology, botany, and genetics has resulted in a range of definitions that may have been suitable at the time they were conceived but

now add to the confusion; (3) rapidly expanding empirical knowledge and the characterization of local developmental sequences results in specialized language that does not transfer well to other regions where similar transformations occurred; (4) agricultural origins are an inherently evolutionary question and, as in any system of descent with modification, categorical or taxonomic distinctions have fuzzy and, for different cases, unevenly and perhaps differently demarcated boundaries; and, (5) food production and agriculture have an impact on multiple features of human societies—e.g., economic, political, social, and ideological, any one of which might be featured in definitions.

Like earlier attempts, our definitions reflect limitations of our knowledge and approach. *Hunting and gathering* entails obtaining daily sustenance through the collection or pursuit of wild foods; wild foods in turn being species whose reproduction and subsistence are not directly managed by humans. Data from around the world indicate that prior to approximately thirteen thousand years ago, all people known archaeologically relied upon hunting and gathering wild foods. Hunting and gathering populations expanded into a broad range of habitats during the Terminal Pleistocene and Early Holocene when foraging strategies diversified (Stiner 2001), in part due to the extinction of previously targeted, large-game species, but also because of the broad array of resource alternatives afforded by warmer Holocene climates (Richerson et al. 2001). Hunting and gathering societies have persisted in various parts of the world (Lee and Daly 1999), but starting after about 13,000 BP (before the present) most foragers evolved into or were subsumed or replaced by groups practicing mixed foraging and cultivation strategies and, ultimately, agriculture (Diamond and Bellwood 2003).

On the other end of a mixed spectrum of subsistence strategies is agriculture. We define *agriculture* as the near total reliance upon domesticated plants or animals; domesticates being varieties or species whose phenotype is a

product of artificial selection by humans, and whose reproduction and subsistence are managed directly by people. For plants, such management almost always involves an investment in seed selection; clearing, systematic soil tillage, terracing to prepare fields, crop maintenance, weeding, fertilization, and other crop maintenance; and, development of infrastructure and facilities from irrigation canals to processing facilities and storage bins. Parallel efforts are entailed in animal husbandry. Even societies practicing the most intensive forms of agriculture may engage in incidental hunting and gathering of wild foods, depending upon their availability or desirability (e.g., deer, blackberries). Dense populations and centralized state-level societies like our own depend upon increasingly complex systems of agriculture (Boserup 1965; Zeder 1991) involving modification to soil texture, structure and fertility (Harris 1989) and sometimes resulting in severe environmental degradation, one of the great challenges of our day (Stockstad and Vogel 2003).

Our definition of agriculture emphasizes *domesticated* plants and animals. Domesticates are new plant or animal varieties or species created from existing wild species through incidental or active selection by humans (Smith 1998). Typically selection leads to biological characteristics that are advantageous to humans; larger seeds, thinner seed coats, greater docility, smaller size animals. Because humans intervene in the natural lifecycle of these plants and animals, many domesticates lose their ability to survive without human management. This outcome is not surprising since it is well known that foragers alter the landscape that they inhabit by burning, transferring plants and animals between habitats, and occasionally interjecting themselves into other species' lifecycles (Hastorf 1999; Smith 1998).

Some plant species were better suited to domestication than others due to their ability to do well in the artificial environments created by humans (Smith 1998). In some instances, the biological changes may have begun incidentally as a co-evolutionary by-product of human exploitation

(Rindos 1984). In other cases domestication may have occurred under conditions of repeated cultivation and harvest (Harlan 1992c; Harris 1989; Ford 1985; Piperno and Pearsall 1998). *Cultivation* is the tending of plants, wild or domesticated; *husbandry* is the parallel term for animal species. Use of the term cultivation specifically acknowledges the possibility that humans tended wild plants for significant time periods before we would classify them as domesticates based on observable genetic alterations (Keeley 1995; Piperno and Pearsall 1998). We reserve the term *cultigen* for domesticated plants under these same conditions.

A variety of stable subsistence economies, extant, historic, and prehistoric, draw upon elements of hunter-gatherer *and* agricultural modes of production. These are difficult to characterize in existing terminologies except as “mixed” economies, engaged in what Smith (2001a) has characterized as *low-level food production*. They typically depend significantly on hunting and gathering while to varying degrees using cultigens or keeping domesticated animals. *Horticulture*, the small-scale planting of domesticated species in house gardens or the use of swidden plots, combined with routine hunting and gathering of wild foods for a significant part of the diet, would be considered a form of low-level food production. Contemporary casual farming by the Mikea hunter-gatherers of Madagascar would be an example of this practice (Tucker 2001; Chapter 2, this volume).

The boundary between low-level food production systems and agriculture is inherently fuzzy. We believe the term agriculture is merited when foraging recedes to an episodic, infrequent or recreational activity, regular provisioning using domesticates takes over daily subsistence, while agricultural work and animal husbandry come to dominate the activity schedules of adults. Although numeric boundaries are somewhat arbitrary and unsatisfactory, agriculture implies that approximately 75% of foodstuffs are acquired from domesticated sources. Although few contemporary societies engage in low-level food production, the archaeological record suggests that

mixed foraging and cultivation/husbandry strategies were common and often stable, in the sense that they were practiced by people for thousands of years before they developed a full commitment and reliance upon agriculture (Smith 2001a).

RESEARCH TRADITIONS IN AGRICULTURAL ORIGINS

Speculation about the origins of food production is probably as old as the first encounter between peoples who recognized that they differed appreciably in their dependence upon domesticated plants or animals. Longstanding traditions in western thought have seen foragers as scarcely removed from animal nature, thus, as societies, simple and primitive, living without the many accoutrements and means of control over nature that we associate with agriculture and industrial culture (Darwin 1874, 643; Powell 1885). Agriculture as an advance was instantly understandable. Hobbes’s famous sentiment that hunting and gathering was a life “solitary, poor, nasty, brutish, and short” (Hobbes 1952, 85) is widely cited, but his views were generally shared in the nineteenth century, for instance by the novelist Charles Dickens (Dickens 1853). We today dismiss this kind of progressive evolutionism as simple-minded ethnocentrism. Foragers may not be the “original affluent society” claimed by Sahlins (1972; Hawkes and O’Connell 1981), but most foraging societies elude the generalizations implied in each of Hobbes’s five famous adjectives. We cannot so easily dismiss questioning just what distinguishes foragers from food producers and how humans evolve, in either direction, from one to the other of these subsistence forms or maintain a mixture of the two for long periods of time.

European scholarly tradition, informed by increasingly reliable ethnography and archaeology, has a long engagement with agricultural origins (see Gebauer and Price 1992b; Redding 1988; Smith 1998). We highlight three of the most popular forces employed by archaeologists to explain the origins of agriculture: demographic pressure, environmental change, and

socioeconomic competition. Demographic pressure and environmental change are exogenous forces and socioeconomic competition is endogenous. None in and of itself satisfactorily explains the origins of agriculture; each was probably an important element of the process, whatever the strength of its causal role. One of the virtues of HBE is its ability to integrate multiple variables like these, with an emphasis on behavioral responses to changing socio-ecological conditions.

DEMOGRAPHIC PRESSURE

Population-resource imbalance caused by demographic pressure is one of several univariate explanations for the origins of agriculture (Cohen 1977; Smith and Young 1972; Smith and Young 1983). In the best known formulation of this idea, Mark Cohen (Cohen 1977) argued that worldwide population growth explained why hunter-gatherers living in different locations independently turned to agriculture at the end of the Pleistocene. The argument was based on the premise that the adoption of agriculture resulted in a net increase in workload and a decrease in food diversity and sufficiency, and therefore an overall reduction in the quality of life, a situation that any rationally minded hunter-gatherer would not enter into freely. Cohen argued that as hunter-gatherers exceeded environmental carrying capacity, food shortages pushed them to experiment with plants and animals and, ultimately, with agriculture. Hunter-gatherers over-filled salubrious habitats worldwide and were compelled to augment their subsistence with food production.

Critics of this position were quick to point out that the archaeological record does not support the idea that environments worldwide were saturated with hunter-gatherer populations on the eve of agricultural development (Bronson 1977; Reed 1977; Rindos 1984). Even localized populations in the primary centers of early domestication appear to be relatively small (Piperno and Pearsall 1998). Others have emphasized the difficulties of measuring population levels in the archaeological record or determining the overall population levels that could be

sustained without significant amounts of environmental degradation and pressure for change (Glassow 1978). There have been attempts to better contextualize demographic change by melding it with ecological models, usually in relation to variations in climate (Bar-Yosef and Meadow 1995; Binford 1971; Flannery 1971; Flannery 1973; Hassan 1977; Henry 1989; Hesse 1982b). These models sometimes lack specificity about the form or degree of demographic pressure required to provoke subsistence change, and they seldom explain why hunter-gatherer populations grew more rapidly and stimulated domestication and agricultural development in certain parts of the world and not others (Keeley 1995).

One response to the early overemphasis on demography has been to heavily discount its importance in the process of domestication and agricultural development (Hayden 1990; Hayden 1995a). This is unfortunate because foragers clearly have dynamic relationships with their living resources and this in turn has population level effects (Winterhalder and Goland 1993; Winterhalder et al. 1988). Even small hunter-gatherer populations alter the distribution and availability of harvested plant and animal species (Stiner et al. 2000). Sometimes this results in decreased availability or resource depression; in other instances, it may result in increased resource abundance. The effects that hunter-gatherers have on the density, distribution, and productivity of resources is well documented in California (e.g., Kumayee; Shipek 1989) and Australia (Gidjngali; Jones and Meehan 1989). Environmental change independent of humans is ubiquitous and can also affect the distribution and availability of important species. Economic decisions by prehistoric foragers to experiment with and ultimately manage certain species of plants and animals occurred within this dynamic context of demographic change and varying plant and animal densities.

ENVIRONMENTAL CHANGE

V. Gordon Childe was one of the first, and certainly the most notable, archaeologists to explicitly hypothesize that changes in climate at the

end of the Pleistocene stimulated the transition to agriculture (e.g., his Oasis or Propinquity Theory; Childe 1928; Childe 1951). According to Childe, agriculture developed rapidly, hence the term Neolithic Revolution, and thus was synchronous with the onset of dry conditions that climate records were suggesting in the Near East at the end of the Pleistocene. To survive, humans and potential domesticates concentrated together in well-watered locations like oases and river valleys, where their close interactions naturally led to domestication and ultimately agriculture. The discovery of sickle blades and grinding stones in the Carmel Caves of coastal Palestine suggested that hunter-gatherers collected wild cereals during the Natufian Period (13,000 BP–10,000 BP), evidence used by Childe in support of this idea (Henry 1989, 6). Although propinquity is overly simplistic (Redding 1988), subsequent paleoenvironmental and archaeological work suggests that regionally specific climatic and biotic changes did occur at the end of the Pleistocene. These surely played a role in shaping spatially local cultural developments, including the domestication of plants and animals and ultimately the adoption of agricultural practices (Henry 1989; Wright, Jr. 1968; Wright, Jr. 1993).

Unfortunately, the overly deterministic nature of the Oasis Theory also provoked a backlash in the broader archaeological community against the importance of changing environmental conditions during the Late Pleistocene and Early Holocene (e.g., Braidwood and Howe 1960; Wagner 1977). For many years the role of climate change was simply ignored or deemphasized relative to other mechanisms perceived to have greater explanatory value. With several noteworthy exceptions (Harris 1996a; McCorrison and Hole 1991; Piperno and Pearsall 1998; Watson 1995; Wright, Jr. 1993), this continues today, even with the development of sophisticated paleoenvironmental techniques (e.g., Piperno 1998) and the aggressive advance of earth system science and high resolution climate records (Hodell et al. 1995;

Hostetler and Mix 1999; Kennett and Kennett 2000; Rittenour et al. 2000; Whitlock 1992; Woodhouse and Overpeck 1998).

These records show that the domestication of key cultigens in the Old and New Worlds occurred during an interval marked by significant fluctuations in global climate (13,000–8,000 BP; Richerson et al. 2001; Piperno and Pearsall 1998). Environmental change at the end of the Pleistocene was most pronounced at higher latitudes as ambient air temperature increased, glaciers receded, sea-levels rose, and forests replaced periglacial tundra (Roberts 1998). Dramatic fluctuations in high latitude environmental conditions parallel substantial changes in temperature and rainfall regimes at lower latitudes (Henry 1989). These changes instigated regional biotic shifts in resource abundance and density. Some regions witnessed the extinction of several large animals, a likely product of environmental change and intensified human predation at the end of the Pleistocene (Lister and Sher 1995; Piperno and Pearsall 1998; cf. Grayson and Meltzer 2003). Others experienced the expansion of wild plant species that were intensively harvested by foragers and, through selective manipulation, became important cultigens (e.g., barley and emmer wheat; Henry 1989, 32). It is under these dynamically changing environmental conditions that foragers altered their subsistence regimes and made dietary choices that led to plant and animal domestication, low-level food production, and ultimately agriculture.

SOCIOECONOMIC COMPETITION

Endogenous social change, particularly the development of prestige economies via socioeconomic competition, has recently become a popular explanation for the transition to agriculture (Bender 1978; Blake et al. 1992a; Hayden 1990; Hayden 1995a; Price 1995b; Smalley and Blake 2003). The mechanism for change in these models is status-seeking individuals, usually men, who encouraged and controlled the growth of potential domesticates to create surpluses for social purposes such as competitive

feasting, alliance formation, and extortion, rather than as primary sources of food. Hayden (1995a, 289) has been the most outspoken advocate of this idea as a general explanation for the transition to agriculture worldwide—from the earliest plant and animal domestication through the development of more intensive forms of food production.

Hayden's model is based on five testable hypotheses (Hayden 1990; see Keeley 1995: 244): (1) domestication and agriculture will emerge in resource-rich, not resource-poor, zones; (2) it will first develop in ranked societies that have marked status inequalities; (3) individuals within these societies will hold competitive feasts; (4) the first plants and animals domesticated will be intoxicants, delicacies, or prestige goods rather than bulk or mundane food items; and (5) evidence for resource stress and malnutrition caused by population pressure or climate change will be absent. In archaeological terms Hayden's scenario implies correlation between plant and animal domestication and agricultural development, and the emergence of socioeconomic complexity, marked archaeologically by a high degree of sedentism (typically large sites with substantial architecture), at least two-tiered settlement hierarchies, intensified production agriculturally or otherwise, storage, specialized production of prestige items or status markers, intensified exchange, acquisition of exotic items by elites, and differential distribution of prestige items in households and burials.

There are several fundamental flaws with the socioeconomic competition model; there are also some intriguing and potentially important insights. As a stand-alone model for agricultural origins, socioeconomic competition fails on two levels. First, it lacks a unifying explanation for why agriculture developed in several independent regions at approximately the same time—other than suggesting it was a historical accident (Piperno and Pearsall 1998, 14). Second, although there is evidence that agriculture often developed in resource-rich habitats (Price and Gebauer 1995b, 8), the initial domestication of most plants and animals occurs well

before conditions promoted socioeconomic competition, at least in Asia, Africa, and the Americas (Piperno and Pearsall 1998, 14; Smith 1998, 209). It appears that many domesticates in Mesoamerica, the Near East, and eastern North America were used by hunter-gatherers at a low level for thousands of years prior to their intensified use (Smith 2001a, 19). This hints that socioeconomic competition is more likely to be significant in the later stages of the transition.

The social significance of food is patent. That some plant species might initially have been grown to brew beer is intriguing; the social aspects of drinking intoxicating liquids are difficult to refute (Blake et al. 1992a; Hayden 1990; Smalley and Blake 2003). However, plants used to brew intoxicating liquids can also serve as valuable food items whether they are fermented or not. This means that multiple currencies must be considered when resource value is assessed by archaeologists. The ability to store surplus food must also be analyzed for its social significance. Individuals who successfully grow, store, and defend food items can use these stores to their social advantage, gaining prestige and influence. Use of surplus food to improve social advantage, at least under certain environmental and demographic conditions, should be examined by scholars employing HBE models.

HBE RESEARCH ON AGRICULTURAL ORIGINS

There is a small HBE literature on agricultural origins. Keegan (1986, 92) made an early and prescient argument that foraging models could be extended to the study of horticultural production. He highlighted horticulture because it represents a mixed subsistence system, transitional between the economies of hunter-gatherers and agriculturalists. Using data from the Machiguenga of Peru, Keegan argued that the key variables of the diet breadth and patch-use models have direct analogs in food production, facilitating the use of these cost-benefit models

in analysis of this system and the evolutionary transitions that gave rise to it. His calculations showed that the Machiguenga generally were stocking their gardens with optimal combinations of cultigens and, with allowance for seasonal and nutritional constraints, making efficient trade-offs among fishing, forest hunting, and gardening.

In a 1991 paper, Layton et al. (1991) described a “complete break” from the standard, evolutionary progression theories of agricultural origins. They proposed instead an approach that sees hunting, gathering, herding, and cultivation as alternative strategies of subsistence that may be taken up alone or in various, stable combinations, depending on socio-ecological circumstances, and without any implication of irreversible directionality to transitions among them. For instance, there is nothing to prevent food producers from evolving into foragers. Various conceptual elements from foraging theory, such as the ranking of resources by pursuit and handling costs, cost-benefit analysis of subsistence trade-offs, boundary defense, and risk minimization are found throughout their argument. In support of their interpretation they summarized numerous ethnographic cases in which these strategies are mixed in shifting and sometimes stable balances, reminiscent of Smith’s (2001a) concept of low-level food production.

Layton et al. stimulated two follow-up papers, both of them making more explicit use of foraging theory to critique or amend specific predictions from their article. Hawkes and O’Connell (1992; cf. Layton and Foley 1992) used a sharper distinction between search, and pursuit, and handling times—the central conceptual distinction of the diet breadth model—to argue that high-ranking resources will *not* drop out of a forager’s diet in response to exploitation and depletion. However rare, they will always be pursued when encountered. Hawkes et al. expand discussion of the circumstances likely to promote subsistence innovation, and argue that “increases in diet breadth result from reduced foraging return rates and so lead to

declines in population growth rates” (Hawkes and O’Connell 1992, 64). They also draw attention to HBE arguments for a gendered division of labor (Hawkes 1991) that might have been important in the evolutionary processes underlying subsistence transitions.

In a second follow-up paper, Winterhalder and Goland (1993) addressed the population growth prediction by Hawkes and O’Connell, cited just above. They used a dynamic, population ecology variant of the diet breadth model to show that declining foraging efficiency associated with expanding diet breadth may result in a decrease or an increase in forager population density. The deciding factors are the density and reproductive potential—together, the sustainable yield—of the low-ranking resources that happen to come into the diet.

Subsequently, Winterhalder and Goland (1997) expanded on these arguments for using a HBE form of analysis in agricultural origins research. They cited three advantages that distinguish HBE from other research traditions: (1) it engages selectionist explanations (Smith and Winterhalder 1992b) that are more powerful than the more commonly used functionalist ones; (2) it has tools for non-normative analysis of unpredictable variation in environmental features and the risk-minimizing adaptive tactics they elicit; and (3) it focuses on localized and immediate resource decisions and their consequences for people “on the ground.” HBE thus engages the behaviors most likely to be causal to evolutionary change: “The changes we summarize under broad concepts such as *domestication* and the *Neolithic revolution* have their origin and form in the ecologically situated choices and actions of individuals” (Winterhalder and Goland 1997, 126; italic in original). Winterhalder and Goland used the diet breadth model to show how foragers might initially come to exploit the organisms that became domesticates, and to speculate on the adaptive consequences of this co-evolutionary engagement. Among the effects examined were the consequences for resource depletion, human population density, and risk management tactics, using evidence

from eastern North America to exemplify their arguments.

Working on the prehistoric development of agriculture in eastern North America, Gremillion (1996a) used diet-breadth and risk-minimization models along with opportunity-cost arguments to generate and evaluate predictions about the circumstances in which new cultigens will be adopted by groups already practicing some agriculture, and whether they will replace existing plant resources, as did maize following a significant delay from its first appearance, or become a supplement, as in the case of peaches. In a second study, Gremillion (1998) analyzed macrobotanical data from the Cold Oak rock shelter in eastern Kentucky to show that increased dependence on cultivation of seed crops around 1000 BC was accompanied by greater anthropogenic disturbance of habitats and a shift in mast resources from acorns to hickory nuts. She developed several HBE hypotheses to address this situation, finding greatest credence for the idea that an increase in the overall abundance of mast resources led to specialization on the most profitable species, in this instance hickory, at the expense of the less highly ranked oak. Alternatively, increases in the ranking of profitability of seed crops such as maygrass, chenopod, and knotweed may have displaced acorns from the diet due to their high processing costs. In each of these applications Gremillion argued that HBE is a fertile source of new and archaeologically testable hypotheses about the subsistence and economic changes associated with the origins of agriculture.

The most thorough existing application of HBE to the question of agricultural origins is Piperno and Pearsall's (1998) monograph, *The Origins of Agriculture in the Lowland Neotropics*. Over half the crop plants domesticated in the Americas are thought to have wild progenitors native to neotropical lowland habitats. Among them are New World staples such as manioc, yams, achira, sweet potato, peanut, gourds, squashes, beans, and perhaps maize. These plants likely were first used by foragers, who cultivated, domesticated, and subsequently

incorporated into specialized agricultural production systems, in seasonal, low elevation forested habitats of the neotropics.

Piperno and Pearsall focus their analysis on the climate and vegetation changes occurring at 11,000 to 10,000 radiocarbon years BP and their likely effects on Neotropical foragers. The first inhabitants of the neotropics encountered a salubrious, open-grassland foraging environment that persisted for only a short time. At around 10,500 BP, the transition to a wetter Holocene climate began to produce a seasonal, deciduous forest cover in the lowland tropics. Piperno and Pearsall hypothesize that due to this habitat shift, and perhaps also to human exploitation (1998, 181), the abundance of the high ranking, "open habitat," plant and animals species decreased, along with foraging efficiency. While the new seasonal forests remained relatively hospitable to mobile hunter-gatherers at low population density (1998, 71), the diets of early Holocene foragers expanded to encompass a broader array of dry-forest plants, species that previously had been ignored. For instance, comparative studies of the efficiency of harvesting tubers suggest they likely were outside of the optimal diet in the late Pleistocene (1998: 85), but moved into that diet as a low-ranked but critical resource once early Holocene habitats became more forested.

The low-ranking, newly important species found in seasonally dry forests were subject to human interest and manipulation, either intentional or inadvertent, routed into cultivation and eventually domesticated (1998; 27, 82). Because they were sparsely distributed over the landscape, hence relatively unattractive to human foragers, there arose an immediate advantage for those who manipulated through burning or harvested species from these habitats so as to increase their density and yield of useful energy or materials.

Piperno and Pearsall cite three rationales for using the diet breadth model in this analysis (1998, 236): (1) the archaeological evidence shows that early hunter-gatherer/horticultural residents of the neotropics had an expanding

diet breadth followed by increasing subsistence commitment to low-ranked species; (2) the prehistoric changes of concern are evident enough that short-term precision in the use of the model isn't necessary (cf. Smith, this volume); and finally (3) evidence from ethnographic tests shows that this model and an energy currency are commonly successful in predicting the economic response of foragers to changing environmental circumstances. They conclude, "[b]ehavioral ecology seems to us to be the most appropriate way to explain the transition from human foraging to food production" (1998, 16).

Many of the dozen or so early HBE papers on domestication and agricultural origins are fairly general and conjectural. They ask, without too much attention to specific cases or the empirical record of prehistoric findings on this topic, how might the ideas of HBE be used to address the question of agricultural origins? By and large, their authors are ethnographers whose experience is with extant hunter-gatherer societies. And, they generally have been written by people who already placed themselves within the research tradition of HBE. By contrast, most of the papers in this volume are based on empirical case studies, and they are written largely by archaeologists. Most are authored by individuals for whom behavioral ecology is a new analytic tool.

We do not claim that the HBE research tradition is a complete replacement for the other approaches that we have identified and briefly described. We view it rather as a sometimes complementary and sometimes competing form of explanation. It is complementary in two respects: (1) HBE takes up issues rarely or never addressed in these approaches; search and pursuit trade-offs in the harvest of low-ranking resource species; risk-sensitive adaptive tactics; and, (2) it frames these issues in quite a different manner than other, sometimes older, anthropological and archaeological research traditions by focusing on the costs and benefits associated with individual-level subsistence decisions in localized ecological settings. This framing difference is determined largely by the analytical

effort of modeling and hypothesis testing within an explicitly selectionist, neo-Darwinian theoretical framework (Smith and Winterhalder 1992b; Winterhalder and Smith 1992). In both respects, HBE provides tools that complement or make other traditions more complete. At the very least, HBE provides a theoretically well-grounded set of tools to begin exploring the transition to agriculture in a variety of environmental and social contexts.

For instance, although Hayden (Hayden 1990; Hayden 2001) presents his competitive feasting model as a sufficient social explanation for the origins of agriculture, in effect as an alternative to models drawing on materialist or ecological explanations, we would prefer a more cooperative form of analytic engagement. We might assume that social stratification and competitive feasting increase the demand for resources and then ask how this source of ecological change would be represented in terms of foraging models—those extant, adapted, or developed specifically for this purpose—and with what consequences for predictions about subsistence choices and the co-evolution of humans and their resources. Taking this a step further, HBE might help us to identify the socio-ecological circumstances and evolutionary processes that combine to generate a competitive social hierarchy like that expressed in feasting (Boone 1992). A signal strength of HBE is its ability to carry into hypothesis generation a wide variety of postulated sources of causation—global climate change to the aggrandizement of dominant individuals.

Nonetheless, to the extent that HBE is successful in addressing the question of agricultural origins, it will raise doubts about or contradict elements of other research traditions. In the process it will help us sort out, appraise and discard faulty elements of these approaches. Thus, for reasons of parsimony as well as theory, those working in the HBE tradition are skeptical of the adequacy of explanations couched at the level of global prime movers such as climate change. Likewise we doubt the efficacy of explanations made in terms of universal, directional pressures,

such as Childe's postulated trend of increasing energy capture (Childe 1965) or ecosystem approaches premised on cybernetic properties such as homeostasis (Flannery 1968).

HUMAN BEHAVIORAL ECOLOGY

HBE has been used to analyze hunter-gatherer economies with favorable results for over two decades. This work is both ethnographic (Hill and Hurtado 1996; Smith 1991) and archaeological (Bettinger 1991b). Because the basics of this approach are well-described elsewhere (Smith and Winterhalder 1992a), we offer here only minimal coverage of assumptions, fundamental concepts, analytic tools, and models and hypotheses, with an emphasis on the models employed by the contributors to this volume and concepts and tools that may be of future use to scholars interested in exploring the problem of agricultural origins.

THE OPTIMIZATION ASSUMPTION

Behavioral ecology begins with an optimization premise. As a result of natural and cultural evolutionary processes, behavior will tend toward constrained optimization (Foley 1985). This assumption makes operational the long-standing view of anthropologists that hunter-gatherers tend to be skilled and effective in the food quest (Winterhalder 2001). Efficiency, say in capturing food energy, is important even if food is not in short supply because it affords hunter-gatherers the time and resources to engage fully in other essential or fitness-enhancing activities (Smith 1979). We state this premise as *constrained* optimization because we do not expect behavior to be fully optimal. Temporal lags in adaptation and compromises among conflicting adaptive goals impede this outcome. Optimization likewise must be determined within the cognitive capacities, beliefs and goals of the organism under study. We adopt the assumption of constrained optimization rather than "satisficing" because the latter—while it may lead to superficially similar predictions—is an empirical concept and is therefore not able to

generate theoretically robust predictions (Elster 1986). Constrained optimization is an analytically powerful starting point that does not entail the belief that behavior is routinely optimal, only that there be a tendency towards optimal forms of behavior.

FUNDAMENTAL CONCEPTS

Behavioral ecology likewise is grounded in the observation, now well confirmed by non-human as well as anthropological studies, that some fundamental economic concepts transcend their scholarly origins in microeconomic attempts to explain the functioning of market-oriented economies. They are useful for studying adaptive decision making whether the questions concern the behavior of capitalists and workers, or the subsistence choices of hunter-gatherers, horticulturalists, and agriculturalists, not to say juncos (Caraco et al. 1980) and bats (Wilkinson 1990). At a minimum this list would include marginal valuation, opportunity costs, discounting, and risk sensitivity.

MARGINAL VALUE. For most tasks we pursue and things we consume, immediate value changes with quantity, be it duration of the activity or the amount of a good obtained or ingested. The first breakfast sausage is more satisfying than the sixth or seventh; an hour-long bath is a delight, but four hours in the tub makes even insipid alternatives attractive. This would be trivial except for the additional observation that the decision to suspend consuming something like sausage or doing something like taking a bath is based on its marginal rather than initial, average or total value. Because of marginal valuation we move from doing one thing to another even though the intrinsic qualities of the options themselves may be unchanging. The formulation of marginal analysis was fundamental to microeconomics (Rhoads 2002), and the careful reader will find marginal trade-offs in each of the foraging models we discuss below.

OPPORTUNITY COSTS. The idea of opportunity costs is closely related: the decision to switch from one behavior—a kind of consumption; a

work activity—to another depends not only on its marginal value, but on the return to be gained from the available alternatives. Thus, one ceases to consume sausage when it becomes more attractive to sip orange juice; one stops bathing when preparing a ceremony is more compelling. More to the point of our subject, one ceases to forage for mussels when the opportunity and benefits of doing something else take precedence. In each case we assess the current activity, be it consumption or purchase against what we might be doing instead. In technical terms, the opportunity cost of an activity refers to the value of the opportunity that is foregone or displaced by continuing it. For instance, the diet breadth model (see below) sets the decision to pursue a particular resource against the opportunity cost of ignoring it in favor of searching for a more profitable resource to pursue.

Much of microeconomics is a logical and mathematical elaboration on the workings of marginal valuation and opportunity costs, as they are manifested in the environment of a market economy. Using these ideas, economists ask how a wage earner's consumption patterns change in response to an increase in her income. By contrast, the behavioral ecologist analyzes how these two concepts play out as an organism interacts with a natural environment of physical processes and other organisms in the roles of predators, competitors, food resources, potential mates, and offspring. She asks, how might the resource choices of a forager shift as a consequence of a decline in the density of a highly valued resource, or an improvement in the technology used to harvest a particular species?

Marginal value and opportunity costs and benefits are at the heart of behavioral ecology models. The most basic claim of the papers in this volume is that these same ideas can be adapted to an understanding of decisions faced by humans during the evolutionary transition between foraging and agriculture.

DISCOUNTING. Discounting refers to the situation in which we assign a future reward less value than if it were available immediately

and with certainty. For instance, we would pay less at planting time for a corn crop which might after all fail, than for that same crop at harvest time when the yield is certain. We discount in this manner when the cost of an activity such as planting occurs immediately but the reward, the harvest, is delayed and, perhaps because of that delay, uncertain. Delay alone can be important because the opportunity to benefit, even from a completely assured harvest in the most extreme case might diminish or pass, were the cultivator to die in the meantime. Delay also offers opportunities for hailstorms, locust plagues and other unforeseen events to reduce the value of the reward itself. For both reasons, effective behavior will hedge, finding it economical to discount delayed rewards. Use of this concept is fairly recent in behavioral ecology theory (Tucker 2001). Because the shift from hunting and gathering to agriculture represents a shift from immediate- to delayed-reward activities (the original terms are those of Woodburn 1982) this basic concept likely will be quite important in economic analyses of the transition from foraging to farming.

RISK-SENSITIVE BEHAVIOR. Basic (or deterministic) behavioral ecology models assume that all environmental variables are constants and that a forager pursuing an optimal set of resources gets the expected (average) reward at all times. By contrast, risk-sensitive models aim to be more realistic by introducing a stochastic element to the relevant environmental variables. All hunters recognize the large role of chance in the discovery and successful capture of game. In a risk-sensitive model the acquisition rate experienced by the forager is expressed by a statistical distribution; outcomes can be assigned probabilities but the actual rate at any time is unpredictable. Therefore, the optimization problem must take into account both the long-term average and the inevitable periods of shortfall. Risk-sensitive models do this. They are generally more realistic and more complicated than deterministic models, sometimes generate like predictions and, given the heuristic nature of the modeling effort, may not always

be the preferred option for analysis (Winterhalder 1986).

There is a well-developed literature regarding the risk-sensitive behavior of foragers and food-producers, taken separately (Cashdan 1990; Halstead and O'Shea 1989; Winterhalder et al. 1999), but little has been written about risk-sensitive adaptation during the transition from one of these subsistence systems to the other (Winterhalder and Goland 1997).

MODEL FEATURES

The concepts just reviewed—marginal valuation, opportunity cost, discounting, and risk-sensitive analysis—signal that behavioral ecology is an attempt to assess the costs and benefits of alternative courses of action under a range of environmental conditions. In operational terms, we accomplish this task with models that have in common four features: an alternative set, constraints, some form of currency, and a goal.

Within a particular model, the range of possible behavioral actions is known as the *alternative set*. For instance, the diet breadth model specifies an alternative set of ranked combinations of potential resources (see below). In the marginal value theorem, the alternative set refers to patch residence times. The alternative set is the dependent variable in the analysis; a particular socioenvironmental factor constitutes the independent variable. The model itself does not specify what might cause the independent variable to take on a certain value, or to change. It thus leaves open the opportunity for exploring how diverse influences such as habitat or climate change, seasonal variations in population density, over exploitation, competition from another predator or pressure to extract a surplus might affect a behavior like resource selection.

The specifics of the organism's capabilities and the environmental features that structure resource selection opportunities are *constraints*. In the diet breadth model constraints include things like the size of the forager, the hunting and gathering technology used, and the distribution and caloric value of the targeted resources. Constraints are all of the elements of the situa-

tion that are taken for granted (more formally, treated with a *ceteris paribus* assumption; see Boyer 1995), in order to focus analysis on one set of effects.

The measure we use to assess costs and benefits is known as the *currency*. While the currency might be any feature of a resource that gives it value, foraging theorists typically assume that food energy is the most important attribute. After oxygen and water, mammals require metabolic energy in large amounts on a nearly continuous basis. The omnivorous diet of most hunter-gatherers makes it likely that meeting one's need for energy entails meeting the needs for other nutrients. This may be more problematic with agriculturalists. The kcal currency is expressed as an efficiency, the net acquisition rate (NAR) of energy. Where energy is not limiting or is less limiting than some other factor—e.g., protein—then that can be used as the currency. For instance, we know that some forms of energy, especially those from large or dangerous game animals, are more prestigious than others (tubers, for instance; Hawkes and Bliege Bird 2002), suggesting that not all kilocalories are equal. Prestige might enter into the currency in some cases. Behavioral ecologists generally emphasize secondary currencies like kcals or mating success because they are more tractable than the primary neo-Darwinian measure of reproductive fitness (Shennan 2002, 108–11).

The final feature of models is the *goal*. A deterministic foraging model likely would have the goal of maximizing energy capture while foraging. A risk-sensitive model would emphasize the goal of avoiding harmful shortfalls of energy. Behavioral ecology models of food transfers in a social group might stress the evolutionarily stable equilibrium of distribution tactics. The polygyny threshold model for mating tactics would emphasize the goal of reproductive success. Different goals usually imply different methods: simple optimization analysis for energy maximization; stochastic models for risk minimization; game theory for frequency dependent behaviors, like intragroup

transfers, that result in evolutionarily stable strategies. The optimization assumption ties together constraints, currency, goal, and the costs and benefits of the alternative set. For instance, given constraints of resource densities and values, and their associated costs and benefits, we predict that organisms will select the alternative that provides them the highest available net acquisition rate of energy. As noted earlier, even when there is no particular shortage of foodstuffs, efficient foraging frees time for alternative activities and lessens exposure to risks associated with foraging. While we don't expect the organism always to engage in the optimal behavior, models based on this assumption have proven to be robust when compared to ethnographic and archaeological datasets (Broughton 1999; Smith 1991).

FORAGING MODELS

Foraging models typically come with a long list of assumptions, awareness of which is critical to their successful use. The models are most often expressed precisely in mathematical formulas or graphs (Stephens and Krebs 1986). In this chapter we provide qualitative and verbal summaries only; explications of greater detail can be found in individual chapters. We trust that the reader wishing to apply the models and understand them more thoroughly and critically will study the references we give for each model.

DIET BREADTH (RESOURCE SELECTION)

The diet breadth or resource selection model (DBM) is one of the oldest and most commonly used (MacArthur and Pianka 1966; Schoener 1974; Winterhalder 1987), particularly by archaeologists (e.g., Broughton 1999; Butler 2000). It is sometimes called the encounter-contingent model because it focuses on the decision to pursue or not to pursue, to harvest or not harvest, a resource once it is encountered. The decision entails an immediate opportunity cost comparison: (a) pursue the encountered resource, or (b) continue searching with the

expectation of locating more valuable resources to pursue. If the net return to (b) is greater than (a), even after allowing for additional search time, then the optimizing forager will elect to pass by the encountered resource, and will continue to do so no matter how frequently this type of resource is encountered.

The general solution to this trade-off is devised as follows: each of k potential resources is ranked in descending order by its net return rate for the post-encounter work to obtain it. This represents a resource's net profitability with respect to pursuit, harvest, and handling costs. The alternative set then is made up of diet breadths from 1 to k , in the form $db = 1$, $db = 1 + 2$, $db = 1 + 2 + 3$, up to $db = 1 + \dots + k$. The derivation of the best-choice diet begins with the most profitable resource (1), and, stepwise, adds resource types, continuing until the first resource ($n + 1$) with a profitability less than the overall foraging efficiency of the diet that does not include it (diet breadth = n). Resources ranked ($n + 1 \dots k$) are excluded because to pursue them would impose an unacceptable opportunity cost: a lower return rate for time spent pursuing them relative to the expected benefits from ignoring them in favor of both searching for and pursuing more profitable types. Think of picking up change in tall grass: if there are enough silver dollars and quarters the income-minded gleaner will ignore the dimes, nickles, and pennies, no matter how frequently they are encountered. Notice that the DBM also entails a marginal decision: It asks, is the profitability of the next ranked item above or below the marginal value of foraging for all resources ranked above it?

Creative use of this or any foraging model entails thought experiments of the form: how will an optimizing forager respond to a change in independent variable x . Predicted responses are confined to options with the alternative set, but the independent variable x might be any change in the environment or the behavioral capacities of the forager that affects the primary model variables: resource encounter rates and profitability. For instance, resource depression,

environmental change, and other factors which diminish encounter rates with highly ranked resources will increase search costs, lower overall foraging efficiency, and as a result, may cause the diet breadth of a forager to expand to include items of lower rank. One or more items that previously ranked below that boundary may now lie above it, making these resources worth pursuing when encountered. The converse is also true. Sufficiently large increases in the density of highly ranked resources should lead to exclusion from the diet of low ranked items. A seasonal elevation of fat content, or adoption of a technology that makes its pursuit, harvest or processing more efficient or any factor that raises the profitability of a particular resource will elevate its ranking, perhaps enough to move into the best-choice diet. It may, in fact, displace resource items previously consumed. Winterhalder and Goland (1997, Fig. 7.4) provide an extended list of factors that might operate through encounter rate and pursuit and handling costs to change resource selectivity.

The diet breadth model also implies that, under a given set of conditions, resources within the optimal diet are always pursued when encountered; those outside the optimal diet will always be ignored. There are no “partial preferences,” such as “take this organism 50% of the time it is encountered.” Likewise, the decision to include a lower-ranked item is not based on its abundance, but on the abundances of resources of higher rank. Think of the small change mentioned earlier.

PATCH CHOICE

In the diet breadth model, we envision a resource that is harvested as a unit with a fixed value (e.g., a steenbok). By contrast, a patch is a resource or set of resources which is harvested at a diminishing rate, either because it is depleted in such a way that makes continued harvesting more difficult; the densest and ripest berries are picked first, or because the continuing presence of the forager disperses or increases the wariness of remaining resource opportunities as in the second or third shot at

a dispersing flock of grouse. Patches can be ranked like resources, by their profitability upon encounter. As a first approximation, the same predictions apply. However, predictions are somewhat less clear for the selection of patches than for resources, because a definitive prediction about patch choice is interdependent with a decision about patch residence time, the focus of the next model.

PATCH RESIDENCE TIME (THE MARGINAL VALUE THEOREM)

If a resource patch—which we envision as a small area of relatively homogeneous resource opportunities, separated by some travel distance from other such locales—is harvested at a diminishing rate of return, it is obvious to ask when the forager should abandon its efforts and attempt to find a fresh opportunity. By moving on, he or she will incur the cost of finding a new patch, but upon locating it, will be rewarded with a higher rate of return, at least for a while. The optimizing solution to this foraging decision is given by the marginal value theorem (Charnov 1976; Charnov et al. 1976; Stephens and Krebs 1986). The marginal value theorem postulates a decline in return rates for time spent in the patch, usually approximated by a negative exponential curve. The optimizing solution specifies that the forager will leave the present patch when the rate of return there has dropped to the average foraging rate. The average foraging rate encompasses the full set of patches being harvested *and* the travel costs associated with movement among them. To stay longer incurs unfavorable opportunity costs because higher returns were available elsewhere. To stay a shorter duration is also sub-optimal, because rates of return are, on average, higher when compared to the costs of moving on to another resource patch.

In this model, short travel times are associated with short patch residence (take the highest return opportunities and move on quickly); long travel times with longer residence times. The forager optimizing his or her patch residence time rarely will completely deplete a patch;

the resources left behind are significant for the recovery of the patch. Finally, the value of harvested patches, upon departure, is the same.

The inter-dependence between the two patch-related models should now be more apparent. Predictions about patch residence time depend on patch choice; reciprocally, predictions about patch choice depend on residence time. Use of one of these models must assume the other; Stephens and Krebs (1986, 32–34) give a more detailed discussion of this model.

HABITAT SELECTION (THE IDEAL FREE DISTRIBUTION)

The ideal free distribution is a model of habitat choice (Fretwell 1970; Sutherland 1996). The distinction between patches and habitats is one of scale: patches are isolated areas of homogeneous resource opportunities on a scale such that a forager may encounter several to several dozen in a daily foraging expedition. Habitats are similarly defined by their aggregate resource base, but at a regional scale. As suggested by their greater relative size, habitats also invoke somewhat different questions, such as where to establish and when to move settlements, and when to relocate by migration. Generally, we ask how populations will distribute themselves with respect to major landscape features like habitats.

In the ideal free distribution, the quality of a habitat depends on resource abundance and the density of the population inhabiting and using it. The model assumes that the initial settlers pick the best habitat, say “A.” Further immigration and population growth in habitat A reduce the availability of resources and the quality of the habitat drops for everyone. Crowding, depletion of resources, and competition are possible reasons for this. The marginal quality of habitat A eventually will drop to that of the second-ranked, but yet unsettled, habitat B. If each individual in the population seeks the best habitat opportunity, further growth or immigration will be apportioned between habitats A and B such that their marginal value to residents is equalized. Lower ranked habitats will be occupied in a similar manner. This model predicts

that habitats will be occupied in their rank order, that human densities at equilibrium will be proportional to the natural quality of their resources, and that the suitability of all occupied habitats will be the same at equilibrium.

In the IFD the creative element resides in imagining how various socioenvironmental settings might affect the shape of the curves representing the impact of settlement density on habitat quality. For instance, it is possible that settlement at low densities actually *increases* the suitability of a habitat. Forest clearing by the newcomers leading to secondary growth might increase the density of game available to them and to emigrants. This is known as the Allee effect. Likewise, some habitats (e.g., small islands; see Kennett et al., this volume) may be quickly affected by settlement, generating a sharply declining curve of suitability as population densities increase, whereas others may be much more resilient. If immigrants to a habitat successfully defend a territory there, then newly arriving individuals will more quickly be displaced to lower ranked habitats, a variant known as the ideal despotic distribution (IDD; see Sutherland 1996).

CENTRAL PLACE FORAGING

Many foragers, human and nonhuman, locate at a dry rock shelter, potable water, or a valuable or dense food source or other particularly critical resource—e.g., an attractive habitation site, or perhaps at a location central to a dispersed array of required resources—and then forage in a radial pattern from that site. Central place foraging models (Orians and Pearson 1979) address this circumstance. They assume that a forager leaving such a home base must travel a certain distance through unproductive habitat to reach productive foraging zones. The goal—optimizing delivery of foodstuffs or other valuables to the central place—must take account of the round trip travel costs between the central place and the foraging site, in addition to the standard considerations about resource selection. The basic prediction of this model is the following: as travel costs out and back increase

with a load on the return trip, the forager should become more and more selective about what is harvested. At long travel distances only the most valuable loads justify the effort.

This model has been adapted in an intriguing way by archaeologists who have used it to address the question of field processing (Bettinger et al. 1997; Metcalfe and Barlow 1992). Field processing entails removing parts of a resource with little or no value, in order to carry more of the valued portions back to the central place. Shelling marine bivalves or removing pinyon nuts from their cones are examples. With data on parameters such as distance, feasible bulk and weight of loads, and the costs and benefits of field processing a particular resource (e.g., Barlow et al. 1993), it is possible to predict rather precisely the travel distance at which the forager will process in the field rather than carry the unprocessed resource back to the central place. Field processing of course improves the efficiency of transportation, but it also commits to processing field time that could have been used to locate, harvest and transport more of the unprocessed resource. This model predicts that field processing will become more likely as travel distance increases.

We cite this adaptation of the central place foraging model in part because it makes the important point that foraging theory is not a closed, off-the-shelf set of tools (Kelly 2000). Rather, it must be, and it has considerable potential to be, adapted to the particular circumstances of human subsistence, whether foragers, farmers, or populations that mix these sources of production.

SETTLEMENT (RE)LOCATION

Settlement models attempt to predict when foragers will relocate their central places, due to localized depletion of resources (Kelly 1992), seasonal or other shifts in the relative values and availability of local and distant resource opportunities (Zeanah 2000). Zeanah's model, for instance, imagines a foraging group whose two most important resources, say lake margin lacustrine species (A) and mountain sheep or

pinyon nuts (B), are found in geographically separated habitats. They also change in their relative seasonal importance. We would expect the forager to locate adjacent to the more dominant of the two food sources (say, A), especially if the resource targeted is difficult to transport, and to harvest the less dominant (B) or easier to transport item through logistic foraging expeditions. Zeanah's model specifies in quantitative terms what shifts in yield and transport costs will lead to the decision to switch the pattern of settlement and logistic procurement, residing adjacent to B, while harvesting A logistically.

Although settlement models have not, to our knowledge, been applied in studies of domestication and agricultural origins, the likelihood that the better foraging and farming sites have non-overlapping distributions, and the implied changes in mobility and sedentism during a transition from foraging, to a mixed foraging & farming, to farming, or back to foraging, offers fertile ground for exploration.

CURRENT DEVELOPMENTS IN FORAGING THEORY

A list of established models might give the sense that behavioral ecology, however useful to interpretation, is a static or completed field. In fact, it is in a rapid state of expansion and development both in ethnography and archaeology. In this section we note several of the more important developments. The trends described here also make it evident why the more encompassing term, behavioral ecology, often is more apt than foraging theory.

BEYOND KCALS

Early applications of foraging models, especially the diet breadth model, adopted a straightforward energy currency to measure the costs and benefits of options in the alternative set. The value of a moose was the weight of its edible tissue represented as kcals. This is consistent with a prime methodological predilection of behavioral ecologists (Winterhalder 2002a): begin simply. Once you understand how the

simple model works and have appraised its relevance to the empirical problem, it is appropriate to relax restrictive and sometimes unrealistic assumptions. Thus, in foraging theory, studies of resource selection led naturally to examination of intra-group resource transfers. This move from issues of economic production to those of distribution drew attention to a different metric: marginal value. After a filling meal or two, the marginal value of the balance of a moose carcass to the forager who obtained it may drop rapidly relative to the kcals it represents. This observation—that medium to large food packets are subject to marginal valuation—is at the heart of behavioral ecology models of food transfers through tolerated theft and reciprocity-based sharing (Blurton Jones 1987; Gurven 2004; Winterhalder 1996; Winterhalder 1997). Of equal importance, there may be some cases in which the marginal value of a resource is the appropriate valuation of its profitability for purposes of the original diet breadth model.

A more radical variation on currency is evident in models devised to help explain an anomaly in early field studies of foraging behavior: although each sex often could do better by harvesting the same set of resources, men sometimes specialize on large game and women on plants and small animals (Hill et al. 1987), each at a cost to their potential foraging efficiency. The show-off (Hawkes and Bliege Bird 2002) and costly signaling (Smith et al. 2003) models assume that resource values—and hence their patterns of acquisition and distribution—will sometimes be predicated on the prestige associated with their use or on the information their capture conveys about the prowess of the hunter. With these models foraging theory has carried us beyond “the gastric” (Zeanah and Simms 1999) and into the realm of social theory (Bliege Bird and Smith 2005), making plausible our earlier claim that foraging theory offers broad grounds for complementing other research traditions in the field of agricultural origins (e.g. Hayden 1995a). Social valuation moves the modeling effort of HBE from the

narrow question of resource selection to broader anthropological issues—the roles of gender, prestige, and power in structuring economic activity (e.g., Broughton and Bayham 2003; Elston and Zeanah 2002; Hildebrandt and McGuire 2002; Hildebrandt and McGuire 2003).

BEYOND DETERMINISTIC APPROACHES

Risk-sensitive and discounting models are another set of variations on early foraging theory efforts. In the original models for diet breadth, patch choice, and patch residence time, all input values were taken to be averages unaffected by stochastic variation. Thus the average search time to locate the next resource was treated as a constant, making foraging a more predictable enterprise than is the case. These models focused on a goal of maximizing acquisition rate during foraging. Risk-sensitive models allow for stochastic variation in the factors influencing foraging decisions, such as encounter rate or pursuit time. They assume that the forager has the goal of risk minimization (Winterhalder et al. 1999). For instance, Stephens and Charnov (1982) modified the marginal value theorem to show that a risk-minimizing forager, in positive energy balance and facing a normal distribution of unpredictable inter-patch travel times, would stay somewhat longer in a patch than a rate maximizing forager whose travel times were a constant.

In general, risk-sensitive models predict that optimizing foragers who are not meeting their average requirements will be risk prone. They will elect the higher variance options from the alternative set because those offer their greatest chance of a survival-enhancing windfall. Foragers in positive energy balance will be risk averse, electing the low variance options that minimize the chance of a threatening shortfall. The implications of these generalities for specific types of decisions must be worked out individually.

A variation on risk-sensitive models is discounting (Benson and Stephens 1996). If the forager has reason to discount, and faces a

choice between a small reward at present or a larger one at some point in the future, he or she may do best by taking the less valuable but immediate option. Tucker (Ch. 2, below; see also Alvard and Kuznar 2001) argues that discounting is likely to be especially important in the transition from foraging to food production.

BEYOND DERIVED AND GRAPHICAL SOLUTIONS

The basic foraging models described above are products of mathematical derivation, often represented graphically. A desire for more realistic variants is associated with new analytic methodologies, such as simulation and agent-based modeling. For instance, Winterhalder and students (Winterhalder et al. 1988) simulated the population ecology of a foraging population interacting with multiple resource species. In this dynamic model, the human population grows or contracts in density as a function of foraging efficiency. It harvests species identified by the diet breadth model, in amounts required to meet its food needs. And, to complete the dynamic circuit, the densities of the resource species themselves expand or contract according to their degree of exploitation and their logistic potential to recover from being harvested. The result is a more realistic application of the diet breadth model: exploitation actually changes prey densities and thus encounter rates in a plausible manner, generating new hypotheses relevant both to agricultural origins (Winterhalder et al. 1988) and conservation biology (Winterhalder and Lu 1997).

Agent-based modeling is another new technique of great promise. Agent-based analyses rely on computer simulations to represent a population of agents interacting with an environment and among themselves. These models iterate a cycle in which the agent collects information from the environment, and then acts in some fashion that changes the agent and environment. The agent-based approach, “emphasizes dynamics rather than equilibria, distributed processes rather than systems-level phenomena, and patterns of relationships

among agents rather than relationships among variables” (Kohler 2000, 2). Agent-based models have the added advantage that they can incorporate basic processes of learning or evolution, for instance by allowing the agent to adjust its behavior according to its monitoring of performance criteria. Because of this property, they are thereby especially useful for simulating adaptive or co-evolutionary processes (see examples in Brantingham 2003; Kohler and Gumerman 2000). Although there are at present no agent-based models of domestication or agricultural origins, behavioral ecology adaptations of the agent-based approach appear an especially promising avenue for research.

BEYOND ETHNOGRAPHY

The specific claim of this volume—that behavioral ecology theory is an essential tool in the analysis of the transition from hunting-and-gathering to agriculture—is set within a broader assertion: that behavioral ecology can be used to understand prehistory in general (Bird and O’Connell 2003; O’Connell 1995). Although archaeologists have been enthusiastic consumers and occasionally developers of foraging theory, the models themselves and the bulk of their testing are the province of biologists and anthropologists working with living species and peoples. As a consequence, the models typically make predictions at the level of individual behavior over very short time scales—minutes to days or perhaps weeks. In contrast, archaeological data on subsistence production, food distribution, mobility, settlement, and the other topics of behavioral ecology represents the aggregate consequences of many individual actions over decades, centuries or longer. Much archaeological data conflate individual, temporal and perhaps spatial variability. This disparity of scale and resolution raises thorny problems regarding how HBE models are to be verified, applied and interpreted in archaeological contexts (e.g., Smith, this volume). How do we get from a chronological sequence of faunal samples, each of which represents perhaps dozens of foraging expeditions by different individuals

over decades or centuries of time, to the seasonally and habitat specific foraging choices of a particular hunter?

This problem is serious but may not be as daunting as appears on first consideration. For instance, careful investigation does occasionally reveal the individual and momentary in prehistory. Enloe and Davis (1992) and Waguespack (2002) both have shown that by analyzing the “refitting” of bones scattered among the different hearths of a campsite it is possible to reliably infer patterns of prehistoric food sharing. In broader terms, Grayson and Delpech (1998; Grayson et al. 2001), Lyman (2003), Broughton (2002) and Gremillion (2002) are exploring how well and under what circumstances various archaeological measures of floral and faunal residues are able to capture foraging behavior changes in diet breadth. A series of reports analyzing broad spectrum type diet breadth changes in late prehistory have made creative use of changing ratios of large, presumably, highly ranked, to small prey (Broughton 1999; Broughton 2001; Butler 2000; Lindström 1996; Nagaoka 2001, 2002) in order to document declining foraging efficiencies and expanding diets. Through a combination of archaeological investigation and population ecology simulation, Stiner and colleagues (Stiner et al. 2000; Stiner 2001; Stiner and Munro 2002) have shown that small prey may be especially sensitive indicators of human resource selection and the impacts of exploitation. We expect these efforts to find archaeologically viable means of using foraging theory to continue.

BEYOND HUNTER-GATHERERS AND FORAGING

The research tradition represented in this volume originated as foraging theory focused on the study of food production in hunter-gatherer populations (Winterhalder and Smith 1981). In both biology and anthropology the approach since has adopted the broader name—human behavioral ecology—as it has expanded its topical focus to encompass resource distribution, group size and structure, mating and reproductive

tactics, and life history evolution, while—in the anthropological case—simultaneously moving into the analyses of societies engaged in other modes of production (reviews in Borgerhoff Mulder 1991; Cronk 1991; Smith 1992a; Smith 1992b; Smith and Winterhalder 1992a; Winterhalder and Smith 2000). The impetus for this expansion has at least four sources: (1) the early empirical success of field studies using the approach; (2) the generality of the neo-Darwinian theory that inspired it; (3) the generality of the underlying concepts of marginal valuation, opportunity cost appraisal, risk-sensitivity, discounting; and, (4) the flexibility of individual models, which often have been readily adapted to problems or settings not foreseen by their original authors. The present volume continues this trend by carrying behavioral ecology theory and models into analyses of domestication and agricultural origins.

The transfer and extension of ideas and concepts in order to bring new topics under the compass of existing theory has obvious scientific merit (Kuhn 1977; McMullin 1983). It also has pitfalls. The failings of early “evolutionist” models of social evolution and their archaeological adaptations, as well as social Darwinist interpretations, are well-rehearsed subjects in anthropology. Contemporary anxieties about the use of neo-Darwinian theory in anthropology are more narrowly and analytically focused, and sometimes not so easy to set aside. A recent example would be debate over the claim by Rindos (1984) that his co-evolutionary account of plant domestication had successfully banished human intent from an explanatory role in this process (Rindos 1985).

In the present volume we take for granted the relevance to agricultural origins of neo-Darwinian and behavioral ecology theory. We reject without explicit argument the substantivist claim of economic anthropology that none of the tools of formalist, microeconomics has any purchase outside of modern capitalist economies (e.g., Sahlins 1972). To the contrary, we believe it evident that the basic concepts of HBE (see above) are fundamental to the

analysis of *any* economy. Close attention to their use in HBE we believe will stimulate new applications and models specifically designed to analyze mixed economies and food production.

We are more receptive to the argument that specific foraging models, developed as they were for foragers, may be only partially appropriate to the analysis of emergent food producers. For instance, the diet breadth model assumes random encounter with resources, a condition increasingly likely to be violated as foragers become involved in the manipulation of individual species. In as much as all models simplify reality and thus violate at least some conditions of their application, the unavoidable judgment is this: does the failure to fit this particular assumption completely vitiate the heuristic or analytical value of the model? With the specific cautions cited in individual papers, we believe the combined weight of the case studies developed in this volume add up to a strong presumption in favor of the utility of foraging theory, even as the foragers being analyzed direct more and more of their effort toward agricultural activities.

We envision three levels where HBE might be applied to the question of agricultural origins. (1) Extant models, although designed for the analysis of foraging, might be applied in the analysis of agricultural origins with little or no alteration in their structure and assumptions. This is the procedure of most authors in this volume. (2) Extant models might be modified so to more directly address questions or situations specific to non-foraging aspects of economy, including cultivation and agricultural production. The modification of central place foraging models to analyze the question of field processing is an especially good example of this. (3) Finally, entirely new models, inspired directly by the problem of explaining human subsistence transitions, might be devised using fundamental behavioral ecology concepts such as opportunity cost or discounting. We think of these options as adopt, adapt, or invent, respectively. While options (2) and (3) hold great potential for novel and perhaps quite interesting analyses, it appears from the papers assembled here that there is much to be accomplished with the simple adoption of existing models.