

Behavioral Ecology and Archaeology

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Abstract Behavioral ecology is the study of adaptive behavior in relation to social and environmental circumstances. Analysts working from this perspective hold that the reproductive strategies and decision-making capacities of all living organisms—including humans—are shaped by natural selection. Archaeologists have been using this proposition in the study of past human behavior for more than 30 years. Significant insights on variation in prehistoric human subsistence, life history, social organization, and their respective fossil and archaeological consequences have been among the more important results.

Keywords Evolutionary ecology · Optimal foraging · Hominin life history · Costly signaling · Hereditary inequality

Introduction

Much of human behavior is highly complex, strikingly patterned, and seemingly purposeful; it has all the characteristics of adaptive design (Williams, 1966). Moreover, human behavior often leaves material traces that can be monitored archaeologically. If behavior does indeed display adaptive design, we might often be able to generate expectations about its past form and variation in specific ecological settings and assess those expectations archaeologically. We explore the extent to which this has been and continues to be a useful proposition.

We begin with some definitions. *Evolutionary ecology* is the study of adaptive design in behavior, life history, and morphology. In the framework of evolutionary biology, behavior is “adaptive” when it tracks environmental variability in ways that enhance an individual’s

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inclusive fitness, defined most generally as its propensity to survive and reproduce (Williams, 1966). *Behavioral ecology* (BE) is the subset of evolutionary ecology that studies the fitness-related behavioral trade-offs that organisms face in particular environments. BE asks why certain patterns of behavior have emerged and continue to persist and looks to their socioecological context in seeking answers (Smith and Winterhalder, 1992, pp. 25–50).

The basic framework for inquiry in BE was established in the 1960s and 1970s by ecologists studying social, reproductive, and foraging patterns in animals (e.g., Alexander, 1974; Hamilton, 1964; Hutchinson, 1965; MacArthur, 1960; Trivers, 1971; Williams, 1966; see Parker, 2005, for recent overview). Ethnographers soon saw the potential of the approach and pursued it in connection with similar issues in the study of human behavior (e.g., Chagnon and Irons, 1979; Winterhalder and Smith, 1981, 1992a). Archaeologists did the same, initially focusing on questions about subsistence (e.g., Beaton, 1973; Wilmsen, 1973) but later addressing issues as diverse as patterns in resource transport, subsistence-related changes in technology, the origin and diffusion of agriculture, the material correlates of social status, early human social organization, the development of social hierarchies, and the evolution of human life history.

Despite these advances, many archaeologists still see behavioral ecology as synonymous with “optimal foraging theory.” Some in fact contend that human evolutionary ecology can and should deal *only* with aspects of foraging (e.g., Schiffer, 1999, p. 167). Such assertions reflect a fundamental misunderstanding of the overall theoretical framework, the breadth of questions it can help address, and the substantive results its application has achieved so far.

Here we seek to counter this misperception by presenting a comprehensive review of archaeological research undertaken from the perspective of behavioral ecology over the last three decades. We begin with a consideration of the kinds of explanations that can be offered about past human behavior, highlighting the ones BE-based analyses can most effectively address. We then offer some general observations on operating assumptions and methods. Next we turn to substantive applications of the perspective, beginning with treatments of various aspects of foraging behavior and continuing through research on life history evolution, costly signaling, and the development of social hierarchies. Many of the examples we cite are drawn from the literature on western North American prehistory, an area in which BE approaches have been especially well developed. We conclude with some general comments on the nature of the enterprise.

Questions about human behavior and its archaeological consequences

Archaeologists deal primarily with two sets of phenomena: past human behavior and its material consequences. All archaeologists study refuse as a matter of routine and have developed a rich and diverse array of methods for doing so. They also have developed a comprehensive body of ideas and information designed to help link those remains with aspects of past behavior. Much of this latter work is referred to as the study of “site formation processes” (Schiffer, 1987), or more precisely as “ethnoarchaeology” (David and Kramer, 2001) or “taphonomy” (Lyman, 1994).

Research on past behavior itself entails two tasks: *reconstructing* it from some particular set of archaeological data, and *accounting* for it as reconstructed. The process of reconstruction relies in part on ethnographic analogy. Although this approach has many advantages, its limitations are also obvious: Some patterns in the archaeological record are the products of nonhuman processes; some have more than one ethnographic referent; some have none. The converse is also partly true: some patterns of behavior may have

more than one archaeological correlate; some fail to generate material residues of any kind. Behavioral ecology has the capacity to mitigate some of these difficulties in that its theoretical framework may help discriminate among alternative behavioral readings of archaeological patterns. It also may guide well-warranted speculation about aspects of past behavior that are unlikely to be represented archaeologically.

However past behavior is reconstructed, the process of accounting for it can take several forms. Following Tinbergen's (1963) model for the explanation of behavior in nonhuman animals, we identify four. *Proximate* explanations of behavior might be called "mechanical." Eating, for example, is prompted or "caused" by the interaction of complex chemical and hormonal processes linking nutrient intake with the state of various internal organs. By themselves, proximate explanations are rarely of great interest to archaeologists.

Ontogenetic explanations emphasize patterns in the development of an individual's behavior through time. They often refer to aspects of physical development, socialization, or to various forms of learning. An ontogenetic explanation of patterns in food consumption might be concerned with how individuals learn what (and what not) to eat. Such arguments have until recently been of limited interest to archaeologists (cf. Henrich, 2004; Shennan, 2002).

Historical explanations typically entail descriptions of local sequences of events and how they create and/or limit opportunities for humans to behave in certain ways. For example, a historical explanation for past changes in diet might involve correlating those changes with shifts in local climate, habitat characteristics, human population size, aspects of social organization, or patterns of trade and exchange, and then proposing a causal relationship. Such explanations have long been developed as a matter of routine by archaeologists. They differ from functional explanations (see below) in emphasizing the unique characteristics of particular historical sequences and thus often reject the proposition that universal processes of any kind might be involved.

Functional explanations are concerned with the survival and reproductive (or "fitness") implications of behavior. They commonly involve the identification of various potential courses of action, an assessment of the fitness-related costs and benefits associated with each, and a hypothesis about which pattern(s) of behavior is (are) likely to be adopted under the stipulated array of constraints, and for what reasons. Functional explanations of subsistence patterns, for example, typically display all of these characteristics. Unlike the narrowest forms of historical explanation, functional arguments almost always involve appeals to processes likely to operate universally.

BE explanations for patterns in human prehistory are "functional" or "adaptive" in the sense just described. Yet while fitness considerations are the primary focus in these arguments, historical, ontogenetic, and even proximate factors may sometimes be seen as relevant to functional analyses in that they help define alternate courses of action and their respective fitness-related costs and benefits.

Assumptions and models of behavioral ecology

Ethnographic and archaeological applications of BE are based on the proposition that behavioral diversity is largely the result of variability in specific socioecological settings, each with a unique set of circumstances that defines the fitness-related "landscape" in which individuals operate. Since many organisms (certainly humans) have the evolved capacity for rapid adjustments favoring advantageous behavior, they are likely to exhibit predictable, short-term, often "real-time" adaptive responses to many social and ecological features of their environment. BE is especially interested in these conditional responses.

As a first-order heuristic for evaluating functional questions, BE often uses a research strategy called the “phenotypic gambit” (Grafen, 1984; see also Winterhalder and Smith 1992b, p. 33). The approach is framed by the proposition that natural selection will favor variants with the *capacity* to solve fitness-related trade-offs efficiently. Phenotypes (including behavior) are products of the interactive effects of complex biological, social, and physical environments. To make adaptive problems tractable, the phenotypic gambit assumes that it is neither feasible nor essential to account for the exact mechanism that generates or transmits a given trait (Smith, 2000, p. 30). This is a calculated analytic risk, but it allows the investigator to avoid unproductive questions about whether a trait is “instinctive” or “learned.” Whether behavior has a “biological” or “cultural” basis is irrelevant from this perspective. BE models are not designed to specify a mode of inheritance; instead, they are tools that help formulate testable hypotheses about the potential fitness-related trade-offs individuals may face in particular socio-ecological contexts.

In developing context-specific predictions about behavior, BE makes use of formal models drawn mainly from optimization analysis (Maynard Smith, 1978) and evolutionary game theory (Dugatkin and Reeve, 1998; Maynard Smith, 1982). Optimality models are designed to evaluate hypotheses about the behavior of individual actors under a specified set of conditions. Game theory (or in the parlance of BE, “evolutionary stable strategy” [ESS] theory) adds a social dimension, where the behavior of one individual depends on that of others. Most applications of BE in archaeology make use of optimality models, though game theory has been deployed to good effect as well.

Formal models in BE provide a framework for organizing testable propositions about behavior. *Models themselves are never tested.* It is the situation-specific assumptions (*hypotheses*) that applications require that are at risk in any analysis. In many BE models, these assumptions pertain to (1) the fitness-related *goal* of behavior, (2) the *decision* variable (or the “conditional strategy”) associated with achieving that goal, (3) the *trade-offs* connected with the decision variable, (4) one or more *currencies* in which to evaluate those trade-offs, and (5) the *constraints* that define or limit the actor’s situational response. Modeled as a series of contingent relationships, these assumptions enable an analyst to generate predictions about behavior under the circumstances so stipulated. Mismatches between predicted and observed (or archaeologically inferred) behavior imply *either* that one or more of the specific hypotheses about goals, decision variables, trade-offs, currencies, and constraints are wrong and in need of reassessment, *or* that the model itself is in some way inappropriate to the behavioral question being addressed.

Applications of behavioral ecology to problems in archaeology

Foraging theory and subsistence strategies

As indicated above, appeals to BE in archaeology focused initially on problems in prehistoric human subsistence, especially those posed by patterned variation in archaeological faunal and floral assemblages and related elements of technology. Most make use of a set of formal models known collectively as “optimal foraging theory” (Charnov and Orians, 1973; Stephens and Krebs, 1986; see Sih and Christensen, 2001, for a recent review). All are based on the assumption that maximizing the rate of nutrient acquisition enhances fitness, either by increasing nutrient intake or by reaching some intake threshold more quickly, thereby freeing time to pursue other fitness-related activities. Though the scope of BE research in archaeology has now broadened considerably, these models still represent the most commonly applied component of the overall approach.

The simplest and best-known foraging model is the “encounter-contingent prey choice model” (PCM), also known as the “basic prey,” “optimal diet,” or “diet breadth” model (Emlen, 1966; MacArthur and Pianka, 1966). It makes a distinction between two mutually exclusive aspects of foraging, *search* and *handling*, the latter defined as including all activities associated with the post-encounter pursuit, capture, or collection of prey, as well as with their preparation for consumption. The model is designed to address a simple question: “Having found a potential prey item, should I handle it or continue to look for another, one that might give me a better return relative to the time spent searching for, collecting, and processing it?” In answering this question, the PCM assumes that the *goal* of foraging is to maximize the rate of nutrient capture. The nutrient *currency* most commonly specified is energy. The model further assumes that the forager knows or can accurately estimate the likely encounter and post-encounter nutrient return rates relative to handling costs for all potential prey types, and also that s/he searches in a patch where prey types are mixed and encountered at random relative to their abundance (*constraints*). Again, the *decision* variable is whether to handle a particular prey type on encounter or to bypass it in search of another more profitable item (*trade-off*).

The PCM holds that foraging efficiency is maximized when the post-encounter profitability of a selected item is equal to or greater than the expected overall foraging return rate, including search. The model predicts that the top-ranked prey type will always be taken on encounter and that less profitable types will be added to the diet in descending rank order until the on-encounter return from the next lowest-ranked type falls below the expected return from searching for and handling all resources of higher rank. Since taking resources of that type will by definition *reduce* the average returns from the patch as a whole, all items of that type and any of even lower rank will be bypassed consistently in favor of continued search for more profitable prey.

Counterintuitively, the PCM also predicts that the inclusion of a given prey type depends *not* on its own abundance or encounter rate, but *only* on its post-encounter profitability and the rate at which all higher-ranked prey are likely to be found. If, for some reason, encounters with the latter decline in frequency, then overall average foraging returns will decline as well. If they drop below post-encounter returns available from relatively low-ranked items not previously taken, then those items will be added to the diet. If, on the other hand, the encounter rate for high-ranked items goes up, then overall average foraging returns will rise as well. As they do, low-ranked prey are increasingly likely to be dropped from the diet.

If encounters with prey are not random relative to abundance but instead are patchily distributed (i.e., “clumped” in time and space), a forager’s decision is *not* “should I search or handle?” but “relative to my other options, should I enter a patch, and once there how long should I stay?” “Patch” models predict that potential foraging locales will be exploited in order of the return rates expected from searching for and handling prey within each, adjusted for the costs of traveling to (and sometimes from) them (Charnov and Orians, 1973; Orians and Pearson, 1979; Stephens and Krebs, 1986, pp. 24–32). Thus a relatively low-ranked patch may be targeted ahead of one yielding higher in-patch returns simply because it is closer. As a patch is exploited, returns from foraging within it often will fall. A rate-maximizing forager should abandon a patch once returns drop below those available from traveling to and foraging within another patch, a prediction formalized in the “marginal value theorem” (Charnov, 1976).

Optimal foraging models have been applied ethnographically since the late 1970s. The best-known early examples include Winterhalder (1981) on prey and patch choice among the sub-Arctic Cree, Smith (1981) on optimal foraging group size among the Inuit, O’Connell and Hawkes (1981) on seed use among the Central Australian Alyawarra (formerly “Alyawara”),

and Hawkes *et al.* on prey choice among the Paraguayan Ache (e.g., Hawkes *et al.*, 1982; Hill and Hawkes, 1983; Hill *et al.*, 1987). Comprehensive reviews of the literature since then are presented in Bettinger (1991), Cronk *et al.* (2000), Hawkes *et al.* (1997), Kaplan and Hill (1992), Kelly (1995), and Winterhalder and Smith (2000).

Early archaeological applications also date to the 1970s (e.g., Bayham, 1979; Beaton, 1973; Jochim, 1976; Keene, 1979; Wilmsen, 1973), but efforts were stalled for a time thereafter, mainly because of problems in quantifying variables needed to operationalize the models. Momentum was regained in the early 1990s as newly acquired ethnographic and experimental data made it possible to address the quantification problem. The number of archaeological case studies in print has since multiplied rapidly (for review see Bettinger, 1991; Kaplan and Hill, 1992; Kelly, 1995; O'Connell, 1995; Shennan, 2002; Winterhalder and Smith, 2000). Much of this work has focused on five general issues: changes in diet breadth among foragers, the origin and diffusion of domesticated plants and animals, links between foraging and technology, constraints on resource transport imposed by central place foraging, and the processes of colonization and competitive exclusion among foragers.

Diet breadth and the question of “intensification”

Archaeologists have long recognized that terminal Pleistocene and Holocene hunter-gatherers exploited a broader array of resources than did their Upper Pleistocene predecessors (e.g., Clark, 1952; Willey and Phillips, 1958). Terms used to mark this pattern include “Mesolithic,” “Archaic,” “resource intensification,” and “broad spectrum revolution.” Standard explanations for this change often make reference to such factors as increasingly comprehensive knowledge of resource availability, the invention or diffusion of critical technology, and declines in the abundance of preferred prey, possibly as a result of climate change and/or human population growth (e.g., Binford, 1968; Braidwood, 1960; Cohen, 1977; Flannery, 1969). Though many of these hypotheses are plausible, there is little in any of them that adequately accounts for the order in which *particular* resources were added to local diets, nor does any imply a clear-cut test.

Early applications of the PCM changed this situation by showing that most newly exploited prey types had very high handling costs relative to energetic yield; that is, they were low ranked compared with previously favored resources (e.g., Bayham, 1979; Beaton, 1973; Botkin, 1980; O'Connell and Hawkes, 1981). Climate- or predation-related declines in the availability of the high-ranked items (those with relatively low processing costs) were consistently identified as critical to the shift to lower-ranked prey. In most cases, test implications were immediately apparent. Many subsequent studies of prehistoric diet change and, to a lesser extent, patterns in patch choice have led to similar inferences (e.g., Cannon, 2000; Edwards and O'Connell, 1995; Erlandson, 1991; Glassow and Wilcoxin, 1988; Grayson, 1991; Jones and Richman, 1995; Mannino and Thomas, 2002; Nagaoka, 2002; O'Connell *et al.*, 1982; Perlman, 1980; Porcasi *et al.*, 2000; Russell, 1988; Simms, 1987; Szuter and Bayham, 1989; Wright, 1994; Yesner, 1989; Zeanah and Simms, 1999; for additional review and discussion see Shennan, 2002; Winterhalder and Smith, 2000).

Three sets of analyses are particularly interesting. Two involve late Holocene changes in the diets of Native Californians. Early 20th century anthropological views of traditional subsistence economies in this region emphasized the abundance and diversity of local food resources (e.g., Kroeber, 1925), the implication being that before European contact Indians living in California rarely if ever suffered from dietary stress. This inference was strongly challenged by the results of initial PCM-based analyses of coastal California shell middens indicating a trend toward increased taxonomic diversity and progressively younger

age structures in late prehistoric molluscan prey populations, a pattern consistent with the depletion of relatively high ranked prey by humans and a corresponding decline in overall foraging return rates (Beaton, 1973; Botkin, 1980).

Subsequent work on these and other aspects of diet, as well as on patch choice, has yielded similar results, including evidence of local declines in populations of high-ranked artiodactyls, fur seals, sea lions, elephant seals, and sturgeon, associated with increased reliance on lower-ranked harbor seals, sea otters, small fish, and small shellfish as well as on high-cost plant foods like tannin-rich acorns and grass seeds at various times and places throughout the Holocene (e.g., Basgall, 1987; Beaton, 1991a; Bouey, 1987; Broughton, 1994; Erlandson, 1991; Hildebrandt and Jones, 1992; Jones, 1995; Kennett, 2005; Raab, 1992; Wolgemuth, 1996).

Of these studies, Broughton's (1994, 1997, 1999, 2002, 2004) analyses of remains from late Holocene sites around San Francisco Bay are especially well developed. Working with museum collections assembled nearly a century ago, Broughton nevertheless is able to demonstrate declines in the relative importance of high-ranked cervids, sturgeon, geese, oysters, and bay mussels relative to lower-ranked forms over periods of several thousand years. Parallel analyses of body part representation show increasing use of more distant, hence costlier patches, consistent with the proposition that returns from more proximate foraging locations had been depressed. Broughton rules out climatic factors as a possible explanation for these changes, arguing persuasively for human predation as the principal cause. This conclusion not only undercuts conventional ideas about Native Californian economies but also challenges widely held views of traditional hunter-gatherers as conservationists, recognizing them instead as active agents of ecological change (see Grayson, 2001; Kay and Simmons, 2002, for more on this topic, especially from an optimal foraging perspective).

The second Californian example comes from areas further south, around the Santa Barbara Channel. There, late prehistoric assemblages show patterns of dietary change paralleling those reported from San Francisco Bay, in this case read partly as a result of human-induced resource depression, partly of climate changes that produced similarly limiting effects on high-ranked prey availability (e.g., Glassow, 1996; Kennett, 2005; Kennett and Kennett, 2000; Raab, 1992, 1996; Raab and Bradford, 1997; Raab and Larson, 1997; Raab and Yatsko, 1992; Raab *et al.*, 1995). In addition to increased taxonomic diversity and declines in prey age structure, these studies also indicate greater human reliance on relatively expensive marine resources, changes in settlement patterns designed to improve access to these resources, and concomitant increases in morbidity and mortality indicators in human skeletal populations, best explained by dietary stress and higher levels of resource competition within and between local human groups (e.g., Kennett, 2005; Lambert, 1993, 1994; Lambert and Walker, 1991; Walker, 1989).

The third set of analyses makes the case for an initial shift toward "broad spectrum" diets much earlier than previously suggested (Stiner and Munro, 2002; Stiner *et al.*, 1999, 2000). Drawing on data from three areas of the Mediterranean Basin, Stiner *et al.* observe that while the overall representation of small vs. large-bodied prey in archaeological assemblages spanning the Middle to Upper Paleolithic transition shows no significant variation, that of different *types* of small-bodied prey changes significantly. Slow-moving, easily captured items (e.g., tortoises, shellfish) are common in Middle Paleolithic components, but decline in frequency and mean body size began in the Upper Paleolithic (<45,000 BP), probably as a result of human overexploitation. Conversely, fast-moving prey (e.g., birds, lagomorphs), lower ranked because they are more difficult to catch, are taken more often. The pattern is consistent with genetic data, indicating a sharp increase in human population size (and so predation pressure) during the mid-Upper Pleistocene (e.g., Rogers, 1995). Stiner and

colleagues suggest that the increase took place in several distinct pulses, each effectively dated (at least in the Mediterranean region) by the shift in small-animal exploitation patterns. Their argument implicitly challenges the idea that these and other changes in human diet and geographical range associated with the beginning of the Upper Paleolithic are best explained by an increase in human intelligence or (more broadly) by the appearance of “modern human behavioral capabilities” (e.g., Binford, 1984; Klein, 1999, pp. 454–463; cf. McBrearty and Brooks, 2000).

An important methodological issue emerging from the work on hunter-gatherer diet breadth involves the question of resource rank and how it is best established. This problem has been addressed satisfactorily for many sessile resources (e.g., plant foods, shellfish) through a combination of ethnographic and experimental work (e.g., Barlow and Metcalfe, 1996; Bettinger *et al.*, 1997; Bird and Bliege Bird, 2000, 2002; Bird *et al.*, 2004b; Cane, 1989; Gardner, 1992; Hawkes *et al.*, 1995a, 1997; Hurtado and Hill, 1989; Madsen and Schmitt, 1998; O’Connell and Hawkes, 1981, 1984; Petruso and Wickens, 1984; Reidhead, 1976; Simms, 1985, 1987; Simms and Russell, 1997; Smith *et al.*, 2001; Talalay *et al.*, 1984; Thomas, 2002; Thoms, 1989); it has proven less tractable for mobile forms (though see Cosgrove and Allen, 2001; Kaplan and Hill, 1992, pp. 168–176; Lindstrom, 1996; Smith, 1991, pp. 227–236).

Some analysts attempt to circumvent the problem by assuming that rank scales closely with prey body size, but this approach fails to consider the costs of pursuit, which are highly variable across taxa and at best loosely related to body weight (e.g., Bliege Bird and Bird, 2005; O’Connell *et al.*, 1988a; Smith, 1991, pp. 230–231; Stiner and Munro, 2002; Winterhalder, 1981, pp. 95–96; see also Hawkes *et al.*, 1991, on the problems of high pursuit failure rates for larger prey). Equally important, larger prey are more likely to be shared with a wider audience, in some cases resulting in relatively low post-encounter returns for the acquirer (e.g., Bliege Bird and Bird, 1997; Bliege Bird *et al.*, 2001, 2002; Hawkes *et al.*, 2001b). The pursuit of these items may still be especially attractive relative to other goals or currencies (e.g., display value), but there is nothing inherent in prey size that always correlates with nutritional profitability for the individual acquirer. Additional ethnographic and experimental data and attention to modeling different pursuit strategies, goals, and currencies should enhance the sophistication and realism of PCM applications to this problem. (See Elston and Zeanah, 2002; Hildebrandt and McGuire, 2002; and sections below on individual constraints and costly signaling theory; also Cannon, 2001; Lyman, 2003a,b; Stiner and Munro, 2002; Ugan and Bright, 2001; for further methodological commentary.)

Origin and diffusion of agriculture

Prey and patch choice models also provide insight on resource cultivation, including the processes underlying the adoption of plant and animal domesticates (e.g., Alvard and Kuznar, 2001; Diehl, 1997; Dominguez, 2002; Foster, 2003; Gremillion, 2004; Hawkes and O’Connell, 1992; Keegan, 1986; Keegan and Butler, 1987; Kennett and Winterhalder, 2006; Layton *et al.*, 1991; Piperno and Pearsall, 1998; Redding, 1988; Russell, 1988; Winterhalder and Goland, 1997).

One of the best illustrations of their potential in this context is provided by Barlow’s (2002) work on the prehistoric diffusion of maize in the American Southwest. Drawing on a detailed analysis of cost/benefit data on traditional farming practices in Central and South America, Barlow observes that maize cultivation includes a range of practices, all of which can be scaled according to work effort, “plant and harvest” being the least expensive, “swidden cultivation,” “typical agriculture” and “intensive agriculture” being progressively

more costly. Although production per unit area farmed generally increases along this same axis, marginal returns generally decline: the more effort devoted to cultivation, the lower the return achieved for each additional unit of effort. Barlow further observes that processing costs impose a ceiling on return rates: regardless of variation in cultivation techniques or resulting yields, farmers grinding dry corn with hand-held stone tools can earn no more than about 1800 kcal per hour of total effort devoted to farming, and this from the *least* expensive cultivation technique. All more intensive forms yield not only lower marginal returns but lower overall average returns as well.

These findings lead Barlow to argue that the choice to adopt maize and the selection of techniques used to cultivate it are likely to have depended on the trade-offs associated with exploiting other resources. In the northern Colorado Plateau and eastern Great Basin, net benefits gained from traditional maize farming broadly overlapped the post-encounter returns available from native plants and small game (e.g., Barlow and Metcalfe, 1996; Simms, 1987). Barlow reckons that in a climatically and topographically complex region like this one, reliance on maize, and the effort devoted to farming it, as opposed to foraging for wild resources, should have varied greatly from time to time and place to place, probably in predictable ways: lowest cost cultivation techniques pursued wherever even modest returns were potentially available, the most expensive ones applied only where related opportunity costs were very low. cursory review of the relevant archaeological literature suggests that she may well be right (Barlow, 2002, pp. 79–82; see also Coltrain and Leavitt, 2002; Coltrain and Stafford, 1999; Madsen and Simms, 1998; Simms, 1986, 1999). Barlow's argument not only merits more serious assessment in the American Southwest, but should also serve as a model for studies of the diffusion of agriculture elsewhere in the world.

Hawkes and O'Connell (1992) phrase the discussion of the trade-offs among foraging, cultivation, and domestication in more general terms, suggesting an even broader range of potential applications. Recall that the PCM divides foraging into two mutually exclusive components: search and handling. Where diets are narrow, more effort is devoted to search, less to handling; where they are broad, the allocation is reversed. Improvements in *search* efficiency are likely to be favored under a wide range of circumstances insofar as they lead to increased encounter rates with more profitable prey and so enhance overall foraging return rates. Improvements in *handling* efficiency, on the other hand, should be adopted *only* where diets are already relatively broad: as the proportion of time devoted to pursuing, collecting, and processing increases, so gains in efficiency in these areas that might have been irrelevant where search effort was high become more critical.

These propositions enjoy significant empirical support. For example, Keeley's (1995) worldwide review of ethnographically known plant cultivation techniques shows that low-cost, large-scale habitat burning designed to improve encounter rates for economically useful plants and animals is common among temperate and tropical foragers with relatively broad diets. Recent work by Bird *et al.* (2004a, 2005) demonstrates that managed burning does indeed have the desired effect on search efficiency (see also Bowman, 1998). Keeley's review indicates that more expensive planting and sowing techniques, also intended to improve search efficiency, are generally practiced only among a subset of groups already engaged in habitat burning. Piperno and Pearsall (1998) argue that a similar trajectory of increasingly intensive cultivation practices, beginning with the planting and sowing of wild geophytes and continuing through relatively high-cost domestication of seed-producing plants, is evident among neotropical foraging populations from the terminal Pleistocene onward. Efforts at improving search efficiency are apparent early in the sequence; those related to handling efficiency (including the domestication process itself) appear later. Finally, Russell (1988) argues that in the Near East initial experiments in animal domestication occurred only

in situations where forager diets were already quite broad and where the principal goal of domestication was the production of milk, an exercise that made otherwise unusable plants or plant parts available for human consumption—in short, improving their handling efficiency.

Technology

Over the past 20 years, discussions of patterns in tool use and their archaeological consequences have increasingly entailed appeals to cost/benefit considerations. Analysts operating from this perspective have paid particular attention to lithics, especially factors that might underlie variation in toolstone source exploitation and implement form, retouch, reduction, and discard patterns. Potential connections between these phenomena and certain aspects of foraging behavior have also been explored in some detail (e.g., Ambrose and Lorenz, 1990; Bamforth, 1986; Binford, 1979; Blades, 2003; Bleed, 1986; Bousman, 1993; Elston and Budy, 1990; Elston and Raven, 1992; Fitzhugh, 2001; Goodyear, 1989; Hiscock, 1994; Jeske, 1992; Kelly, 1988; Kuhn, 1995; Parry and Kelly, 1987; Shott, 1996; Simms *et al.*, 1997; Tomka, 2001; Torrence, 1983; Vierra, 1995; for comprehensive review see Bamforth and Bleed, 1997; Jochim, 1989; Nelson, 1991; Odell, 2001).

Results of this work have been mixed. Despite the attention to costs and benefits, sometimes to foraging theory in particular, few of these studies make substantive use of formal models in which goals, decision variables, trade-offs, currencies, and constraints are clearly stipulated. Most are more casually framed and so yield less than fully compelling outcomes. Even where formal treatments are undertaken, key variables have often proven difficult to quantify, especially those related to toolstone utility and the costs and benefits associated with the use of different implement forms and reduction strategies.

These and other problems notwithstanding, some of the work cited above makes excellent use of the BE framework. Kuhn (1994), for example, develops a formal model of toolkit composition for mobile foragers, focusing on the optimal type, size, and number of implements. Key constraints are *transport costs*, measured by implement weight, and *utility*, defined by the potential of different implement forms to produce fresh working edges of suitable length. Kuhn's analysis suggests that operators should generally avoid including cores in their kit, given that a significant fraction of their mass will be discarded as waste in the course of tool production. Trade-offs between implement size, weight, and utility suggest that carrying flakes or tool blanks is the better option.

Elston and Brantingham (2002) assess the costs and benefits of adopting microlithic technology for use in projectile weapon systems. Drawing on both ethnographic and experimental data, they show that while bone or wooden points equipped with microblade insets are significantly more expensive to produce than either stone or simple organic points, such items are also less likely to fail and are more readily repaired when they do and, therefore, should be preferred under certain climatic and demographic circumstances. Elston and Brantingham also assess trade-offs associated with the use of various types of blade cores, concluding again that more expensive forms should be favored in some settings, despite their cost, mainly because of the advantages they provide in weapon maintenance. Building on these results, Elston and Brantingham offer a series of predictions about the spread of various elements of microblade technology in northeast Asia during the late Upper Pleistocene relative to changes in climate, human population density, and degree of reliance on food storage.

Drawing more directly on the prey choice model, Bright and colleagues (Bright *et al.*, 2002; Ugan *et al.*, 2003) explore the relationship between diet breadth and technology, specifically the proposition that investments in collecting and processing gear, designed to

improve handling efficiency, are likely to increase in tandem with diet breadth (Hawkes and O'Connell, 1992). Bright *et al.* use this idea to account for changes in late prehistoric assemblage composition in the Great Basin, showing that as encounters with relatively high-ranked animal prey declined and diet breadth increased, less effort was devoted to the manufacture and maintenance of chipped stone hunting and processing tools and considerably more to the grinding stones needed for processing high cost seeds. Ugan *et al.* carry the argument further by developing a predictive model of investment in subsistence technology that takes into account the costs of making and maintaining gear, the returns gained as a result, and the time period over which the technology is to be deployed.

Several important implications follow from this work. First, all else equal, archaeological indications of increased investment in handling technology can be read as evidence of greater diet breadth. The high-cost processing tools and facilities (e.g., ceramics, large-scale roasting facilities, seed and nut grinding gear) that became more common in many parts of the world from the late Pleistocene onward are an obvious example. Most were associated with the adoption of low-ranked, hard-to-handle plant foods such as seeds and toxic or chemically complex geophytes and mast resources (e.g., Basgall, 1987; Clarke, 1976; Wandsnider, 1997; Wright, 1994). Even in the absence of the remains of such resources themselves, the presence of the technology alone indicates a relatively high investment in processing and a correspondingly low nutrient return ratio.

The increased investment in projectile weaponry (atlatl, bow and arrow, complex armatures) evident in the Eurasian Upper Paleolithic offers a less generally recognized but equally important example (e.g., Knecht, 1993; Kuhn and Stiner, 2001). These technologies are expensive to make and maintain (Elston and Brantingham, 2002), and marginal returns from deploying them are likely to be relatively low (Ugan *et al.*, 2003). The inference that their increasingly frequent use from early Upper Paleolithic times onward signals a general increase in human diet breadth is consistent with Stiner *et al.*'s (1999, 2000) more narrowly drawn argument based on small-animal remains (see Grayson and Delpech, 1998; O'Connell, 2005; for further discussion).

This leads to a further point about *efficiency*. It is often said that the adoption of more expensive subsistence technology marks an improvement in this aspect of food procurement: better tools make the process more efficient. This is true in the sense that such technology often enables its users to extract more nutrients per unit weight of resource processed or area of land harvested. If, on the other hand, the key criterion is the cost/benefit ratio, the rate of nutrient gained relative to the effort needed to acquire it, then the use of more expensive tools will often be associated with *declines* in subsistence efficiency. Increased investment in handling associated with the use of high-cost projectile weapons, in plant foods that require extensive tech-related processing, and in more intensive agriculture all illustrate this point.

Central place foraging: alternative goals, individual constraints, and the implications of differential resource transport

The strength of basic foraging models lies in their simplicity and generality. But as many have observed, the hypotheses they use to frame and test are sometimes falsified: in short, foragers (including humans) are sometimes found *not* behave as one might initially expect (e.g., Sih and Christensen, 2001). When this happens, the analyst is forced to reconsider his/her expectations, either by reformulating one or more first-stage hypotheses about goals, currencies, constraints, and so forth, or by turning to a model better suited to the question at hand. Archaeological applications of foraging models commonly confront an additional problem, namely, that the connection between foraging behavior and its archaeological

consequences may be complex, making predictions derived from even the simplest model applications to problems in prehistory potentially difficult to test.

Analysts have addressed these difficulties by developing more sophisticated ways of using basic foraging models and by exploring more effective means of confronting what has sometimes been called the “archaeological transform” problem (e.g., Schiffer, 1972). Studies of hunter-gatherers as central place foragers, folks who operate from a residential base to which they return between foraging bouts, offer some especially good examples of these approaches.

One involves the question of residential site location. Simply as a result of anisogamy, males and females often have different reproductive goals and correspondingly different strategies for achieving them (Trivers, 1972). Generally speaking, female reproductive success is constrained by access to resources critical for offspring survival. Male fitness, on the other hand, is limited by mating opportunities. As behavioral ecologists working with traditional hunter-gatherers have shown, this often translates into different foraging strategies: women targeting resources that maximize the efficiency with which they provide food for themselves and their offspring on a daily basis; men favoring prey whose occasional capture provides a “public good” of great interest to many, thereby drawing favorable, potentially fitness-enhancing attention to the provider (see below under “costly signaling”). These tendencies pose an important problem for central place foragers operating in patchy habitats: Given their respective foraging goals, the optimal residential site locations for women may be different from those for men. Hence the question: which location to favor when establishing a residential base?

Working in the Carson Desert of western Nevada and building on earlier research by Raven and Elston (1989) and Kelly (2001), Zeanah (2004) attacked this problem by (1) identifying the resources potentially available to late prehistoric foragers, (2) isolating those most likely to be targeted in pursuit of men’s and women’s foraging goals, respectively, (3) plotting their distribution across a wide range of different habitat types, then (4) determining which locations maximized the flow of resources to consumers on a daily basis. Under the climatic and environmental conditions thought to have prevailed in this region over the last several thousand years, sites located closest to resources predicted to have been favored by women proved to be the optimal solution most of the time, a result consistent with the actual distribution of late prehistoric archaeological sites identified as residential bases. Given this constraint, the optimal strategy for men would often have involved working from logistically organized “field camps” (*sensu* Binford, 1980) located well away from residential bases in areas where encounter rates with large animal prey were likely to be most frequent, an expectation again met by the archaeological record.

In a related study, Elston and Zeanah (2002) carried the argument further by modeling climatic and environmental conditions for the terminal Pleistocene in another part of the Great Basin, leading to a different set of predictions about preferred base camp locations, one that has not yet been rigorously tested but nevertheless seems consistent with most features of the relevant archaeological record as currently understood (e.g., Beck and Jones, 1997).

Another problem commonly encountered in this domain is that central place foragers sometimes cannot easily move all the resources they have gathered from the point of acquisition back to their residential base. Examples might include all parts of a large animal or an especially heavy load of acorns or shellfish. If the forager’s goal is to maximize the rate at which a certain *utility* (say, calories) is delivered to the base, the choice under these conditions is either to discard parts of the take or to devote more effort to transport—make as many trips as necessary to and from the base to move the entire load. The trade-off is

important because its resolution has obvious implications for the distribution of archaeological residues across the landscape (e.g., Binford, 1978).

Building on earlier work by Orians and Pearson (1979), Metcalfe and Barlow (1992) explored this trade-off with a formal model designed to predict the point at which “field processing and partial discard” as opposed to “bulk transport” will maximize delivery rates to a central place. Key elements of the model include the distance from prey acquisition site to base, the collector’s transport capabilities, the structure of the resource (number of component parts and their respective utilities), and the cost in time to process it in order to improve the utility of the load. Generally speaking, the larger the resource “package” relative to transport capability, the greater the distance from acquisition site to base, and/or the lower the costs of field processing, the more likely foragers will handle and abandon relatively low-utility elements in the field. Applications of the model have so far been limited by the absence of critical data, especially on processing costs, but useful results have nevertheless been reported for resources as diverse as big game, small seeds and nuts, toolstone, and shellfish (e.g., Barlow and Metcalfe, 1996; Beck *et al.*, 2002; Bettinger *et al.*, 1997; Elston and Raven, 1992; Lupo, 2001; Lupo and Schmitt, 1997; O’Connell and Marshall, 1989; Zeanah, 2000).

Bird and associates (2002, 2004b) have combined data on prey and patch choice and the effects of individual forager constraints with information on resource processing and transport costs in an analysis of patterns in midden composition on the Meriam Islands of eastern Torres Strait (for pertinent background see Bird, 1996, 1997; Bird and Bliege Bird, 1997, 2000, 2002; for similar examples of the same general approach see de Boer, 2000; Thomas, 2002). Their particular concern is the striking difference between the frequency with which contemporary Meriam foragers collect various species of shellfish and the representation of those species in archaeological deposits, both prehistoric and modern. Their analysis shows that ethnographic patterns of prey selection “in patch” are consistent with the goal of maximizing energy gained per unit of time devoted to search and handling, given the important caveat that children and adults walk at different speeds and so encounter higher-ranked prey at different rates. Patterns in acquisition-site processing and subsequent transport to base are further constrained by age-related differences in processing time and transport capability. Although it limits collecting time, processing the shellfish before transport increases the utility of a load. Beyond a predictable point, field processing can consistently increase the rate at which the meat of certain shellfish can be delivered to a base; hence the difference between what was collected and what shows up in the middens at central places. Patterns in the archaeological assemblages that Bird and colleagues examined are consistent with an age-specific goal of maximizing acquisition *and* delivery rate. These different goals and constraints are likely to affect the archaeological consequences of foraging in most intertidal environments (e.g., Meehan, 1982). The same reasoning can be applied to the analysis of relationships between prey choice and its archaeological consequences in other settings as well (e.g., O’Connell *et al.*, 1988a, 1990).

Colonization and competitive exclusion

Foraging theory also has been used in the study of regional colonization (e.g., Beaton, 1991b; Keegan, 1995; Keegan and Diamond, 1987; Kelly, 1999; Meltzer, 2002). Some of the best examples make use of the “ideal free distribution” model (Fretwell and Lucas, 1970), which envisions a region containing several separate patches ranked by quality, as measured by the costs and benefits of exploiting their respective subsistence resources. All else equal, colonists entering the region should occupy the highest-ranked patch first. Through time,

the quality of this patch should decline as a function of colonizer population growth. When returns fall to the level of those available in the second-ranked habitat, colonizers should occupy that one as well. The process is expected to continue until all patches are occupied and the marginal returns from exploiting them are at equilibrium – in other words, when there is no incentive for any resident of any patch to relocate.

Kennett *et al.* (2006) use this model to frame an argument about the colonization of Oceania. They contend that patterns in the initial occupation of this region should be a function of three variables: colonizer subsistence strategies, island size (and related ecological diversity), and distance from initial point of entry. Generally, foragers should deplete higher-ranked resources on any given island fairly quickly, and so should occupy all parts of the region in relatively short order, depending on the costs of interpatch travel. On the other hand, colonists practicing intensive agriculture should initially improve patch quality in ways that support population growth over longer periods of time and so display a slower rate of movement between patches. Preliminary review of the archaeological record indicates a relatively close match with predicted patterns.

Colonization of regions already occupied by other humans presents a different set of problems. Particularly interesting examples involve populations with similar subsistence economies and technologies (e.g., Moratto, 1984, pp. 529–574; Smith, 2004). The key questions are how the invaders manage to displace residents and why the latter fail to prevent the formers' advance, say by adopting some version of the invaders' own tactics.

Bettinger and Baumhoff (1982) offer an interesting answer to the first question in their analysis of a case from the Great Basin. At European contact, this region was occupied by speakers of six closely related Uto-Aztecan languages, collectively referred to as Numic (Miller, 1986). The languages themselves reached their historic distributions within the last thousand years or so (Lamb, 1958). Since humans have occupied this part of North America for at least the last 11,000 years (Grayson, 1993), a model of recent language spread is read by many to imply a related process of population displacement (Madsen and Rhode, 1994). Genetic data from late prehistoric human skeletal remains appear to support this inference (Kaestle and Smith, 2001).

Drawing on the logic of the prey choice model, Bettinger and Baumhoff (1982) argue that incoming Numic speakers displaced resident groups by a process of *competitive exclusion*, mainly by taking a broader but more expensive set of resources than those used by members of the resident population. This purportedly allowed the invaders to occupy a wider range of habitats at higher densities for longer periods of time, effectively eliminating the resident population's opportunity to maintain its economic *status quo* (see also Winterhalder and Goland, 1993), and so either pushing it off its range or absorbing it. The fitness advantages that should have been associated with the narrower diets of the residents were rendered moot, simply because that strategy could no longer be pursued in the presence of competitors willing to accept a lower marginal return on foraging effort (see Simms, 1983, for a critique).

O'Connell (2005) applies essentially the same line of reasoning to the problem of Neanderthal displacement by anatomically modern humans in western Eurasia, and in the process attempts to come at the second question noted above, the residents' failure to counter the invaders' tactics. Upper Paleolithic "moderns," particularly men, took a broader range of prey than did Neanderthals, a practice that may have given them a competitive advantage similar to that enjoyed by Numic speakers in the Great Basin. While Neanderthals' failure to expand their own diets in response might be attributable to what some see as their limited cognitive capabilities (e.g., Klein, 2003; Mellars, 1996), O'Connell suggests that gender-specific, fitness-related opportunity costs may have been a more important consideration. If Neanderthal men's big-game hunting tactics were key to the acquisition of mating

opportunities, as is the case among modern foraging groups (e.g., Hawkes *et al.*, 1991, 2001b), then any departure from them might have been avoided because of the near-term costs in male–male competition, even at the expense of ultimate extinction.

Life history theory and the evolution of genus *Homo*

To this point, our review has been concerned with the most common applications of BE to problems in archaeology, those involving subsistence and related features of technology and settlement patterns. Recently, a second major area of BE-oriented research has developed within archaeology, different from the above in that it attacks a broader set of questions, at a greater depth in time, and appeals to a more comprehensive set of models and related arguments and data sets in doing so. The central issue is the initial evolution of genus *Homo*.

The problem

Humans are distinguished from their nearest living relatives, chimpanzees, by a familiar list of traits: larger body and brain size, obligate bipedality, different (arguably simpler) dental and digestive anatomies, a slower life history, very different patterns of social organization and reproduction, a much wider geographical range, more variable diets, and a greater degree of reliance on technology. Our most recent common ancestor, a chimpanzee-like form, lived about 5–7 million years ago (Ma) (Glazko and Nei, 2003). Obligate bipedality (or something close to it) was present in our lineage, the hominin line, by at least 4 Ma (White *et al.*, 1994), and some of our other distinctive traits—larger body size, modern (or near-modern) human anatomical proportions, human (or human-like) dental and alimentary anatomy, and broad (extra-African) geographical range—emerged as a set, probably in the late Pliocene (1.9–2.4 Ma), a development identified by some as marking the first appearance of genus *Homo*, embodied in the taxon referred to either as “early African” *H. erectus* or *H. ergaster* (e.g., Wood and Collard, 1999).

Recent work on life history theory and related analyses of the hominin fossil record add important details to this picture (Hawkes *et al.*, 1998). Key features of mammalian life history—age at first reproduction (α), average adult lifespan ($1/M$, the inverse of adult mortality), and average annual fertility (b)—have been shown to vary in tandem across most taxa (Charnov, 1993, 2001). Charnov argues that this variation is controlled by adult mortality (M), which determines the point at which resources previously devoted to growth should be allocated instead to reproduction. Generally speaking, it is better to delay this shift to grow larger and so have more production to put into offspring. But delay increases the risk of dying before reproducing. The lower the adult mortality rate, the lower this risk; hence, the later the predicted age and the larger the body size at maturity, such that the ratio of α to average adult lifespan (αM) is constant. Larger adult body size in turn generally correlates with longer gestation, larger neonates, later age at weaning, and lower fertility.

Like nearly all other living primates, chimpanzees fit this model fairly well (Alvarez, 2000; Charnov and Berrigan, 1993). They are relatively large, mature late (at about age 12–13 years), have relatively low adult mortality rates, live to age 50 or more, have large babies, nurse them until they are about age 5, and so have relatively long interbirth intervals and correspondingly low fertilities (Goodall, 1986; Nishida *et al.*, 2003; Robson *et al.*, 2005).

Humans fit the model in some ways but differ strikingly in others (Alvarez, 2000; Robson *et al.*, 2005). Humans can live much longer than chimpanzees, and so mature later (at about 18–20 years) and are larger as adults. But relative to adult body size, humans wean their babies early and so may have relatively *short* interbirth intervals and correspondingly

high fertilities. Among the best-known modern hunter-gatherer populations, *b* is roughly twice what the general primate model would lead one to expect relative to age at maturity (e.g., Hawkes *et al.*, 1998, 2003). Furthermore, unlike nearly all other mammals (except possibly elephants and some cetaceans), their reproductive systems undergo senescence well in advance of other components of their physiology. Specieswide, human females reach menopause at about 50 ± 5 years (Hawkes, 2003; Pavelka and Fedigan, 1991), making their age at reproductive senescence similar to that in chimpanzees. Yet unlike chimpanzees most women who reach that age have many years of additional life ahead of them: in those same well-known hunter-gatherer populations, *on average*, about two decades (Hawkes, 2004).

Opinions differ on when the modern human pattern of life history began to emerge. In our view, the balance of available data indicate that prehuman hominins (*sensu lato*, “australopithecines”) matured at about the same age as modern chimpanzees and so may have had similar life histories (Wood and Collard, 1999; cf. Dean *et al.*, 2001). *H. ergaster* marks the first definite move away from this pattern, with an age at maturity significantly later than that in australopiths (e.g., Clegg and Aiello, 1999; Dean, 2000; Ruff and Walker, 1993; Smith, 1993; Smith and Tompkins, 1995; see also Caspari and Lee, 2004; Dean *et al.*, 2001; Hawkes and O’Connell, 2005). Maximum life spans for members of this taxon may have been intermediate between those of chimpanzees and modern humans. Assuming that age at reproductive senescence was the same as that in chimpanzees and modern humans, the initial appearance of midlife menopause then dates to this point in our lineage (Hawkes *et al.*, 2003; O’Connell *et al.*, 1999). In short, near-modern human life histories seem to have appeared in tandem with other major changes in morphology, physiology, and ecology associated with the emergence of the earliest clear-cut representatives of our genus.

Hunting and the embodied capital hypothesis

The conventional explanation for the evolution of early humans, commonly called the “hunting hypothesis,” models it as a reaction to late Pliocene climate change (see Cartmill, 1994, for background; Lovejoy, 1981; Washburn and DeVore, 1961; Washburn and Lancaster, 1968, for influential argument; O’Connell *et al.*, 2002, for recent review and discussion). Cooler, drier, more seasonal conditions established at this time allegedly reduced the availability of plant foods important to ancestral hominins, forcing them to rely more heavily on meat, especially from large ungulates. More meat may have meant lower somatic processing costs, hence, the development of a simpler dental and digestive anatomy. The demands of hunting favored increased reliance on technology and greater intelligence, leading to a significant increase in brain size. Bigger brains posed an “obstetrical dilemma” for mothers, causing them to deliver their babies at an earlier stage of development. This not only increased the costs of child care but also limited mothers’ ability to hunt and gather, making them at least partly dependent on other adults for nutritional support. The extended juvenile period implied by the combination of early weaning and delayed maturity further increased these costs. Men’s big game hunting purportedly underwrote all of this in exchange for more restricted mating arrangements and correspondingly greater confidence of paternity. Nuclear families, marked by a strong pattern of male parental investment, are said to have been among the results.

Kaplan *et al.* (2000) have recently updated this hypothesis, with specific reference to current life history theory and the “embodied capital” model from economics (Becker, 1975). They propose that bigger brains required more time devoted to growth, which meant more time available for learning (embodied capital) and in turn not only more adult productivity but also lower adult mortality and later age at maturity. Kaplan *et al.* emphasize the role of hunting as central to the coevolution of a longer juvenile period and lower adult mortality (see

also Hill and Kaplan, 1999; Kaplan and Robson, 2002; Robson and Kaplan, 2003). Selection should have favored investments in “experience-based embodied capital,” especially insofar as this led to increased payoffs from complex foraging activities, hunting being the prime example. Longer childhoods may thus be both *cause* and *effect* of learning complex foraging skills: longer childhood increased experience-based capital; more experience-based capital increased adult productivity and reduced adult mortality, favoring still further delays in age at maturity.

Archaeological data have long been seen to provide crucial support for this hypothesis. The earliest sites appear at roughly the same time as early *Homo*; some contain the remains of large animals in close association with stone tools (e.g., Isaac, 1997; Leakey, 1971). Many analysts take this as clear evidence of big game hunting and the transport of meat to central places to share with mates and offspring, in short, for nuclear families and paternal provisioning (e.g., Clark, 1997; Isaac, 1978; Kaplan *et al.*, 2000; Rose and Marshall, 1996). The coincidence with the appearance of early *Homo* is seen as strong support for a causal relationship.

Despite its continuing appeal and Kaplan and associates’ recent theoretical contributions, there are reasons to be skeptical of this hypothesis. 1) On strictly theoretical grounds, males of most sexually reproducing species, including humans, are unlikely to favor the provisioning of offspring over investment in mating opportunities, given that the potential reproductive payoffs from the latter will usually be significantly greater (e.g., Hawkes *et al.*, 1995b; see Blurton Jones *et al.*, 2000, for empirical support).

2) The hunting hypothesis has relied heavily on the idea that big-game hunting serves as a paternal provisioning strategy among ethnographically known hunter-gatherers and so probably played a similar role in the distant past. In fact, paternal provisioning is actually not practiced among the best-documented low-latitude foraging populations, including those occupying habitats most similar to the ones in which early humans evolved. Hunters in these situations routinely target resources and distribute their take in ways that neither contribute optimally to the daily subsistence needs of their respective families nor provide the latter with unusually sizable shares when the hunter is successful (e.g., Bliege Bird, 1999; Bliege Bird *et al.*, 2001; Hawkes, 1990, 1991, 1993; Hawkes *et al.*, 1991, 2001a,b; Panter-Brick, 2002).

3) The Kaplan *et al.* argument that learning-related delays in age at maturity favored lower adult mortality and extended longevity actually reverses the chain of causality posited by Charnov (1993). In Charnov’s model, extended adult life expectancy drives prolonged adolescence, not the other way around. The Kaplan *et al.* argument also fails to account for the retention of the ancestral age of reproductive senescence and the resulting development of midlife menopause, a specieswide life history pattern among modern humans that arguably emerged for the first time in early *Homo*.

4) The idea that prolonged adolescence is essential to the development of “skill-intensive” foraging practices, a theme central to most versions of the hunting hypothesis and elaborated by Kaplan *et al.*, is at least partly undercut by the results of recent ethnographic work on children’s foraging practices. This work shows that larger body size is the primary requirement for success in the acquisition of “nutrient-rich” resources, *not* learning or intelligence (e.g., Bird and Bliege Bird, 2002; Bliege Bird and Bird, 2002; Blurton Jones and Marlowe, 2002; Blurton Jones *et al.*, 1997).

Most important from the perspective of this particular review is the Kaplan *et al.* handling of the relevant archaeological data. One issue involves their assertion that because evidence of the use of plant foods is absent from the Plio-Pleistocene material record, these resources did not play a major role in early human diets—an unlikely proposition at best. Another is

their continuing adherence to the view that the large-animal bone accumulations at sites such as Olduvai and Koobi Fora do indeed indicate big-game hunting on the part of early humans, a reading contradicted by more than 20 years of comprehensive taphonomic research, nearly all of which points to scavenging on kills made by other predators as the primary role played by humans in the creation of these sites (e.g., Binford, 1981; Blumenschine and Marean, 1993; O'Connell *et al.*, 2002). If this interpretation is accurate, then meat from big game is unlikely to have been the key element of the diet of early *Homo*. Inherent limitations on the amounts of edible tissue available from scavenging and the frequency and reliability with which it can be obtained make it impossible for this food source to have played the regular family provisioning role envisioned by proponents of the hunting hypothesis (O'Connell *et al.*, 2002). The earliest indication of a level of hunting success consistent with this classic argument dates to about 500 ka BP (Stiner, 2002), more than a million years *after* the emergence of the genus its development is argued by Kaplan *et al.* to explain.

Grandmothering and the low mortality hypothesis

Observations among the Hadza, a traditional East African foraging population, provide the basis for an alternative hypothesis (Hawkes *et al.*, 1995a, 1997a). Hadza children are remarkably effective at feeding themselves (Blurton Jones *et al.*, 1989; Hawkes *et al.*, 1995a). But they still need support from others until they are well into their teens, particularly at times when foods they can take and process on their own are unavailable. Some of this support comes from men's big-game hunting, a source that is unreliable on a day-to-day basis. Despite substantial effort, men manage to acquire large carcasses on average only about once every 30 hunter-days, and periods of ten days or more have been recorded in which little or no meat was available in study camps (Hawkes *et al.*, 1991, 1997b). Moreover, most of the meat children eat comes from men other than their own fathers (Hawkes *et al.*, 2001a,b). Support from a child's mother is much more consistent, but her ability to provide it is significantly reduced during the late stages of a pregnancy and for the first year or so postpartum. At these times, her weaned but still dependent children must look elsewhere for help. Most of it comes from mother's postmenopausal female relatives, usually her own mother or mother's sister (Hawkes *et al.*, 1989, 1997b). Senior Hadza women are able to acquire key resources at rates comparable to those earned by their younger adult kin; since they often work longer hours they are frequently more productive. In cases where mother is heavily pregnant or nursing, her weaned children's nutritional welfare is found to correlate closely with "grandmother's" foraging effort.

Hawkes and colleagues (Hawkes, 2003; Hawkes *et al.*, 1997b, 1998, 2003; O'Connell *et al.*, 1999, 2002) use these observations to formulate an alternative scenario for the evolution of early *Homo*. They assume that ancestral hominin (australopith) life histories were similar to those of modern chimpanzees and that weanling australopiths were able to feed themselves with little or no assistance. They further assume that late Pliocene climate change reduced the availability of foods these younger juveniles could handle on their own. Under these circumstances older females, at or near the end of their own reproductive careers, would have gained a selective advantage by supporting the offspring of their younger female kin with foods they themselves could acquire reliably and at relatively high rates but that young children could not. Examples of such resources include geophytes, which are readily collected and processed by adults, often provide a substantial proportion of modern forager diets, but commonly require more upper body strength, manual dexterity, and judgment to handle effectively than younger human juveniles possess (e.g., Coursey, 1973; O'Connell *et al.*, 1999; Wrangham *et al.*, 1999). Feeding weanlings with resources like these would

have allowed local hominin groups to transcend the habitat restrictions imposed by juvenile foraging capabilities: unlike chimpanzees, and by analogy, australopiths, they could have operated in situations where youngsters were unable to feed themselves, opening the door to the occupation of a much broader range of habitats. If senior females did the feeding, their daughters could have weaned their children earlier and moved to the next pregnancy sooner, the net result being closer birth spacing and higher fertility. The more vigorous the older female, the better able she would have been to provision her grandchildren, and so the higher their survivorship. Tendencies to live longer and be more active past menopause would have persisted and spread as a result. As adult life expectancy increased, age at maturity would have been delayed in order to grow longer and so reap the benefits of larger body size (Alvarez, 2000).

This model is similar to the hunting hypothesis in that it identifies late Pliocene climate change and its implications for ancestral hominin subsistence as critical to the evolution of early *Homo*. Like the Kaplan *et al.* version of that argument, it makes the effects of those changes on hominin life history the central focus of attention. It also appeals to the same body of theory (Charnov, 1993) as the framework for analysis. Unlike the Kaplan *et al.* formulation, it sees lower adult mortality and extended longevity, *not* delayed maturity, as the main force behind other life history changes. Long periods of learning are thus seen as a consequence of, *not* the catalyst for, extended juvenility. Finally, given that the selective effects of grandmother's provisioning are likely to have been greater with respect to her daughter's children than those of her son, with whom her relationship will sometimes have been less certain, the model predicts that transgenerational sets of uterine-linked kin are likely to have been important features of early human social organization. Nothing about nuclear families or central place foraging is entailed in any of this argument (cf. Clark, 1997; Foley and Lee, 1989).

Though only recently formulated, the grandmother hypothesis has already been challenged on several key points. Some question whether grandmother's help, particularly as a provisioner, can ever have had a significant effect on either her daughter's fertility or the survivorship of her grandchildren (e.g., Hill and Hurtado, 1996, pp. 427–434; Kaplan *et al.*, 2000). Several recent empirical studies show that it not only can but often does (e.g., Jamison *et al.*, 2002; Lahdenperä *et al.*, 2004; Nath *et al.*, 2000; Ragsdale, 2004; Sear *et al.*, 2003; Voland and Beise, 2002). Other critics hold that the pattern of extended postmenopausal longevity purportedly central to further changes in human life history is in fact a relatively recent development, dating no earlier than the appearance of fully modern humans, possibly to the last few centuries (e.g., Caspari and Lee, 2004; Kennedy, 2003; Trinkaus, 1995). This objection is misplaced on two grounds. First, it ignores the allometric relationship between age at maturity and adult lifespan documented across a broad sample of living primates, including modern humans (Alvarez, 2000; Hawkes and O'Connell, 2005). A commonly estimated maturation age of 15 years for early *Homo* implies, perforce, a lifespan that extends well beyond menopause. Second, the idea that this point can be countered by maximum age estimates of 50 years for the skeletal remains of early humans ignores both the inherent inaccuracy of those estimates and the consistent, taphonomically related underrepresentation of seniors in skeletal samples that they were known to have been part of at the time of interment (Hawkes and O'Connell, 2005).

Further evaluation of this hypothesis requires at least two things: 1) The nature of the life history shift associated with the emergence of early *Homo* needs to be clarified. While on balance the available data appear to indicate a pattern intermediate between those of chimpanzees and modern humans, respectively, there is room for skepticism. Not all features of life history can be monitored skeletally, but two that are central to the grandmother

hypothesis, age at maturity and weaning age, can be. Testing hypotheses about the former (e.g., Caspari and Lee, 2004; Dean *et al.*, 2001; Smith, 1993) and exploring promising ways of establishing the latter (e.g., Rabb, 2005; Wright and Schwarcz, 1998) are the obvious next steps.

2) The proposition about key resources must be evaluated. According to the model, these must be readily and reliably available, collectable by adults in quantities large enough to support more than one person on a daily basis, and difficult for young juveniles to handle effectively. Geophytes as a class are the most obvious candidates on all three counts. That the earliest humans out of Africa quickly moved as far north as latitude 40°–45° (e.g., Gabunia *et al.*, 2000; Zhu *et al.*, 2001) and then held at that threshold for more than a million years is consistent with the idea that roots, tubers, and corms were a critical component of their diet: This is roughly the outer limit for reliance on geophytes as a staple among historically known foragers (e.g., Thoms, 1989). Evidence for the controlled use of fire and archaeological, chemical, or genetic markers of starch consumption would provide further critical support for this hypothesis.

Wasteful behavior versus costly signaling

A third area of BE-oriented research in archaeology involves aspects of human behavior that might at first glance seem inexplicable from a Darwinian perspective. Common examples include stylistic attributes of artifact form, elaborate grave goods, competitive feasting, long-distance trade in nonutilitarian commodities, monumental architecture, and investments in “public goods.” These and other similar phenomena are alike in that their production often entails significant costs in time and effort. The question is what fitness-related benefits, if any, they confer on their producers. Answers offered by archaeologists drawing on concepts derived from behavioral ecology can be grouped under two headings: those that regard “wasteful behavior” as somehow crucial to group survivorship, and those that see it as central to differences in the reproductive success of individuals.

Wasteful behavior and group survivorship

Advocates of the “group survivorship” argument routinely cite Dunnell (1989) as their primary inspiration (e.g., Kornbacher and Madsen, 1999) but sometimes also make reference to standard BE formulations, notably Seger and Brockman’s (1987) bet-hedging model (e.g., Aranyosi, 1999; Madsen *et al.*, 1999). Their efforts have been directed primarily at explaining investment in monumental architecture and costly burial practices. They propose that these “wasteful” efforts absorb resources that would otherwise be devoted to reproduction and so prevent populations that invest in them from exceeding local habitat carrying capacities. These populations are thus better prepared to survive occasional drops in resource availability than are those that invest more directly in fitness.

References to the BE literature notwithstanding (and counter to Seger and Brockman (1987) in particular), this is a group-selectionist model of the sort that has been rejected by behavioral ecologists for more than 40 years (e.g., Maynard Smith, 1964, 1976; Williams, 1966; cf. Dunnell, 1999). The arguments against it are compelling. Theoretical and empirical work consistently shows that selection nearly always favors behavior that maximizes *individual* reproductive success, *regardless* of its implications for the welfare of the group of which that individual is a part (e.g., Blurton Jones and Sibly, 1978; Grafen, 1984; Michod, 2000; Olson, 1965; Winterhalder and Smith, 2000; for comprehensive review see Keller, 1999). Individuals who sacrifice their reproductive interests for the sake of the group are

nearly always at a selective disadvantage in competition with those who favor their own. Exceptions to this generalization are highly unusual and occur only under well-known, narrowly defined circumstances (Grafen, 1984; Harpending and Rogers, 1987; Maynard Smith, 1964, 1976; Rogers, 1990; see also Shennan, 2002: pp. 239–244, 253–256), none of which have yet been shown to apply in the Dunnellian “wasteful behavior” literature. Until they are, this line of work seems unlikely to produce reliable insights about “wasteful behavior” in the past.

Costly signaling

Another, much more promising line of argument for “wasteful” or “irrational” behavior, one that draws on evolutionary game theory, has been developed under the heading of “costly signaling theory” (CST) (e.g., Grafen, 1990; Johnstone, 1995, 1997; Zahavi, 1975, 1977, 1990, 1995; Zahavi and Zahavi, 1997; see also Veblen, 1899). It holds that in contests between individuals, the ability to provide an honest index (or *signal*) of each individual’s quality or motivation can frequently be in the best interests of both signaler and recipient (Getty, 1998; Maynard Smith, 1982, 1991). Often the costs of producing the signal offer the best (sometimes the only) indication of its validity: More able, more highly motivated individuals can afford to provide more expensive (“more wasteful”) signals. Demonstrating the ability to bear those costs may benefit both signaler and recipient. For example, the attention-attracting behavior of a mobile prey item (e.g., babbler alarm calls, stotting by gazelles) guarantees its condition to a potential predator. The higher the quality signaled, the less likely that even more energy will be wasted on either side in a costly, often pointless chase. Both predator (recipient) and prey (signaler) gain from the exchange of information.

CST has been applied productively in BE-oriented studies of several aspects of human behavior over the past decade (e.g., Bliege Bird and Smith, 2005; Bliege Bird *et al.*, 2001; Boone, 1998, 2000; Boone and Kressler, 1999; Hawkes, 2000; Hawkes and Bliege Bird, 2002; Neiman, 1997; Smith and Bliege Bird, 2000, 2005; Smith *et al.*, 2003; Sosis, 2000, 2003; Sosis and Bressler, 2003). Three elements of this work, involving material display, hunting strategies, and competitive feasting, have important implications for archaeology.

Material display

Humans often use material media, in the form of art, ornament, or the stylistic aspects of artifacts, to communicate information about themselves and/or their social milieu, a practice widely identified as the essential archaeological diagnostic of modern human cognitive and behavioral capability (e.g., Klein, 2000; McBrearty and Brooks, 2000). Though it is clear that information is routinely transmitted in this way, it is equally clear that such information may be difficult for outsiders to decipher (e.g., Hodder, 1982).

CST offers a useful approach to this problem by focusing attention on the cost of the message and the circumstances that make paying it worthwhile. Neiman’s (1997) analysis of Maya calendrical monuments provides an example. Maya construction required substantial investments in stone quarrying, transport, and engraving, as well as in the maintenance of the relevant intellectual and craft-specialist infrastructure. The inscriptions themselves reported the history of the responsible lineage, documenting its antiquity and setting forth the basis for its claim to control both the emplacement site and its surrounding economic “support zone.” These were classic costly signals, effectively impossible to fake. Neiman contends that investment in monuments is likely to have varied directly with both polity size and influence and the intensity of interpolity competition, which in turn should have been related

to such factors as agricultural productivity, current climatic conditions, and demographic pressure on the resource base. He uses this argument as a basis for evaluating alternative hypotheses, developed on other grounds, concerning the scale of regional political organization, the factors responsible for its disintegration, and the reactions of local populations to the beginning of that collapse.

Though Neiman's lead has so far encouraged few followers (but see Kohn and Mithen, 1999), it could be pursued along a much broader front. The most intriguing point of attack involves the assumptions referred to above, that signaling via material media is both ubiquitous among and unique to modern humans. On the contrary, not all modern human populations invest much if anything in material display, certainly not in ways that are likely to be reflected archaeologically (e.g., Jones, 1977; Speth, 2004), but at least some *nonhuman* species do (e.g., Diamond, 1986, 1991; McKaye, 1991). Consistent with the spirit of Neiman's argument, it is interesting to speculate that differences in the degree of human investment in material display during the late Pleistocene and Holocene reflect differences in the intensity of interpersonal and/or intergroup competition, say as a function of changes in population density. If so, then it may be, as Kuhn *et al.* (2001) and others have suggested, that the widely touted "explosion" in evidence for symbolic communication beginning at about 50 ka is driven not by a sudden increase in human cognitive capability but instead by the larger human population sizes and higher levels of resource competition (Rogers, 1995; Stiner *et al.*, 1999). Similarly, it may be that the intermittent appearance of style, art, and ornament in the African MSA can be read as evidence of earlier transient increases in human population density and competition. And it also may be that the near-complete absence of material display in the west Eurasian Middle Paleolithic says more about Neanderthal demography than it does about their cognitive or behavioral capabilities. Clearly, this line of argument raises many more questions than it resolves, but taking those questions seriously seems to be a step in the right direction (Speth, 2004).

Hunting strategies

One of the more interesting results emerging from the use of foraging models in analyses of hunter-gatherer subsistence is the observation that men's prey choices are often inconsistent with the goal of maximizing daily nutrient return rates. Men routinely bypass items they can easily take at relatively low but consistent rates (e.g., plant foods) in favor of other resources (e.g., big game) that yield higher but much less reliable daily returns (Bliege Bird, 1999; Bliege Bird and Bird, 2005; Bliege Bird *et al.*, 2001; Hawkes *et al.*, 1991; Hill *et al.*, 1987; Hurtado and Hill, 1989; Wiessner, 2002). For example, Hadza men specialize in hunting large ungulates, yet succeed in acquiring them, on average, only one hunter-day in 30, a daily failure rate of 97% (Hawkes *et al.*, 1991). This practice does not serve the commonly suggested goal of family provisioning (Hawkes *et al.*, 2001a,b). Hadza men concerned with insuring the nutritional welfare of their wives and children would do better by taking a broader array of prey, including small game and plant foods, partly because they are far more reliably acquired, partly because they can usually be reserved for the hunter's own household. Big game are not only taken less predictably but also are shared much more widely, usually with no special allocation to the hunter's own family. The more successful the hunter, the bigger the difference generally observed between what he gives away and what he and his household receive in return. Hence the question: What benefits flow to the hunter from specializing in the pursuit of large animal prey?

Hawkes and colleagues argue that big-game hunting is often a form of costly signaling, a means by which men establish and maintain social position relative to their peers and

competitors, not just among the Hadza but among foragers in general (Hawkes, 1990, 1991, 1993, 1996, 2000; Hawkes and Bliege Bird, 2002; Hawkes *et al.*, 1991, 2001a,b). To the degree the hunter is successful, two ends are achieved. First, because big-game hunting is a risky, skill-intensive undertaking, the good hunter marks himself as a powerful ally and dangerous adversary. His relationships with others are likely to be structured accordingly. Equally important, his successes make available a “public good,” one that is of interest to all, unpredictably acquired, readily divisible, and thus likely to be shared widely (Blurton Jones, 1987), considerations that draw still more favorable attention his way. That attention might include deference to his wishes, support in disputes, positive dealings with his spouse and children, and more frequent mating opportunities (Hawkes and Bliege Bird, 2002).

Bliege Bird, Sosis, and colleagues (Bliege Bird and Smith, 2005; Bliege Bird *et al.*, 2001; Sosis, 2000, 2003) argue that in some cases the “display” quality of an activity alone may be enough to warrant its performance, regardless of whether it produces a public good. For example, Meriam men routinely spearfish on the reef in clear view of their home village. This activity generates an average 80% lower return than that available from collecting shellfish in the same area, yet men generally disregard the latter activity apparently because of the performance value of skill-intensive spearfishing, especially when pursued within sight of one’s main competitors—other men (Bliege Bird and Bird, *n.d.*; Bliege Bird *et al.*, 2001).

These observations and the theory that accounts for them have so far been applied in three archaeological case studies involving hunting and aggressive scavenging. 1) Hildebrandt and McGuire (2002, 2003; McGuire *et al.*, 2004, pp. 130–135) use CST to account for the correlation between sustained human population growth and a proportional *increase* in large mammal remains from Middle Archaic (4000–1000 BP) faunal assemblages in many parts of California and the western Great Basin. The pattern is seen to be inconsistent with the predictions of standard prey choice model: If big game are high ranked and thus typically pursued on encounter while foraging, then (all else equal) larger human population sizes and correspondingly greater pressure on resources should result in a *drop* in the abundance of large mammal remains relative to those of other prey types. Hildebrandt and McGuire contend that the observed proportional increase in these remains is more consistent with increasing benefits from the signaling value of certain resources that, successfully acquired, ensure that the qualities of the acquirer are displayed to larger, more concentrated local audiences. Coincident increases in the production and widespread transport of hunting tools made from relatively “showy” toolstone and in the investment made in hunting-related rock art are also seen to be consistent with this hypothesis. In short, the overall pattern reflects an increase in the level of social competition and a corresponding change in the value of hunting for prestige.

2) As indicated above in the section on competitive exclusion, O’Connell (2005) suggests that the failure of Neanderthal males to broaden their prey selection pattern in the face of competition from Upper Paleolithic “moderns” parallels Hadza men’s reluctance to pursue small game in addition to hunting and scavenging large animal prey. As just noted, if Hadza men targeted a broader, more reliably acquired range of prey, they could provision their families more effectively (Hawkes *et al.*, 1991, 2001a,b). But by pursuing this strategy, they risk falling behind in costly signaling competition with other men and thus lose out on the benefits that flow from success in that competition, notably better mating opportunities. O’Connell proposes that the same explanation may account for the Neanderthal pattern of targeting large game with close-range weapons (e.g., thrusting spears or javelins). Neanderthal men who took fewer risks by targeting large animal prey at greater distances with more sophisticated arms, like those used by Upper Paleolithic “moderns,” or by hunting and trapping small game arguably had lower social status than their more aggressive peers, and

so did less well in competition for mates, a losing strategy in the short term, regardless of its potential implications for long-term Neanderthal survivorship as a population.

3) O'Connell *et al.* (2002) use a related line of argument to account for the archaeological record of competitive scavenging reported for late Pliocene East Africa. Conventional wisdom holds that this record is evidence of increased hominin reliance on meat from large animal carcasses as a source of food for mates and offspring, a shift that contributed directly to the emergence of genus *Homo* (e.g., Isaac, 1978). O'Connell *et al.* contend that causality in fact ran in the opposite direction. Shifts in hominin female foraging and food-sharing practices, none of them involving meat, arguably provide a better explanation for the emergence of genus *Homo*. One of the more important consequences of this development, larger adult body size, increased hominin males' chances of success at competitive scavenging, defined as a form of costly signaling (O'Connell *et al.*, 1988b, 2002, pp. 859–862). Driven by the social benefits that emerged from that activity, investment in it is likely to have increased, despite the probability that resulting nutritional gains were often low and always unpredictable.

Broughton and Bayham (2003; see also Byers and Broughton, 2004) have weighed in on the first of these cases, arguing that the increase in large animal remains encountered archaeologically in parts of Middle Archaic western North America says nothing about costly signaling. Instead, it reflects a climate-driven increase in the abundance and encounter rates for this prey type, an inference derived from the basic prey choice model. Two assumptions are critical to this argument: (1) that profit scales closely with prey body size, (2) that the goal of big-game hunting is the maximization of short-term foraging return rates. If so, increased evidence of big-game hunting should reflect either an increase in large animal population densities or a decline in human population sizes. Absent any evidence of lower human populations (the record shows just the reverse), Broughton and Bayham draw attention to data indicating cooler, wetter late Holocene climates that should have favored larger big-game populations. They contend that human populations exploiting this development grew in size, ultimately depressed big-game populations, and so were forced to broaden their diets to include more small game and plant foods, resulting in the Late Archaic pattern discussed above. In short, they contend, appeals to CST are not needed to account for the phenomenon of interest when the basic prey choice model does so as well or better.

Regardless of which argument proves correct, the dispute prompts us to underline an important point, namely, that Broughton and Bayham's assumptions about resource rank and men's foraging goals are fragile. They might be valid in this case, but there are good reasons to be skeptical about them, not only in this particular situation but also as general rules, and so to pursue the type of argument that Hildebrandt, McGuire, and others have begun to develop. The best reported hunter-gatherer ethnographies (Ache, Hadza, Meriam, and !Kung) all show that men's prey choices are inconsistent both with predictions derived from the basic prey choice model and with the goal of family provisioning. This is and probably always has been a common pattern (e.g., Hawkes *et al.*, 1995b). Widely held assumptions about nuclear families as units of common economic and reproductive interest and about a "sexual division of labor" that serves that interest are drawn into question as a result (e.g., Hawkes *et al.*, 2001a,b). Novel arguments about key developments in human evolutionary history are provoked accordingly. Broughton and Bayham's critique sidesteps these important issues. In our view, the interesting question is not *whether* men consistently favor costly signaling over rate maximization (or the reverse) while foraging, but *under what circumstances* they are likely to prefer one or the other and how the alternatives might be distinguished archaeologically (see Hawkes, 2000, for a trial formulation).

Competitive feasting

Status and the production of costly foods used to achieve or reinforce it are common elements in arguments about subsistence intensification and the development of social complexity (e.g., Dietler and Hayden, 2001; Gummerman, 1997; Hayden, 1996, 1998, 2001; Kirch and O’Day, 2003; van der Veen, 2003; Wiessner and Schiefenhoevel, 1996). An important problem with much of this work is the absence of a theoretically consistent basis for identifying the conditions under which high-cost, status-related food production and distribution might be expected to develop.

Costly signaling theory may provide a useful avenue for constructing such a framework, allowing us to recast questions about the use of “luxury foods,” feasting, and their role in escalating socioeconomic contests (Bliege Bird and Smith, 2005). Luxury foods are generally characterized by (1) the expense of acquiring or producing them and (2) the notion that they are functionally unnecessary (van der Veen, 2003). Where competition for relative social position conditions success, luxury foods are in some cases functional requirements for condensing and conveying information. The expense of producing such goods often limits their distribution to special occasions—feasts—that can be arranged only by those who can afford them (Jennings *et al.*, 2005). By conspicuously paying such costs, sponsors advertise differences in ability to access resources and control labor. The audience viewing the advertisement gains from the information conveyed and in some cases from the goods distributed (Bliege Bird and Smith, 2005; Boone, 1998; Smith and Bliege Bird, 2000).

Ritualized feasting is a tangible way of standardizing display and broadcasting social power, allowing both fine-grained judgment of an individual’s influence within a group and an honest signal of a corporate group’s political will and strength. In some contexts, large game animals are “requisite luxuries” whose distribution is analogous to feasting and required for hunters to stay in place on the positional treadmill within a group (Bliege Bird *et al.*, 2001; Hawkes and Bliege Bird, 2002). Smith and Bliege Bird (2000, 2005) cite many examples of other types of within-group competition related to feasting. Moreover, a corporate group’s internal cohesion and access to power over other groups, resources, and reproduction are often highly dependent on ritualized feasting (e.g., Adams, 2004, 2005; Boone, 2000; Boone and Kressler, 1999). From this perspective, feasting and warfare are often two sides of the same coin, with feasts serving as an “altruistic threat” whereby the costs of all-out conflict between groups are avoided by showing off how much the sponsor can afford to lose, advertising a concrete and reliable index of underlying competitive ability (Zahavi and Zahavi, 1997, pp. 141–143).

Fitzhugh (2003, pp. 121–129) has drawn explicitly from CST to model the role of feasting in the emergence of complex socioeconomic stratification in the Kodiak Archipelago. The model is of interest for both its theoretical grounding and its capacity to generate hypotheses amenable to archaeological test. With initial conditions of environmental asymmetry and circumscription, minor differences in the ability of individuals or corporate groups to access and hold productive resources can lead to socioeconomic “arms races.” This feeds back to increase the benefits of making resource patches defensible. Endemic warfare may emerge among competitors of similar ability. This increases the payoffs for clearly communicating underlying quality with reliable indices of power: control over resource patches and the means of production are enforced by direct defense and advertisements of resource-holding potential through accumulations of wealth, elaborate feasts, and conspicuous destruction of property. Those unable to engage in symbolic feasting are marginalized and, if circumscribed, supported as subordinates or forced into slavery. Fitzhugh makes a logical case that without

the emergence of a political economy based on signaling competitive strength through feasting, despotic corporate groups are unable to assert control over the labor of others.

The evolution of hereditary inequality

The fourth and final topic covered by this review is the evolution of hereditary inequality, defined here as a pattern of privileged control over key resources, including the labor of nonkin, that can be passed to one's descendants. Conventional archaeological approaches to this problem have long focused on the role of agriculture as an important factor (often purportedly the main catalyst) in the development of such patterns (e.g., Childe, 1946). But a large body of work published over the last two decades underlines the frequently forgotten observation that hereditary inequalities also have emerged among certain hunter-gatherer populations (see Arnold, 1996; Kelly, 1995, pp. 293–331; Price and Brown, 1985; Price and Feinman, 1995; Sassaman, 2004, for review). Commonly referred to as *complex* hunter-gatherers, these groups are (or were) further marked by the presence of high population densities, large settlements, low residential mobility, moderate to heavy reliance on stored foods, ownership and defense of resources, hierarchical political organization, high levels of interpersonal competition and intergroup conflict, ritual feasting, prestige goods, and moneylike currencies. By definition, *simple* hunting and gathering societies lack most of these characteristics. BE-oriented archaeologists interested in the development of inequality have focused on complex hunters for two reasons: 1) these societies are relatively small and so comparatively tractable analytically; 2) the exercise allows investigators to build on the growing body of work on hunter-gatherer economies grounded in optimal foraging and costly signaling theory (e.g., Erlandson and Jones, 2002; Fitzhugh, 2003; Kelly, 1995; Kennett, 2005; Raab and Larson, 1997).

Keeley (1988) shows via comprehensive literature review that complex hunter-gatherers are restricted to habitats where potential subsistence resources are abundant, predictably available, and relatively defensible (see also Dyson-Hudson and Smith, 1978). He argues convincingly that population growth is the driving force behind the emergence of the “complex” pattern. The obvious question is how the two are linked: What processes connect demographic pressure with the development of hierarchical forms of economic, social, and political organization?

Vehrencamp's (1983) model for the evolution of *egalitarian* versus *despotic* societies provides a useful starting point for discussion (see also Boone, 1992; Hawkes, 1992, for further treatment of this and other models of competition and cooperation). The model assumes that competition over resources is ubiquitous, even within local groups of closely related individuals. It stipulates that where some group members (*dominants*) are able to secure a disproportionate share of resources for their own use, others (*subordinates*) are confronted with the choice of either tolerating that *bias* or leaving. Ecological circumstances define both the benefits of remaining with the group and the options for relocating, and so determine the degree of bias subordinates are likely to endure before moving (see also Diehl, 2000, for more on intragroup competition).

Keeley's argument about the catalytic effect of population pressure helps identify those circumstances and their implications for other aspects of behavior. Higher population densities are generally correlated with greater diet breadth and the occupation of a wider range of habitats. The greater the degree of environmental packing that results, the fewer the opportunities for subordinates to relocate as bias develops. Moreover, depending on the nature of the resources being exploited, there may be an increasing benefit to subordinates for staying in place, even where bias is high. Broader diets are by definition associated with

greater investments in handling effort. The greater the concentration of those resources in space, the narrower the period of availability, and the greater the potential for mass storage, the greater the payoff to larger groups of processor/consumers organized to take advantage of those periodic, relatively short-term resource “flushes.” Subordinates who help accumulate the store and share in its consumption gain from the availability of larger quantities of food over longer periods of time, despite the “rake-off” by dominants. Dominants gain from the potential to control and redistribute to their own fitness-related benefit increasingly disproportionate shares (a *surplus* relative to their own immediate subsistence needs) as a function of subordinates’ greater tolerance for bias. Vehrencamp’s model further indicates that the degree of bias likely to be sustained varies directly with the strength of intragroup kin connections: The more closely related subordinates are to dominants, the higher the level of bias they should be prepared to accept before defecting. Hierarchically ranked, coresident kin groups are a likely outcome in these situations.

These same considerations also determine patterns of *intergroup* competition and cooperation. Particularly favorable locations—those offering relatively reliable access to relatively abundant storable foods—are likely to become the focus of competition among local groups, especially where fluctuations in resource abundance at various locations are asynchronous (Blurton Jones, 1987). The higher the degree of demographic packing, the fewer the options for movement to unoccupied patches in the face of local resource shortfalls, the more likely it is that “have-nots” will be willing to bear the cost of aggressive competition for control of perennially favorable locations. Dominants already occupying those locations may be able to offset such forays by deploying some of their surplus resources, either to “buy off” the impending threat or to enlist the support of other relatively disadvantaged parties to help defend against it. Depending on degrees of interpatch variation in resource abundance and reliability, shifting patterns of alliance and enmity are likely to result. Continued population growth exacerbates these tendencies. Nevertheless, the greater the relative value of key locations, the better able those in control of them will be to maintain that control over relatively long (i.e., intergenerational) periods of time.

As indicated above, costly signaling (e.g., via competitive feasting) should play an important role in these situations. Dominants are likely to pursue it as a means of displaying their relative power and ability to defend the critical resource base, and thus inhibit aggressive moves by potential rivals. In-group subordinates are likely to support it with their labor (as opposed to denying it by defection) as long as it remains their best fitness-related strategy. Potential out-group clients should be alert to its benefits and adept at distinguishing the merits of competing patrons.

Obvious tests for this line of argument lie in the ethnographic and archaeological records of the Northwest Coast of North America. At the time of European contact, societies all along this coast were marked by features typical of complex hunter-gatherers, including (but not limited to) high population densities, hereditary differences in social status, ownership and defense of resources, reliance on stored foods, and relatively high levels of interpersonal competition and intergroup conflict, the latter two often involving classic examples of costly signaling, including competitive feasting and gift giving and the ostentatious destruction of valuable property (Suttles, 1990). It is widely recognized that these patterns display a broad latitudinal gradient; those in the northern half of the region generally represent more extreme versions, those to the south more attenuated forms (e.g., Kroeber, 1939).

The overall richness of the resource base is clearly responsible for the relatively high human population densities reported for the northwest coast. Variation in the costs and benefits of exploiting salmon and other anadromous fish, crucial resources all along the coast, arguably accounts for much of the intraregional patterning in socioeconomic complexity.

Schalk (1977) has shown that the attractiveness of these resources as targets for intensive exploitation varies broadly with latitude and local human population density. To the south, anadromous fish and other resources are available throughout much of the year, limiting the incentive for storing any of them. To the north, the availability of all resources narrows seasonally, increasing that incentive. Anadromous fish are especially suitable for storage because of the size of their runs. But the tasks of collecting, processing, and storing large quantities of fish have significant technological and organizational costs, all of which become heavier the larger the quantity of resource to be handled and the narrower the time window available for doing so. The higher the local human population, the easier these costs may be to bear and the more important it is that they be met. Opportunities for the development of despotic forms of social organization, those that favor centralized management and organizational efficiency in the handling of stored foods at the expense of subordinates' individual autonomy, may emerge as a result. Topographic factors add a further constraint: some spots (e.g., falls and rapids) are especially well suited for the capture of anadromous fish in large quantities. Payoffs to human consumers from control of such locations can be very high, making them especially attractive targets for competition. Unpredictable short-term variation in the size of runs (e.g., Suttles, 1968) adds a further incentive for such competition.

Collectively, these factors lead one to predict that key elements of social complexity, including the level of reliance on storage, degree of social inequality, intensity of intergroup competition, and patterns in costly signaling, will all vary at least in part with latitude, the nature of coastal and riverine topography, and the density of local human populations (Schalk, 1977). The ethnographic record appears to be at least superficially consistent with these expectations, though comprehensive analysis from a BE perspective, perhaps along the lines pioneered by Neiman's (1997) treatment of Maya calendrical monuments, clearly would be useful.

Elements of the general model outlined above, based on Keeley's and Vehrencamp's work, are anticipated and elaborated in Fitzhugh's (2003) study of socioeconomic evolution in the Kodiak Archipelago. Patterns in the early prehistory of Kodiak (7500–3500 BP) are generally consistent with predictions grounded in the prey choice, ideal free distribution, and technological innovation models reviewed in the section on foraging theory. The earliest residential groups were small, diets were narrow, and related investments in collecting and processing technology were relatively limited. Foraging ranges were large and seasonal mobility was high. As population grows through time, all of these patterns are reversed. Evidence of more efficient collecting and processing tools, seasonal occupation of sites especially suitable for mass harvesting of anadromous fish, and reliance on storage appears by 3500 BP. After 2000 BP, and especially after 800 BP, patterns typical of the region at the time of European contact emerged: heavy investment in residential, collecting, storage, and defensive facilities, initially at the best locations for salmon harvesting and later at less favorable spots; greater diversity in the size and internal organization of residential structures and increased evidence of traffic in prestige goods—all consistent with an increase in socioeconomic hierarchy. As Fitzhugh contends, the evidence fits with the idea that long-term population growth and the related depletion of higher-ranked resources drive economic intensification, ultimately resulting in this situation in heavy reliance on food storage and the development of social hierarchies. Whether the latter were hereditary in nature has yet to be resolved archaeologically, but it seems reasonable to infer from both theoretical considerations and the regional ethnography that this was the case. Again, further analysis from this perspective here and elsewhere on the Northwest Coast, and indeed anywhere similarly complex patterns of socioeconomic organization are indicated archaeologically

would seem to be in order (see Kennett, 2005, on the evolution of complex hunter-gatherer economies along the Santa Barbara Channel).

Conclusion

It should be clear from this review that the BE perspective is broader and more sophisticated than many of its critics maintain and its utility to archaeologists more substantial than they imply. Its reach equals (in fact, exceeds) the span of the archaeological record; its grasp encompasses problems long identified as classics in the field—from the evolution of genus *Homo* through the origins of agriculture and the development of hereditary inequalities. It has already produced novel, testable solutions to many of these problems, and one can readily imagine still further potentially productive applications.

Critics may object to BE's inherent reductionism and implicit rejection of "culture" as an explanation for human behavior. In our view, these are among its most important virtues. Reducing a problem to its key elements and attacking them one at a time is the essence of good science: It is the most effective way of eliminating problematic answers and identifying and pursuing more promising ones. One might argue that most of BE as applied to humans pertains to "culture," but unlike many schools of thought in anthropology, BE generally attempts to explain patterns in cultural behavior rather than explain them away as a function of culture. Equally important, discounting the uniqueness of human culture opens the door to a comprehensive appreciation of the similarities and differences between humans and their nearest relatives and to a better understanding of how these may have evolved—impossible goals if our species is always held analytically apart from the rest of creation.

Critics also may contend that the approach is overly concerned with cross-cultural generalizations and is insufficiently attentive to the importance of more or less independent cultural traditions as determinants of human behavior, another version of the charge of inappropriate reductionism. In our view, an anthropological perspective requires both, and BE does better than its competitors at meeting that requirement. Attention to the details of socioeconomic context is essential to the BE perspective.

Behavioral ecology does not answer every question about the evolution of human behavior, but it does provide useful and productive insight on many. We look forward to further developments.

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