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Evolution in Archaeology

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Darwinian archaeology, cultural transmission, cultural lineages, dual inheritance theory, human behavioral ecology, optimality modeling

Abstract

This review begins with a brief outline of the key concepts of Darwinian archaeology. Its history is then summarized, beginning with its emergence as a significant theoretical focus within the discipline in the early 1980s; its main present-day currents are then presented, citing examples of recent work. The developments in archaeology are part of broader trends in anthropology and psychology and are characterized by the same theoretical disagreements. There are two distinct research traditions: one centered on cultural transmission and dual inheritance theory and the other on human behavioral ecology. The development of specifically archaeological methodologies within these two traditions for testing evolutionary hypotheses relating to diachronic questions using archaeological data is discussed. Finally, this review suggests that the greatest challenge for the future lies in finding ways of using archaeological data to address current major debates in evolutionary social science as a whole concerning, for example, the emergence of large-scale cooperation.

INTRODUCTION

The term evolution in archaeology has accumulated an enormous range of meanings, with different implications, over many years. Traditionally, however, when not referring to the biological evolution of putatively ancestral species, it has occurred most commonly in the phrase cultural evolution (sometimes used interchangeably with social or sociocultural evolution), referring to the history of what are conceived as the key long-term trends in human history: from foraging to farming, or from farming to the origins of civilization and the state, accompanied by such developments as increased population, greater social complexity and inequality, and more complex technologies. More recently, the term has increasingly come to refer to the idea that the processes producing cultural stability and change are analogous in important respects to those of biological evolution: On this view, just as biological evolution is characterized by changing frequencies of genes in populations through time as a result of such processes as natural selection, so cultural evolution refers to the changing distributions of cultural attributes in populations, likewise affected by processes such as natural selection but also by others that have no analog in genetic evolution. In fact, to understand changing patterns of human behavior and organization we need to take account of both the biological and the cultural dimensions. It is this latter, Darwinian rather than Spencerian, sense of evolution that will be the focus of this review, but the reader will see that the Darwinian perspective also has things to say about social evolution in the traditional sense.

In this review I briefly outline the key concepts that form the basis of what it is useful to call Darwinian archaeology, then provide a summary review of its history beginning with its emergence as a significant theoretical focus within the discipline in the early 1980s, and finally outline its main present-day currents, citing examples of recent work. The developments in archaeology are part of broader trends in anthropology and psychology more gener-

ally (see e.g., Auinger 2000, Cronk et al. 2000, Dunbar & Barrett 2007, Durham 1991, Smith & Winterhalder 1992b, Sperber 1996), but the types of data dealt with by archaeologists and the diachronic questions they generally address have led to an emphasis on some theoretical perspectives rather than others and to the development of specifically archaeological methodologies for obtaining information relevant to testing evolutionary hypotheses.

THE PROCESSES OF CULTURAL EVOLUTION

The extent to which cultural processes may be modeled in evolutionary terms remains disputed (e.g., Bamforth 2002; Fracchia & Lewontin 1999, 2005), although the way in which cultural entities and processes closely match Darwin's original formulation of the theory of evolution has recently been shown in detail by Mesoudi et al. (2006). In the most general terms, they involve parallel mechanisms for inheritance, mutation, selection, and drift.

In the case of culture, the inheritance mechanism is social learning: People learn ways to think and act from others. Of course, the routes through which culture is inherited are much more diverse than those for genes (Cavalli-Sforza & Feldman 1981), and different routes have different consequences for the patterning of cultural change through time. Variation in what is inherited is generated by innovations. These may be unintended copying errors, but they can also be intentional changes, perhaps arising from trial-and-error experimentation, that lead an individual to stop doing what they had previously learned and to start doing it differently, or even to do something different altogether. Whether this will be widely adopted depends on a range of selection and bias mechanisms, many of which have no equivalent in genetic evolution but whose existence and importance have formed the subject of major developments in the theory of cultural evolution over the past 30 years (especially Boyd & Richerson 1985, Cavalli-Sforza & Feldman 1981). These mechanisms form the theoretical

foundation for what follows and, given the complexities involved, it is important to spell them out (see also Eerkens & Lipo 2007).

Natural selection in the narrowest sense affects humans as it does members of all other species; for example, other things being equal, individuals whose genes give them dispositions toward behavior that is more advantageous in enabling survival and reproductive success are more likely to survive and reproduce than are those who do not have such dispositions and those genes will be more widely represented in future generations. However, natural selection can also act on cultural attributes in the sense that those individuals who inherit or acquire certain cultural attributes may have a greater probability of surviving and/or reproducing than would those who do not, a process that will continue so long as those possessing the cultural attributes pass them on to their children; thus, those cultural attributes will become increasingly prevalent. For example, in many parts of the world, adopting an agricultural rather than a hunting-and-gathering way of life clearly led to greater reproductive success because population densities increased considerably; as a result, the cultural traits that characterize agriculture spread and, in some cases, subsequently influenced genetic evolution (e.g., the ability to digest lactose: Burger et al. 2007). An analogous process of cultural selection can also operate if individuals with certain cultural traits are more likely to be taken as models for imitation than others are, by virtue of those traits, and these in turn become successful models. The traits concerned will become more prevalent even if they have no bearing on reproductive success whatsoever, and indeed, even if they are deleterious to it. This is because if an attribute is passed on other than by parents to children, there is no reason for its success to depend on the reproductive success of the individuals concerned. For example, if celibate priests are more likely than other adults to be teachers and if, as a result of what they teach, their pupils are more likely to become celibate priests and teachers, then the values they teach will increase in frequency relative to others.

However, in addition to these selection mechanisms, a number of bias processes can affect what is transmitted; these refer to factors that affect what and who people try to copy when they are learning from others. Thus, results bias refers to the situation where people look at what other people do, for example, the crops they plant, compare the results with what they are doing themselves, and then change what they do because the other way of doing things seems to be more effective. Content biases are affected by features of transmissible phenomena that make them intrinsically more or less memorable for reasons relating to the structure of the mind or the strong reactions they provoke; examples might be fairy tales or so-called urban myths (see also Washburn 2001). Context biases are aspects of the context of learning that affect what is transmitted; thus, something may be copied simply because the person initially doing it is prestigious (prestige bias) or because it is what most people locally do (conformist bias). In these latter two cases, whether a particular cultural attribute or practice becomes more prevalent in a population has nothing to do with its intrinsic properties but only with the context of learning.

Finally, there is the cultural equivalent of genetic drift. The frequencies of particular cultural attributes can change for essentially chance reasons not involving any preference for a particular attribute. Who or what one copies may simply be a random choice dependent on who or what one meets.

None of these different mechanisms in themselves specify the tempo or mode of cultural evolution, whether it occurs gradually or in a punctuated fashion, or by means of episodes of branching cladogenesis or continuity within a single lineage. Many views assume, implicitly or explicitly, that the emergence of new culturally inherited phenomena with natural selection consequences for human populations, such as agricultural practices, is the key motor for episodes of branching cladogenesis, especially through population dispersal (e.g., Bellwood 2001; Prentiss & Chatters 2003), but here too drift processes may play a key role

HBE: human behavioral ecology

in the initial stages of the process (Rosenberg 1994).

A BRIEF CONCEPTUAL HISTORY OF DARWINIAN ARCHAEOLOGY

Darwinian archaeology attempts to account for the patterns observed in the archaeological record in terms of the processes outlined above. The work carried out under this heading is extremely varied but can be roughly divided up into two categories: studies that emphasize the role of natural selection in affecting human behavior and do not attach that much importance to culture, and those that emphasize the importance of understanding changing cultural traditions. These two approaches are generally seen as opposed to one another, although in many respects they are complementary. The opposition goes back to the beginnings of Darwinian archaeology, which had its origins in two very different traditions.

One was Dunnell's (1980) evolutionary archaeology, which took the view that the material remains making up the archaeological record could be seen, like human skeletal remains, as an element of the hard part of the human phenotype, which had the property of surviving after death; they were therefore analogous to the paleontological fossil record. Artifacts, or attributes of artifacts, either had a function, in which case they would be subject to natural selection, or they did not, in which case the only process affecting their frequency over time would be drift (Dunnell 1978). The job of evolutionary archaeology was to distinguish the operation of these factors in different cases. One could criticize many things in Dunnell's approach (see e.g., Shennan & Wilkinson 2001), and his terminology was a source of confusion rather than clarification. For example, under natural selection he included all forces affecting the replicative success of particular artifact forms, not just those relating to the reproductive success of their makers and users (see Bentley et al. 2008 for further discussion), but the key importance of his ap-

proach for archaeology was that it focused on the archaeological record. Whereas other varieties of evolutionary anthropology focused on human decision makers and the factors affecting their decisions, Dunnell asked what the operation of evolutionary forces would look like from the point of view of the cultural attributes or artifacts themselves—their prevalence over time and the modifications that occur in them—when we do not have direct observational access to people's decision making. This perspective has its origins in the culture historical archaeology of the first half of the twentieth century. It remains an issue of central importance for archaeology.

The other evolutionary perspective was human behavioral ecology (HBE), one of the two evolutionary approaches that emerged out of the human socio-biology of the 1970s (the other being evolutionary psychology, which has had much less influence on archaeology and is therefore not considered in this review). HBE postulates that people are behaviorally plastic in the context of general dispositions toward courses of action that tend to lead to improved survival and reproductive success and of an ability to perceive and react appropriately to relevant environmental cues; these perceptions and reactions may be conscious or unconscious. Accordingly, people should tend to respond optimally from the point of view of survival and reproductive success to the various challenges posed by their local adaptive environment, even if that is a novel one. It is the environment that is the motor for change or stability; people are sufficiently plastic behaviorally to respond to new conditions and cultural traditions have no role, a position very close to the cultural ecology of processual archaeology. HBE research is carried out using naturalistic studies that identify the adaptive constraints and opportunities that characterize particular situations and then collect data to test whether people are indeed acting optimally.

The differences between evolutionary archaeology (*sensu* Dunnell) and HBE emerged most clearly in a debate between Lyman &

O'Brien (1998) and Boone & Smith (1998). It revolved around the role of transmission and selection and focused specifically on an ethnographic example, the process by which Cree Indians gave up using snow shoes for snowmobiles (Ramenofsky 1995). For Boone & Smith it was a matter of cost-benefit decision-making based on behavioral plasticity underpinned by selection-influenced capacities. For Lyman & O'Brien, the demise of the snow shoe, an artifact type with a long history conditioned by its functional requirements, i.e., subject to selection, and its replacement by the snowmobile, a different artifact with essentially a shorter but more complex history of transmission, could indeed be seen as a Darwinian process in the strictest terms—involving the increasing replicative success of snowmobiles compared with snowshoes, although that process need not be related to the survival or otherwise of the population of users. Clearly both are right in this case—the difference is one of perspective—and the complementarity of the two approaches has been increasingly recognized. Nevertheless, the distinction between those evolutionary approaches that attach importance to the role of culture and cultural transmission and those that see relatively little role for them remains an important one and will provide the basis for structuring the remainder of this review.

CULTURAL TRANSMISSION AND THE ARCHAEOLOGY OF CULTURAL TRADITIONS

In the past 15 years there have been major theoretical and methodological developments in this domain as well as a rapid growth in the number of concrete case studies putting the ideas and methods to work. The main theoretical development has been the absorption of Dunnellian evolutionary archaeology within the framework of Boyd & Richerson's dual inheritance theory (DIT). This combination has broadened the range of concepts and mechanisms now considered relevant to understanding the evolution of culture (Eerkens & Lipo

2007). Dunnell's natural selection can now be seen as a catch-all category covering a range of very diverse forces acting on what is transmitted through time, and the distinctions are important ones. Thus, in the famous example discussed above, snowmobiles became more prevalent among the Cree as a result of results bias, not natural selection on the survival and reproductive success of the users. Indeed, making this distinction is at the root of some of the most long-standing debates in archaeology, for example, whether the spread of farming into Europe was a process of indigenous adoption (involving results bias) or demographic expansion and extinction (natural selection acting on the bearers of cultural traditions). In effect, evolutionary archaeology *sensu* Dunnell has to be seen as an artifact-focussed subset of the dual inheritance approach. However, the match is not perfect. As formulated by Boyd & Richerson and their students, DIT focuses on the individual decision-making and does not take what might be called the meme's eye view that the evolutionary study of archaeological traditions requires. Thus, whether it is possible to distinguish the different mechanisms on the basis of archaeological data and to identify the operation of one rather than another is an area of active research (see below). However, the basic procedures of an evolutionary archaeology of cultural traditions are now clear. It is necessary to identify histories of transmission to show that an ancestor-descendant relationship exists, if indeed it does (O'Brien & Lyman 2000), and then attempt to understand the forces shaping it, all on the basis of patterned variation in the archaeological record. In practice, however, these operations are not necessarily sequential, and the information to make the distinctions required may simply not exist. Thus, if a particular cultural attribute, for example, the sharpness of a lithic cutting edge, is very strongly determined by its function, then it will contain no signal of its transmission history, even though it is likely that it had one (as opposed to being discovered anew by every novice flint knapper through trial-and-error learning).

Characterizing Cultural Lineages

The first issue to address is whether a given diachronic sequence of archaeological observations is the result of a transmission process. Clearly, transmission implies continuity but continuity does not necessarily imply transmission. It might arise, for example, from the continuity of environmental conditions or of a particular function. In practice, probably the most important technique for characterizing transmission has been seriation. This is a very well-known technique with a long history and involves putting phenomena in a linear order on the basis of some measure of their similarity to one another (Lyman & O'Brien 2006, O'Brien & Lyman 2000). The assumption that things that are more similar to one another are close together in time provided an important basis for culture-historical chronology building. However, with independent evidence of the chronological order, we can test whether the phenomena that are most similar to one another are indeed closest to one another in time. To the extent that they are, continuity is implied. Thus, if successive assemblages linked by transmission, for example, of counts of different ceramic types, are put in order, then the changing frequencies of the types will show the characteristic battleship curve pattern of first appearance, increasing popularity, and decline. Ultimately, however, our conviction that cultural transmission is the predominant force accounting for the pattern is also based on other knowledge, for example, that the making of pottery is an activity acquired by social learning. Other situations are a priori less clear cut. Thus Schibler (2004) showed that through-time fluctuations in the proportional and absolute frequencies of wild and domestic animal bones did not relate to changing cultural preferences but to climatic fluctuations because hunting became predominant at times of a cool, wet climate, which could be demonstrated by independent evidence.

As Lyman and O'Brien (2006) have pointed out, seriation is based on the idea of tracing a single cultural lineage through time, but if we take the example of frequency seriation of

ceramic assemblages, based on the successive appearance, rise, and decline of new variants within the assemblages, then the new variants can also be looked at from a different perspective: They represent new branches on the evolutionary tree of that ceramic tradition, characterized by innovations that differentiate them from the ancestral state. Of course, the idea that cultural relationships can be represented as an evolutionary tree analogous to those that are used to represent the relationships among biological species is the basis of traditional historical linguistics. It also has a very long history in cultural anthropology, as does the idea that the branches of cultural trees can grow back together again, split, and join together once more, producing complex patterns of hybridization or reticulation. In recent years, the nature of cultural evolutionary trees has once again become the center of major debate because of the use of modern methods of cladistics derived from evolutionary biology as a basis for inferring the existence of cultural lineages and the relationships among them.

These methods are based on the assumption of branching evolution from a single origin; the entities under study, specific artifact types, for example, are placed on a tree such that those branches that have the most similar common histories in terms of shared mutations with respect to particular characters are most closely linked (O'Brien & Lyman 2003). This notion presupposes that the characters are homologous, that is, the artifact types or other entities share specific values for those characters because they are linked by descent from a common ancestor, rather than because they have undergone similar selection pressures (analogous characters or homoplasies; see e.g., O'Brien & Lyman 2003 for the complex terminology of cladistic analysis). A given set of descriptive traits of, for example, an artifact type may be made up of a mixture of homologous and analogous attributes, and these need to be distinguished or reconciled by methods that produce an overall cladogram consistent with the largest number of characters (see, e.g., Collard et al. 2008). Moreover, not all the traits that

characterize a complex object or entity will have had a common history (Boyd et al. 1997). Some of the attributes of a given ceramic tradition, decorative motifs, for example, may have been borrowed from a different ceramic tradition by a process of horizontal transmission, and tree-building methods based on the assumption of branching differentiation from a single ancestor will not do this justice. These issues have resulted in a great deal of debate (for doubts and concerns see Borgerhoff Mulder 2001, Lipo 2006, Temkin & Eldredge 2007, Terrell et al. 1997; contra, e.g., Gray & Jordan 2000, Kirch & Green 2001, Mace & Pagel 1994) and critical analysis (e.g., Eerkens et al. 2006, Nunn et al. 2006) but also produced important methodological developments (e.g., Bryant et al. 2005, Page 2003; for an archaeological example, see Riede 2008). Gray et al. (2008) argue on a variety of methodological and theoretical grounds that pessimistic conclusions about the role of cultural phylogenetics are unjustified.

Many examples of the use of such phylogenetic techniques to construct cultural lineages and identify the forces affecting them have appeared in the archaeological literature in recent years (e.g., Coward et al. 2008, Darwent & O'Brien 2006, Foley & Lahr 1997, Harmon et al. 2006). Many examples from anthropology have major archaeological implications. Gray & Atkinson (2003), for example, used phylogenetic methods to estimate the most probable date of the root of the Indo-European language family tree, obtaining a result that fits much better with Renfrew's (1987) agricultural dispersal model of Indo-European spread than with the so-called Kurgan hypothesis, which fits the dates estimated by traditional historical linguists.

In fact, as Neff (2006) has emphasized, formal seriation and phylogenetic analyses are not the only means of characterizing cultural lineages and the forces acting on them. He himself uses scientific methods of ceramic composition analysis which he links to raw material zones to develop and test hypotheses concerning cultural lineages in Mesoamerican pottery and the factors that affected them.

Modelling Lineage Change

As noted above, to identify and characterize cultural lineages, indeed to claim their existence, is already to make inferences about the processes that produced them and to exclude some of the possible reasons for similarity among different phenomena, for example, that they arise from environmental continuities or convergent adaptations. Distinguishing the action of different forces such as those postulated by DIT requires researchers to make many more distinctions than Dunnell did (see above), which has caused problems for archaeologists. Although the basic mathematical framework of DIT was defined more than 20 years ago, progress has been slow in finding ways to operationalize it through the analysis of patterned variation in archaeological data (Eerkens & Lipo 2007).

One example is Bettinger & Eerkens's (1999) analysis of variation in arrow points in the western United States. They examined the patterns of correlation among different attributes of early arrowheads in central Nevada and eastern California and found that there was a generally high level of attribute intercorrelation among the arrowheads in the former area and much more variable correlations between different attributes in the latter. On this basis, they proposed that in central Nevada, arrowheads were adopted by a process of prestige bias without examining the functional efficacy of their different attributes, but in eastern California, local populations experimented with the different attributes, which led to greater variation and more independence between them. In effect, the size and nature of the covarying package of attributes (Boyd et al. 1997) can be extremely informative about specific processes of cultural transmission and the factors affecting them.

There is clearly much more scope for taking forward the identification and analysis of cultural packages, but the main single topic on which the characterization of processes has focused is the identification of drift. The key achievement here was Neiman's (1995) demonstration of the way the mathematics of the

neutral theory of evolution could be used to generate quantitative expectations of what a distribution of artifact frequencies should look like if drift is the only factor affecting it, rather than simply making a priori judgments. In effect, the methods provide the basis for a null hypothesis. If a particular distribution fails to depart from neutrality, there is no reason to postulate anything other than drift as the process producing it (Bentley et al. 2004). If there is a departure, then something further needs to be invoked to account for it (Shennan & Wilkinson 2001). It is important to note that drift as a process can exist only in the context of an evolutionary model, which includes transmission. It has no role in HBE, nor in any other approach that lacks an inheritance concept.

Following the logic of genetic drift, in cultural drift, variation is the result of random copying of cultural attributes, with some possibility of innovation, and the results of the process depend solely on the innovation rate and the effective population size, itself dependent on the scale of interaction. It is very unlikely that any individual act of copying, for example, of a ceramic decorative motif, will be random, but if everyone has their own reasons for copying one person rather than another, the result will be that there are no directional forces affecting what or who is copied. Neiman's original case study indicated that patterning in the rim attributes of eastern North American Woodland period pottery was a result of drift, but Shennan & Wilkinson (2001) showed that patterning in the frequency of decorative attributes of early Neolithic pottery from a small region of Germany indicated a pronovelty bias in the later periods and Kohler et al. (2004) in a case study from the U.S. Southwest were able to show a departure in the direction of conformity. Thus, these methods do provide a potential basis for distinguishing some of the transmission forces postulated by DIT. All these studies followed Neiman in using an assemblage diversity measure to identify drift, but subsequently Bentley & colleagues (2004) also showed that the frequencies of different variants resulting from a random copying process followed a power law,

with a small number of the variants attaining very high frequencies but most occurring only very few times. In such cases, although one can predict that a small number of variants will attain very high frequencies, it is impossible to predict which ones. It is increasingly clear that such processes occur in an enormous range of phenomena and follow universal laws (Bentley & Maschner 2008).

Eerkens & Lipo (2005) have developed a similar approach to the characterization of neutral variation in continuous measurements and the measurement of departures from it. They applied it to explaining variation in projectile point dimensions in Owens Valley and in Illinois Woodland ceramic vessel diameters. They showed that drift was sufficient to explain the variation in projectile point thickness, but base width showed less variation than expected, so some biasing process leading to a reduction in variation must have been operating while, in the case of the pottery vessel diameters, variation-increasing mechanisms were at work.

One of the points that emerges very clearly from all the work with drift models is that there cannot be a radical separation between function and style, or between the operation of selection and biasing forces and drift. There is a continuous spectrum from pure drift to very strong selection/bias, just as certain activities depend very strongly on transmission and others are most strongly conditioned by variation in the environment facilitated by behavioral plasticity.

HUMAN BEHAVIORAL ECOLOGY IN ARCHAEOLOGY

As noted above, the starting point for HBE is the assumption that humans, like other animals, have evolved under the pressure of natural selection to maximize their reproductive success, and that behavioral plasticity enables them to respond speedily and adaptively to changes in the environment. In effect, of all the different evolutionary forces listed above, this approach assumes that natural selection acting on humans as it does on other animals is the

only one that matters, by giving them adaptive capacities to make good decisions. Some of HBE's advocates believe strongly that this is substantively the case and that culture and cultural transmission are therefore unimportant; however, it is not necessary to accept this idea to believe that HBE provides a powerful starting point for many kinds of archaeological investigation because of the specific hypotheses that follow from its assumptions, which are underwritten by their success in accounting for behavioral strategies in nonhuman animals.

Thus, HBE theory provides the basis for setting up cost-benefit models of what is optimal to do in specific circumstances, which may depend on what other people are doing (the province of evolutionary game theory, e.g., Skyrms 1996). For archaeologists, it provides a strong basis for generating specific hypotheses to account for patterning in the archaeological record so long as certain conditions can be satisfied, but those conditions are arguably quite stringent. It is necessary to know, or have a sound basis for making assumptions about, the range of options available, the currency in terms of which they will be evaluated, and therefore by implication the relevant goals of the people concerned, as well as constraints that affect the payoffs (Bird & O'Connell 2006, p. 5; Lupu 2007, p. 146; Winterhalder & Kennett 2006, pp. 13–14). The area of research where these criteria have been most fully developed and discussed has been in the use of optimal foraging theory to account for patterning in the remains of plants and animals found at archaeological sites, especially those of nonagriculturalists. However, archaeologists are increasingly using HBE ideas to explain patterning in archaeological data relating to a wide range of other areas of human activity in response to theoretical developments within HBE and their application in other areas of anthropology. Although it is impossible to cover even a small fraction of the work that is now being carried out, the main areas of research will be indicated below (see also reviews by Bird & O'Connell 2006, Lupu 2007).

Optimal Foraging

Over the past 20 years, optimal foraging theory (OFT) has been the basis of numerous studies. Researchers usually assume that people are seeking to maximize their rate of calorific intake when they are engaged in food-getting activities, on the further assumption that, other things being equal, natural selection will favor those individuals that are most efficient. The diet breadth model postulates that an individual will make the choice whether to exploit a particular encountered resource by determining whether the postencounter returns obtained after pursuing (if necessary) and processing it into a form in which it can be eaten will be greater than those to be obtained by ignoring that resource and looking for something better. Thus, resources can be ranked in terms of their postencounter returns. Highly ranked resources will always be taken on encounter, but lower ranked ones will be ignored. This decision is important and, in some respects, counterintuitive. Whether a resource is exploited does not depend on its own abundance but on that of the resources ranked higher than it. Resource ranks may be assessed on the basis of experimental or ethnographic work in the present (e.g., Barlow 2002, Kaplan & Hill 1992). In terms of archaeological evidence, significant taphonomic and sampling issues potentially arise, but assuming that these can be overcome, faunal assemblages, for example, can be evaluated in terms of some measure of their likely productivity or resource rank. Because animal body size is correlated with handling costs and is readily assessable using archaeological faunal data, the proportion of large-bodied vs. small-bodied animal bones has very frequently been used as a diet-breadth measure (e.g., Broughton 1994; see also Ugan 2005; for within-species size variation see, e.g., Mannino & Thomas 2002). Stiner and colleagues (2000) have used the proportions of slow-moving vs. fast-moving (and therefore hard to catch) small game as a diet breadth measure in their studies of faunal exploitation in the east Mediterranean later Palaeolithic. Despite its simplicity, the diet

breadth model has been remarkably successful in accounting for variation in faunal assemblages, especially in the context of diachronic sequences showing resource depression (e.g., Broughton 1997, Butler 2000).

This simple model can be modified in various ways. For example, central place-foraging models (Lupo 2007, pp. 151–53) have been developed to make predictions about the effects of transport costs on what resources will be exploited where and the extent to which they will be processed before being brought back to a base for consumption (Metcalf & Barlow 1992). Nagaoka (2002) relates changing prey representation at the Shag River Mouth site in New Zealand to changing hunting and transport distances as a result of resource depression.

Many of the most interesting issues arise when initial predictions of such optimal foraging models are apparently not met. Thus, Stiner & Munro's (2002) analysis of the faunal remains from the Natufian period (~13–10 ka) at Hayonim cave in the Levant found that for the first three phases, the proportion of fast-moving small game was high and of slow-moving game was low, but, contrary to the resource depression that might be expected as a result of long-term occupation, in the final two phases the situation was reversed, with slow-moving game now in a majority. It appears that these slow-moving game populations were able to recover and exploitation was now not sufficiently intense to reduce them again. In fact, we know independently, from regional data on site sizes and occupation intensities, that in the Early Natufian phase sites were large and occupation intensity was high, whereas in the Later Natufian, population declined as a result of the onset of the Younger Dryas cold and dry climatic phase ~11 ka.

Clearly the matter of distinguishing causes for patterns observed in faunal and plant remains assemblages is fundamental. Inferences of resource depression as a result of human overexploitation, for example, need to exclude factors such as climate change. However, some of the most interesting recent debates have concerned the nature of the fitness-related cur-

rency which is being maximized in a particular context. As noted above, standard of models assume that the rate of energy extraction is being maximized. However, some researchers have proposed that, as far as big-game hunting is concerned, it is more probably prestige, in the context of costly signaling. The basis of this argument is that ethnographically big-game hunting does not seem to lead to calorie maximization for the hunter and his immediate family when compared with possible alternatives, but the sharing of meat that results from hunting success gives prestige and other political benefits in alliances, which lead to greater reproductive success (Hawkes 1991). Costly signaling theory, another set of ideas from BE, proposes that apparently costly or wasteful behavior can be favored by natural selection if it provides an honest signal of underlying, otherwise invisible, fitness-related qualities that are of interest to observers such as potential mates or rivals. Only individuals of high quality can afford to pay the costs of the most expensive signals. Bliege Bird & Smith's review (2005) of costly signaling in the context of human behavior showed that in many ethnographic contexts, costly signaling provides a coherent explanation of instances of apparently extravagant generosity or consumption. Hildebrandt & McGuire (2002, McGuire & Hildebrandt 2005) have proposed that the increase in big-game hunting in the Middle Archaic of the Great Basin should be seen as representing an increase in costly signaling, which occurred because populations were increasing, leading to increased social competition and larger numbers of receivers of the costly signals being produced (cf. Neiman 1997). They contrast the pattern in presumptively male-dominated hunting with that indicated by the plant remains, which suggests increasing diet breadth and intensification. They reject the counter arguments proposed by Byers & Broughton (2004) that the increase in big-game hunting resulted from an increase in animal populations as a result of climate change and is explicable in OF terms. However, their proposal has been further criticized by Coddington & Jones (2007) on the grounds, among



others, that provisioning activities would always have been dominant and would therefore make up the vast proportion of faunal remains in the archaeological record, even if prestige hunting was occurring. McGuire et al. (2007) respond with an analysis of faunal remains, which suggests that the logistically organized hunting of bighorn sheep, which was driving the increase in big-game hunting, could not have been efficient in terms of gaining calories under even the most advantageous assumptions. It is clearly important to be able to distinguish the factors affecting hunting priorities in particular cases rather than assuming a priori that one or the other must be the case. As Bird & O'Connell (2006) point out, the interesting question then becomes understanding the factors that lead the priorities to vary. Thus, for example, differences in social status may affect the currencies that individuals maximize in particular contexts (Lupo 2007).

OFT is increasingly being applied to understanding past plant exploitation and food production (e.g., Barlow 2002, 2006; Kennett et al. 2006b), and issues of risk and time-discounting are also being introduced (e.g., Tucker 2006).

Technology

Technology potentially raises problems for HBE approaches in the sense that the assumption of immediate adaptive responses to environmental change effectively implies that technological solutions will automatically arise when specific problems appear that the technology could solve. Although this notion may be more or less true in the case of some simple technologies, it is very unlikely for more complex ones, which will have a specific culturally transmitted history of accumulated successful innovation. Nevertheless, this does not make it any the less worthwhile to analyze technology from an HBE perspective in terms of how the costs and benefits of available alternatives affect the likelihood of their adoption.

The issues are clearly laid out by Ugan et al. (2003, pp. 1315–16). Determining how much time and effort it is worth to put into produc-

ing an artifact depends on a number of factors—what it is used for and how frequently, the extent to which increased effort in manufacture produces improved performance—as well as on the opportunity cost of the time spent in making the artifact—time that could have been used for some other activity. Many artifacts figure directly in the optimal foraging calculus because they are concerned in some way with improving the postencounter handling costs of particular resources. The optimality assumption predicts maximizing efficiency in this context, while acknowledging that there may be conflicting priorities leading to the need for trade-offs. Conversely, of course, demonstration of a lack of efficiency in production may indicate that costly signaling considerations are relevant (Bliege Bird & Smith 2005, pp. 230–31).

Bettinger et al. (2006) propose a model different from that of Ugan et al. but within the same optimality framework. It leads to different results for the comparison between different technologies in terms of the number of hours of use required for a more expensive technology to substitute for a less expensive one. Bettinger et al. use the method to explore the history of projectile weapons in prehistoric California.

Social Evolution

As noted above, one of the triggers for the emergence of a specifically Darwinian evolutionary archaeology was the rejection of the study of social evolution in the sense of trends toward increasing complexity. In fact, many HBE concepts are relevant to understanding social processes and changing patterns of social organization and have been used in illuminating ways to understand ethnographic and historical phenomena. They include the contrast between scramble and contest competition (Boone 1992), parental investment theory (Mace 1998), reproductive skew theory (Bird & O'Connell 2006, pp. 26–27; Summers 2006; Vehrencamp 1983), and theory concerning the relation between the density and predictability of resources and territoriality (Dyson-Hudson & Smith 1978; see also Shennan 2002 for a

general discussion of these and other issues). These theories and their existing applications demonstrate that HBE is not a set of ideas restricted to the analysis of optimal foraging in hunter-gatherer societies but is relevant to a vast range of social processes in societies of all sorts [and is closely akin in many respects to the so-called New Institutional Economics (North 1981)]. These ideas have been much slower to enter the specifically archaeological literature, partly because they raise significant issues about how they can be operationalized in terms of archaeological data, but also because, whereas students of hunter-gatherer foraging behavior very often have a strong background in biological evolution, this is much less the case with students of, for example, state-level complex societies.

One example that has entered the literature is costly signaling theory, as described above; other studies, more wide-ranging in their use of HBE theory, have begun to appear (e.g., Fitzhugh 2003, Kennett 2005). Like Kennett (2005, also Kennett et al. 2006a), Shennan (2007) used the concepts of the “ideal free distribution” and the “ideal despotic distribution” (Fretwell & Lucas 1970, Sutherland 1996) to provide a basis for understanding the consequences of the patch colonization process represented by the spread of farming into Central Europe. The ideal free distribution proposes that, as new areas are colonized, individuals occupy the resource patch that gives them the best returns. As more individuals occupy the patch, the returns to each individual decline to the point that the returns to an individual from the best patch are no better than those from the next best patch, which has no occupants. Once the returns from both patches are equal, they will be occupied indiscriminately until population growth reaches the point at which an equal benefit can be gained by occupying a still worse patch, and the process is repeated. When there is territoriality, however, the situation is different. Here the ideal despotic distribution applies. The first individual occupying the area can select the best territory in the best patch. Subsequent individuals settling there do not affect

the first arrival but have to take the next best territory, and so on, until there comes a point at which the next settler will do just as well by taking the best territory in the next best patch. Subsequent individuals will then take territories in either patch where the territories are equally suitable. In contrast to the ideal free distribution, where new settlers decrease the mean return for everybody, including those who arrived first, in the case of the ideal despotic distribution, the returns depend on the order of settlement so that the initial settlers of the best territory in the patch will do best.

In the case of the expansion of farmers into Central Europe, the first to arrive at favorable settlement patches settled in the best locations; indeed, the founding settlements almost invariably remained the most important ones. Individual microregions filled up relatively rapidly, as the detailed local data make clear. Cemeteries came into existence to represent an ancestral claim to territory in the face of increasing competition as local carrying capacities were reached. Isotope analyses point to the emergence of patrilineal corporate groups (e.g., Bentley et al. 2002). One can postulate that over time the senior line of the lineage in a given patch would have maintained control of the prime location and its territory and is represented archaeologically by the larger houses in the founding settlements. The junior branches, however, would be in increasingly inferior positions and would have relatively little option to go elsewhere (Vehrencamp 1983), hence the increasing number of smaller houses in the settlements.

In the later occupation phases of many settlement microregions, ditched and/or palisaded enclosures appeared. These may have been ritual and/or defensive, but they represent the emergence of a new type of social institution integrating large numbers of people. Once institutions emerged that integrated larger numbers of people into a cooperating unit that could be more successful in competition than groups not integrated in this way, other groups had little option but to copy them if they wished to avoid potentially disastrous consequences.

The nature of those disastrous consequences is indicated by the evidence for massacres occurring at this time; the evidence for large numbers of dead—more than 60 in one case—points to a large number of attackers. This situation may be seen as a prisoner's dilemma. The fates of individual households would have become increasingly dependent on those of the larger entities of which they became a part (Read & LeBlanc 2003). Not adopting this new form of organization was not an option at the local level, but at the global level it might have been better for all concerned if it had not occurred, in the sense that the conditions of life deteriorated with the appearance of warfare; the extent of exchange, visible in the materials making up lithic assemblages, declined drastically and so too did population, leading to regional abandonment in some places.

One could argue that what has been presented is no more than a plausible scenario described in evolutionary terms. Nevertheless, the model provides a strong set of natural-selection-based predictions about the kinds of things that happen during colonization and population-expansion processes, and the available archaeological evidence corresponds closely to the predictions. Others who have not adopted an HBE framework have interpreted the settlement and social patterns of these colonizing farmers in ways that are similar to those outlined above (e.g., van der Velde 1990), so the description is not simply a circular consequence of the framework and models adopted.

FUTURE DEVELOPMENTS

Developments in all areas of evolutionary archaeology will continue, but two key areas may be identified: comparing and testing in specific cases the predictions of HBE approaches with those of DIT perspectives in which culture

plays a significant explanatory role, and especially developing and testing social evolutionary hypotheses involving the sorts of mechanisms outlined above. Indeed, the number of different theoretical models and hypotheses framed within a Darwinian perspective available in the literature, usually on the basis of evolutionary game theory and often making evolutionary psychology assumptions, is now almost overwhelming. Many such studies refer more or less in passing to archaeological evidence, make assumptions about prehistoric states of affairs on the basis of ethnographic generalizations, or have archaeological consequences that have not been explored. It is only possible to give one example here.

Many of the most important current debates in evolutionary social science concern the emergence of human altruism and large-scale cooperation. Some (e.g., Henrich 2004) depend on cultural group selection. Others propose very different mechanisms. Choi & Bowles (2007), for example, have developed a model of what they call parochial altruism and warfare, which shows that altruism to the members of one's own group and hostility to nongroup members could evolve if such attitudes contributed to the group's success in warfare and the parochial attitudes actually encouraged intergroup conflict. Their simulations show that in conditions such as those that were likely relevant to late Pleistocene societies, neither altruism nor parochialism could have been successful on their own, but they could have prevailed jointly by encouraging intergroup warfare.

It remains to be seen how much archaeology will contribute to such debates. As always, the extent to which it can do so depends on archaeologists' ability to identify and characterize variation in the archaeological record in relevant ways that lead to the development and testing of causal hypotheses.

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The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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