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Patterns, Processes, and Parsimony: Studying Cultural Evolution with Analytical Techniques from Evolutionary Biology

Mark Collard and Stephen J. Shennan

Over the past twenty-five years, there has been growing appreciation that the processes involved in the evolution of genes and culture are sufficiently similar that cultural evolution can be legitimately studied within the Darwinian framework that is used to study genetic evolution (Durham 1979; Dunnell 1980; Pulliam and Dunford 1980; Cavalli-Sforza and Feldman 1981; Lumsden and Wilson 1981; Boyd and Richerson 1985; Teltser 1995; Maschner 1996; O'Brien 1996; Barton and Clark 1997; Lyman and O'Brien 1998; Shennan 2002b; Mesoudi et al. 2004). Our goal in this chapter is to highlight a growing body of work in which this view of cultural evolution has been taken to its logical conclusion and evolutionary biological methods have been applied to cultural data with a view to shedding light on events in prehistory and on debates regarding cultural evolutionary processes. We will begin by discussing in more detail the conceptual foundations of this novel approach. We will then outline cultural evolutionary applications of population genetic models and of the cladistic method of phylogenetic reconstruction. Last, we will examine studies in which phylogenetic comparative methods have been applied to cultural datasets.

Conceptual Foundations

Proponents of three closely related schools of thought have applied evolutionary biological methods to cultural data. The first of these schools is referred to as gene-culture coevolutionary theory, or more usually now dual inheritance theory (Durham 1979, 1990, 1991, 1992; Pulliam and Dunford 1980; Cavalli-Sforza and Feldman 1981; Lumsden and Wilson 1981; Boyd and Richerson 1985; Richerson and Boyd 1992; Laland et al. 1995). In dual inheritance theory, genes and culture are viewed as two distinct systems of information transmission. They both involve the transmission of phenotype-influencing information but operate via different mechanisms. The genetic system is based on reproduction, while the cultural one involves social learning. With this difference in mind, dual inheritance theorists hold that genetic evolution and cultural evolution are similar in that they are both based on the process that Darwin referred to as descent with modification, but they also accept that the nature of social learning is such that cultural evolution is influenced by forces that have no obvious equivalents in genetic evolution. Most notably, individuals can choose to copy practices from nonkin, and they are also able to modify or discard practices in the light of experience. The significance of these processes is that cultural evolution cannot be assumed to be always in step with genetic evolution. Sometimes it will be, but frequently it will not. Our ability to learn from nonkin means that cultural patterns will often not coincide with genetic patterns. Likewise, our ability to learn from other individuals and to pass on those behaviors to yet other individuals throughout our lives means that cultural evolution will often be faster than genetic evolution. Dual inheritance theory even allows for the possibility that the transmission of some cultural traits might be maladaptive from a genetic point of view (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Shennan 2002b).

The second school of thought is called selectionist archaeology, or more often evolutionary archaeology (Dunnell 1980, 1989; Leonard and Jones 1987; Neff 1992; O'Brien and Holland 1995; Ramenofsky 1995; Abbott et al. 1996; Lipo et al. 1997; Lyman and O'Brien 1998; O'Brien and Lyman 2000; Leonard 2001; O'Brien and Lyman 2003). The central tenet of evolutionary archaeology is that artifacts are just as much a part of the human phenotype as are our bones, muscle, and skin (Dunnell 1989; Lyman and O'Brien 1998; O'Brien and Holland 1995; Leonard 2001). The corollary of this is that artifact variation through time and space should be explained in exactly the same way as paleobiologists account for the temporal and geographic variations in bony morphology that are documented in the fossil record, namely as the result of natural selection and drift (Lyman and O'Brien 1998; Ramenofsky 1995; Abbott et al. 1996; Leonard 2001). The former is the process by which the composition of the pool of heritable information that influences the phenotypic characteristics of a lineage is altered by some individuals out-reproducing others as a consequence of possessing characteristics that are more effective in current conditions. The latter is the process by which the composition of the aforementioned pool of heritable information is altered by some individuals out-reproducing others due to chance alone. Some evolutionary archaeologists recognize that cultural evolution and genetic evolution involve different transmission mechanisms (Dunnell 1989; Lyman and O'Brien 1998). Indeed, one prominent proponent of evolutionary archaeology has argued that the replicative success of cultural traits should not be assumed to be reducible to the reproductive success of individuals (Leonard 2001). However, in practice, evolutionary archaeologists do not normally allow for the possibility that genes and culture may have different evolutionary dynamics (Ramenofsky 1995; Abbott et al. 1996; Leonard 2001).

The third school of thought is known as human behavioral ecology (Borgerhoff Mulder 1991; Cronk 1991; Smith and Winterhalder 1992; Smith 2000; Winterhalder and Smith 2000; Smith et al. 2001; Shennan 2002b). Linked to a substantial body of work in evolutionary biology (Krebs and Davies 1993), human behavioral ecology seeks to explain human behavior in terms of its ongoing adaptive significance. That is, human behavioral ecology attempts to understand how a particular behavior contributes to an individual's reproductive success or that of their relatives given the prevailing environmental (including social) conditions. The key assumption of human behavioral ecology is that humans are sufficiently flexible for the vast majority of behavioral differences among them to be primarily the result of diversity in environmental conditions rather than differences in genes or in cultural inheritance (Smith 2000; Shennan 2002b). Thus, human behavioral ecologists concentrate on the relationship between behavioral strategies and ecological circumstances and pay little attention to the mechanisms by which behavioral differences among individuals can potentially arise (Smith et al. 2001). One substantive consequence of this "black box" approach is that human behavioral ecology does not take into account population-level phenomena such as drift. Another is that human behavioral ecology makes no allowance for the possibility that some behavioral traits may not be adaptively significant because they were acquired as part of a package of traits. The first of these distinguishes human behavioral ecology from both dual inheritance theory and evolutionary archaeology. The second further distinguishes human behavioral ecology from dual inheritance theory.

Population Genetics-Based Cultural Evolutionary Models

One of the surprises in genetics in the 1960s was the discovery that much DNA does not actually code for proteins. In fact, it apparently does not code for anything and hence cannot be under any form of selection. It was found that the only factors that affect the chances of a new mutation surviving or going extinct in this DNA are the mutation rate and random drift, which is dependent on population size. This is the basis of the neutral theory of evolution (Kimura 1983). Recently, evolutionary anthropologists have begun to apply the neutral theory to cultural data to great effect.

In the mid-1990s, drawing on the distinction between artifact style and function made by Dunnell (1978), Neiman (1995) used the neutral theory to develop a series of predictions about the amount of variation to be expected in the decoration of a pottery assemblage if the decoration were neutral in terms of adaptation. He analyzed rim decoration on pottery assemblages from seven successive phases of the Woodland period in Illinois and found that it matched the expectations of the neutral model. He concluded that the patterns of variation depended on changing levels of intergroup contact, which started low, increased, and then declined again. The time of highest interaction was also a time when exotic trade goods were widespread. Because the successful transmission of pottery-making traditions depends on long-lasting relationships between teacher and learner, Neiman suggested that the changing levels of intergroup contact related to changes in the level of long-term residential movement of potters between groups.

More recently, Shennan and Wilkinson (2001) used the neutral model in a study of patterns of pottery decoration from two settlements of the Linear Pottery culture in western Germany. This culture is thought to represent the archaeological trace of an early agricultural population that spread across much of Central Europe between about 5700 and 5400 BP. The Linear Pottery culture is especially well documented in the valley of the Merzbach on the Aldenhovener Platte in western Germany as a result of excavations carried out in advance of strip mining. In Shennan and Wilkinson's study, ceramic sequences from the founding Merzbach valley Linear Pottery culture settlement, Langweiler 8, and from a later settlement, Laurenzburg 7, were analyzed in the light of the neutral model. Shennan and Wilkinson found that the expectations of the neutral model and the amount of variation in the pottery assemblages coincided only in the early phases of occupation. In the later phases, the diversity of the assemblages indicated that there had been deliberate selection for novel decoration types rather than simple drift. Shennan and Wilkinson proposed that the potters might have been doing this because they wanted to establish their own local identity and distinguish themselves from neighboring groups. This work has been taken further by Bentley and Shennan (2003) using decorative attribute frequencies rather than assemblage diversity measures.

Population genetics models in which innovations affect fitness have also been used in cultural evolutionary studies. Shennan (2001), for example, has investigated the impact of population size on cultural evolution with the aid of a model developed by Peck et al. (1997) to assess the relative benefits of sexual and asexual reproduction. In Peck et al.'s model, mutations can be either beneficial or deleterious; there is a correlation between an allele's fitness prior to mutation and its postmutation fitness; and many mutations produce only very small changes in fitness. Shennan employed two cultural evolutionary models in his study. To create the first, he altered Peck et al.'s model so that transmission was possible from one "cultural parent" to one "cultural offspring." To produce his second model, Shennan modified Peck et al.'s model to allow transmission between individuals belonging to different generations where the older individual is not the biological parent of the younger individual. In simulation trials, Shennan found a marked increase in the mean fitness of the population as effective population size increased. In the trials of the first model, the mean fitness value of the population increased ten thousand-fold as effective population size increased from five to fifty. In trials of the second model in which cultural traits were adopted from nonbiological parents 5 percent of the time, the population's mean fitness value increased one thousand-fold as the effective population size increased from five to twenty-five, and then increased by around five times as effective population size increased from twenty-five to seventy-five. Shennan's simulation studies showed that larger populations have a major advantage over smaller ones when it comes to cultural innovation because of the decreasing role of sampling effects as populations get larger. When effective population size is large, there is a far greater probability of fitness-enhancing cultural innovations being maintained and deleterious ones being lost than when effective population size is small. In the latter situation, innovations that are maintained tend to be less beneficial in terms of reproduction and less attractive for imitators. Recently Henrich (2004) has developed another cultural evolutionary model based on population genetics theory. His model also shows the importance of population size in maintaining and increasing technological complexity but is based on the greater probability of *more complex* skills being invented and maintained when populations are larger.

The studies described in the last three paragraphs, along with the work of Lipo et al. (1997), Hahn and Bentley (2003), Bentley et al. (2004), and Kohler et al. (2004), demonstrate the considerable potential of population genetics-based models to shed light on cultural evolution. Crucially, such models provide a baseline of great epistemological value. Where cultural patterns agree with the patterns predicted by a model, we can invoke the principle of parsimony and discount processes that are more complicated than the modeled process. In contrast, where the cultural and modeled patterns disagree, we can legitimately disregard the modeled process and seek a more complex explanation. As such, the application of population genetics-based cultural evolutionary models allows us to narrow down the range of possible explanations for cultural evolutionary patterns in a controlled manner.

Cladistic Analysis of Cultural Data

Cladistics is currently the dominant method of phylogenetic reconstruction used in biology (Kitching et al. 1998). Based on a null model in which new taxa arise from the bifurcation of existing ones, cladistics defines phylogenetic relationship in terms of relative recency of common ancestry. A pair of taxa are deemed to be more closely related to one another than either is to a third taxon if they share a common ancestor that is not also shared by the third taxon. Exclusive common ancestry is indicated by evolutionarily novel or derived character states. Two taxa are inferred to share a common ancestor to the exclusion of a third taxon if they exhibit derived character states that are not also exhibited by the third taxon.

Recently, researchers have begun to apply cladistics and related phylogenetic methods to cultural data in order to shed light on events in prehistory (e.g., Foley 1987; Foley and Lahr 1997, 2003; Gray and Jordan 2000; O'Brien et al. 2001, 2002; Holden 2002; Forster and Toth 2003; Gray and Atkinson 2003; O'Brien and Lyman 2003, 2005; Rexová et al. 2003; Robson-Brown 1996). This approach is well illustrated by the historical linguistic studies of Gray and Jordan (2000), Holden (2002), and Gray and Atkinson (2003), and the archaeological work of O'Brien and colleagues (O'Brien et al. 2001, 2002; O'Brien and Lyman 2003).

Gray and Jordan (2000) employed cladistic methods to assess the two main competing models regarding prehistory in the Pacific, the express train model and the entangled bank model. The former suggests a rapid dispersal of Austronesian speakers from a homeland in Taiwan around six thousand years ago, whereas the latter contends that the Polynesian colonizers derived from a population in eastern Melanesia that had been there for tens of thousands of years. The entangled bank model also avers that the cultural and linguistic patterns that are visible among the Polynesian islands are at least as much the result of continuing contact subsequent to initial colonization as they are the result of the colonization process itself. Gray and Jordan first used cladistics to produce a phylogeny of Pacific languages. Then, they mapped the archaeological and geographic steps suggested by the express train model onto the language phylogeny. This analysis indicated that the links predicted by the express train model were a close fit with the language phylogeny, much closer than would be predicted to occur by chance. Gray and Jordan pointed out that proponents of the entangled bank model argue that genes, languages, and culture are constantly combining and recombining, so that patterns of language relationships say little about the history of the language speakers and reflect only geographic proximity. Gray and Jordan's results conflict with this suggestion because they were able to recover a relatively robust phylogeny, and because proximity on the language phylogeny did not correspond to geographic proximity.

Holden (2002; see also Holden et al. 2005) used cladistics to reconstruct the relationships among seventy-five Bantu and Bantoid African languages from ninety-two items of basic vocabulary. As in the Polynesian case, researchers disagree about the history of the Bantu languages. Some contend that the Bantu languages evolved rapidly in conjunction with the expansion of farming in sub-Saharan Africa during the Neolithic and Iron Ages, and that a tree can therefore represent the relationships among the languages. Others hold that the tree model is flawed because diffusion of Bantu words among neighboring speech communities is likely to have been common. Holden's cladistic analysis returned a relatively small set of equally parsimonious cladograms and indicated that the majority of characters were consistent with the most parsimonious cladograms. Holden concluded that the latter finding offered strong support for the tree model of Bantu language history. Subsequently, Holden compared the most parsimonious cladograms with a model for the spread of farming in sub-Saharan Africa that archaeologists have constructed based on pottery styles and dates. She found that the branching order and geographic distribution of the major branches of the Bantu language trees were consistent with the archaeological model. She concluded, therefore, that the dispersal and diversification of the Bantu languages were linked to the expansion of farming during the Neolithic and Iron Ages, and that since that time Bantu-speaking communities have not moved to any great extent.

Gray and Atkinson (2003) used phylogenetic methods and an Indo-European lexical dataset to test the two main hypotheses for Indo-European origins—Gimbutas's (1973) Kurgan expansion hypothesis, which suggests that Indo-European spread with Kurgan pastoralists beginning around 6000 BP, and Renfrew's (1987) Anatolian farming hypothesis, which contends that the Indo-European languages expanded with the spread of agriculture from Anatolia around 9500–8000 BP. Gray and Atkinson first used cladistics to reconstruct the phylogenetic relationships among the Indo-European speech varieties, and then employed a Bayesian Markov chain Monte Carlo method to estimate the divergence times of the main speech variety groups suggested by the cladistic analysis. The divergence times estimates obtained by Gray and Atkinson provide strong support for the Anatolian farming hypothesis of Indo-European origins. The initial divergence of Indo-European was suggested to occur between

7800 and 9800 BP, which is close to the time of divergence proposed by Renfrew based on the archaeological record. Interestingly, Gray and Atkinson also found evidence for a rapid divergence of several speech variety groups around the time posited for the Kurgan expansion, which they suggested may indicate that the two hypotheses are in fact compatible.

O'Brien et al.'s (2001, 2002; O'Brien and Lyman 2003) archaeological application of cladistics focused on the long-standing problem of the evolution of projectile point form in the southeastern United States during the Paleoindian period. They began by recording three qualitative and five quantitative characters on a sample of 621 specimens representing a range of projectile point types, including Clovis, Dalton, and Cumberland. They then subjected the specimens to paradigmatic classification to cluster them into taxa with unique combinations of character states. In the next part of the study, O'Brien et al. carried out a cladistic analysis of the seventeen taxa that contained at least four specimens. One of the seventeen taxa was selected as the outgroup based on least-step occurrence seriations and chronological considerations; the remainder were treated as the ingroup. The cladistic analysis yielded a single most parsimonious cladogram. O'Brien et al. evaluated the fit between the cladogram and the dataset with a goodness-of-fit index called the Consistency Index (CI). This index ranges between 1.0 and 0.0, with values close to 1 indicating a good fit between the cladogram and the dataset and values close to 0 indicating a poor fit. The cladogram obtained by O'Brien et al. had a CI of 0.59, which suggests that it is a reasonable depiction of the relationships among the taxa. In the final part of their study, O'Brien et al. used the cladogram to investigate the character state changes that occurred in the course of the evolution of Paleoindian projectile point form.

Another group of researchers has applied cladistics to cultural data in an effort to resolve an ongoing debate about the processes involved in cultural evolution (Tehrani and Collard 2002; Jordan and Shennan 2003). To date, the debate in question has concentrated on two competing hypotheses, which have been termed the branching hypothesis (also known as the demic diffusion or phylogenesis hypothesis) and the blending hypothesis (also known as the cultural diffusion or ethnogenesis hypothesis; Romney 1957; Kirch and Green 1987; Moore 1994, 2001; Bellwood 1996; Tehrani and Collard 2002). According to the former, the cultural similarities and differences among human populations are primarily the result of cultural assemblages dividing as the communities that produce them repeatedly grow and split. The branching hypothesis predicts that the similarities and differences among cultures can be represented by a cladogram, and that there will be a strong association between cultural variation and linguistic, morphological, and genetic patterns (e.g., Ammerman and Cavalli-Sforza 1984; Renfrew 1987). In contrast, supporters of the blending hypothesis (Terrell 1988, 2001; Moore 1994, 2001; Dewar 1995; Terrell et al. 1997, 2001) contend that it is unrealistic "to think that history is patterned like the nodes and branches of a comparative, phylogenetic, or cladistic tree" (Terrell et al. 1997:184). Instead, they argue that the biological, linguistic, and cultural evolution of our species is best characterized by "a constant flow of people, and hence their genes, language, and culture, across the fuzzy boundaries of tribes and nations" (Moore 2001:51). The blending hypothesis predicts that a reticulated graph can best represent the similarities and differences among cultures (Terrell 2001), and that there will be a close relationship between cultural patterns and the frequency and intensity of contact among populations.

Tehrani and Collard's (2002) study examined decorated textiles produced by Turkmen groups between the eighteenth and twentieth centuries. Two sets of cladistic analyses were carried out. The first focused on the period before the Turkmen were incorporated into the Russian Empire. These analyses indicated that in the precolonial period, the evolution of Turkmen textile designs was dominated by branching. A randomization procedure (the permutation tail probability test) suggested that the data contain a phylogenetic signal, and parsimony analysis indicated that the data fit the bifurcating tree model associated with cultural branching reasonably well. The fit between the model and data was not perfect, indicating that blending played a role in the evolution of Turkmen culture. However, goodness-of-fit statistics (CI, Retention Index) and a second randomization procedure (bootstrapping) suggested that blending was markedly less important than branching. According to the goodness-of-fit statistics, about 70 percent of the similarities among the assemblages are homologous, and approximately 30 percent are homoplastic. This is compatible with the borrowing of designs and motifs being responsible for a third of interassemblage resemblances, although the possibility of independent invention as a source of homoplastic similarities cannot be completely discounted. Tehrani and Collard's second set of analyses dealt with weavings produced after the defeat of the Turkmen by the Russian military. These analyses suggested that the social and economic changes experienced by the Turkmen after their incorporation into the Russian Empire led to a greater role for blending in Turkmen cultural evolution. Branching remained the dominant cultural evolutionary process, but the importance of blending increased. The goodness-of-fit statistics indicated that approximately 60 percent of the interassemblage resemblances are homologous, and approximately 40 percent are homoplastic. Thus, there is a 10 percent increase in the number of homoplastic resemblances among the woven assemblages from the period of Russian domination. This is consistent with more intertribal borrowing of designs and motifs, but again independent invention cannot be entirely discounted as a source of the homoplasies. Tehrani and Collard concluded that the two sets of analyses supported the branching hypothesis more strongly than they supported the blending hypothesis.

Jordan and Shennan (2003) reached a contrasting conclusion. These researchers used cladistics to examine variation in Californian Indian basketry in relation to linguistic affinity and geographic proximity. They carried out three sets of cladistic analyses. In the first, they used the permutation tail probability test to determine whether their basketry datasets (coiled baskets, twined baskets, all baskets) contain a phylogenetic signal. These analyses suggested that a significant phylogenetic signal is present in all three datasets. In the second set of analyses, Jordan and Shennan used the CI to assess the fit between the datasets and the bifurcating tree model. These analyses suggested that the phylogenetic signal detected by the permutation tail probability test is weak. In the third set of analyses, Jordan and Shennan used a statistical test developed by Kishino and Hasegawa (1989) to assess the fit between the datasets and trees reflecting linguistic relationships, geographic distance, ecological similarity, and adjacency. This test enabled them to distinguish between two different potential sources of homoplasy—independent invention and blending. In an analysis of the complete sample of baskets, the fit between the dataset and the adjacency tree was considerably better than the fit between the dataset and the other trees. This suggests that blending had a bigger impact on the distribution of similarities and differences among the basketry assemblages than branching or adaptation to local environments.

In an analysis of just the coiled baskets, blending was also found to play a more significant role than branching or adaptation to local environments. The analysis of the twined baskets contrasted with the preceding analyses in that the language tree fit the dataset better than the other trees. This suggests that branching was more important than blending or adaptation to local environments in generating the twined baskets. On the basis of these results, and the results of a range of multivariate analyses, Jordan and Shennan concluded that the evolution of Californian Indian baskets is best explained by ethnogenesis. Jordan and Shennan (2005) have recently reported similar results from a finer-grained analysis of basketry traditions in northern California.

In our view, the studies discussed in this section suggest that cladistics can be a useful tool for tackling certain cultural evolutionary problems. It offers a well-understood model that can be fit to material culture and linguistic datasets in a straightforward manner. Where the fit between a cultural dataset and the tree model is close, we can invoke the principle of parsimony and legitimately conclude that the similarities and differences among the cultural units are primarily the result of branching. On the other hand, where there are numerous homoplasies and the fit between a cultural dataset and the tree model is consequently poor, we can justifiably infer that borrowing or convergent evolution played a more important role in generating the similarities and differences among the cultural units. The instances of homoplasy can then be investigated with biological phylogenetic methods that are not based on the bifurcating tree model (Hendy and Penny 1992; Bandelt and Dress 1992; Hurles et al. 2003; Bryant et al. 2005; Greenhill and Gray 2005).

With regard to further applications of biological phylogenetic methods to problems in prehistory, there are some cases where we can predict quite confidently that a tree model is likely to be relevant, where the data patterns seem to point in this direction even though formal analyses remains to be done. As we mentioned earlier, the spread of farming into Central Europe seems to have involved a fast initial colonization process followed by more local population expansion, mirrored by the increasing regionalization of pottery styles. A similar pattern of initial uniformity followed by increasing regionalization seems apparent in the case of Bell Beakers, but it is by no means clear that the mechanisms are the same, since the pattern seems to be restricted to a limited part of the Bell

Beaker cultural inventory, especially the Beaker vessels themselves. Here, and more certainly in subsequent periods that seem to have had large sedentary populations, it seems likely that cultural innovations relating to different aspects of social life and originating in different places would have spread through those populations more or less independently, resulting in multiple cultural lineages rather than a single cultural core (Boyd et al. 1997).

Phylogenetic Comparative Methods

Correlation-based cross-cultural comparisons have often been used to test hypotheses regarding the influence of environmental factors on cultural practices. They have also frequently been used to test hypotheses about the coevolution of cultural practices. However, it has long been recognized that this form of analysis is problematic. Correlation analysis requires cases to be independent of one another, but multiple instances of a particular cultural practice cannot be assumed to be independent, because human populations are related by descent. It is possible that populations exhibit the same cultural practice as a result of independent, convergent evolution, but a more parsimonious explanation is that they exhibit the cultural practice because they inherited it from their last common ancestor. Anthropologists have attempted to overcome this problem primarily by means of stratified sampling. Populations are clustered into groups that are deemed to be independent of one another, and then a representative population from each group is selected for inclusion in the analysis. This was the approach used to generate the well-known standard cross-cultural sample (Murdock and White 1969). Unfortunately, as Mace and Pagel (1994) have pointed out, the stratified sampling approach has serious shortcomings. The most important of these is that it does not actually remove the problem of nonindependence. Because all humans are related to one another, the groups into which the populations are clustered in the first step of the process are not independent of one another. They are simply more distantly related than the populations within each group. Thus, the problem of historical relatedness persists, albeit less obviously. Another important problem with the stratified sampling approach is that it rules out cross-cultural analyses of closely related populations, which means that many interesting hypotheses cannot be tested.

Recently, a number of researchers have turned to a cluster of techniques known as phylogenetic comparative methods to deal with the impact of population relatedness on cross-cultural analyses (e.g., Mace and Pagel 1994; Holden and Mace 1997, 1999, 2005; Sellen and Mace 1997; Mace and Jordan 2005; Pagel and Meade 2005). These methods were developed by evolutionary biologists to deal with an analogous problem—the nonindependence of species included in tests of hypotheses regarding adaptation and coevolution (Harvey and Pagel 1991). The phylogenetic comparative method used most frequently by evolutionary anthropologists—independent contrasts (or independent comparisons) analysis—focuses on quantitative data and seeks to determine how much change in the dependent variable is explicable by change in the independent variable after phylogeny is taken into account. The independent contrasts method proceeds via several steps (Mace and Pagel 1994; Harvey and Pagel 1991). First, the dependent and independent variables are measured in a sample of taxa. Next, the values for the dependent and independent variables are mapped onto the tips of an estimate of the phylogeny for the taxa. Thereafter, the common ancestors implied by the cladogram are assigned the averages of the values exhibited by their descendants for the dependent and independent variables. Subsequently, the differences between the values exhibited by sister taxa are calculated. These are the independent contrasts. They are called this because they represent the change that has taken place since the taxa last shared a common ancestor. Last, the independent contrasts derived from the dependent variable values are regressed against the independent contrasts obtained from the independent variable.

A number of long-standing anthropological hypotheses have been tested with phylogenetic comparative methods (Mace and Pagel 1994; Holden and Mace 1997, 1999, 2005; Sellen and Mace 1997; Mace and Jordan 2005; Pagel and Meade 2005). We will mention two here. In the paper that introduced phylogenetic comparative methods to anthropology, Mace and Pagel (1994) evaluated the idea that African pastoralist populations adopt camel herding in order to cope with dry environments. They focused on nine pastoralist populations from East Africa whose phylogenetic relationships can be inferred from linguistic evidence. Mace and Pagel found that the distribution of camel herding among the nine populations can be most parsimoniously explained by four independent instances of cultural change. They also found that the four populations that herd camels live in drier areas than the populations that herd cattle. Thus, Mace and Pagel concluded that camel herding is indeed an adaptation for living in dry environments. More recently, Holden and Mace (1997) have used independent comparisons analysis to investigate the evolution of postinfancy high lactose-digestion capacity. Three hypotheses have been proposed to explain the distribution of this heritable trait, which is common only in populations of northern European and circum-Mediterranean origin. The first suggests that postinfancy high lactose-digestion capacity is an adaptation to millennia of pastoralism and milk consumption. The second avers that postinfancy high lactose-digestion capacity is an adaptation to high-latitude environments. According to this hypothesis, populations that live at high latitudes drink milk because it is a good source of vitamin D and they are at risk of vitamin D deficiency due to limited sunshine. The third hypothesis suggests that post-infancy high lactose-digestion capacity is an adaptation to highly arid environments. In this hypothesis, the water content of fresh milk is posited to increase the survival chances of individuals who are able to digest lactose compared to maldigesters. Holden and Mace tested the three hypotheses with the aid of phylogenies derived from genetic and linguistic data. Their analyses provided strong support for the hypothesis that post-infancy high lactose-digestion capacity is an adaptation to millennia of pastoralism and milk consumption. The other two hypotheses were not supported by the analyses.

The use of phylogenetic comparative methods to test hypotheses regarding the evolution of human behavior has been criticized (Cashdan and Rogers 1997; Rogers and Cashdan 1997; Borgerhoff Mulder 2001). However, in our view the arguments for using phylogenetic comparative methods are stronger than those for not using them. For example, while it is true that the results they produce are dependent on the accuracy of phylogeny employed, the alternative, nonphylogenetic approach is even more problematic. Not using a phylogeny effectively assumes that all populations are equally closely related to one another, which is implausible (Mace and Pagel 1994). It is also true that phylogenetic comparative methods provide conservative tests of adaptive and coevolutionary hypotheses (Cashdan and Rogers 1997; Rogers and Cashdan 1997). However, we believe that in studies of this kind, false-negative results are less damaging than false-positive results, which is what the conventional, nonphylogenetic approach can be expected to produce (Mace and Pagel 1994). Accordingly, we consider phylogenetic comparative methods to be an important addition to our analytical toolkit. Nevertheless, as far as their application to archaeological problems is concerned, further theoretical development is required. The trees that have been used in comparative tests to date are all based on languages or genes, whereas archaeological versions of these tests would have to be based on trees derived from material culture data. Until the method is explored using trees of relationships based on archaeological data with a reasonable phylogenetic signal, it is unclear how useful this approach will be.

Concluding Remarks

Applying evolutionary biological methods to cultural data with a view to shedding light on cultural evolution is a relatively new approach. However, we think its potential is already clear. Perhaps its greatest benefit is epistemological. Most work on cultural evolution involves identifying patterns in datasets and then trying to determine which processes are likely to have produced those patterns. Evolutionary biological methods are advantageous in this regard because they tend to be based on well-characterized process models. As such, when we apply them to our cultural datasets, we can be confident about the implications of the results we obtain. If the method indicates a good fit between the data and the model, we can invoke the principle of parsimony and discount processes that are more complicated than the model. Conversely, if the method suggests that the fit between the data and the model is poor, we can legitimately disregard the modeled process and seek a more complex process to explain the data. Evolutionary biological methods, therefore, allow us to select process explanations for cultural patterns in a rigorous manner. A further important benefit of applying evolutionary biological methods to cultural data is that it allows cultural archaeologists, anthropologists, and historical linguists to provide information about patterns and processes of cultural evolution that can be linked with contemporary genetic data and with the increasingly available evidence for past human mobility from studies of stable isotopes and ancient DNA. We believe this combination has the potential to give us unparalleled insights into the interrelations among populations and the genetic, linguistic, and nonlinguistic cultural attributes associated with them.

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