THEORIES OF EVOLUTION FOR ARCHAEOLOGY

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Cowboy Ecology: Essays in Honor of R. L. Bettinger
One of the hallmarks of Robert Bettinger’s contribution to archaeology is the attention he pays to ecological and evolutionary theory. Archaeology and the other historical sciences must deal with limited and noisy data. Theory that integrates information from many case studies and from experiments is an essential tool for interpreting particular archaeological sequences. Both genetic and cultural evolutionary theory are based on mathematical models of ecological time scale microevolutionary processes. Theorists consider what happens to a population of individuals as they live out their lives in one generation and pass on their genes and culture to the next generation. Then they imagine that these processes are repeated for many generations. One might think that microevolutionary processes would be hard to infer in the archaeological record but Bettinger and his colleagues have been able to make such inferences in favorable circumstances. However, archaeology makes a more important contribution to the study of macroevolution. Macroevolution occurs on time scales that are too long to be captured by experiments or observation of living creatures or cultures. On such time scales, phenomena like changes in climate and geomorphology become appreciable. Some of the most difficult but most interesting questions in science are macroevolutionary ones. Major changes in genes and culture give rise to new adaptive syndromes, some quite revolutionary. For example agricultural innovations starting around 11 kya eventually transformed most human societies. Almost all of the data we have to infer the hows and whys of macroevolution come from the historical sciences—archaeology, paleoclimatology, paleontology, and allied disciplines. For example, the human lineage exhibits a number of long term trends such as increasing brain size and increasingly sophisticated technology. Are such trends due to internal constraints on the rate of evolution of complex organs and technologies or are the externally driven by environmental change? Both processes are certainly important in general, but perhaps are differentially important at different time scales. Archaeology and its companion historical disciplines furnish ever higher resolution data to test any theory derived hypotheses about such matters. Improvements in data analytic methods are providing powerful new tools to analyze such data.
It might seem natural that evolutionary theory should be the foundation of archaeology. Archaeologists, after all, recover sequences of evidence related to changes in human behavior over time, evidence of evolution. However, complexities related both to archaeology and to evolutionary theory have made providing an evolutionary foundation for archaeology a challenging task. Our Cowboy has been a pioneering contributor (Bettinger 1980; Bettinger et al. 2015; Bettinger 1991). In his 1980 review he noted that the theoretical tools available to explain the diversity of hunting and gathering behavior were in their infancy. By the time of his 1991 book, fields such as behavioral ecology and cultural evolution had significantly matured. By 2015 many more developments were worth reviewing.

Some of the special difficulties of archaeology include the incompleteness of the record and the extreme complexity of the actual events that generated that record. Archaeologists are often interested in explaining the events in a particular historic sequence, such as the Numic expansion into the Great Basin (Bettinger and Baumhoff 1982). As the highly cited applied ecologists Burnham and Anderson (2002: 20) put it “we believe that ‘truth’ (full reality) in the biological sciences has essentially infinite dimension.” The social sciences are just biology with some extra dimensions thrown in! As our Cowboy recognized early in his career, theory is an essential tool in the face of complexity. It brings in knowledge from many critical fields like human biology, ecology, and evolution. Well tested theories have had explanatory success in many cases and are candidates to be applied to new ones. Theories summarize knowledge drawn from many specific historical trajectories and are often tested explicitly with comparative data (e.g. Bettinger 2015; Turchin et al. 2017).

The plan for this chapter is as follows: First I review the state of the art in theory building in very complex situations like evolving human societies. Second, I discuss the particular contribution cultural evolution and gene–culture coevolution introduce into the interpretation of archaeological sequences. Third, I introduce the distinction between microevolution and macroevolution, arguing that while archaeologists can and do make contributions to microevolution, their main contribution to evolutionary theory is in the realm of macroevolution. Finally, I sum up. In all parts I summarized the past contributions of archeology to the issues reviewed and its stake in future discussions of them.

THEORY AND EMPIRICAL COMPLEXITY

INCREASED SOPHISTICATION OF EMPIRICAL INFERENCE METHODS

As Burnham and Anderson (2002) explain it the first two chapters of their book, the high dimensionality of biological systems is a serious challenge for empirical science. See also (Burnham and Anderson 2004). It is sometimes called the “curse of dimensionality (Keogh and Mueen 2017).” As the number of dimensions of a system increase, the amount of data necessary to accurately characterize it increases exponentially. In practice, data are expensive to come by and are plagued by noise. The problem confronting the empiricist is how to use a relatively small amount of noisy data to learn as much as possible about a system that is potentially impossibly complex (Efferson and Richerson 2007). Burnham and Anderson argue that the task is to fit models to data in such a way as to extract as much information as possible from the limited data. These might be standard linear statistical models or models of the actual processes the analyst thinks are candidates to explain the data. Modelers want to avoid either under- or overfitting their data. An example of underfitting is to fit a straight line to data that have a pronounced curvature. There is some information about a second, or perhaps more, dimensions in such data. Overfitting is to create a model so complex that it fits the noise in the data as well any real
information in it. Overfit models have poor estimates of the real parameters and hence, when applied to out-of-sample data, predict it poorly. Burnham and Anderson endorse using an information theoretic goodness of fit measure, the Akaiki Information Criterion. AIC penalizes models for their complexity, a theoretically sophisticated version of Occam’s Razor. They also endorse formulating a set of a priori plausible models and competing them to best explain the data using AIC and related information theoretic goodness of fit measures. For example, it is often sensible to consider a “full” model with K terms and various simpler versions with <K terms. Unlike the case of using variance explained as a goodness of fit measure, the penalty AIC assigns to more complex models reduces the risk of overfitting.

One of interesting features of the derivation of information theoretic goodness of fit measure is that the concept of the true model (full truth) drops out of the analysis. This reflects the fact that if the full truth is of very high dimension and the amount of data we have is comparatively small. We can never be sure that the set of models we are testing contain the full truth. What we can estimate is how close the models we are testing are to full truth, relative to other models in the set we are testing. We may be able to say with considerable confidence that one is the closest to full truth and that others are distinctly further away. But because we don’t know what full truth is we can’t say how close our best model is to full truth! This is a formalization of the classic fallibilist model of scientific epistemology (Campbell 1974). We can be pretty confident that some hypotheses (models) cannot explain the data we are analyzing, but we also expect that with more data or better models our current best model is likely to be superseded in the future. A given set of data, say a particular archaeological sequence, may be the product of one or a few dominant processes. Another sequence may be dominated by a different set of processes. We can only detect the operation of dominant processes out of the tantamount to infinite ones that could in principle be important. Thus, we can anticipate that different systems will dominated by different processes. Even within a sequence there can be “regime shifts” in which the most important causal processes change. For example, in Western North America, the advent of the bow and arrow (Bettinger 2015; Bettinger and Eerkens 1999) and intensive plant based resource use (Bettinger and Baumhoff 1982) seems to have caused sociopolitical and subsistence revolutions that probably count as regime shifts.

A second statistical development of interest to archaeologists is the use of cheap computing power to implement Bayesian analyses (Gerbault et al. 2014; McElreath 2015). Computational techniques like Markov Chain Monte Carlo (MCMC) essentially simulate data for a range of plausible parameter values (priors) and compare the predicted data to the actual data. The emphasis is on models that are plausible candidates to actually explain the data. For some range of priors the predicted data are a more or less good fit to real data, giving plausible posteriors given the data. These methods are still computationally very demanding for all but models so simple they are likely to underfit the data. This has led to innovations in Approximate Bayesian Computational methods (ABC) that sample proposed parameter values rather than try to exhaustively compute all possible values of the posteriors. This is much like MCMC except that it is computationally much less demanding, at some cost in terms of the quality of posterior estimates. ABC methods are an active area of statistical research and, together with decreasing costs of computation, promise to put powerful new tools in the hands of practitioners. Already ABC methods have made important contributions to such archaeological topics as the evolution of dairying and adult lactase persistence (Gerbault et al. 2011) and to the study of plant and animal domestication (Gerbault et al. 2014). Other Bayesian methods have been applied by archaeologists to changes in facial form as a function of cultural practices (Katz et al. 2017).

A third important development is the creation of synthetic data-bases that can support more ambitious comparative and model fitting analysis. Some of these data are longstanding, such as Jorgenson’s (1980)
Western Indians ethnographic database, the Human Relations Area Files (Ember 1988). Others are more recent such as D-PLACE (Kirby et al. 2016), and the Pulotu Austronesian database (Watts et al. 2015). Such data can be analyzed in a comparative way using phylogenetic methods borrowed from biology (e.g., Bouckaert et al. 2012; Currie et al. 2010) and other statistical techniques (Mathew and Perreault 2015). A more ambitious approach is to reconstruct time series based on historical and archaeological data. Historians and archaeologists collectively have an enormous amount of data on evolution but it is reported in temporally short, geographically local segments. The trick to making this information usable is to join up the spatio-temporal segments to make a continuous record. One also wants to construct enough sequences to get a good representation of geographic variability. Such databases include Seshat (Turchin et al. 2017), and the Database of Religious History (Slingerland and Sullivan 2017). A rapidly growing accumulation of ancient DNA data that can help to track ancient population movements (Reich 2018). The Western North American archaeological record seems to me to be sufficiently complete to support the construction of such a database (Bettinger 2015; Schwitalla et al. 2014). Similarly, the Holocene archaeological record in Europe is sufficient to support quite sophisticated analyses (Shennan et al. 2015).

These three innovations promise to put evolutionary theory much more directly at the heart of the historical sciences generally, and archaeology particularly, than has heretofore been possible. The vision that our Cowboy articulated so clearly nearly 40 years ago (Bettinger 1980) is getting new sets of legs!

TEMPO AND MODE OF HUMAN EVOLUTION: THE PROPER ROLES OF GENES AND CULTURE

HUMAN NATURE VERSUS GENE-CULTURE COEVOLUTION

Much of evolutionary human science is based on the theory of genetic evolution. This approach was termed human sociobiology by E.O. Wilson (1978). It advances the idea that human nature is a real phenomenon based on the evolution of genes by natural selection. In this picture, culture and other systems of phenotypic pay a strictly subordinate proximal role in evolution (Richerson 2018). Wilson argued that the case for human nature rested on two (alleged) facts. First, that human evolution was predominately genetic throughout most of our evolutionary history. Second that genes laid down a detailed cognitive map early in development that then controlled phenotypic systems like learning and social learning via what he called “epigenetic rules.” On this account human evolution follows the dictates of the Modern Synthesis (Huxley 1942). The Modern Synthesis holds that the inheritance of acquired variation was Darwin’s greatest error. Yet culture is a system in which acquired variation is often inherited. What I learn for myself I can teach you. If culture plays any fundamental role in human evolution this bit of Modern Synthesis dogma would have to be relaxed, at least in the special case of humans. Ernst Mayr (1961) buttressed the Modern Synthesis with his famous argument that evolution (the ultimate cause) selected for adaptive proximate mechanisms (developmental circuits, physiology, neurobiology, learning mechanisms). Such proximate mechanisms only affect evolution via the genes that code for them according to his view. This picture of the evolutionary process has strong defenders today, even as it applies to humans (Dickins and Rahman 2012; Scott-Phillips et al. 2011).

Both legs of the empirical argument that Wilson made in 1978 have been subject to forceful critiques in recent years. The fundamental critique is that culture has played a leading role in the human adaptation via culture led gene-culture coevolution. Our most important biological adaptations, such as our long juvenile period, evolved to exploit the advantages of culture in a dynamic world (Bettinger 2009; Gintis
Archaeologists and paleoanthropologists have a large stake in this debate because these sciences provide important tests for gene dominant versus culture dominant hypotheses regarding human evolution. Since must cause must proceed effects, these historical sciences are our main source of information about when cultural events precede genetic ones and vice versa. Our recent ability to retrieve ancient DNA sequences has provided an important new tool to assess when genetic changes occurred, setting up more critical tests of the two hypotheses (Gerbault et al. 2011; Reich 2018; Sahle et al. 2018).

The stone tool record goes back to around the inception of our genus but likely before (Lewis and Harmand 2016). By Oldowan times (2.6-1.7 mya) intra- and inter-site variability in knapping practices suggest a fairly sophisticated adaptation to raw material variation. Some of this variation could represent varying cultural traditions (Roche et al. 2018). Comparisons of chimpanzee toolmaking with Oldowan tools suggest that early Oldowan knappers were considerably more adept. The reason is having hands that were specialized for the accurate, forceful blows necessary to knap stone efficiently (Toth and Schick 2009; Whiten et al. 2009). The australopithecine Paranthropus apparently used bone tools to excavate termite mounds (d’Errico and Backwell 2009). Good evidence suggests that Australopithecus afarensis used stone tools to access meat (McPheron et al. 2010). Stone tools are the earliest machine tools—tools that make other tools. It seems likely that early Homo had a fair repertoire of tools executed in perishable materials such as wood and hide. It is true that the final modernization of the human cultural adaptation is rather late in time (the last 40-200 krys) (Marean 2015; Will et al. 2019). This may be because ongoing increases in the high frequency climate variation were selecting for progressively more sophisticated cultural capacities in the Late Pleistocene (Richerson and Boyd 2013). It is harder to say how culturally transmitted social institutions were evolving. We do know that cultural evolution will be a greater advantage the more variation learners are exposed to. The important biased transmission forces work more strongly the more variation individuals can assess (Boyd and Richerson 1985). As human brains grew larger mothers would need more allomaternal support. Institutions of marriage and kinship were likely early socio-cultural innovations that both supported mothers and gave social learners access to more cultural variation (Burkart et al. 2009; Chapais 2008). Likely, social institutions existed deep in our lineage. Gintis’ (2016) argument that culture has played a pervasively leading role in human evolution is quite plausible. It requires much more work, including archaeological and paleoanthropological work, to be firmly established.

ARCHAEOLOGY VERSUS COGNITIVE INNATISM

One of archaeology’s greatest contributions to our understanding of human evolution is its increasingly detailed documentation of the pattern of human evolution over the last 50 krys (Flannery and Marcus 2012; Klein 2009). As Flannery and Marcus outline, this work documents several important features that theories of human evolution must be constrained to fit. First, the hunter-gathers of the NW European Upper Paleolithic, and similar traditions elsewhere, appear to have been innately capable of virtually all of the behavior that we think of as characterizing humans today. The dominant mode of evolution over this time period appears to have been cultural and culture led gene-culture coevolution (Laland et al. 2010; Ross and Richerson 2014). During the last ice age under a highly variable climate, humans remained hunter-gatherers, albeit sophisticated ones. As the climate stabilized after the sharp Younger Dryas cool arid period (12.9-11.7 cal ky BP) human populations underwent what amounts to a cultural adaptive radiation based on progressively intensifying exploitation of local subsistence resources, most commonly plant resources (Richerson et al. 2001). Societies also tended to become more complex during the Holocene. Complexity in turn tended to be accompanied by a greater or lesser degree of inequality. Any general theory of human evolution has to be consistent these patterns.
Evolutionary Psychologists developed a highly nativist hypothesis, deductively based on Modern Synthesis first principles, about the mode of human evolution under the rubric “massive modularity” (Frankenhuis and Ploeger 2007). The massive modularity hypothesis is similar in most respects to Wilson’s (1978) human nature hypothesis. It does have a much more conservative picture of genetic evolution. See Lumsden’s (2006) introductory essay in the 25 Anniversary edition of his book with Wilson. Barkow, Cosmides and Tooby (1992) imagined that cognition was a collection of hundreds or thousands of information rich, encapsulated, special purpose modules evolved to deal with the regularities of Pleistocene environments. Holocene humans thus inherited powerful innate adaptations for the Pleistocene that could not be expected to be adaptive to the Holocene due to the conservatism of organic evolution. Hence, they argued, it is fruitless to apply adaptationist reasoning to Holocene behavior. This line of reasoning is flatly inconsistent with the archaeological record of the last 50 ky. As sophisticated as last glacial hunter-gathers were, they were never very numerous. The Holocene adaptive radiation led to increasingly abundant populations. Humans were much more successful in the Holocene than in the Pleistocene. The deductive theory of conservative massive modularity is utterly inconsistent with the empirical discoveries of archaeology.

Robert Boyd’s and my intuition about what big brains, and the sophisticated cognition it supports, are for is diametrically opposite to the massive modularity hypothesis. Virtually the only regularity in the Pleistocene was the lack of regularity. In theory, a costly capacity for culture can be supported by large amounts of spatial or temporal variation. Spatial and especially temporal variation was abundant in the Pleistocene (Richerson et al. 2005). The limited temporal variation in the Holocene seems to have led to the locality specific pattern of subsistence intensification documented by archaeologists (Richerson et al. 2001). The massive modularity hypothesis takes cognitive adaptations to be similar to anatomically fixed adaptations like eyes. The cultural evolutionary hypothesis takes them to be similar to the adaptive immune system, largely an organ for phenotypic plasticity. Culture, in effect, puts phenotypic flexibility on steroids. It allows individuals to learn complex traits by teaching and imitation, traits that might incorporate the individual innovations of many ancestors (Boyd et al. 2011). The task of discovering just what is innate is quite difficult. Children are already extracting some information about their mother’s diet and language before they are born. After birth infants rapidly develop considerable social learning skills (Carey 2009). Of course, the mind is plausibly a mixture of innate modular elements and acquired skills, much as the immune system is divided into innate and acquired-adaptive components (Barrett 2015).

Recently, a Bayesian theory of development has been proposed in which inheritance systems like genes and culture transmit priors which are then subject to modification by data (Richerson 2018). The data collected by various systems of phenotypic flexibility such as individual learning and the immune system are integrated. Being sick is an aversive experience, for example. Updating is iterative throughout the entire lives of individuals. Current behavior need not necessarily carry much, if any, trace of the inherited priors that initiated its development. The cultural evolutionary hypothesis fits the archaeological data much better than the massive modularity hypothesis. This is not surprising given that theory started with the basic archaeological patterns as the things to explain!

**COGNITIVE NEUROSCIENCE FAVORS THE CULTURAL EVOLUTIONARY HYPOTHESIS**

Archaeologists may be interested in how the Evolutionary Psychologists’ massive modularity version of the human nature hypothesis as fared on its home turf of cognitive neuroscience. What does the accumulating evidence in that field suggest about the degree to which cognitive modules are built by
genes in evolutionary time versus by cultural transmission, learning and other components of
phenotypic flexibility during development? In the case of humans, I think it supports a rather radical
version of the cultural evolutionary hypothesis.

The story begins with the fate of Noam Chomsky’s Language Acquisition Device hypothesis. Chomsky
thought an innate LAD was necessary because he thought children receive far too little information of
the structure of their language from their caregivers to reconstruct its syntax. However, a careful
reanalysis of a corpus of mother-infant speech, much cited by linguistic innatists, showed that mothers
give a lot of linguistically informative feedback to kids, including about syntax (Moerk 1983). A recent
quantitative analysis of the information content of language estimates that syntax represents a tiny
fraction of the total, implying that syntax should be easy to learn compared, especially, to the lexicon
(Mollica and Piantadosi 2019). At one point Chomsky proposed a “principles and parameters” model of
syntax. Languages should have the innate principles of grammar in common and language differences
should stem from a few alternate parameters per principle (Pinker 1994). Some comparative linguists
tried hard to put empirical flesh on these bones and failed (Newmeyer 2004). The principles the
grammars of different languages used were too diverse. In the face of such evidence Chomsky himself
became a minimalist as regarding the innate features of language cognition (Fitch et al. 2005). Many
contemporary linguists subscribe to a highly cultural hypothesis of language acquisition and evolution
(Deutscher 2005; Everett 2012; Hurford 2011; Tomasello 2005).

Recently, cognitive neuroscientists have developed a model of how the brain develops that I think fits
quite comfortably with a radical cultural culture hypothesis. It goes back to an old ideas of Gerald
Edelman’s (1987) and Klaus Immelmann’s (Immelmann 1975). Edelman pointed to the astronomical
number of synapses in the brain of infant humans. The functional organization of the brain develops by
pruning these synapses after birth based on what he called “neuronal group selection.” Basically, it is
difficult to imagine how genes can specify the detailed synaptic organization of the neocortices of mammal
and bird brains, much less human neocortices. This must be accomplished by developmental processes.
Immelmann’s question was about the developmental process of imprinting. Why was the imprinting
mechanism so easily disrupted by environmental contingencies, as when Konrad Lorenz caused graylag
goslings to imprint on him? Immelmann suggested that it might be very hard for genes specify a detailed
picture of a graylag goose by arranging directly for the requisite synaptic pattern. But it could take
advantage of the early developing visual system to, as it were, take a picture of the first attentive animal
the gosling experienced and called that Mom. The system can be tricked by a mischievous ethologist but
works well enough in normal circumstances.

Several recent books and papers have modernized the Edelman/Immelmann argument based on new
findings in cognitive neuroscience (Anderson 2014; Colagé and d’Errico 2018; Ellis and Solms 2017;
Heyes 2018; Krubitzer and Stolzenberg 2014; Panksepp and Biven 2012; Striedter 2005). The neocortex
does seem to be largely an organ of phenotypic flexibility in which functional cognitive circuits are
organized and reshaped by experience during development. Cortical resources are organized into
functional circuits such that they typically make use of a number of cortical regions. Any given cortical
bit typically participates in a number of functional circuits. Thus, for much of the cortex, the
phenotypical picture of the brain as a collection of innately structured regions each devoted to a
particular cognitive function seems to be wrong. This makes sense energetically. Brain metabolic
overhead is high and it should be used as efficient as possible. Any given small bit of cortex should be
busy as often as possible in order minimize brain size and therefore its overall metabolic cost. Therefore,
nurons are extensively recycled from one cognitive task to the next as one goes about daily life.
The cortex has a number of powerful mechanisms for self-organization during development, most particularly associative learning (including reinforcement learning) and social learning. Reinforcement based learning is particularly important in connecting cognitive development adaptively to environmental contingencies. Reinforcement is generated by the emotional and appetitive circuits in the brain stem and adjacent structures. Eating when you are hungry is reinforcing. Pleasant social interactions when you are lonely likewise. Fear is unpleasant and tends to extinguish behavior that causes it. The emotional and appetitive circuits are ancient and highly conserved parts of vertebrate brains but they project extensively to the neocortex and receive projections from it. This mutual modulation means that the emotional circuitry can have a big impact on what is learned but also that what is learned can modulate the emotions and appetites. Thus, rather general reinforcement mechanisms can shape learning and cultural evolution but culture and individual learning can reshape reinforcement. For example, in many cultures, capsicum, the pain causing compound in red peppers, comes to be experienced as rewarding by most participants. This Bayesian neurobiological and cognitive picture of the neocortex as a highly flexible knowledge acquisition system guided by reinforcement matches neatly the adaptive analysis of culture as an adaptation to environmental variability (Baum 2017; Boyd and Richerson 1985; Boyd et al. 2011). The impact of reinforcement can be quite weak at the individual level but with accurate cultural transmission it can adaptively shape cultural traits over cultural evolutionary time. In essence, the “cognitive revolution” started by Chomsky’s (1959) critique of Skinner (1957) made an epic mistake. It opposed innate cognitive explanations to behaviorist ones based on reinforcement. The Bayesian proposal is that inherited priors are combined with new information in a principled way (Richerson 2018). Genetic (and cultural) priors and reinforcement based on environmental contingencies are equally important parts of systems of adaptive phenotypic flexibility.

WHAT ROLE DO GENES PLAY?

Genes contribute the emotional priors that generate the reinforcement the shape cognition in developmental time. Humans also make unusually heavy use of cultural priors. This generality of reinforcement mechanisms and their evolutionary conservatism might seem as if it would preclude species-specific adaptations. Massive modularity critics of “blank slate” arguments (Pinker 2002) depict reinforcement based theories as general purpose mechanism unable to deal with species-specific behavior. This is nonsense (Baum 2017)! There are plenty of ways for such behavior to arise via species specific reinforcing mechanisms. The emotional circuitry can be directly re-tuned by genetic and cultural evolution (Seelke et al. 2016). For example, humans form strong affiliative bonds with mates, family, and friends based on the modification of ancient emotional circuitry that generates mother-infant attachment (Chisholm et al. 2016). In many otherwise solitary mammals the only attachments that form are mother-infant, but in humans attachment has evolved to support a much wider social network. In the animal model of monogamous versus promiscuous voles, the neurobiological mechanisms generating the bonding of mates in the monogamous case are well understood (Stetzik et al. 2018). Similarly, anatomical and physiological adaptations will generate species specific patterns of reinforcement. Ungulates have a digestive system well adapted to fiber rich diets and eat fresh grass avidly. Humans might eat grass during a desperate famine but in normal times will not find it a reinforcing dietary item. Humans’ whole dietary system is adapted to more nutrient dense, lower fiber diets. Despite strong nutritional constraints, human diets are wondrously diverse. This variety is a major component of our Holocene cultural adaptive radiation. Our skeletal anatomy virtually guarantees that most of us will learn to walk on our hind legs, though certain rare deleterious mutations related to gait can cause people to learn to be (awkward) quadrupeds (Ozcelik et al. 2008).
In the case of human culture, reinforcement becomes important through what Boyd and I (1985) called decision-making forces. People can learn as individuals and they are selective imitators and teachers. Like natural selection, the choices that social learners and teachers make can be potent evolutionary forces in the long run even when they are weak at the individual level. For example, human hunters build up an impressive knowledge of the plants and animals they exploit (Blurton Jones and Konner 1976). Most animals are wary and cryptic when they are subject to human predation. Building up this knowledge is a non-trivial exercise in natural history. It depends on a collaborative, multi-generation, science-like exercise of observation and hypothesis testing (Liebenberg 1990).

AN EXTENDED EVOLUTIONARY SYNTHESIS?

Much of the current general critique of the Modern Synthesis has been articulated under the call for an Extended Evolutionary Synthesis (EES). Proponents of the EES argue that developmental systems play an active role in the evolutionary process. They violate the supposed firewall between proximate and ultimate causation (Gould 1980; Laland et al. 2011; Laland et al. 2015; Pigliucci 2007; West-Eberhard 2005). My favorite version of the general argument is Levis and Pfennig’s (2016) case for “plasticity first.” They observe that the many mechanisms of phenotypic flexibility are the first line of defense against environmental variation. But they are generally an expensive mode of adaptation and the adaptive phenotypes they generate may only be partially effective. Genes that lower the cost of phenotypic flexibility or improve the effectiveness of the phenotypic adaptation will “assimilate” to the acquired adaptation. Arguments along these lines go back to the Baldwin Effect in the late 19th century (Baldwin 1896).

Whatever the outcome of the general debate between proponents of the Modern Synthesis and the Extended Evolutionary Synthesis, human culture is an example of how a supposedly proximate mechanism can have major ultimate effects. Bettinger and Baumhoff’s (1982) paper on the Numic spread is a nice example. The Numic peoples of Eastern California evolved a plant intensive subsistence system a few hundred years ago. This system turned out to give them a competitive advantage over the hunting specialists that heretofore dominated the Great Basin. The three linguistic branches of the South-eastern Californian Numics rapidly radiated across the Great Basin due to this subsistence advantage. The hunting specialists couldn’t or didn’t adopt the Numic subsistence system by way of defense. This is a case of natural selection acting on cultural variation. If the criterion for an ultimate cause is natural selection acting on heritable variation, cultural evolution can be an unambiguous ultimate factor. This sort of pattern seems to be common, as Bettinger and Baumhoff remark. For example, the first farmers to spread into Europe extended a subsistence system pioneered in the Fertile Crescent westward across the subcontinent (Shennan 2018). In many parts of the world these subsistence strategies became based on domesticates, but in places like Western North America and Australia increasingly sophisticated hunter-gathers persisted until the European conquest. Arguably, the Holocene adaptive radiation of humans was set in motion when the cold, dry, temporally variable climates of the last glacial gave way to warmer, wetter, more stable Holocene climates (Richerson et al. 2001).

CULTURE LED GENE-CULTURE COEVOLUTION

Another way that culture can influence the evolutionary process is via culture led gene-culture coevolution. As the discussion on gene-based reinforcers above notes, genes certainly influence cultural evolution. But equally, culture can act as an evolutionary force on genes via culture led gene-culture coevolution (Laland et al. 2010; Richerson et al. 2010; Ross and Richerson 2014).
First, culture creates systems of institutionalized social selection that acts variation in behavior (Boehm 2012). Take psychopathy. The various subscales of psychopathy seem to be moderately to highly heritable (Dhanani et al. 2017). Psychopaths are highly disruptive to normal human social systems (Boddy 2014). As a consequence people take measures ranging from divorce and resignation from jobs to incarceration and execution to defend themselves from psychopaths. To the extent that these defenses are effective they are liable to limit the reproductive success of people who behave psychopathically. Hence they exert social selection against any genes correlated with psychopathic behavior. Our cooperative social projects can only exist if psychopathy is kept to a low frequency since they provide rich pickings for unscrupulous if not defended. On the other hand, those that conform to the rules benefit from successful social projects. Most likely, the evolution of egalitarian human social systems from the ancestral primate pattern of dominance structured societies owes to this process (Boehm, 2012).

Second, human technology substantially constructs the environments in which we live and such environments will exert selective forces on genes (Odling-Smee et al. 2003). The best worked out example is adult lactase persistence in some populations with a history of dairying. The analysis of milk fat residues on potsherds allows archaeologists to confidently attribute dairying to early Neolithic farmers in Western Europe (Roffet-Salque et al. 2017). Normally lactase production is down-regulated in mammals after weaning as there is no other source of lactose is the diet. In many early Western European dairying populations lactase persistence genes came under strong selection (Leonardi et al. 2012). The exact selective advantage of being able to digest lactose is debated. My own suspicion is the energy in lactose might have become a critical famine food. The hungriest time in famines is the spring and early summer in the temperate zone, and the rainy season in the tropics, while the new year’s staple crops are still unripe (Vaitla et al. 2009). But these seasons will be when grass has greened up and dairy stock will be producing maximum milk. Survival at such times might have been enhanced by the calories in lactose in persistent individuals. Many lactase non-persisters can become lactose tolerant. They were probably the majority in early farming populations. But by using bacteria to ferment lactose they would lose most of the calories in the sugar. Lactose contributes about 40% of the calories in milk, not insignificant if milk was a famine food. Archaeologists might be able test such hypotheses. For example, ancient DNA, together with paleopathology data might test whether lactase persisters show less signs of seasonal calorie deficiency.

CULTURAL GROUP SELECTION

One of the most radical culture driven gene-culture coevolution arguments is that group selection on cultural variation played a definitive role in shaping our innate social psychology, such as our lifelong enjoyment of social attachments (Boyd and Richerson 1982; Richerson et al. 2016; Richerson and Henrich 2012). This idea has roots in Darwin’s treatment of human evolution in the Descent of Man (Darwin 1874). He proposed that selection on the level of ancient tribes would have selected for prosocial emotions like sympathy and patriotism that in turn favored cultural rules to structure cooperation. Examples of cultural groups replacing other cultural groups are a staple of the archaeological record as exemplified by the Numic expansion into the Great Basin. Two principal legs of the human adaptive system are our ability to cumulatively evolve (1) complex technology and (2) complex forms of social organization that involve substantial cooperation between non-relatives. Neither of these features are as well-developed in any other vertebrate species. The Numic expansion seems to be an example of the latter. The success of the Numic peoples in the Great Basin involved a reorganization of the division of labor to emphasize women’s economic roles (Bettinger and Baumhoff 1982).
Our social systems are underpinned by institutions, rules that structure societies into social roles and prescribe the behaviors appropriate to each role. Institutions of marriage and kinship are much studied examples. Much evidence supports the hypothesis that institutions vary from society to society (and sub-society to sub-society), that societies and sub-societies often compete, and that these institutional differences are often consequential in such competition. Thus, cultural group selection exemplifies the Darwin's basic syllogism for the operation of natural selection (Richerson et al. 2016). Although the paleoanthropological details are distressingly incomplete, by the latest Pleistocene human technology and social organization seem generally equivalent to that of ethnographic hunter-gatherers in sophistication. One might imagine that institutionalized cooperation is quite ancient. Australopithecines and early Homo would seem to have been more exposed to predation than their arboreal ancestors by virtue of being terrestrial pedestrians. Yet early Homo, at least, had access to hunted or scavenged carcasses. Perhaps the Early Pleistocene terrestrial hominins evolved rather large-scale cooperative strategies to collectively defend themselves and aggressively contest carcasses. Reno et al. (2003) present data suggesting that sex dimorphism is Australopithecus afarensis was similar to that of modern humans. This suggests that male conflicts over mates were modest and that A. afarensis could have been rather cooperative. A mob of australopithecines armed with stones to throw and basic wood or bone clubs would be a formidable force if they were prepared to cooperate.

The radical phenotypic flexibility/culture hypothesis thus holds that the whole trajectory of human evolution was organized by an increasing specialization for evolving and deploying cultural adaptations. Our hands evolved to make and use tools, our bipedalism freed our hands and an gave us a low-cost gait effective for hunting and gathering, our emotions evolved to support institutionalized social systems, and our brain evolved to support the acquisition and use of complex technological and social behaviors. It is sometimes said that human evolution is a case of humans domesticating themselves. The competing human nature hypothesis has faltered in the face of the evidence, some old, some new. Paleoanthropologists and archaeologists have produced the data on which this hypothesis rests and will be instrumental in refining and testing it.

MICROEVOLUTION AND MACROEVOLUTION

DEFINITION

Microevolution is the genetic or cultural change that occurs on time scales short enough to be observed directly in the field or subject to experiments in the lab. Some classic biological studies continue for a goodly number of generations, for example Peter and Rosemary Grant’s (2002) 30 year study of the evolution of Darwin’s finches on the Galapagos. Cultural evolution is sometimes very fast. Miu et al. (2018) studied cumulative cultural evolution in computer tournaments with horizontal transmission of code that spanned a week. Macroevolution is evolution that occurs on long time scales typically observed by paleontologists, archaeologists and historians. In favorable circumstances, historical scientists can produce a quite high resolution record, but generally the data are incomplete in various ways that demand theory for their interpretation.

ARCHAEOLOGY AND MICROEVOLUTION VERSUS MICROEVOLUTION

Archaeologists can sometimes make use of microevolutionary theory to interpret patterns in the archaeological record (Bettinger and Eerkens 1997; Bettinger and Eerkens 1999; Eerkens et al. 2006;
Eerkens and Lipo 2007). High resolution archaeological records can support sophisticated model fitting exercises to understand particular microevolutionary trajectories (Itan et al. 2009). However, it seems to me that the most important evolutionary questions for archaeologists and other historical scientists are the macroevolutionary ones. Increasingly high resolution records are becoming available (Bevan et al. 2017; Shennan et al. 2013) together with the already mentioned improved methods to analyze that data. Microevolution can be studied by direct observation and experiment, but only historical scientists have the data to address macroevolutionary questions. Experimental macroevolutionary studies of microbes are an interesting exception (Lenski and Travisano 1994).

WHY MACROEVOLUTION IS AN INTERESTING AND IMPORTANT PROBLEM

It might be thought one could straightforwardly extrapolate microevolutionary processes to the longer time scales of macroevolution. Theory derived from microevolutionary studies would be the theory of macroevolution. For several reasons, things are not so simple.

First, both genetic and cultural evolutionary rates are time scale dependent (Gingerich 2009; Perreault 2012). On short time scales evolution looks fast, but at long time scales it looks much slower. It is as if, on the short time scale, strong selective forces move gene and cultural trait frequencies at quite high rates but more or less at random. On longer time scales, short term noise mostly averages out. The longer term mean of selective forces changes much more slowly than short term rates would suggest. In the Grants’ (2002) study alternations of drought and rain drove the evolution of finch beaks quite rapidly, but the mean climate change is probably considerably slower, resulting in much microevolution being a back-and-forth responses to short term variation. Only a small amount of the noisy back-and-forth contributes to long term change However, slow as it is, macroevolutionary processes generate the large-scale trends and novelties that we are most curious about. Why did our hyper-cultural species evolve in the Pleistocene instead of some other species in some other geological era? Why did agricultural systems evolve in the Holocene but not in previous interglacials? Why did human populations and cultural complexity explode in the last half millennium instead of earlier in the Holocene? Archaeology (and paleontology) are popular evolutionary sciences with the general public because they deal with the most interesting and most important evolutionary events.

Second, environmental variation is also scale dependent. There is generally more variation in environmental time series at low frequencies (long time scales) than at high frequencies (short time scales). This pattern is often called “red noise” (Whitehead and Richerson 2009). We are all familiar with the concept of white noise, a variance pattern with equal variance at all frequencies. Red noise is a variance pattern with disproportionate variance at low frequencies, producing a low roar rather than the bland hum of white noise if converted to sound (https://en.wikipedia/wiki/colors_of_noise). One way to think of red noise is that, on average, the more distantly separated two points are in time, the more different they will be. This seems to be true out to the lowest frequencies we can observe on earth (Ward and Kirschvink 2015). The earth’s climate varies between high CO₂-low O₂ hothouse conditions and low CO₂-high O₂ icehouse conditions on time scales of hundreds of millions of years. To the extent that genetic and cultural evolution is a response to environmental variation, the most interesting evolution will be macroevolution in response to the low frequency part of the environmental variation.

Third, evolution, as we have seen in the case of cultural evolution, cannot necessarily be boiled down to natural selection acting on genes to create adaptations. Gould and Eldredge (1977) famously argued that macroevolution was driven by species selection not by selection on genes within species. Microevolution creates species, essentially at random, and these species competed to be represented in
future ecological communities. This is strikingly similar to the ecologists’ old idea of primary succession
in which potentially invading species do or do not succeed in entering an ecological community as the
environment changes, while current members of the community persist or exit. Often successional
change is faster than Darwinian change. When environments change, local populations will experience
selection but also competitive pressure from species already well adapted to the new environment. An
ill-adapted species may often be competitively excluded before selection can adapt its genes to the new
environment. Daniel Axelrod’s (1973) studies of fossil plants in Western North America found that the
larger woody species changed very little morphologically in the last 100 MY. However, as climates and
topography changed ecological communities changed by succession. For example, as California’s climate
acquired its summer-dry Mediterranean climate, drought tolerant oaks moved north from the semi-arid
mountains of Northern Mexico while trees needing summer water, like coast redwoods, retreated to a
narrow coastal belt where fog drip was sufficient to furnish summer water. Similarly, the end of the last
ice age caused a massive reorganization of the world’s biomes as plants and animals expanded and
contracted their ranges following the dramatic climate change. For example, Tundra, Boreal Forest, and
Temperate Deciduous Forest largely replaced the former Mammoth Steppe biome (Guthrie 2001).
Because the biological sub-disciplines of ecology, evolution and paleontology have historically had
modest interactions, macroevolutionary theory is still relatively undeveloped (Grether et al. 2017). Aside
from simple linear responses to environmental drivers, biotic interactions in ecological communities are
highly non-linear and give rise to complex dynamics that can include long term out-of-equilibrium
transients (Hastings et al. 2018). Just because an ecosystem doesn’t change for appreciable periods
doesn’t necessarily mean that it is at a stable equilibrium.

Fourth, evolving systems are subject to factors internal to the evolutionary process as well as to the
external environment. The influences of the external environment are plain to see. For example, the last
65 MY have witnessed an irregular but persistent cooling and drying trend in the earth’s climates
accompanied by increasing variability (Zachos et al. 2001). Savannas, steppes, and deserts expanded at
the expense of forests and former forest browsers like horses evolved lineages specialized for eating
productive but abrasive grasses. Brain size increased as spatial and temporal environmental variability
increased (Jerison 1973) in line with the hypothesis that brains are mainly organs designed for
phenotypic plasticity.

The processes internal to the evolutionary systems we study are also important. Evolutionary processes
act by “descent with modification,” modifying existing phenotypes. Thus, “preadaptations” are often
important. Australopithecines had relatively large ape brains, free hands, binocular vision, and were
probably fairly to highly social. These traits could be readapted, “exapted” as some say, to the human
adaptation based on culturally acquired technology and social institutions (Neco and Richerson 2011).
While many browsing herbivores adapted to grazing niches, the human lineage has not faced
competition from other lineages converging on our hyper-cultural adaptation. It is true that many
species use cultural transmission to adapt to variable environments and these could be parallel
adaptations to the same increases in climate variation that influenced our evolution (Jesmer et al. 2018;
Laland 2017; Whitehead and Rendell 2015; Whiten et al. 2016). Were essential preadaptations
somehow more fortuitous in our lineage or was it just that our increasing cultural sophistication
crowded out other potential entrants into highly culture-dependent niches?

Another kind of internalist argument supposes that human evolution was dependent on a key, or
several key, breakthroughs. For example, Washburn (1959) argued that the evolution of upright posture
in our lineage set off a positive feedback cycle in which free hands allowed us to make primitive tools
and larger brains evolved to make better tools. Subsequently a number of such key innovations
arguments have been proposed (Hrdy 2009; Tomasello 2014; Wrangham 2009). For example Richard Klein (2000) proposes that a mutation occurring about 50 kya in the Anatomically Modern Human lineage led to the final modernization of our lineage's behavior. The evolutionary scenario these authors seem to imagine is one in which the external environment is constant and the pace of human evolution has been regulated by the appearance of mutations or other forms of innovation. There is no doubt that these proposals point to important components of the human adaptive complex. We would a very different species if we had failed to evolve cooperative breeding, cooking, joint attention, and artistic expression.

I think the right questions to ask are: what is the rate limiting step in an evolutionary sequence, and on what time scale? Evolutionary processes can be fairly fast, particularly cultural evolutionary processes, but they are not instantaneous. Even phenotypic adaptations take some time to develop. The immune system often gets ahead of attacking microbes and saves our lives. But it often doesn’t, so immunization was a medical miracle. So, at short time scales internal factors limit the rate of response to selective processes. At long time scales, external environmental change is clearly important, as the examples given above show.

The empirical and theoretical investigation of rates evolution has a long history (Walker and Valentine 1984). In the case of cultural evolution see (Diamond 1997; Perreault 2012). One question analysts have asked is how many empty niches exist at any given time. The more empty niches, the more evolution is out of equilibrium with the prevailing environment and presumably the more important are internal processes in regulating the rate of evolution. Walker and Valentine estimated that perhaps 30% of marine invertebrate niches were empty based on a model in which species origin rates and extinction rates were both dependent on standing diversity. However, their model, and many others like it, did not attempt to relate origin and extinction rates to environmental change. Thus, if extinctions are just chance events unrelated to environmental change, the internal constraints necessary to result in 30% of niches being empty would seem to be considerable. On the other hand, if these niches are being actively emptied by ongoing environmental change, a more externalist picture of the 30% figure would be warranted. A more convincing case for the importance of internal factors and the time scale over which they might operate is the case of recoveries from mass extinctions. Aloy (2008) used a high quality paleontological database to look at recoveries from near-instantaneous mass extinction events. His analysis suggests that recovery from such events takes on the order of tens of millions of years, again suggesting that internal constraints are important. However environmental change in the aftermath of the extinction were not taken into account. Perhaps environmental recovery after a mass extinction is slow or ongoing background environmental change slows the approach to a diversity equilibrium.

Biologists have begun to use Bayesian MCMC methods to extract estimates of evolutionary rates from phylogenetic trees (Rabosky 2014). These sorts of studies need to incorporate data on environmental change in order to estimate adaptive lags. We know from the aforementioned studies of Adult Lactase Persistence that genetic evolution in culturally novel environments can be quite rapid (Leonardi et al. 2012). However ALP is based on one gene with high penetrance and the simplicity of the trait is perhaps atypically conducive to rapid evolution.

In the case of cultural evolution, the Pleistocene-Holocene transition is an interesting natural-experimental case. The transition was quite abrupt and rather shortly led to people focusing more heavily on plant resources in many places around the world. It was as if the world 11,000 years ago was suddenly rich in empty niches for humans (Richerson et al. 2001). Surprisingly, estimates of long term population growth rates of early farmers in Western Eurasia and Holocene hunter-gathers in North America both come in at about 0.05% per year. Hunter-gatherers innovating more plant intensive
foraging techniques seemingly could grow at the same rate as farmers innovating new domesticates and
new techniques for processing them, at least for a prolonged period (Zahid et al. 2016). Bettinger and
Baumhoff’s (1982) study of the Numic spread and Bettinger’s (2015) study of subsistence and political
evolution in Western North America postulates a macroevolutionary pattern of cumulative cultural
innovations that among other things drive population expansions as a result of those innovations.
Patterns of violence (Schwitalla et al. 2014), direct evidence on subsistence (Wohlgemuth 2010), ancient
DNA (Raff et al. 2011), and population movements inferred from language distributions (Shaul 2014)
paint generically similar pictures. This suggests that internal constraints were important even to cultural
evolution on the time scale at least 11 millennia. This contrasts with Alroy’s (2008) ten million year time
scale for biotic recovery in the face of mass extinctions. The internal constraints on cultural evolution
would seem to be much weaker than those on genetic evolution, if still appreciable.

Evolutionary Psychologists have suggested that individual level “improvisational intelligence” obviates
the need for cultural evolution in explaining human adaptive diversification (Cosmides and Tooby 2001;
Pinker 2010). If so, internal constraints on would be very weak or non-existent. But eleven millennia of
progressive change in subsistence documented by archaeologists are apparently not consistent with
such a strong version of improvisational intelligence. A weaker form of improvisational intelligence
combined with cultural evolution probably explains why cultural evolution is so much faster than organic
evolution yet has millennial scale lags (Boyd and Richerson 1985).

Contrary to the cultural evolution explanation, Douglas Kennett (2005) tells the cultural history of the
Channel Islands Chumash entirely using theory from human behavioral ecology and climate change
providing a completely external interpretation of post-Pleistocene events there. A relatively invariant
climate notwithstanding, the Holocene is not without progressive environmental change. Such change
could conceivably account for some, if not much, of the progressive change in subsistence systems. High
sea levels have led estuaries to silt up and coastlines to retreat. River flood plains have enlarged and
soils have weathered (Bull 1991). Many geomorphic processes have been so much accelerated by
human activity in the Holocene that some want to call all or part of it the Anthropocene. Conceivably,
subsistence evolution in the Anthropocene has been mainly a pattern progressive niche construction in
which many environmental effects have been internalized (Ellis et al. 2013). Sorting out the roles in
external and internal factors in cultural (and genetic) macroevolution will clearly require new models,
the new approach to model fitting to data, and the better sets of data that I have briefly described here.
The work of archaeologists will of course be critical to theory building and theory testing in this
endeavor.

SUMMARY AND CONCLUSIONS

Our Cowboy articulated the importance of theory to archaeology at the beginning of his career, and has
practiced what he preached to this day. He has also contributed to building the kind of databases in
California, the Great Basin, and Northwestern China to which theory can be fruitfully applied. Over the
last 40 years we have learned how to be more humble about the complexity of systems such as even
small-scale human societies interacting in a complex and dynamic landscape. This humility has led to the
development of more powerful model fitting and hypothesis testing strategies.

At the same time, evolutionary theory has grown more sophisticated. Cultural evolutionary theory has
grown from a handful of provocative ideas to a major enterprise. Application of these ideas to empirical
cases has likewise grown. We are beginning to be able to place human cultural and genetic evolution into a paleoclimatological and paleoecological frame. We are beginning to see how genes, culture, and other mechanisms of phenotypic flexibility are integrated into complex adaptive systems.

To my way of thinking, sorting out the macroevolutionary roles of external environmental push and pull factors, versus internal opportunities and constraints, is the biggest issue in the historical sciences generally. The internalization of environmental factors via niche construction is potentially a very important phenomenon (Odling-Smee et al. 2003). George Gaylord Simpson’s (1944) *Tempo and Mode in Evolution* was the main paleontological contribution to the Modern Synthesis. In it Simpson argued that a straightforward extrapolation of the then standard microevolutionary theory developed the other architects of the synthesis was a sound basis for understanding paleontology. As we have seen, this idea has lately become controversial. So there remains a major macroevolutionary project to accomplish. Archaeologists have played and will continue to play a major role in the human part of it, particularly the cultural evolutionary and gene-culture coevolution parts of the problem. They have already developed impressive data with enough resolution to fit models to it. Exciting new sources of data like ancient DNA are starting to have an impact.

The younger readers of this book will note that your elders have left you more problems than neatly solved puzzles. We have done our best to leave tools in your hands that make you smarter than we are. Certainly, the vast majority of the progress in the field of cultural evolution over the last quarter century has been has been at the hands of younger scientists (Henrich 2016; Mesoudi 2011)! It looks like a recipe for a lot of fun for you-all!

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Whiten, Andrew, Christine A. Caldwell, and Alex Mesoudi


Whiten, Andrew, Kathy Schick, and Nicholas Toth


Will, Manuel, Nicholas J. Conard, and Christian A. Tyron


Wilson, Edward O.


Wohlgemuth, Eric


Wrangham, Richard


Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups


Zahid, H. Jabran, Erick Robinson, and Robert L. Kelly