

Towards a unified science of cultural evolution

Alex Mesoudi

Centre for Social Learning and Cognitive Evolution and School of Psychology, University of St. Andrews, St. Andrews, Fife KY16 9JP, Scotland, United Kingdom; and Department of Anthropology, University of Missouri – Columbia, Columbia, MO 65211; and W. Maurice Young Centre for Applied Ethics, University of British Columbia, Vancouver, British Columbia V6T 1Z2, Canada.
MesoudiA@missouri.edu **www.missouri.edu/~mesoudia/**

Andrew Whiten

Centre for Social Learning and Cognitive Evolution and School of Psychology, University of St. Andrews, St. Andrews, Fife KY16 9JP, Scotland, United Kingdom.
aw2@st-and.ac.uk **www.st-and.ac.uk/~aw2/**

Kevin N. Laland

Centre for Social Learning and Cognitive Evolution and School of Biology, University of St. Andrews, St. Andrews, Fife KY16 9TS, Scotland, United Kingdom.
knl1@st-and.ac.uk **www.st-andrews.ac.uk/~seal**

Abstract: We suggest that human culture exhibits key Darwinian evolutionary properties, and argue that the structure of a science of cultural evolution should share fundamental features with the structure of the science of biological evolution. This latter claim is tested by outlining the methods and approaches employed by the principal subdisciplines of evolutionary biology and assessing whether there is an existing or potential corresponding approach to the study of cultural evolution. Existing approaches within anthropology and archaeology demonstrate a good match with the macroevolutionary methods of systematics, paleobiology, and biogeography, whereas mathematical models derived from population genetics have been successfully developed to study cultural microevolution. Much potential exists for experimental simulations and field studies of cultural microevolution, where there are opportunities to borrow further methods and hypotheses from biology. Potential also exists for the cultural equivalent of molecular genetics in “social cognitive neuroscience,” although many fundamental issues have yet to be resolved. It is argued that studying culture within a unifying evolutionary framework has the potential to integrate a number of separate disciplines within the social sciences.

Keywords: cultural anthropology; cultural evolution; cultural transmission; culture; evolution; evolutionary archaeology; evolutionary biology; gene-culture coevolution; memes; social learning.

1. Introduction

Parallels or analogies between biological and cultural evolution have been noted by a number of eminent figures from diverse fields of study (e.g., Darwin 1871/2003; Dawkins 1976; Dennett 1995; Dobzhansky et al. 1977; Hull 1982; Huxley 1955; James 1880; Medawar 1982; Popper 1979; Skinner 1981), and in the last few years a burgeoning literature exploring this relationship has emerged (e.g., Aunger 2000b; 2002; Blackmore 1999; Boyd & Richerson 2005; Danchin et al. 2004; Mace & Holden 2005; Mesoudi et al. 2004; Mufwene 2001; Pagel & Mace 2004; Plotkin 2002b; Richerson & Boyd 2005; Runciman 2005; Shennan 2002; Wheeler et al. 2002; Ziman 2000).

The implication of this growing body of theory is that culture exhibits key Darwinian evolutionary properties. If this is accepted, it follows that the same tools, methods, and approaches that are used to study biological evolution may productively be applied to the study of

human culture, and furthermore, that the structure of a science of cultural evolution should broadly resemble the structure of evolutionary biology. In the present paper we attempt to make this comparison explicit, by examining the different approaches and methods used by evolutionary biologists and assessing whether there is an existing corresponding approach or method in the study of cultural evolution. Where such an existing correspondence is not found, we explore whether there is the potential to develop one. We also explore potential differences between biological and cultural evolution.

The purpose of this comparison is primarily to stimulate a more progressive and rigorous science of culture. Although evolutionary biology has become enormously productive since Darwin’s theory of evolution was formulated, the discipline that professes to be most directly engaged in the study of culture – cultural or social anthropology – has been much less demonstratively productive over the course of the same time period, particularly in terms of establishing a secure body of data and theory

that earns and deserves the attention of researchers working in sister disciplines. This is increasingly acknowledged by many of its own practitioners (e.g., Bennett 1999; Bloch 2000; Kuper 1999). For example, in a recent review of the history of anthropology, Bennett (1999) states that “the cultural side of the discipline tends to smother its data with personal and arcane theorizing” (p. 951), while another anthropologist, Bloch (2000), states that cultural anthropology “with time, has become theoretically more and more vague, pretentious and epistemologically untenable” (p. 202).

Why has biology been so much more successful than anthropology and many related fields of social science during the past 150 years? We do not believe that biologists are on average more able than researchers who have traditionally studied culture, nor is biology significantly easier to study than culture. Rather, we suspect that two factors are of particular importance. First is the relative willingness of biologists to make simplifying assumptions and use what may be comparatively crude but workable methods, in order to make complex systems tractable and contribute to the steady accumulation of reliable knowledge that will ultimately form the basis of a sophisticated understanding of the phenomena in question. Although many social scientists frequently

object that human culture is too complex to be amenable to such simplifying assumptions and methods, the relative success of biologists in studying enormously complex biological systems renders such objections open to question.

Second, and particularly relevant to this article, the theory of evolution encompasses and integrates a multitude of diverse subdisciplines within biology, from behavioural ecology to paleobiology to genetics, with each subdiscipline stimulating and contributing to several others (see Mayr [1982] for further details of this “evolutionary synthesis”). The social sciences, in contrast, have no such general synthesising framework, and the greater part of disciplines such as cultural anthropology, archaeology, psychology, economics, sociology, and history remain relatively insular and isolated, both from each other and from the biological and physical sciences. Adopting an evolutionary framework can potentially serve to highlight how these disciplines are, in fact, studying complementary aspects of the same problems, and emphasise how multiple and multidisciplinary approaches to these problems are not only possible but necessary for their full exposition. At present, many of the individual studies considered below are the result of independent developments at the fringes of separate fields of study. Placing these disparate studies side-by-side within a broader evolutionary framework, as is done here, will, we hope, contribute towards creating a coherent unified movement and bring evolutionary analyses of cultural phenomena into the mainstream.

An evolutionary framework also brings with it a set of proven methods that have rich potential within the study of culture. We note below a number of cases in which methods developed within evolutionary biology have been adapted for use in the study of culture, such as phylogenetic analyses or population genetic models. As we shall see, several of these evolutionary methods have already contributed to significant advances over more traditional non-evolutionary methods.

The left side of Figure 1 illustrates the overall structure of evolutionary biology, as described by Futuyma (1998, pp. 12–14) in what is, perhaps, the most widely used undergraduate textbook in the field. The study of biological *macroevolution* deals with change at or above the species level, whereas biological *microevolution* concerns changes within populations of a single species. The former comprises systematics, paleobiology, and biogeography, whereas the latter involves population genetics (theoretical, experimental, and field-based), evolutionary ecology, and molecular genetics. In sections 2 and 3, we examine each of the subdisciplines of evolutionary biology in turn, first outlining their general methods and then briefly describing examples of recent studies to illustrate how those methods are applied and the kind of results they yield. This is followed in each case by a discussion of existing analogous or equivalent methods within the social sciences regarding human culture, again describing recent key studies. These cultural disciplines, and the way in which they map onto the structure of evolutionary biology, are illustrated on the right side of Figure 1.

Although there may be no obvious precedent for two distinct fields to exhibit the same internal structure, the similarity of underlying processes (Mesoudi et al. 2004) leads us to expect a correspondence. We believe that this mapping will (1) help make sense of actual

ALEX MESOUDI is a Postdoctoral Fellow at the University of British Columbia. He was educated at University College, London (B.Sc. in Psychology) and the University of Liverpool (M.Sc. in Evolutionary Psychology) before recently completing his Ph.D. in Psychology at the University of St. Andrews. His research interests include the experimental study of human cultural transmission and evolutionary approaches to human culture. Previously published articles include “Is human cultural evolution Darwinian? Evidence reviewed from the perspective of *The Origin of Species*” in the journal *Evolution*. He recently has been conducting experimental simulations of changes in the archaeological record in collaboration with evolutionary archaeologist Michael O’Brien.

ANDREW WHITEN, a Fellow of the Royal Society of Edinburgh and the British Academy, is Professor of Evolutionary and Developmental Psychology and Wardlaw Professor of Psychology at the University of St. Andrews. He is the Coordinator of the recently established Centre for Social Learning and Cognitive Evolution. Numerous publications on social learning, traditions and culture in human and nonhuman primates include, most recently “The second inheritance system of chimpanzees and humans” (*Nature*, 2005).

KEVIN N. LALAND is Professor of Biology at the University of St. Andrews, where he heads the Social Evolution and Learning Group and is a core member of the Centre for Social Learning and Cognitive Evolution. Laland has previously held BBSRC and Human Frontier Science Program postdoctoral fellowships and a Royal Society University Research Fellowship. His research focuses on animal behaviour and evolution, incorporating experimental studies of fish, birds and primates and a variety of theoretical methods. He has written five books and more than 100 scientific articles, largely on the topics of animal social learning, gene-culture co-evolution and niche construction.

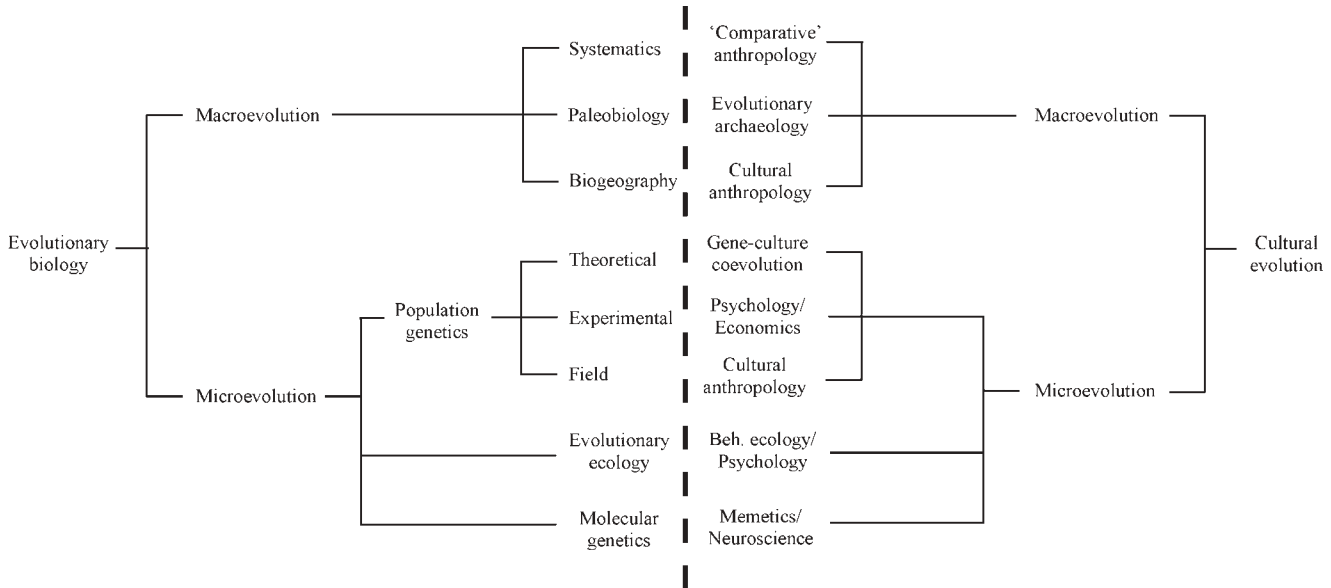


Figure 1. Major subdivisions within evolutionary biology (left side; after Futuyma 1998) and corresponding disciplines currently or potentially employed in the study of cultural evolution (right side).

developments in the study of cultural evolution; (2) suggest new research programmes and hypotheses; and (3) help identify the most promising research strategies.

It is important first to define “culture” explicitly and to specify the precise theory of cultural evolution that we are advocating. Following Richerson and Boyd (2005), we define *culture* as “information capable of affecting individuals’ behaviour that they acquire from other members of their species through teaching, imitation, and other forms of social transmission” (p. 5). “Information” is employed as a broad term incorporating ideas, knowledge, beliefs, values, skills, and attitudes. *Cultural evolution* is characterised as a Darwinian process comprising the selective retention of favourable culturally transmitted variants, as well as a variety of non-selective processes, such as drift (Boyd & Richerson 1985; Cavalli-Sforza & Feldman 1981). This contrasts with the progressive, unilinear theories of “cultural evolution” (e.g., Tylor 1871), in which human societies were seen as progressing through a fixed set of stages, from “savagery” through “barbarism” to “civilisation.” This erroneous view of evolution drew more from Spencer than Darwin, and such flawed evolutionary ideas persisted within anthropology until the mid-twentieth century (e.g., Steward 1955; White 1959). The development of a genuinely Darwinian theory of cultural evolution remained in its infancy (e.g., Campbell 1960) until the pioneering works of Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985). These researchers not only provided a rich theoretical groundwork for analysing culture in terms of modern evolutionary theory, but also developed rigorous mathematical treatments of cultural change inspired by population genetic models (see Richerson & Boyd 2005 for an accessible account of this work).

We also emphasise that the theory of cultural evolution is distinct from the field of *evolutionary psychology* (e.g., Barkow et al. 1992; Pinker 1997), which deals with *biologically* evolved features of the human mind shaped by genetic rather than cultural inheritance. Evolutionary

psychology therefore more accurately belongs on the left side of Figure 1 (although it is not shown) and should be distinguished from the separate cultural inheritance system outlined on the right side. Although some evolutionary psychologists tend to downplay the role of transmitted culture (e.g., Tooby & Cosmides 1992, pp. 115–117), there is ample evidence that culture plays a powerful causal role in determining human behaviour and cognition (Richerson & Boyd 2005; Tomasello 1999). Of course, biologically evolved features of cognition do affect cultural processes in important ways, as emphasised by gene-culture co-evolutionists (e.g., Durham 1992b). This interaction is discussed further in section 3.4.2.

To illustrate the Darwinian nature of a modern evolutionary theory of culture, and build an empirical case for such a theory, Mesoudi et al. (2004) explicitly compared the empirical evidence for biological evolution presented by Charles Darwin in *The Origin of Species* (1859/1968) with present-day evidence from the social sciences regarding human culture. In *The Origin of Species*, Darwin presented meticulous evidence for *variation* in the characteristics of individuals within a species, for the *selection* (natural or artificial) of individuals possessing certain characteristics, and for the *inheritance* of those selected characteristics to the next generation. Mesoudi et al. (2004) collated equivalent evidence that culture similarly exhibits these key properties. For instance, there is evidence for considerable *variation* in terms of the diversity of cultural knowledge, beliefs, and artifacts, as illustrated by the 4.7 million patents issued in the United States since 1790 (Basalla 1988) and the 6,800 languages spoken world wide (Grimes 2002). Cultural *selection* occurs as a result of competition for limited attention, memory, and expression. For example, psychologists have demonstrated interference in the recall of similar (competing) words (Baddeley 1990), and archaeologists have tracked increasing frequencies of one artifact and the corresponding decreasing frequencies of competing artifacts (O’Brien & Lyman 2000). The *inheritance* of

successful cultural traits has been demonstrated in numerous studies of the transmission of skills and beliefs in traditional societies (e.g., Cavalli-Sforza, Feldman, Chen & Dornbusch 1982; Hewlett & Cavalli-Sforza 1986) and in studies of social learning in children (e.g., Bandura 1977; Whiten et al. 1996).

These three basic characteristics (variation, selection, and inheritance) generate a number of other phenomena observed by Darwin in biological evolution and which are also evident in human culture (Mesoudi et al. 2004). Cultural traits go *extinct* as a result of competition, as occurred with the gun in Japan (Perrin 1979) and with bone tools in Tasmania (Diamond 1978). Basalla (1988) amassed extensive historical evidence for the gradual *accumulation of modifications* through time, such as Joseph Henry's 1831 electric motor, which borrowed many features from the steam engine, or Eli Whitney's 1793 cotton gin, which was based on a long line of Indian devices. Cultural traits can be said to *adapt* to their environment, as demonstrated by the work of human behavioural ecologists (Smith & Winterhalder 1992). Evolutionary principles can account for the *geographical distribution* of cultural variation, such as the diffusion or descent of various traits in African societies (e.g., Hewlett, De Silvestri & Guglielmino 2002). Culture exhibits the *convergent evolution* of similar forms in unrelated lineages, such as the tendency for both teddy bears (Hinde & Barden 1985) and cartoon characters (Gould 1980) to become increasingly neotenous over the course of time. Finally, cultural traits *change in function* or become *vestigial*, as documented by Basalla (1988) for numerous technological artifacts, such as the no longer optimal QWERTY keyboard layout of Edison's gramophone, which was originally used for dictation. A more detailed account of the case for cultural evolution can be found in Mesoudi et al. (2004) and Richerson and Boyd (2005). Finally, Mesoudi et al. (2004) noted that, just as Darwin formulated his theory of evolution with little understanding of genes or Mendelian inheritance, a theory of cultural evolution likewise does not necessarily have to rest on the existence of memes or particulate cultural transmission, a topical issue but one of great contention (Henrich & Boyd 2002; Aunger 2000b).

This last point highlights the fact that, although there are many fundamental similarities between biological and cultural change, the two processes are certainly not identical, and biological methods and models cannot and should not be unthinkingly applied to cultural phenomena without careful consideration of any potential differences (Plotkin 2002b). On the other hand, critics (e.g., Bloch 2000; Gould 1991; Pinker 1997) commonly reject outright any evolutionary analysis of culture by appealing to putative differences that are frequently illusory or unfounded. In the following sections and in section 4 we assess the validity of each of these potential differences and their implications for a science of cultural evolution.

2. Macroevolution

This section sketches the principle approaches to macroevolution adopted by biologists, namely systematics, paleobiology, and biogeography, and considers corresponding approaches in the study of cultural evolution.

2.1. Systematics

2.1.1. Biology. *Systematics* is the study of the diversity of organisms and of the relationships between them. Modern systematists adopt the principles of *cladistics*, which holds that these relationships should be based exclusively on *phylogeny*, or descent (Futuyma 1998; Harvey & Pagel 1991; Hennig 1966). Hence modern systematists seek to reconstruct the evolutionary history of species based on similarities in their morphological, behavioural, or genetic characters. (A biological *character* is defined as an inherited trait or feature, whereas a *character state* describes the form or value of that character. For example, "blue" and "brown" are character states of the character "eye colour.") This section concerns only the analytical techniques used to identify these relationships, rather than the methods used to obtain the geographical or archaeological data used in these analyses, which are discussed in the following sections.

Two species might share a character or character state either because they each inherited it from a common ancestor (*homology*) or because the character evolved independently in the two species' separate lineages (*analogy*). In order to eliminate the latter and determine phylogenetic relationships, systematists identify *shared derived characters*, that is, traits that evolved only once in a pair of species' common ancestor but are not observed in close relatives. Because shared derived characters are unique to species directly related by descent, they can be used to identify branching points in the phylogeny. The principle of parsimony (or some equivalent method) can then be used to construct a phylogenetic tree which requires the fewest number of these branching points, often using computer programs such as PAUP (Swofford 1998) or MacClade (Maddison & Maddison 1992).

For example, Burns et al. (2002) recently applied phylogenetic analyses to the morphological features of 88 species of Darwin's finches of the Galapagos Islands, finding that all were descended from a common ancestor originating in the Caribbean, rather than South America as had commonly been thought. The evolutionary history of specific traits can also be studied using phylogenetic methods, such as Whiting et al.'s (2003) finding that, although the common ancestor of all insects is thought to have possessed wings for flight, the common ancestor of the stick insects was wingless, and wings re-emerged in the stick insect lineage on a number of independent occasions.

Phylogenetic methods are also used to identify general patterns of evolution. For example, Goodwin et al. (1998) found that "mouthbrooding" behaviour in cichlid fish, in which eggs are incubated in the mouth of the parent, has evolved on 10 to 14 independent occasions from the ancestral state of guarding eggs in nests, illustrating convergent evolution. The association of mouthbrooding with reduced fecundity and larger eggs additionally illustrates the selective effects of one trait on others.

2.1.2. Culture. Just as biologists seek to reconstruct a species' evolutionary history using shared characters, anthropologists seek to reconstruct the history of groups of people based on cultural traits, such as language, tools, customs, or beliefs. In doing so, anthropologists have faced the same problem as evolutionary biologists, that of

distinguishing between homologous and analogous traits. Indeed, this was recognised within anthropology as long ago as 1889 by Francis Galton, which has led to it being referred to as “Galton’s problem” (Galton 1889, p. 270).

The fact that Galton’s problem is virtually identical to the problem faced by biologists has recently led a number of anthropologists to adopt the same solutions. Mace and Pagel (1994) argued that the phylogenetic analyses used by systematists are superior to previous attempts to solve Galton’s problem, such as Murdock’s cross-cultural sample (Murdock & White 1969) or the statistical removal of inherited traits (e.g., Dow et al. 1984), both of which involve the loss of important aspects of the data. Mace and Pagel (1994) treated cultural traits as equivalent to biological characters, with independent instances of cultural change occurring when a cultural trait is invented, acquired from another culture, changed, or lost. Shared, derived characters can then be identified, and the parsimony-based computer programs developed by systematists can be used to reconstruct the most likely evolutionary history of those cultural traits of interest.

For example, Holden (2002) applied cladistic methods to linguistic data from 75 Bantu languages spoken in sub-Saharan Africa. Items of basic vocabulary whose meanings were common to all groups (e.g., “man,” “woman”) were taken as characters, and the different lexical forms used to represent these meanings were treated as character states. A shared character state was therefore one in which the same word form was used for the same meaning in both languages. Geographical and archaeological data were also obtained (see next sections). It was found that the linguistic data showed a good fit with the phylogenetic tree model, and that this tree correlated with geographical proximity and archaeological data suggesting that language was associated with the spread of farming across prehistoric Africa. A further study on the same populations (Holden & Mace 2003) suggested that the acquisition of cattle led to a change from matrilineal to patrilineal inheritance of wealth.

Using similar methods, Gray and Jordan (2000) found that the distribution of 77 Austronesian languages was most consistent with a single common ancestral form in Taiwan which rapidly spread through the region, and Gray and Atkinson (2003) found evidence supporting the theory that the Indo-European language group was associated with the spread of agriculture from Anatolia around 8,000 to 9,500 years ago.

The recognition that cultural traits may be directly acquired from other cultures, that is, transmitted horizontally (within a generation), raises possible objections (e.g., Gould 1991; Moore 1994) to the use of these biological methods, which were originally developed to deal only with vertical (parent-to-offspring) transmission and hence might be unsuitable for studying some cultural evolution. However, as noted by Mesoudi et al. (2004), any putative dichotomy contrasting a “divergent, branching biological evolution” with a “convergent, cross-fertilising cultural evolution” is a distortion of both biology and culture. Significant cross-lineage transfer occurs in biological evolution, especially for microbes (Doolittle 1999; Rivera & Lake 2004) and plants (Abbott et al. 2003), whereas the convergent nature of culture is an empirically testable hypothesis rather than a statement of fact. Tackling the issue systematically and quantitatively, Tehrani

and Collard (2002) found a greater role for branching “phylogenesis” than convergent “ethnogenesis” in Turkmen textile patterns, and Collard et al. (2005) have found that the best available cultural data sets show just as good a fit with a branching phylogenetic model as do biological data sets. In the short term, there are likely to be plenty of data sets for which these methods may be useful, whereas ultimately, it may be mutually beneficial for biological and cultural evolutionists to develop mathematical techniques that incorporate both horizontal transfer and vertical descent.

Another potential objection to the use of cladistic methods in anthropology is the difficulty of identifying distinct “characters” in cultural artifacts (see also criticisms of memetics in section 3.5.2.). The identification of characters in culture is undoubtedly difficult (O’Brien & Lyman 2003, p. 143), but it is important to acknowledge that it is also difficult for biological characters, and this difficulty has not prevented biologists from producing valuable work using the character concept (Wagner 2000).

2.1.3. Conclusions. Treating cultural traits as equivalent to biological characters allows anthropologists to apply the same rigorous phylogenetic methods to cultural data as are used by evolutionary biologists. This is because anthropologists and biologists share the same crucial goals: to reconstruct the history of certain traits and to identify general patterns of change. A number of studies applying phylogenetic methods to cultural data demonstrate that such methods can be successfully used to achieve these goals, for example in determining whether a group of traits are related by descent, whether their spread was associated with other traits, or whether they generated selection for other traits.

2.2. Paleobiology

2.2.1. Biology. The aim of paleobiology is to use the fossil record to identify prehistoric species and reconstruct their evolutionary history (Futuyma 1998; Simpson 1944), consequently helping to explain the present diversity and distribution of living species. The principle methods involve the collection of fossils and analysis of their features, with age and environment reconstructed based on these features and the characteristics of the surrounding rocks. Analysis of these data often involves the use of the phylogenetic methods described above in order to distinguish between homologous and analogous traits. The fossil record is a much more direct (albeit incomplete) source of evidence about the evolutionary past than the distribution of existing species, and, additionally, allows paleobiologists to provide an absolute timescale for evolutionary events using radio-decay dating techniques.

For example, Zhou et al. (2003) describe exceptionally well-preserved fossils from north-eastern China from the Early Cretaceous period, the forms of which support the theories that birds are direct descendants of the dinosaurs, that feathers evolved before flight, and that there was rapid adaptive radiation of bird ancestors. Seiffert et al.’s (2003) phylogenetic analysis of strepsirrhine primate fossils, meanwhile, suggests that the group is much older than was previously thought and has an Afro-Arabian origin. These studies, and countless others, show that fossil evidence can be used to date evolutionary events, support

hypotheses concerning the origin of traits, and reveal general evolutionary patterns such as adaptive radiation.

2.2.2. Culture. In general, archaeologists have similar goals to paleobiologists: identifying prehistoric artifacts, reconstructing lineages of these artifacts and of the people associated with them, and revealing the evolutionary relationships between these lineages. The basic methodology – extracting specimens from the ground – is also similar. It is only recently, however, that some archaeologists have begun to adopt explicitly evolutionary models and tools (for overviews, see O'Brien & Lyman 2002b; Shennan 2002). The key assumption underlying both paleobiology and archaeology is that similar forms that vary through time are causally connected by inheritance (which O'Brien & Lyman [2000] term the assumption of “heritable continuity”). Such sequences of causally connected forms constitute evolutionary lineages. Simpson (1961) proposed that evolutionary lineages should be used as a means of defining a species, rather than requiring reproductive isolation (Mayr 1963), and this “evolutionary species” concept is increasingly being used in evolutionary biology (Wiens 2004). The same lineage-based-species concept has been suggested by Hull (1982) for culture, and extended by O'Brien and Lyman (2000) specifically for prehistoric artifacts.

O'Brien and Lyman (2000) have argued that evolutionary lineages can be reconstructed using the method of *seriation*, in which a collection of artifacts is ordered according to their similarity: the more features two artifacts share, the closer they are in the order; the fewer they share, the further apart they are placed. Where such orderings exhibit gradual, overlapping change, it can be assumed that the seriation represents an evolutionary lineage causally connected by cultural transmission.

Early archaeologists used the method of seriation to identify lineages of coins (Evans 1850), stone tools (Pitt-Rivers 1875), and Egyptian pottery (Petrie 1899). The method fell out of favour, however, in the mid-twentieth century, which O'Brien and Lyman (2000) attribute to the increased popularity of an essentialist stance in archaeology, in which types are perceived to have distinct “essences” and change occurs only when one type suddenly transforms into another. This contrasts with evolutionary “population thinking” (Mayr 1982), which recognises naturally occurring variation within populations rather than focusing on typological essences. O'Brien and Lyman (2000) have consequently made efforts to reintroduce seriation into archaeology as a method of studying evolutionary change in artifacts. This is demonstrated by their analysis of projectile points from the Southwestern United States, which, they show, exhibit continuous, gradually changing variation rather than a small number of distinct types. O'Brien and Lyman (2000) argue that forcing artifacts into distinct categories often distorts their true phylogenetic relationships.

The method of seriation is nonetheless vulnerable to the same problem as similar methods in paleobiology: distinguishing between homologies and analogies. Hence, O'Brien et al. (2001) and O'Brien and Lyman (2003) have argued that it is also necessary to adopt the cladistic methods described above to reconstruct evolutionary lineages accurately. For example, O'Brien et al. (2001) and O'Brien and Lyman (2003) carried out a phylogenetic

analysis of 621 Paleo-Indian projectile points from the Southeastern United States (see Fig. 2), and Tehrani and Collard (2002) used similar methods to reconstruct the history of Turkmen textile patterns.

Other evolutionary archaeologists have adapted neutral drift models from evolutionary biology (e.g., Crow & Kimura 1970) to account for “stylistic variation” in artifacts. For example, Neiman (1995) demonstrated that changes in decorative styles of Illinois Woodland ceramics can be predicted by a model incorporating the selectively neutral but opposing forces of drift and innovation. Bentley and Shennan (2003) found that the frequencies of West German pottery decorations over the course of 400 years can be predicted by a similar model of unbiased cultural transmission, with some anti-conformist bias in later periods.

As well as prehistoric artifacts, past cultures – unlike past species – have often left detailed written records or

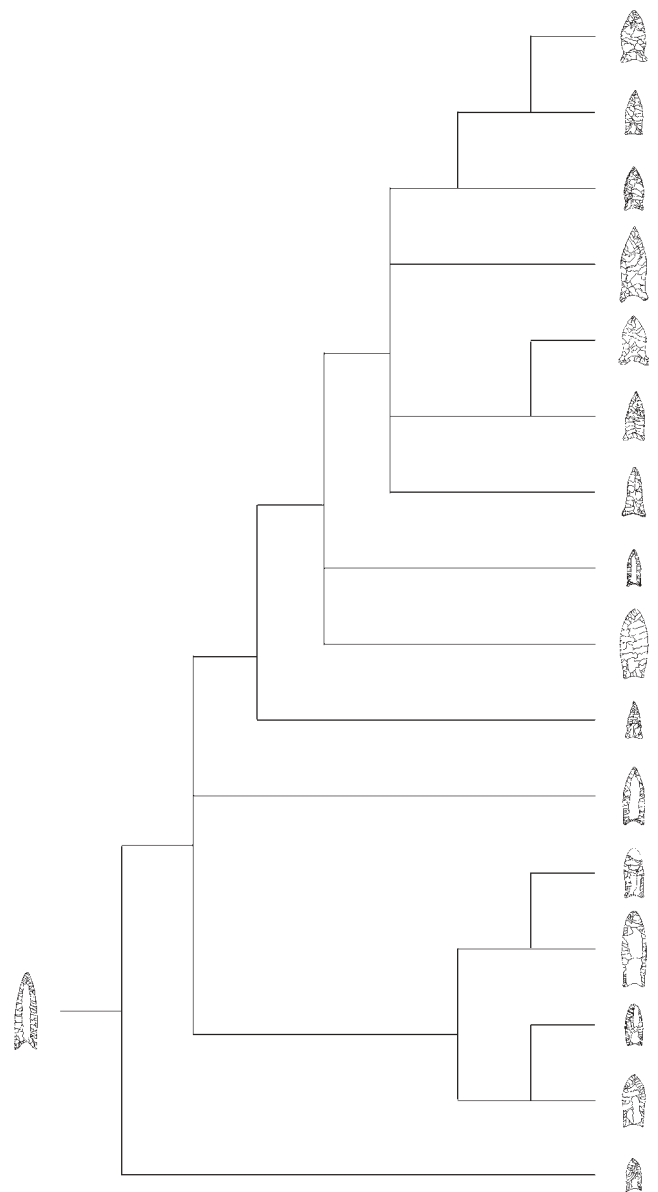


Figure 2. A phylogenetic tree of 17 projectile points from the Southeastern United States, from O'Brien and Lyman (2003), illustrating divergence from a single common ancestor.

direct historical evidence of their knowledge, skills, and technology. For example, Hinde and Barden (1985) found that the facial dimensions of teddy bears became increasingly baby-like during an 80-year period, which they attributed to a biologically evolved human preference for baby-like faces. Basalla (1988), meanwhile, collected numerous examples of technological change which exemplify the gradual modification of preceding technology (see also Petroski 1994; Ziman 2000). For example, although Eli Whitney's cotton gin is commonly described as unprecedented, it was in fact based on existing mechanical cotton gins used to extract other varieties of cotton seed, which were in turn derived from previous Indian gins and before that from an even older sugar-cane press (Basalla 1988, pp. 32–33). Such gradual, cumulative change suggests the presence of evolutionary lineages of artifacts linked by cultural transmission.

Methods developed within evolutionary biology can also be applied to relatively recent historical data. Howe et al. (2001) describe how different manuscript versions of the same text can be used to reconstruct the evolution of that text. This was demonstrated by Barbrook et al. (1998) who used cladistic methods to reconstruct the historical relationships between 58 different manuscripts of Chaucer's *Canterbury Tales*, improving on previous non-phylogenetic reconstructions. Bentley et al. (2004), meanwhile, found that the frequencies of first names and patent applications in twentieth-century United States both conform to a simple model of random copying originally developed in evolutionary biology (Crow & Kimura 1970). This neutral model represents a useful null hypothesis describing the case where no selection is operating.

2.2.3. Conclusions. Archaeologists face essentially the same task as paleobiologists – to identify earlier forms of the phenomena of interest (often now extinct or superseded) and reconstruct their history. It is therefore not surprising that the tools and approaches used by paleobiologists have been successfully imported into archaeology. Adopting evolutionary “population thinking” (O'Brien & Lyman 2000), using the methods of cladistics (Mace & Holden 2005), and importing models of selection or drift (Neiman 1995) can produce a more accurate understanding of the past than traditional archaeological methods. Historical records of cultural artifacts will often be more complete and accurate than the fossil record, offering a potentially important role for historians in the study of cultural evolution.

2.3. Biogeography

2.3.1. Biology. Biogeography is the study of how biological, ecological, geographical, and historical factors determine the spatial distribution of organisms (Brown & Lomolino 1998; Futuyma 1998). Members of a population may adapt to their new environments when they disperse, or populations may be divided by physical barriers and evolve distinctively. Islands are often of particular interest to biogeographers (e.g., MacArthur & Wilson 1967) because of their isolation from other terrestrial ecosystems. Long-term geographical factors such as climate change or tectonic plate movement can affect organisms' spatial distribution, as can shorter-term ecological factors such as competitors or pathogens. Fossil evidence and

phylogenetic analyses are used to infer the past distribution of organisms, which can help to explain their present distribution, and which has led biogeography to become intimately linked with both paleobiology and systematics.

The methods of biogeography can be classed as either descriptive or analytical. Descriptive methods consist of documenting the present distribution of organisms in space, along with their ecology and physical environment. Once these data have been gathered, analytical models, including the cladistic techniques described above, can be constructed and tested to try to explain this distribution.

For example, Stephens and Wiens (2004) sought to explain the geographical distribution of emydid turtles in eastern North America, which exhibit two broad patterns of community structure. Phylogenetic analyses of morphological and molecular data combined with details of habitat and diet revealed that the differences between the two groups are predominantly owing to “phylogenetic conservatism” (i.e., descent from two distinct evolutionary lineages), although the dispersal of several species from one group to the other has reduced these differences.

Roca et al. (2004) used fossil data to explain the distribution of an island species. Phylogenetic analyses of genetic and fossil evidence suggest that around 76 million years ago the solenodons – small, burrowing insectivores from the West Indies – diverged from other insectivores rather than from the tenrecs or the rodents. This date coincides with the separation of the islands from mainland North America on account of tectonic movement and/or rising sea levels, supporting the hypothesis of divergence due to geographical separation.

2.3.2. Culture. The geographical distribution of cultural traits is shaped, at least in part, by factors similar to those affecting the distribution of organisms. Just as the past dispersal of organisms can help to explain the present distribution due to biological inheritance, cultural traits can also persist through time because of transgenerational cultural transmission. Whereas organisms can disperse to new environments, cultural traits can spread by the movement of culture-bearing people or the diffusion of ideas and technology among non-kin. Cultural traits may also arise as adaptations to local ecological conditions.

The field of social science most equivalent to biogeography is again anthropology. One of the main goals of cultural anthropology has been to document and map the worldwide distribution of cultural traits, in a manner resembling the descriptive methods of biogeography. This has resulted in databases such as Murdock's *Ethnographic Atlas* (Murdock 1967), the Human Relations Area Files (Murdock et al. 1987), and, for languages, the *Ethnologue* (Grimes 2002).

More recently, evolutionarily informed analytical models have been developed to attempt to account for the distributions of cultural traits captured by these databases. The field of human behavioural ecology (see section 3.4.2) operates, with some success, on the premise of a correspondence between cultural and ecological variation (Smith & Winterhalder 1992). Other researchers have endeavoured to distinguish ecological from “inherited tradition” explanations. Guglielmino et al. (1995), for example, used the *Ethnographic Atlas* to analyse the distribution of 47 cultural traits in 277 African societies. Most of

the traits, particularly family and kinship traits, correlated with linguistic group, suggesting vertical transmission. A minority of traits were distributed according to geographical proximity, consistent with horizontal diffusion between groups, whereas the distribution of none of the traits could be explained by ecology alone.

Similarly, Hewlett et al. (2002) combined data from the *Ethnographic Atlas* and the *Ethnologue* with newly emerging genetic data to study the distribution of cultural traits in 36 African populations. Twenty of these traits were distributed according to language and/or genes, suggesting vertical cultural transmission, twelve traits correlated with geographical proximity, suggesting diffusion, and four followed ecology, suggesting independent adaptation to local conditions.

A further parallel with biogeography lies in the use of cladistic methods to help explain the present distribution of cultural traits, which we have already seen, for example, for African and Austronesian languages (Gray & Jordan 2000; Holden 2002). Yet another parallel lies in the value of physical barriers in studying the spatial distribution of culture. For example, Cavalli-Sforza and Wang (1986) applied a “stepping-stone” model, developed within biology to study genetic distributions, to linguistic data from 17 Micronesian islands, finding that the degree to which languages shared words declined with the negative exponential of the distance between those islands, just as has been found for biological traits.

Another example of the use of islands to study cultural evolution involves the case of the prehistoric inhabitants of Tasmania, whose cultural repertoire significantly decreased in size and complexity after their isolation from mainland Australia (Diamond 1978; McGrew 1987). Henrich (2004b) developed a model showing that the reduction in population size caused by this physical separation was sufficient to cause the breakdown and loss of relatively complex cumulative skills and tools, because of the paucity of models from which to learn such skills. Henrich’s analysis demonstrates the interactive effects of demography and geography on the distribution of cultural traits.

2.3.3. Conclusions. There is a clear parallel in the aims, methods, and findings of biogeography and anthropology. Both disciplines aim to explain the spatial distribution of traits, and do this descriptively by documenting spatial variation in forms and analytically by developing theoretical models to account for patterns in this variation. Whereas the descriptive stage has been carried out by anthropologists for decades independently of a Darwinian model of cultural evolution, analytical models have benefited from biological tools such as the methods of cladistics and population-genetic and fitness-maximisation models. Similar factors have, moreover, been found to influence the distribution of biological and cultural traits, such as transmission dynamics (e.g., vertical/descent or horizontal/diffusion), geographical phenomena (e.g., physical barriers), and ecological factors.

However, we see potential here for the science of cultural evolution to become more predictive, along the lines of evolutionary biology, by specifying a priori which traits should follow these different evolutionary dynamics and under which conditions. For example, Boyd and Richerson (1985) predict that cultural traits that constitute

adaptations to relatively rapidly changing environmental conditions should be transmitted horizontally, whereas cultural traits that constitute adaptations to environmental conditions that are stable across biological generations (although not stable enough to have become genetically specified) should show evidence of conservative vertical transmission. Further predictions are given in section 3.3.

2.4. Macroevolution: General conclusions

The evidence concerning macroevolutionary patterns reveals a broad fit between the methods and approaches of evolutionary biology and those of the social sciences. This is primarily because a number of anthropologists and archaeologists are already importing biological methods and models into their fields, with considerable success. Phylogenetic methods have been used by anthropologists to explain the spatial distribution of various cultural traits, and by evolutionary archaeologists to reconstruct evolutionary lineages of material artifacts. As this suggests, there is already considerable cross-fertilisation of ideas and methods in these disciplines, which, we argue, is a key benefit of adopting a unified evolutionary framework. We have also seen cases where the evolutionary methods have proved significantly more effective than traditional non-evolutionary methods, such as the adoption of evolutionary “population thinking” in archaeology, or the cladistic solution to Galton’s problem.

3. Microevolution

One of the central principles of the evolutionary synthesis of the 1930s was that large-scale macroevolutionary patterns of change are the result of small-scale microevolutionary changes in gene frequencies within populations (Mayr 1982). A complete theory of cultural evolution would therefore require studies of small-scale changes in populations of cultural traits. The following sections outline the approaches to microevolution developed by evolutionary biologists – population genetics (theoretical, experimental, and field), evolutionary ecology, and molecular genetics – along with corresponding methods in the study of cultural evolution.

3.1. Theoretical population genetics

3.1.1. Biology. Significant advances were made in the study of biological evolution before its molecular basis was understood, in no small part through the use of simplified mathematical models, pioneered by Fisher (1930), Wright (1931), and Haldane (1932). In the simplest models, sexually reproducing individuals in a large (“infinite-sized”) population all contribute to an aggregate gene pool. Under the assumptions of random mating, and with no migration, selection, or mutation, allele frequencies will remain constant through successive generations (the Hardy-Weinberg principle). Deviations from this simple case can be incorporated into population genetic models, such as mutation, non-random (e.g., assortative) mating, or the impact of processes such as natural selection or random genetic drift. Overall allele or genotype frequencies in successive generations can be tracked mathematically to simulate the process of

evolution, often to find out whether a particular genetic trait can invade and spread through a population, and if so, to explore the possible evolutionary consequences of this invasion.

For example, McKone and Halpern (2003) developed a population genetic model of androgenesis, a rare phenomenon seen in freshwater clams, Saharan cypress trees, and stick insects, where the offspring acquire nuclear DNA from the male parent only. The model predicts that mutations causing androgenesis will often spread rapidly to fixation in an initially non-androgenetic population, and in some cases cause extinction of that population because of the loss of females, perhaps explaining the rarity of such mutations.

3.1.2. Culture. Models of *cultural evolution* and *gene-culture coevolution* adopt essentially the same methods as above. The latter (sometimes also referred to as *dual-inheritance theory*) assimilates cultural inheritance into population genetic models, developing mathematical models that incorporate both biological and cultural evolution simultaneously and interactively, whereas “cultural evolution” models are formulated exclusively at this cultural level (Boyd & Richerson 1985; Cavalli-Sforza & Feldman 1981; Feldman & Cavalli-Sforza 1976; Laland et al. 1995a). These models exploit parallels in the demographic consequences of biological and cultural change with, for example, differential adoption and innovation in culture modelled as equivalent to natural selection and mutation within biology, and with other processes such as drift, migration, and assortative mating operating equivalently in both cases.

In gene-culture coevolution models, each individual is often described in terms of a combination of genetic and cultural traits, or “phenogenotype.” This requires that transmission rules for both genes and culture must be considered, with selection on genes affecting the adoption of cultural traits, and vice versa. As well as adopting the same general methods and principles as population genetics, in many cases gene-culture coevolution researchers have adapted specific established population genetic models to render them suitable to features of culture that are not directly analogous to their biological counterpart.

Researchers in these fields recognise that cultural transmission can be very different from biological transmission. Whereas the latter is primarily vertical, Cavalli-Sforza and Feldman (1981) have modelled the consequences of horizontal and oblique (from unrelated members of the parental generation) cultural transmission. Boyd and Richerson (1985) and Henrich and Boyd (1998) have demonstrated mathematically that a “conformist” cultural bias, in which individuals are predisposed to adopt the most popular cultural trait in a group, can evolve in a wide variety of environmental conditions and leads to stable differences between cultural groups, potentially leading to cultural group selection (Boyd & Richerson 1985). Other models consider a variety of other forms of transmission biases (Boyd & Richerson 1985; Cavalli-Sforza & Feldman 1981; Feldman & Cavalli-Sforza 1976). Importantly, many of these biases are unique to cultural transmission and will generate evolutionary dynamics with no obvious parallel in biology. Such differences do

not, however, invalidate an evolutionary analysis of culture.

Models have also been developed for specific cases of gene-culture coevolution. For example, Feldman and Cavalli-Sforza (1989) modelled the coevolution of genes for lactose absorption and the cultural trait of dairy farming, finding that the allele for lactose absorption will spread provided there is a high probability that the offspring of dairy farmers themselves become dairy farmers, but not otherwise, even with a significant viability advantage. Another case study examined the evolution of handedness (Laland et al. 1995b), proposing a model that gave a better fit to patterns of handedness in families and among twins than do leading purely genetic models.

As well as population genetic methods, biological models of neutral genetic drift (Crow & Kimura 1970) have been adapted to study the evolution of cultural traits such as names and patents (Bentley et al. 2004), demonstrating that the distribution of such traits can be accounted for by chance events. Boyd and Richerson (1985), meanwhile, have developed a model of runaway cultural selection similar to runaway sexual selection, which they argue can account for a range of cultural traits, from oversized yams in Ponape to extensive tattooing in Polynesia (paralleling elaborate sexually selected biological traits such as the peacock’s tail).

Mathematical models such as these are often treated with suspicion and even hostility by some social scientists, who consider them to be oversimplifications of reality (see Laland et al. 1995a, and associated comments). The alternatives to gene-culture coevolution analyses, however, are usually either analysis at a single (purely genetic or purely cultural) level or vague verbal accounts of “complex interactions,” neither of which we believe to be productive. Gene-culture analyses have repeatedly revealed circumstances under which the interactions between genetic and cultural processes lead populations to different equilibria than those predicted by single-level models or anticipated in verbal accounts (Laland et al. 1995a), as illustrated by the aforementioned examples of dairy farming and handedness.

Interestingly, fifty years ago the same reservations about simplifying assumptions were voiced about the use of population genetic models in biology by the prominent evolutionary biologist Ernst Mayr (1963). He argued that using such models was akin to treating genetics as pulling coloured beans from a bag (coining the phrase “beanbag genetics”), ignoring complex physiological and developmental processes that lead to interactions between genes. In his classic article “A Defense of Beanbag Genetics,” J. B. S. Haldane (1964) countered that the simplification of reality embodied in these models is the very reason for their usefulness. Such simplification can significantly aid our understanding of processes that are too complex to be considered through verbal arguments alone, because mathematical models force their authors to specify explicitly and exactly all of their assumptions, to focus on major factors, and to generate logically sound conclusions. Indeed, such conclusions are often counterintuitive to human minds relying solely on informal verbal reasoning. Haldane (1964) provided several examples in which empirical facts follow the predictions of population genetic models in spite of their simplifying assumptions, and noted that models can

often highlight the kind of data that need to be collected to evaluate a particular theory.

Ultimately, Haldane won the argument, and population genetic modelling is now an established and invaluable tool in evolutionary biology (Crow 2001). We can only echo Haldane's defence and argue that the same arguments apply to the use of similar mathematical models in the social sciences (see also Laland 1993; Laland et al. 1995a; Mace & Pagel 1994; Pagel & Mace 2004).

3.1.3. Conclusions. A number of researchers have imported the methods of theoretical population genetics to study the coevolution of genes and culture, and the dynamics of cultural change through time. These methods have provided a rigorous analysis of many cultural evolutionary processes and case studies. The differences between biological and cultural inheritance are not ignored and do not invalidate such models, and many of the criticisms of the use of such analytical models in the social sciences have been addressed in a parallel debate within evolutionary biology.

3.2. Experimental population genetics

3.2.1. Biology. As well as using the theoretical models described above, population geneticists have studied microevolutionary processes experimentally by breeding multiple generations of study organisms in the laboratory, in order to simulate evolution under controlled conditions. Laboratory-based experiments have been used to estimate the rate and effect of mutation, detect adaptation to experimentally induced environmental conditions (e.g., different temperatures), and measure responses to the artificial selection of single or multiple traits (Futuyma 1998; Hartl & Clark 1997).

In a typical artificial selection experiment, a population of a species, such as *E. coli* or *Drosophila*, is measured for some desired trait (e.g., temperature resistance). In each generation only a subset of the population is allowed to reproduce, with the reproducing individuals chosen according to the desired trait (e.g., those most resistant to high temperatures). After a number of generations, the population is again tested for the trait to estimate the response to this selection regime.

For example, Torres-Vila et al. (2002) employed a laboratory-based artificial selection paradigm to investigate the genetic basis of polyandry (females mating with more than one male) in a normally non-polyandrous species of moth. Initially 150 pairs of moths were allowed to mate freely, and all of the fertilised females were assessed for their tendency to solicit further matings. In five subsequent generations only females displaying polyandrous behaviour were allowed to mate, resulting in a significant increase in the frequency of polyandry and indicating the successful artificial selection of this trait.

Natural selection can be simulated by manipulating environmental conditions and allowing the population members to compete naturally amongst themselves, with those individuals best suited to the imposed conditions out-breeding less-suited individuals. After a number of generations, the population is tested for adaptation to the imposed conditions. Kennington et al. (2003), for example, experimentally simulated the natural selection

of body size in *Drosophila* in response to humidity. Separate populations were maintained at either high or low humidity and were allowed to breed freely. After 20 weeks (5–10 generations) it was found that the low humidity lines were significantly larger than the high humidity lines, which Kennington et al. argued occurred because large flies have a low surface area relative to weight, lose less water, and so are better adapted to low humidity. This experimental result also helps to explain the geographical distribution of *Drosophila* in the wild, with large body sizes found at high latitudes with low humidity.

3.2.2. Culture. One parallel with this work lies in laboratory-based psychological experiments simulating cultural transmission. Where population genetic experiments simulate biological evolution by studying the transmission of genetic information from generation to generation through the reproduction of individuals, psychological experiments can potentially simulate cultural evolution by studying the transmission of cultural information (e.g., texts or behavioural rules) from one individual to another through social learning.

One method for simulating cultural evolution was developed by Gerard et al. (1956) and Jacobs and Campbell (1961). A norm or bias is established in a group of participants, usually by using confederates, and one by one these participants are replaced with new, untrained participants. The degree to which the norm or bias remains in the group after all of the original group members have been replaced represents a measure of its transmission to the new members.

For example, Baum et al. (2004) studied the transmission of traditions using a task in which participants received financial rewards for solving anagrams. Groups of individuals could choose to solve an anagram printed on either red or blue card: the red anagrams gave a small immediate payment, whereas the blue anagrams gave a larger payoff but were followed by a "time-out" during which no anagrams could be solved. By manipulating the length of this time-out, the experimenters were able to determine which of the two anagrams gave the highest overall payoff (i.e., where the blue time-out was short, blue was optimal, and where the blue time-out was long, red was optimal). Every 12 minutes one member of the group was replaced with a new participant. It was found that traditions of the optimal choice emerged under each experimental condition, with existing group members instructing new members in this optimal tradition by transmitting information about payoffs and time-outs, or through coercion.

Key similarities exist between this study and the experimental simulations of natural selection described above. In Kennington et al.'s (2003) study with *Drosophila*, where the experimentally determined conditions of low humidity favoured large body size, larger individuals out-reproduced smaller individuals. Hence, genetic information determining "large body size" was more likely to be transmitted to the next generation through biological reproduction, and the average body size of the population became gradually larger. In Baum et al.'s (2004) study, where the experimentally determined conditions favoured red anagrams (when the blue time-out was relatively long), choosing red anagrams gave a larger payoff to the participants. Hence, the behavioural rule "choose red" was more

likely to be transmitted to the new participants through cultural transmission, and the overall frequency of choosing red gradually increased.

Baum et al.'s (2004) method could easily be adapted to study the cultural evolution of attitudes or beliefs. Groups of participants could be asked to discuss a contentious issue, then for every generation the participant with the most extreme opinion in a certain direction would be removed and replaced with a random participant. After a number of generations, the group should hold more extreme views (in the opposite direction to those of the removed participants) than average members of the larger population.

Experimental economists have also recently begun to study the transmission of behavioural traditions that emerge when chains of successive participants play economic games. For example, Schotter and Sopher (2003) had successive pairs of participants play a game in which two players chose one of two options without communicating. If they chose different options, neither got any payoff, encouraging coordination. If both chose the first option, then the first player benefited more than the second, whereas if both chose the second option, the second player benefited more, creating conflict. Transmission was effected by allowing each player to view the behavioural history of all previous players and/or to receive explicit advice from the preceding player in the chain. It was found that stable conventions emerged in which both players consistently chose one option, and that these conventions were mainly due to explicit advice rather than behavioural history.

A similar methodology exists within experimental psychology. The *transmission chain method*, as developed by Bartlett (1932), involves a text or picture being passed along a linear chain of participants. The first participant in such a chain reads or views the stimulus material and later recalls it. The resultant recall is then given to the next participant in the chain to recall, the result of which is given to the third, and so on along the chain. Studying how the material changes as it is transmitted, and comparing the degradation rates of different types of material, can reveal specific biases in cultural transmission (e.g., Mesoudi & Whiten 2004; Mesoudi et al. 2006).

Mesoudi and Whiten (2004) used this method to study the cultural transmission of event knowledge. Everyday events, such as going to a restaurant, are thought to be represented in memory hierarchically, in which a global high-level proposition (e.g., "go to restaurant") can be subdivided into lower-level propositions (e.g., "sit down," "order," "eat," "pay"), each of which can be subdivided further (e.g., "look at menu," "select food," "call waiter"). Mesoudi and Whiten found that when descriptions of such events expressed entirely at a low hierarchical level were passed along multiple chains of participants, they were spontaneously transformed into higher hierarchical levels.

Linear transmission chain studies such as those of Schotter and Sopher (2003) and Mesoudi and Whiten (2004) bear less similarity to the experimental paradigms of population genetics. Nevertheless, Schotter and Sopher's study provides important data on the mode of cultural transmission (explicit advice versus behavioural history), data which might be needed as a preliminary to more advanced experimental manipulations. Studies

such as Bartlett (1932) and Mesoudi and Whiten (2004), although not imposing a selection regime on the transmission of cultural traits, are in a sense simulating selection "in the wild" (see section 3.3.2), as cultural information is being shaped by the minds of the participants it passes through. In Mesoudi and Whiten (2004), the implicit hierarchical structure of memory causes the selection of event knowledge at high hierarchical levels; hence, there is selection due to evolved or implicit features of human cognition. A design more explicitly along the lines of a natural-selection population genetic experiment might involve exposing different chains of people to different experimental conditions, or having each chain composed of different types of people with alternative pre-existing knowledge.

Finally, as well as simply detecting the *presence* of directional selection, population geneticists may obtain quantitative estimates of the *strength* of selection. Cultural transmission experiments would benefit from the development of similar measures, and once again there are opportunities to borrow usefully from biology. Stabilising selection might also be studied in this manner, by testing whether certain beliefs or ideas are converged upon following an experimentally induced deviation (see section 3.3).

3.2.3. Conclusions. Although laboratory-based experiments are an established approach to the study of biological evolution, relatively little experimental work exists in psychology or economics that has studied the dynamics of cultural transmission. Such studies are essential for a full understanding of cultural evolution. Psychological studies of cultural transmission would benefit from explicitly drawing on the methods of experimental population genetics, both in the design of experiments and in the analysis of data.

3.3. Population genetics: Field studies

3.3.1. Biology. The third approach within population genetics is the study of evolution in naturally occurring populations. Observational studies or field experiments can give estimates of the heritability of traits by measuring parent-offspring correlations, and measures of mortality and reproductive success can be used to estimate the mode and strength of selection on those traits (Endler 1986; Futuyma 1998).

The *mode* of selection (Endler 1986; Simpson 1944) refers to whether selection is *directional* (i.e., individuals at one end of a distribution are favoured, causing a change in the mean trait value), *stabilising* (i.e., intermediate individuals are more successful than those at the extremes, decreasing variation in the trait), or *disruptive* (i.e., extreme individuals do better, increasing variation in the trait).

The *strength* of selection is commonly represented by the *selection gradient*, a multiple regression-based measure of the relationship between relative fitness and variation (Arnold & Wade 1984; Lande & Arnold 1983). Selection gradients have become a common currency within evolutionary biology for estimating the strength and mode of selection, and for making comparisons between populations (e.g., Endler 1986; Hoekstra et al. 2001; Kingsolver et al. 2001). The actual methods used

to obtain these measures are varied. Endler (1986) lists ten common methods for detecting natural selection in the wild and for the corresponding results that would suggest its operation, as summarised in Table 1.

There are literally hundreds of examples of natural selection being demonstrated in natural populations of organisms by the above methods (Endler 1986). Recent examples include Donley et al.'s (2004) analysis of similar morphological and biomechanical specialisations in lamnid sharks and tuna, such as a "thunniform" body shape, in both cases caused by selection for fast movement through water. This convergent evolution (Endler's third method) has occurred independently during the 400 million years since the two groups diverged from a common ancestor. Marko (2005), meanwhile, found evidence for character displacement (Endler's second method) in two closely related species of rocky-shore gastropods. Significant differences in shell shape were observed only where the two species overlapped, caused by divergent selection as a result of competition.

3.3.2. Culture. Cultural traits have similarly been studied in natural human populations, although mostly not within an explicit evolutionary framework and hence without the formalised hypotheses, methods, and measures of selection employed within evolutionary biology, as seen above. We briefly discuss three relevant research traditions – anthropological field studies, rumour research, and the diffusion of innovations – before outlining how more formal, theoretically driven methods developed within biology might be applied to cultural data.

First, anthropological field studies have examined the acquisition of cultural knowledge in traditional societies. Members of a community are typically interviewed to find out from whom they acquired their knowledge or skills. For example, Hewlett and Cavalli-Sforza (1986) interviewed members of the Aka of central Africa, finding that the majority (80.7%) of practical skills were said to be acquired from parents, 5.2% from other family

members, and 12.3% from unrelated individuals. Similarly, Aunger (2000a) found that food taboos are acquired predominantly from biological parents in a horticultural society in the Democratic Republic of Congo, with a subsequent less influential phase of learning from non-kin.

Second, the field of social psychology devoted to rumour research (Rosnow 1980; 1991) has generated a number of field studies examining the transmission of rumours through naturally occurring populations. A rumour is defined as a belief passed from person to person without secure standards of evidence being present (Allport & Postman 1947, p. ix). Studies have used questionnaires to track either naturally occurring or experimentally introduced rumours through a small population. Jaeger et al. (1980), for example, used confederates to plant a rumour in a college that some students had been caught smoking marijuana during final exams, with Jaeger et al. obtaining details of transmission using questionnaires. Bordia and Rosnow (1998) have more recently studied the transmission of a rumour through an Internet community, with the electronic record of communications allowing the longitudinal study of all stages of transmission, rather than relying on retrospective accounts.

Finally, research in sociology on the diffusion of innovations (Rogers 1995) examines how new ideas and technologies are transmitted through naturally occurring populations. Typically, questionnaires or interviews are employed to assess the past and present use of the innovation by the respondent, and used to compile a picture of diffusion through the population. Classic studies have examined the diffusion of new types of seed among farmers (Ryan & Gross 1943) and antibiotic among doctors (Coleman et al. 1966). A recurring finding from more than 3,000 diffusion studies is an S-shaped cumulative adoption curve (Rogers 1995), which indicates a slow initial uptake, followed by a rapid increase in adoption, and finally another slow period as the population reaches saturation (similar sigmoidal dynamics characterise the diffusion of alleles).

Table 1. *Methods for the detection of natural selection in the wild and results that would suggest the presence of selection as given by Endler (1986, Ch. 3, esp. Table 3.1)*

Method	Result indicative of selection
1 Exploring the relationship between a trait and an environmental factor (source of selection)	Correlation between the trait and an independent environmental (selective) factor
2 Comparing closely related species living in the same region	Homologous traits affected in same manner, e.g., divergence in similar traits due to competition (character displacement)
3 Comparing unrelated species living in similar habitats	Similarities in analogous traits due to convergent evolution
4 Comparing gene frequencies with those predicted by a null (no selection) model	Deviation of gene or genotype frequencies, number of alleles, or disequilibrium from the null model
5 Long-term study of trait distribution	Long-term stability or regular directional change in the trait
6 Perturbation of natural populations	Trait divergence from the new postperturbation mean
7 Long-term study of demography (e.g., survivorship, fecundity)	Particular demographic patterns associated with particular trait values over time
8 Comparing the trait distribution of different age – classes or life-history stages	Differences in trait frequency distributions between age classes
9 Using knowledge of fitness, genetics, physiology, etc., to predict short-term change in a trait	Predictions confirmed
10 Using fitness-maximisation models to predict an observed trait frequency or distribution at equilibrium	Predictions confirmed

Many of these diffusion studies, however, can be criticised for not clearly identifying a priori the putative selection pressure responsible for the diffusion and then testing this prediction in natural populations, as is commonly done in evolutionary biology (Endler's first method). Instead, diffusion of innovations research has produced a list of a posteriori and somewhat vague qualities that supposedly explain diffusion rates, such as "trialability" or "complexity" (Rogers 1995). One recent study that *did* specify a priori a hypothesised selection pressure is Bangerter and Heath's (2004) study of the "Mozart effect," the idea that exposure to classical music enhances intelligence, especially during childhood. Although it has very weak scientific support, this idea has gained wide currency in the United States mass media, which Bangerter and Heath (2004) hypothesised was because it offers a cheap and easy way of supposedly enhancing one's child's development. This hypothesis predicts that the Mozart effect should be more prevalent in the mass media of states where there is poor academic performance and low spending on education, which Bangerter and Heath showed to be the case.

3.3.3. Conclusions. There are some weak similarities between the methods used by evolutionary biologists to study evolution in naturally occurring populations of organisms and those which have been used to study cultural change "in the wild." Rumours and innovations are studied as they colonise novel environments, whereas anthropological studies provide estimates of heritability. The shorter timescale of some cultural evolution and the ability of people to report its means of transmission suggest that cultural evolution might be easier to detect than biological evolution (although such verbal reports would need to be supplemented with observational data).

The study of cultural evolution, however, is distinctly lacking in formal tests for cultural selection, as opposed to other forms of cultural change such as drift. Laland and Brown (2002) have argued that each of Endler's (1986) methods for detecting natural selection in the wild (Table 1) can be adapted for studying the selection of naturally occurring cultural traits. As mentioned above, sociological studies have successfully tracked changes in the frequencies of various traits following their natural or artificial introduction into a novel environment. The next step would be to demonstrate that these changes in frequency are the result of *selection*, for example, by comparing the frequency of a newly introduced idea with the frequency of the idea in the parent population from which it diffused, predicting directional change. An alternative approach would be to test whether stabilising selection was operating on the character prior to the perturbation by investigating whether it returns to the original equilibrium, as predicted. We also encourage more studies like that of Bangerter and Heath (2004), which identifies a priori a putative selection pressure – anxiety about child development – responsible for the spread of a cultural trait, and successfully predicts the distribution of the trait from that selection pressure.

Another method is to investigate cultural character displacement, in which two competing cultural lineages in the same region diverge in order to reduce direct competition (Laland & Brown 2002). We might, for example, predict that the religious beliefs of people who live side

by side with people of different, opposing beliefs (e.g., Muslims and Jews in the West Bank, or Catholics and Protestants in Northern Ireland) will be more divergent and extreme than the beliefs of people not in immediate contact with competing beliefs (e.g., Muslims in neighbouring Islamic countries such as Syria and Jews in Jewish-only regions of Israel, or Catholics in the Republic of Ireland and Protestants in mainland Britain).

Convergent cultural evolution, meanwhile, might be detected where cultural lineages from distant yet similar environments have evolved similar features. History is likely to be littered with examples of similar, independently evolved solutions to common problems, such as the independent evolution of writing by the Sumerians around 3000 B.C., the Chinese around 1300 B.C., and the Mexican Indians around 600 B.C., all in response to a need for stocktaking (Diamond 1998).

Studies of cultural evolution could also adapt the measures of selection strength developed by biologists, such as the selection gradient. Quantitative measures of the rate of microevolution, like the darwin or the haldane (Hendry & Kinnison 1999), might also be adapted to the cultural case. There is much opportunity here for the fertile transfer of good ideas from biology to the social sciences, with many of the methods currently being used by evolutionary biologists to investigate natural selection in the wild yet to be tried by researchers studying culture.

3.4. Evolutionary ecology

3.4.1. Biology. Ecology is the study of interactions between organisms and their environments (Begon et al. 1996). Evolutionary ecology focuses on the evolutionary processes by which organisms have become *adapted* to their environments (Cockburn 1991; Futuyma 1998). Such environmental features can be *abiotic*, such as temperature or rainfall, or *biotic*, such as food sources, predators, parasites, competitors, or helpers of both the same and different species. Ecologists have adopted a range of methods to study these processes, including field studies, natural and laboratory experiments, and mathematical models. There is, therefore, a great deal of overlap with biogeography and population genetics.

For example, Korpimäki et al. (2002) set out to determine whether predation was responsible for the 3-to-5-year cycles in population densities of voles in northern Europe. By experimentally reducing numbers of the voles' predators, Korpimäki et al. (2002) were able to show a corresponding increase in the population density of voles compared to non-manipulated vole populations. This response was supported by a demographically based population model which predicted that reduced predation produces a shift from 3-to-5-year cycles of vole population density to 1-year cycles.

3.4.2. Culture. Cultural traits can also be said to interact with, and adapt to, their environment. The environment in this case can be divided into three categories, two of which roughly correspond to the abiotic and biotic features that affect organisms. Hence, cultural traits may adapt to physical features of the environment such as temperature or rainfall. Cultural traits may also compete with and adapt to other cultural knowledge, equivalent to the

biotic environment. Finally, cultural traits may adapt to biologically evolved or implicit features of human cognition. This has no exact equivalent in the biological world, although perhaps there is a loose parallel in genetic or developmental constraints on adaptation, or in the coevolution of symbionts and hosts (Dennett 2001; 2002).

As their names suggest, cultural ecologists (e.g., Steward 1955) and human behavioural ecologists (e.g., Smith & Winterhalder 1992) have studied the adaptation of cultural traits to the physical and social environment. We discuss here the rigorous and explicitly Darwinian field of human behavioural ecology, which is directly equivalent to (and indeed emerged from) behavioural ecology within biology, usually using the same theoretical tools and models, such as optimal foraging theory (Stephens & Krebs 1986). Although human behavioural ecologists often choose to downplay transmitted cultural processes, such work is valuable within a cultural evolutionary framework in specifying the microevolutionary process of cultural adaptation and the adaptive cultural characters that may be transmitted to subsequent generations.

The practical methods of human behavioural ecology, like those of anthropology in general, involve observing and recording behaviour in natural environments, typically in small communities within traditional societies. Unlike conventional anthropology, however, these observations are guided by the predictions of formal mathematical models. This fieldwork, as well as the theoretical models it is designed to test, resembles the methods of evolutionary ecology. An example is the occurrence in Tibet of polyandry, which has been shown to be functionally adaptive under the particularly harsh environmental conditions of the region (Crook & Crook 1988).

As well as adapting to the physical environment, cultural traits may also adapt to other pre-existing cultural information. The study of this form of adaptation would incorporate competition between cultural traits, for which ecological concepts such as exploitation or interference might be useful. Mufwene (2001) has recently proposed a detailed ecological theory of language evolution along these lines.

Finally, because cultural traits rely predominantly on human minds for their storage and transmission, there is the possibility of adaptation to biologically evolved or developmentally acquired cognitive features of those minds. Hence, transmission experiments and field studies can draw on findings from cognitive and developmental psychology concerning implicit memory structures, such as Mesoudi and Whiten's (2004) demonstration that the hierarchical structure of memory shapes the cultural transmission of event knowledge. Evolutionary psychology (e.g., Barkow et al. 1992) also provides a rich theoretical and empirical body of research on biologically evolved features of human cognition that might be predicted to bias cultural transmission in particular directions. Sperber and Hirschfeld (2004) similarly argue that the diversity of some cultural traits, such as religious beliefs or classifications of animals and plants, is the result of adaptation to biologically evolved domain-specific cognitive capacities (e.g., folk biology; Atran 1998). There is also evidence that biomechanical properties of the human vocal apparatus significantly constrain the form of words (MacNeilage & Davis 2000). The infant vocal tract, for example, favours simple consonant-vowel

alternations such as “dada” and “mama” (MacNeilage & Davis 2000), which may explain why such word forms are used in many languages to denote parents.

Of course, cultural knowledge does not exist solely in human brains and does not rely exclusively on face-to-face communication for transmission. It may also be fruitful to study the adaptation of cultural traits to alternative transmission media such as printed documents or the Internet, and to examine whether such media are merely direct extensions of cognitive capacities or whether they generate their own novel transmission constraints (see Donald 1991).

3.4.3. Conclusions. Cultural traits may adapt to the physical environment, to other cultural knowledge, or to biologically evolved or implicit features of human cognition. Although behavioural and cultural ecologists have produced a large body of work relating ecological factors to cultural beliefs, knowledge, and skills, there is much less work on adaptation to the latter two “cultural environments.” Anthropological fieldwork and psychological experiments are needed which measure features of these environments (pre-existing cultural knowledge and biologically evolved or implicit aspects of cognition) and make testable predictions regarding corresponding features of culture.

3.5. Molecular Genetics

3.5.1. Biology. One of the major achievements of twentieth-century biology was the discovery that sequences of DNA comprise the major part of the molecular basis of biological inheritance. Considerable progress has been made in biology as a result of this knowledge. The fields of molecular biology and genetics involve the study of the structure of DNA, RNA, and proteins and the processes involved in their inheritance and expression (Futuyma 1998; Watson et al. 1987).

Molecular genetics has a number of specific uses in evolutionary biology (Futuyma 1998). As mentioned above, molecular markers can be used to reconstruct and date phylogenetic relationships, as well as provide information on genetic variation, population structure, and gene flow. Molecular techniques can also be used to investigate the functions of specific genes in the development of biochemical, morphological, or behavioural phenotypic features.

3.5.2. Culture. One approach to culture that is explicitly analogous to genetics is *memetics*. In order to illustrate the universality and substrate-neutrality of his replicator-centred theory of evolution, Dawkins (1976) coined the term *meme* to describe a cultural replicator, or a unit of cultural transmission. Memetics has been developed further by Hull (1982), Dennett (1995), Blackmore (1999), and Aunger (2000b; 2002), amongst others. A common assumption of memetics is that cultural knowledge is stored in brains as discrete packages of semantic information, comparable to how biological information is stored as genes. Once expressed in behaviour or artifacts, these packages of learned information can be replicated in the heads of other individuals through social learning.

The recently burgeoning literature promoting memetics has attracted a number of criticisms (Laland & Brown

2002). Some of these, such as the need to accommodate the merging of lineages, apply equally to a general theory of cultural evolution and have been discussed elsewhere in this target article. Specific to memetics is the criticism that culture cannot be divided into discrete units with clearly specified boundaries (Bloch 2000; Midgley 2000).

However, the same putative “criticism” could equally be levelled at modern concepts of the gene (Laland & Brown 2002). As documented by Portin (1993; 2002), the concept of the gene has undergone significant changes through the past 150 years. The classical view, held from the time of Mendel (1866) until the 1930s, saw the gene as an indivisible unit of transmission, recombination, mutation, and function. That is, a gene is a unit of information that is transmitted whole, within which no recombination occurs, which mutates independently from other genes, and which produces a single molecular product (as captured by James Watson’s famous canon, “DNA makes RNA makes protein”). This simple and dated gene concept seems to be the view of the gene held by many social anthropologists who are critical of memetics.

Advances in genetics since the 1930s, however, have shown this unitary gene concept to be inadequate and overly restrictive. Further reconceptualisation began in the 1970s following the discoveries of such phenomena as *overlapping genes*, where the same stretch of DNA codes for more than one protein; *movable genes*, DNA sequences that move around the genome; and *nested genes*, which reside inside other genes. Such revised conceptions have continued in the wake of modern discoveries, such as alternative splicing, nuclear and messenger RNA editing, cellular protein modification, and genomic imprinting.

In alternative splicing, for example, one of several alternative versions of an exon is transcribed into a coding segment. Depending on which one is chosen, different proteins can be produced from the same gene. Exons can even be spliced in from other genes, and in some cases this produces not just one or two variants, but hundreds or even thousands. Alternative splicing is not a rare or occasional event and it seems to occur in approximately half of all human genes (Modrek & Lee 2002). Gone is the notion of “one gene–one protein.” In fact, genes seem much more like ideas – information that can be expressed in a multitude of different ways.

The modern concept of the gene is hence characterised as abstract, general, and open, with fuzzy boundaries that change depending on the context in which the term is used (Portin 1993; 2002). Indeed, there are now multiple, mutually incompatible gene concepts prevalent within biology (Stotz & Griffiths 2004). So, although the critics of memetics are probably correct in pointing out the vaguely and flexibly specified nature of the meme concept, exactly the same problem applies to the gene concept, which undoubtedly has been of enormous value in the study of biological evolution. The crucial point here is that both empirical and theoretical traditions within population biology have thrived in spite of this biological complexity, by using simple, discrete gene concepts.

However, there is still a gap between the detailed understanding of the cellular and molecular bases of genetic inheritance and the somewhat informal ideas of memetics. A more detailed picture of the mechanisms of cultural transmission requires an understanding of how the brain processes relevant information. Here, the most obvious

analogy might be between molecular genetics and the molecular and cellular bases of learning and memory. However, such learning can be usefully studied at levels other than the molecular, ranging from purely cognitive analyses that say little directly about underlying neural bases, to studies that explicitly focus on supracellular aspects of how imitative and related processes are executed in the brain, studied through methods such as fMRI. These considerations suggest that because the storage and transmission of culturally transmitted information is so physically different from the genetic, it is here that scientists studying cultural transmission will need to venture further beyond the analogies between cultural and biological evolution that we have focused on so far. Already, one can perceive the beginnings of what has been called a “social cognitive neuroscience” that aims to integrate all the required levels of analysis. Three of these levels – the neural, the whole-brain, and the cognitive – are outlined here.

First, at the *neural* level, the social learning community (see Hurley & Chater 2005) has hailed as highly significant the discovery of “mirror neurons” in the prefrontal cortex of monkeys, which activate both when the monkey observes a specific goal-directed hand action, such as grasping an object, and also when the monkey performs that same action (Gallese et al. 1996; Rizzolatti et al. 1996). This match between observation and execution of motor actions has led some researchers to suggest that the mirror-neuron system forms the basis both for *imitation* (Meltzoff & Decety 2003; Rizzolatti et al. 2002; Williams et al. 2001), which is one possible cultural transmission mechanism, and for *theory of mind* (Gallese & Goldman 1998), which has also been argued to be important in human cultural transmission (Tomasello 1999; Tomasello et al. 1993).

However, it has long been argued that rather than single memories or functions being determined by single neurons, memory is more likely to be determined by patterns of activation within neural circuits and the resulting connection strengths between neurons (Hebb 1949). Phenomena such as long-term potentiation (Bliss & Lomo 1973) and long-term depression (Dunwiddie & Lynch 1978), as well as a multitude of pre- and post-synaptic changes in neural tissue, offer potential electrophysiological and biochemical mechanisms underpinning certain long-term memories (see Keyser & Perrett 2004 for a Hebbian-based model of social cognition). These views of memory, in which single neurons are implicated in a range of functions, and functions are determined by more than one neuron, resemble the complexity found in the genetic system discussed above, where one gene has a potentially wide range of functions and expressions.

Aunger (2002) has recently attempted to integrate memetics with neuroscience, arguing that a robust conceptualisation of the “meme” must specify its material basis in the brain. He proposes that memes should be seen as electrochemical states of multiple neurons, and offers a definition of a “neuromeme” as “a configuration in one node of a neuronal network that is able to induce the replication of its state in other nodes” (p. 197). As Aunger acknowledges, however, any attempt to provide a more detailed description and theory of a neuromeme is severely limited by the current lack of understanding within neuroscience concerning the precise neural and molecular basis of how learned information is stored in the brain. One problem specific to the present discussion

is that rat and monkey models may be limited in their relevance to studying culturally acquired information, given these species' limited capacity for culture, whereas invasive single neuron recordings are not performed on humans and other great apes.

Notwithstanding these complications, there is evidence from cognitive neuropsychology that cultural knowledge is often chunked and aggregated into higher-order knowledge structures that may be separable (Plotkin 2002b). For example, there are several reports of category-specific naming impairments of human patients with brain damage who have been found to recognise and correctly name all items except those in a specific category, such as fruits and vegetables or country names (Crosson et al. 1997). Such studies suggest that at least some learned knowledge stored in human brains is organised into separable semantic categories. There is also recent evidence that single neurons in the human medial temporal lobe respond to the higher-order abstract representation of a specific person or building (Quiroga et al. 2005).

Second, the charting of imitation and related processes at the *whole-brain* level has focused principally on humans, including the study of neurological cases such as apraxia and its associated imitation deficits (Goldenberg & Hermsdorfer 2002) and fMRI studies of imitation in normal (Iacoboni et al. 2001; Rumiati et al. 2004) and other groups, such as autistic individuals who experience difficulties in imitation (Avikainen et al. 1999).

Third, if neuronal studies have been largely restricted to monkeys and whole-brain studies to adult humans, it is research at the *cognitive level* regarding social learning in great apes and, more recently, human children that has generated the richest current taxonomies of cultural learning, delineating such processes as program-level imitation, emulation, and affordance learning (Byrne & Russon 1998; Tomasello et al. 1993; Want & Harris 2002; Whiten & Ham 1992; Whiten et al. 2004). Cognitive models that seek to explain how these operate have begun to proliferate but remain few and quite crude in comparison to our understanding of genetic transmission mechanisms; they include Meltzoff and Moore's (1997) active intermodal matching (AIM), Heyes's (2005) associative sequence learning (ASL), and Byrne's (1999) string parsing models. Interestingly, all of these models appeal to a foundation of mirror-neuron function, leading Whiten (2005a) to question whether they really solve, or instead merely assume to be solved, the essential "correspondence problem" (Nehaniv & Dautenhahn 2002) of mapping between equivalent actions in a model and a cultural learner. Others have explicitly tackled this problem in offering neural network models proposed to be capable of learning the appropriate correspondences (Keyesers & Perrett 2004; Laland & Bateson 2001). Keyesers and Perrett (2004) review data consistent with their hypothesis that in monkeys this is achieved by circuits linking premotor area F5, inferior parietal cortex PF/PFG, and the superior temporal sulcus, and by the homologues of these areas in humans.

3.5.3. Conclusions. Whereas genetic information is represented in sequences of DNA molecules, cultural information is represented primarily in the brain. Viewing culture as comprised of discrete units of information, or memes, can potentially make a complex system

theoretically and empirically tractable, in the same way as the gene concept advanced biologists' understanding of biological evolution. Although memes can be characterised as vague entities with flexible and fuzzy boundaries, so can the modern concept of the gene. It should be remembered that there were at least 50 years of productive investigation into biological microevolution before the molecular basis of genetic inheritance was determined, and even now it is only partly understood.

A deeper understanding of the neural and molecular basis of culturally acquired information must rely on technological advances in, for example, neuroimaging techniques. However, we should also reserve the possibility that the same cultural information is specified by different neural substrates in different brains, severely limiting such methods for studying cultural transmission. In this case there may be no cultural equivalent to molecular biology, although models and methods examining cultural transmission at the behavioural and cognitive levels can still provide important insights.

Another possibility is that such methods will reveal that certain aspects of cultural transmission are *not* particulate and are better characterised in terms of a blending process. Even in this case, however, evolutionary models are still applicable (Henrich & Boyd 2002). Indeed, Darwin formulated his theory of evolution with little understanding of genes or Mendelian inheritance.

Delineation of the neural basis of cultural information will also bear on another oft-cited putative dis-analogy between biological and cultural evolution: that there is no clear equivalent to the genotype-phenotype (or replicator-interactor) distinction in culture. Loosely, we can speak of culturally acquired semantic information stored in brains as replicators and the expression of that information in behaviour or artifacts as their interactors. However, without further advances in memetics and neuroscience, such a division is somewhat speculative. It may prove that forcing cultural inheritance too tightly into the biological model is in this case unproductive (Aunger [2002], for example, has developed an alternative model of cultural transmission based on signal theory).

The delineation of the genotype-phenotype distinction will also bear on whether cultural inheritance can be described as "Darwinian" or "Lamarckian," the former maintaining Weismann's barrier between replicator and interactor, and the latter involving the inheritance of acquired phenotypic variation. Ultimately, we do not think that researchers should get too distracted by whether strict analogies to the replicator-interactor distinction can be drawn or whether cultural inheritance is Darwinian or Lamarckian, especially when the necessary neuropsychological evidence is lacking. Many of the methods described elsewhere in this article can be pursued despite a poor understanding of cultural transmission at the neural level.

3.6. Microevolution: General conclusions

The comparison between biological and cultural microevolution has produced mixed results. First, a well-developed body of theory exists which has drawn on the mathematical population genetic models within biology to provide a rigorous and successful analysis of cultural evolution. This is predominantly the work of gene-culture

coevolution, although neutral models of genetic drift have recently also been successfully applied to cultural traits.

Second, experimental and field studies of cultural microevolution typically lack the rigour of equivalent studies within experimental and field population genetics. Explicit tests for selection, such as the artificial selection paradigm or Endler's (1986) various tests for selection in natural populations, and quantitative measures of the strength of that selection, such as selection gradients, have not yet been employed. A number of opportunities exist for psychologists, field anthropologists, sociologists, and experimental economists to adapt some of these tools and methods developed in biology to the study of cultural microevolution.

Third, there is currently a limited correspondence between our understanding of molecular genetics and the molecular or neural basis of cultural inheritance. This is primarily due to limitations in the tools of neuroscience, such as imaging techniques, which cannot yet reveal exactly how information is acquired by and stored in the brain, nor the relationship between models of social learning and models of memory. Much potential exists, however, to develop further cognitive models of social learning.

4. Differences between biological and cultural evolution

Despite the plethora of studies reviewed above, which we have argued can be viewed as part of a larger field of cultural evolution, many of these studies, as well as the evolutionary approach in general, have yet to gain acceptance by mainstream cultural anthropology and related social sciences. One reason for this resistance is that many social scientists see a number of fundamental differences between biological and cultural change that, they argue, invalidate an evolutionary analysis of culture. We have already seen that upon closer examination of either the biological or the cultural evidence, a number of these purported differences become either illusory or unimportant to the validity of the comparison (e.g., the horizontal transfer of cultural information causing cultural lineages to blend and merge [sect. 2.1.2]; the apparent lack of discrete particles in culture equivalent to genes [sect. 3.5.2]; and the lack of a clear equivalent to the genotype-phenotype distinction and the related issue of Lamarckian inheritance [sect. 3.5.3]).

Another putative difference is the frequent argument that, whereas biological evolution is "blind" with respect to long-term goals (i.e., mutation is independent of selection), cultural change is often intentionally directed toward some specific goal (e.g., Bryant 2004; Pinker 1997, pp. 208–210). However, the extent to which culture is intentionally directed and the precise effect of this intention on long-term cultural change are empirical issues. In fact, studies of technological innovation (e.g., Basalla 1988) and creativity (e.g., Simonton 1995) suggest that successful inventions and discoveries are frequently either the result of trial and error or the unintended by-products of attempts to solve unrelated problems. Conversely, biological evolution is also to a degree directed in the sense that potential mutations, particularly the minority that will be subject to selection, are

heavily constrained by a species' history of selection (see Hull et al. 2001; Mesoudi et al. 2004). This is not to suggest that there are no differences here – on the contrary, "smart variants," biologically evolved biases in cognition and other cultural traits, may guide behaviour in a non-random direction (Laland et al. 2000). There is evidence of both directed and undirected variation in human culture, and the relative importance of each is currently unknown. We maintain that critics must empirically demonstrate that the existence of intent does in fact invalidate an evolutionary account of human culture, and moreover, must explain why many of the evolutionary methods discussed above (e.g., the phylogenetic analyses) work equally well for both biological and cultural evolution despite this alleged difference.

One potentially valid criticism of some accounts of cultural evolution is the treating of all cultural traits as equivalent. In previous sections we have described beliefs, behaviour, technological artifacts, languages, and social systems as examples of a somewhat simplistic notion of the "cultural trait." Undoubtedly, cultural evolutionary processes will sometimes act differently on different forms of cultural variation, frequently generating distinct evolutionary dynamics for each. It is already well established that vertically and horizontally transmitted traits, conformist transmission, and direct and indirect biases will each exhibit different but characteristic dynamics (Boyd & Richerson 1985). We have no doubt that the pattern and intensity of selection acting on fads and fashions will be quite different from that acting on established norms and institutions. In a sense, this is not too dissimilar to the biological case, where alternative traits may be subject to different forms of selection and where multi-level selection models are commonplace.

Plotkin (2002b) has furthermore argued that "social constructions," cultural traits such as justice or money that exist only because of shared agreement, require a fundamentally different explanation from concrete traits such as technological artifacts, and have no real equivalent in the biological domain. Like Plotkin, we do not believe that this invalidates an evolutionary approach to culture; rather, it requires a different evolutionary treatment from the one developed within biology. An evolutionary consideration of social constructions and a detailed taxonomy of cultural traits are, however, beyond the scope of this article. The important point is that deviations from the biological case such as this do not necessarily invalidate an evolutionary approach to culture; they merely require novel treatments of cultural phenomena within a general evolutionary framework.

5. Nonhuman culture

We end by considering the burgeoning literature that has emerged in the last few years regarding nonhuman social learning and culture (see Avital & Jablonka 2000; Byrne et al. 2004; Frigaszy & Perry 2003; Laland & Hoppitt 2003; Whiten 2005b; Whiten et al. 2003), which suggest parallels with the work on human learning and culture discussed above. Irrespective of the similarities and differences between human and animal culture, here we ask whether the above methods can be fruitfully employed to study the behavioural traditions of other species.

First, there is evidence from a number of species of behavioural traditions not obviously attributable to genetic or ecological differences, and hence thought to constitute socially learned cultural patterns. For example, Whiten et al. (1999; 2001) documented 39 putative cultural traits in chimpanzees from various regions of Africa, such as tool usage and grooming behaviour. Similar regional differences inferred to be cultural in origin have been observed in orangutans (van Schaik et al. 2003) and capuchins (Fragaszy & Perry 2003; Perry et al. 2003a), as well as in the vocalisations of birds (Catchpole & Slater 1995) and mammals (especially cetaceans: Janik & Slater 1997), and behavioural traditions in fish (Helfman & Schultz 1984; Warner 1990). There are obvious parallels here with the databases compiled by cultural anthropologists documenting worldwide geographical variation in human culture.

Second, Mercader et al. (2002) have used traditional archaeological techniques to excavate a site in Africa used by chimpanzees for at least the past 20 years to crack nuts using stone hammers and wooden anvils. Considerable evidence of past nut-cracking behaviour was uncovered, specifically nutshell and fractured stone, the latter of which the authors claimed was indistinguishable from a subset of the earliest and simplest stone tool assemblages left by hominid ancestors. Although the finds were probably very recent compared with the cultural artifacts studied by archaeologists, this study suggests that the same methods can potentially be used to uncover evidence of past nonhuman cultural behaviour.

Third, a number of studies have tracked the diffusion of innovations within nonhuman communities, paralleling the research tradition of the same name for human technology (Rogers 1995). The most famous case is the diffusion of potato-washing in a community of Japanese macaques (Kawai 1965). Lefebvre (1995) found that 16 of 21 reported cases of the diffusion of foraging innovations in primates exhibit a rapid accelerating pattern of adoption characteristic of cultural transmission (an example of which is the S-shaped distribution reported by Rogers 1995), although Laland and Kendal (2003) and Reader (2004) have expressed reservations about inferring learning mechanisms from diffusion curves. Whiten et al. (2005) have recently employed a more experimental approach to studying the spread of alternative foraging techniques in different groups, creating the potential to track diffusion dynamics more reliably.

Fourth, population genetic modelling has been used to analyse patterns of nonhuman culture, specifically birdsong. Lynch and Baker (1993) found that the geographical distribution of chaffinch songs can be accounted for by a neutral model in which mutation, migration, and drift are at equilibrium. Lachlan and Slater (1999) adopted gene-culture coevolution methods to find that vocal learning can be maintained in a “cultural trap” formed by the interaction between genes (which specify the constraints on songs) and culture (the songs themselves). Gene-culture coevolutionary methods have also been used to explore how song learning might affect speciation (Beltman et al. 2004) and the evolution of brood parasitism (Beltman et al. 2003).

Fifth, the experimental transmission chain method devised by Bartlett (1932) has been used to study the social learning of mobbing in blackbirds (Curio et al. 1978) and food preferences in rats (Laland & Plotkin 1990; 1993). Jacobs and Campbell’s (1961) replacement

method has been used to study the transmission of food preferences in rats (Galef & Allen 1995) and route preference in guppies (Laland & Williams 1997; 1998).

These various studies demonstrate that many of the same methods used to investigate biological evolution or human cultural evolution can be applied to nonhuman culture. Studying human and nonhuman culture within the same theoretical framework is likely to provide important insights into the evolutionary origins of human culture and the psychological mechanisms underpinning it.

6. Conclusions

The evidence discussed in this article suggests that much potential exists for a comprehensive science of cultural evolution with broadly the same structure as the science of biological evolution, as outlined in Figure 1. This potential is already being realised for the study of cultural macroevolution and the mathematical modelling of cultural microevolution, with methods developed within evolutionary biology, such as phylogenetic analyses and population genetic models, being applied to cultural data. A number of opportunities exist for psychologists, sociologists, and experimental economists to adopt the experimental methods and tools developed in population genetics to simulate cultural microevolution and detect cultural evolution “in the wild.” Finally, the study of the neural basis of cultural transmission is seemingly dependent on advances in new technologies that should reveal how culturally acquired information is represented in the brain.

We have also seen some examples where the explicit adoption of an evolutionary framework or evolutionary methods has provided significant advances over traditional nonevolutionary methods. For example, phylogenetic analyses have provided a solution for Galton’s problem when comparing societies related by descent, and evolutionary “population thinking” allows more accurate descriptions of archaeological artifacts than does an essentialist perspective.

One reason why evolutionary biology has been relatively successful is that a unifying evolutionary framework encourages and stimulates cross-disciplinary work. Some cross-disciplinary borrowing has already been seen in the study of cultural macroevolution, with phylogenetic methods increasingly used in both archaeology and cultural anthropology. As more researchers adopt the evolutionary framework outlined here, we anticipate the occurrence of more such borrowing. For example, experimental studies of cultural transmission might explicitly test the predictions of theoretical models, and empirical findings might in turn be used to inform the assumptions of further models. Experimental work might also simulate the findings of archaeologists and anthropologists to determine the possible transmission mechanisms underlying certain historical and geographical macroevolutionary patterns.

Although we advocate the adoption of a number of methods and approaches developed within evolutionary biology, we do not advocate the slavish and dogmatic imitation of evolutionary biology. Cultural inheritance is undoubtedly different in many respects from biological inheritance, and novel mathematical analyses and

empirical investigations into cultural dynamics that deviate from the biological case are necessary (Richerson & Boyd 2005). As noted above, cultural phenomena such as social constructions have yet to be dealt with in evolutionary terms. At the same time, however, these deviations do not invalidate an evolutionary framework. For example, subtle refinements of traditional biological methods have been found to enhance the validity of the mathematical modelling tradition described in section 3.1.2.

Furthermore, despite the impression perhaps given in this target article, we should also bear in mind that evolutionary biology is, like any other science, far from perfect and is continually changing and updating its methods. Indeed, evolutionary biologists may well benefit from considering evolutionary systems alternative to their own, or from utilising methods developed by social scientists.

In short, we submit that the argument that culture exhibits a number of key Darwinian properties is well supported and we advocate taking advantage of this in order to use evolutionary biology as a model for integrating a multitude of separate approaches within the social sciences and, where appropriate, borrowing some of the methods developed by evolutionary biologists to solve similar problems. Putting disparate studies from presently unconnected disciplines together into a broad evolutionary context adds value to each of the individual studies because it illustrates that the degree of progress in this area is far more impressive than hitherto conceived. We suggest that these studies can now be said to be aligned within a unified “movement” and that if this Darwinian evolutionary movement could be better coordinated, a more persuasive and important direction could be given to much work in the social sciences.

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Open Peer Commentary

Culture evolves only if there is cultural inheritance

Robert Aunger

Hygiene Centre, London School of Hygiene and Tropical Medicine, London WC1E 7HT.

robort.aunger@lshtm.ac.uk www.robortaugner.net

Abstract: Mesoudi et al. argue that the current inability to identify the means by which cultural traits are acquired does not debilitate their project to draw clear parallels between cultural and biological evolution. However, I suggest that cultural phenomena may be accounted for by biological processes, unless we can identify a cultural “genotype” that carries information from person to person independently of genes.

In their Introduction, Mesoudi et al. argue that culture is socially acquired information, and that cultural evolution is the selective retention of favourable cultural variants (plus drift). They also argue that cultural phenomena exhibit the necessary characteristics of an evolutionary process: variation, selection, and inheritance. Here, I would like to suggest that the cultural evolutionary literature has not yet determined whether the inheritance relation holds for cultural traits.

The authors argue that cultural evolutionary studies are currently in the state that characterized evolutionary biology prior to identification of genes as the unit of inheritance – we merely lack our Watson and Crick to identify the “memes” of culture. However, this historical analogy is a false one, because culture need not be independent of biology – indeed, genetic evolution may be able to account for the phenomena we consider to be cultural. The lack of knowledge about inheritance relationships was not such a problem for evolutionary biology because it was obvious that some sort of transmission process was necessary to account for the intergenerational similarity of phenotypes, with variation, observed in populations of organisms. However, it is possible for genetic or environmental processes to account for what many consider to be cultural behaviour, making cultural explanation superfluous (Aunger 2002). Richerson and Boyd (2005) argue, on the contrary, that there are many cases where the only explanation for group-specific behaviours is cultural transmission, because no environmental variable correlates with the distribution of such behaviours spatially, making an environmentally determinist explanation impossible. Such a case, they believe, implies the existence of cultural genotypes being passed from person to person through a social learning process which operates independently of physical environments.

However, evolutionary psychologists counter with the “jukebox model” – the idea that evolution may have stored sophisticated behavioural repertoires in our brains through prior natural selection which are triggered by environmental cues, much as a jukebox plays a particular record when a specific button is pushed (Tooby & Cosmides 1992). In the case of jukebox-like causation, the cues could be social, and as complex as the observation that most people in the local area are exhibiting a particular behaviour. The consequence is thus a change of behaviour by the observer of conspecifics – but the cause of the behaviour itself is not acquired as a result of observing the conspecific, only the choice of the behaviour. What has occurred is simply the operation of a bias rule: “when in Rome ...” Such rules, coupled with the retrieval of pre-existing behavioural knowledge from a mental storehouse, could account for the apparent group-specific and frequency-dependent nature of many cultural traits. Both the cultural transmissionist and jukebox accounts involve a form of social learning; however, the resulting evolutionary dynamics are quite different, because the jukebox model suggests that new behaviours are acquired only through individual learning and genetic assimilation, whereas the cultural transmissionist account can rapidly produce novel behaviours through a Lamarckian process of knowledge exchanged through imitation.

Neuroscientific advances concerning how brains acquire and store information can help us understand how individuals learn from their surroundings. However, even a precise understanding at a molecular level of how the brain stores information does not answer the central cultural evolutionary question: whether information is replicated through transmission between individuals. We need to establish that, in the process of communication, one brain produces speech (for example), and that this speech transforms the hearer’s brain. But we also need to know that the communication introduces new information to the hearer’s brain which resembles the information in the speaker’s brain that caused the speech in the first place. That would be a true relationship of inheritance and would constitute a process of information acquisition from others through a mechanism other than gene replication (Aunger 2002). Hence, models of

social learning must be matched to models of memory before we can determine whether units of cultural inheritance (cultural genotypes) exist.

A related argument often used to justify the assumption that there must be cultural transmission is the fact that human culture is cumulative: For each generation, there seems to be a larger store of knowledge which cannot have arisen through genetic causes; culture changes too fast to be genetic, in effect (Tomasello et al. 1993). However, it is possible that this accumulation is occurring not in people's brains but in the technological world we have created. Niche construction can result in the inheritance of information through the persistence of information-bearing artefacts from generation to generation (Odling-Smee et al. 2003). The interaction of social learning with artefacts makes humans such a powerful force for environmental change (Aunger 2002; Donald 1991). Again, the exact nature of the exchange of information between people and their technological products is not clear. It is possible that much of the "knowledge" associated with technological practices is embodied in "cognitive artefacts" themselves (Hutchins 1995), which "afford" humans the perception of increased intrinsic power (Norman 1988).

There are obvious examples of Darwinian processes involving information replication – and hence inheritance – through processes not involving genes. In one case, units of computer code – call them "instructions" – exist as states of computer memory (the instruction's genotype), but also have consequences that lead to the production of exact replicas in other machines through infection – epidemics of computer viruses, in effect. Similarly, prions are infectious proteins which can cause other proteins to acquire their information by reshaping them; the prion's genotype is an abnormal shape that can be duplicated through a process of refolding of another protein via contact with an existing prion molecule (Prusiner 1995). In both cases, non-genetic information is duplicated and spreads through a population of hosts (computer memory and protein molecules, respectively).

In some ways, it is thus clearer that evolutionary processes are occurring in the environment than in social groups of human beings. This is because it is still not known whether culture as normally considered – as a pool of information in people's heads modified via the inter-individual transmission of information – involves the transfer from person to person of a cultural genotype. As a result, it is still unclear whether culture evolves independently of DNA. We therefore need to identify a cultural inheritance process – and thereby exclude the possibilities of jukebox-like recall or niche construction as accounts of how individuals come to exhibit similar "cultural" behaviours – before the analogy the authors make between genetic and cultural evolution will be secure. How this project will be undertaken is not clear.

Vertical/compatible integration versus analogizing with biology

Jerome H. Barkow

Department of Sociology and Social Anthropology, Dalhousie University, Halifax, Nova Scotia, B3H 4P9, Canada.

Barkow@dal.ca <http://is.dal.ca/~barkow/home.htm>

Abstract: Vertical/compatible theoretical integration provides an alternative way of unifying sociocultural anthropology and related disciplines. It involves analyzing theoretical statements for their implicit and explicit assumptions at multiple levels of analysis and then determining whether these assumptions are compatible with consensus in the relevant disciplines (e.g., does the sociological theory include an assumption at odds with consensus psychology?). Incompatibilities indicate a need for further research. This approach is much more likely to salvage the bulk of humanities-oriented anthropology than is that of the authors.

Mesoudi et al. are to be congratulated for their survey of biology, and I agree with much of what they say. For example, sociocultural anthropology clearly has not progressed in the cumulative fashion of evolutionary biology. (Goody [1982, p. 8] is probably right in arguing that the former field tends to mistake mere changes in emphasis for progress.) I also agree with the authors' implicit position that training in biology (and psychology!) should be a prerequisite for training in anthropology. But here our reasons differ.

Biology may owe its integration to Darwin, but not necessarily its success. I have met biologists who know little of Darwin, whereas that branch of biology known as medicine achieved much even in its pre-Darwinian, pre-Ewald, and pre-Nesse and Williams days (Ewald 1994; Nesse & Williams 1994). No doubt the social sciences would benefit if more of its practitioners were trained in some area of biology. I suspect, however, that had the authors' expertise combined meteorology and anthropology, they would have made a similarly convincing case for the former field's probabilistic models promise of unity for the human sciences.

The authors' proposal neglects most of sociocultural anthropology and related fields. What they include is worthy, but they pay scant attention to the likelihood that very few of the field's practitioners are interested in modeling their endeavor on *any* science, whether biology or meteorology. Perhaps this is why we are reading this article where we are reading it, and not in *Current Anthropology*. Most of sociocultural anthropology has, in the past 25 to 30 years, joined the humanities. When social scientists speak of "theory" nowadays, they usually mean social philosophy and political commentary, and the research they conduct only occasionally involves hypothesis testing. This is not the place to discuss why this is true, but a glance at the table of contents of any issue of the *American Anthropologist* will confirm that it is indeed so. My point, however, is neither to condemn nor to lament this state of affairs but to recommend salvage.

Rather than seeking to rebuild the social sciences (largely) from those bits and pieces that have analogues in biology, an alternative both more modest and more feasible exists: the approach of vertical/compatible explanation (Barkow 1989a; 1989b; 2006; Cosmides et al. 1992; Walsh 1997). Not just biology but the sciences as a whole have been so successful in part because they take vertical integration for granted. This means, for example, that a chemist does not seek to reduce chemistry to physics but does assume that the principles of physics apply to every chemical process. Biologists do not reduce evolution to nothing but chemistry but do assume that biological processes are compatible with what we understand of chemistry. Scientific psychologists take care to ensure that their theories are compatible with biology (including evolutionary biology), as well as with chemistry and physics. And so forth. If we are to apply this idea to sociocultural anthropology and the rest of the human sciences, then their theories must be tested for compatibility with psychology (and biology, etc.). This is not a reductionist argument, and "compatible" does not imply "nothing but" – each level has its own theories, and no one would think to reduce ecology to chemistry or the social sciences to psychology. The approach is not necessarily even entirely hierarchical – theories of consciousness need to be compatible with what we know of neurophysiology but they may or may not be at the same level of organization.

Vertical/compatible integration is usually ignored in the human sciences as a matter of ideology (confusingly labelled "theory"). Most of sociocultural anthropology and sociology interprets Emile Durkheim as having established the principle that one must ignore the psychological. In practice, a non-psychological (often anti-psychological) approach is a group-identity marker and hence never questioned (see Barkow 1989b for discussion and exceptions). But vertical/compatible integration can, unlike the admittedly useful analogize-with-biology approach argued by the authors, rescue (in the

sense of “become part of mainstream science”) much of sociocultural anthropology and related fields.

The “rescue” involves applying the compatibility test. This task is possible and worth doing but not necessarily easy, given the often vague vocabulary and ever-changing buzzwords of the disciplines involved. The goal is to salvage the bulk of existing sociocultural anthropology – all those studies of that change-in-scale phenomenon now labeled “globalization,” all those multi-sited ethnographies, all those moral mission ethnographies seeking to expose social injustice – all of this simply wonderful, even if humanities-rather-than-science-oriented – anthropology. The material now becomes ore to mine and then to refine by passage through the compatibility sieve. Wherever a sociological assumption (e.g., the “glass ceiling” is socially constructed rather than a reflection of different male/female fitness interests) rings the incompatibility bell, there is a problem to be addressed. Perhaps one discipline is right and the other wrong, perhaps both are wrong – let us seek a grant to study the issue.

Academic disciplines are fairly autonomous, and it is very doubtful that most sociocultural anthropologists will pay attention either to the authors’ call for biology or to my own for vertical/compatible integration. Instead, humanities-oriented anthropologists will probably simply lose the turf war as policy-makers and the educated public turn to the hypothesis testers, the data gatherers, the mathematical model builders for their understanding of human societies. But I think that vertical/compatible integration represents a way of salvaging much of the existing discipline. Both the efforts advocated by the authors and the approach for which I am here spreading propaganda, are entirely compatible, and I would like to see both proceed.

Why we need memetics

Susan Blackmore

31 Berkeley Road, Bishopston, Bristol BS7 8HF, United Kingdom.

susan.blackmore@blueyonder.co.uk

<http://www.susanblackmore.co.uk/index.htm>

Abstract: Memes are not best understood as semantic information stored in brains, but rather, as whatever is imitated or copied in culture. Whereas other theories treat culture as an adaptation, for memetics it is a parasite turned symbiont that evolves for its own sake. Memetics is essential for understanding today’s information explosion and the future evolution of culture.

Mesoudi et al. have helpfully situated memetics within the framework of theories of cultural evolution. I disagree with parts of their formulation and suggest some further reasons why memetics is essential for understanding cultural evolution.

First, Mesoudi et al. claim that “A common assumption of memetics is that cultural knowledge is stored in brains as discrete packages of semantic information” (target article, sect. 3.5.2, para. 1). I disagree. This was not assumed by Dawkins (1976) when he invented the term “meme” thirty years ago this year, nor by Dennett (1991; 1995), nor by me (Blackmore 1999; 2001). Aunger (2002) does take this view, but otherwise it is mostly the critics of memetics who do so – aiding their attempts to demolish memetics.

There are at least three issues here: whether memes must be stored in brains, whether they are discrete, and whether they consist of semantic information. The discreteness issue is clearly dealt with by the authors, so I shall comment on the other two. Like others, I have argued that memes need not exist in brains, and this follows directly from Dawkins’s original formulation. He derived the term “meme” from the Greek *mimeme*, meaning “that which is imitated,” giving as examples “tunes, ideas, catch-phrases, clothes fashions, ways of making pots or of building arches.” Ideas (if such a vague term can be

pinned down) may arguably be thought of as semantic information in brains – depending on one’s definition of “idea” – but what about skills and fashions? A new skill copied from someone else undoubtedly involves changes in the brain, but these changes are not “semantic information” and in any case they are not what is copied; somehow, through the complexities of the human capacity for imitation, a second person ends up acquiring a new skill from having observed the first. By definition, whatever is copied in that process is the meme. This may be a hard concept to pin down and to build theories upon, but we miss the point if we think of memes as little bullets of information inside heads.

Mesoudi et al. also claim that “cultural information is represented primarily in the brain” (sect. 3.5.3). Since it is hard to measure quantities of cultural information, I cannot dispute this, but I would like to point out that as every day passes, more and more cultural information is being stored in computers and digital media of various kinds. Just as we can reconstruct a little of ancient Greek philosophy from the memes left behind by its proponents, so a future civilisation might reconstruct a great deal of our culture from the far more extensive memetic debris left behind. Memetics can handle this far better than other theories of cultural evolution, including the possibility that memes might continue to thrive and evolve even if all humans died.

Mesoudi et al. comment that there is no clear equivalent of the genotype/phenotype distinction in culture, an issue bearing on the vexed question of whether cultural inheritance is “Darwinian” or “Lamarckian.” I agree with them that without further advances the distinction is speculative, but I would like to go further.

Memes are relatively new on this planet, and their replication and storage has not yet settled down to anything like the efficient system adopted by genes. If evolutionary systems themselves evolve, then we should expect improvements in their copying and storage systems over time. The process of separating the genotype and phenotype protects against information loss and is an obvious improvement (more generally conceptualised as a shift from “copy-the-product” to “copy-the-instructions”; Blackmore 1999).

We can see that this shift has happened in memetic evolution in the past and it is still going on today. Unaided human imitation is crude and unreliable, entailing huge information loss, but human meme machines were only a first step in the coevolution between memes and their copying machinery. The evolution of language improved fidelity, and writing and printing presses improved fecundity and longevity, but more recently new processes have appeared that have a clear distinction analogous to Weismann’s barrier. An example is the program with which this commentary is being written – Microsoft Word. All over the planet there are millions of copies of this program that are all identical, or very nearly so. Yet each copy of Word leads to completely different documents, and it is the success of these documents that prompts people to buy copies of Word and the factories to turn out more of them. Copying the instructions for making documents leads to much faster evolution than copying the documents themselves.

So do we need memetics? Yes, because of the fundamental difference between memetics and all other theories of cultural evolution. This is best illustrated by Dennett’s (1995) powerful question “Who benefits?” According to other theories, culture is an adaptation, and (in spite of occasional maladaptive cultural traits) the genes will always, as Wilson puts it, “keep culture on a leash” (Lumsden & Wilson 1981). In this view humans or their genes are the ultimate beneficiaries. Until recently Boyd and Richerson’s theorising appeared to be close to memetics, but they have now made it clear that they do not consider memes to be replicators that evolve for their own sake (Richerson & Boyd 2005). So for them, too, culture is an adaptation.

According to memetics, culture is not and never was an adaptation. It began as a by-product of the evolved capacity for imitation that then took off on its own evolutionary trajectory, using us

humans to grow and evolve for its own benefit. It is more like a parasite turned symbiont than an adaptation.

This makes a big difference not only to how we understand human evolution but to our predictions for the future. Memetic evolution constructed human brains and is now building better, higher fidelity meme machines, including computers, the Internet, and digital media. For the moment we humans are essential to the further evolution of the memosphere, but there are already many memes created that never have contact with a human being, and there will be more. Memetics alone makes sense of this and will help us understand what is happening.

Analogies are powerful and dangerous things

Monique Borgerhoff Mulder,^{a,b} Richard McElreath,^{a,b} and Kari Britt Schroeder^b

^aDepartment of Anthropology, Graduate Group in Ecology, Population Biology Graduate Group, University of California at Davis, Davis, CA 95616;

^bDepartment of Anthropology, University of California at Davis, Davis, CA 95616.

mborgerhoffmulder@ucdavis.edu

<http://www.anthro.ucdavis.edu/faculty/monique/MBMWeb/>

[Moniqueshomepage.htm](http://www.moniqueshomepage.htm) mcelreath@ucdavis.edu

<http://arbeit.ucdavis.edu/mcelreath/> kbschroeder@ucdavis.edu

http://www.anthropology.ucdavis.edu/anthro/gprofile/gradprofile_e.cfm?id=70

Abstract: The analogy between biological and cultural evolution is not perfect. Yet, as Mesoudi et al. show, many of the vaunted differences between cultural and genetic evolution (for example, an absence of discrete particles of cultural inheritance, and the blurred distinction between cultural replicators and cultural phenotypes) are, on closer inspection, either illusory or peripheral to the validity of the analogy. But what about horizontal transmission? We strongly agree with the authors that the potential for horizontal transmission of cultural traits does not invalidate an evolutionary approach to culture. We suggest, however, that it does require a different evolutionary treatment.

Here, not to admonish the authors for oversight but to emphasize potential pitfalls in conceiving of the culture–biology analogy too narrowly, we list some common misconceptions about transmission modes.

1. First, any trait can be fed into a software program to produce, or map, a phylogeny. This does not mean that the phylogeny is the most accurate depiction of the trait’s history, nor that vertical transmission best accounts for its distribution. This may seem obvious, but a number of studies cited in the target article are founded on such erroneous logic.

The absolute value of a goodness-of-fit measure, such as RI or CI or even the familiar R^2 , is rarely informative. Rather, the same data must be analyzed with multiple models to make sense of measures of fit. Statistical measures developed to test for “treeness” are also of little help. They are based on strong assumptions about evolutionary process that cannot be casually applied to data produced by any evolutionary process. Indeed, all existing phylogenetic methods make strong assumptions about independence of lineages, rates of evolution, and other important aspects of descent, and biologists rarely employ any such method without first exploring its sensitivity to violations of these assumptions with simulated data. We fail to see how, without explicit models of cultural evolution and simulation studies, we can infer from published work that phylogeny provides the most accurate depiction of a trait’s history.

2. Most cultures are of course made up of multiple traits, each of which may have a different phylogeny. Untangling the distinct phylogenies of separate traits is complicated (McElreath 1997), but assuming that all traits have the same tree simply avoids the issue. Using a narrow range of conserved vocabulary to construct language classifications yields a narrow view of

language evolution – other aspects of language typically have different histories (Thomason & Kaufman 1988). Even among well-behaved biological species, different loci sometimes have different phylogenies (Enard & Pääbo 2004). Indeed, few geneticists would even attempt to construct a single phylogeny for the entire genome. The bulk of what we know about human history suggests strong mixing at many scales. Hence, assuming populations evolve independently, as typical maximum likelihood does, for example, is something few biologists are now willing to assume (Relethford 1998).

3. The authors support the use of a phylogenetic approach in comparative analyses to deal with Galton’s problem, claiming (sect. 4, para. 2) that “evolutionary methods . . . (e.g., the phylogenetic analyses) work equally well for both biological and cultural evolution.” Unfortunately, this is not true. A recent simulation study shows that as the prevalence of horizontal transmission of cultural traits between populations increases, so do Type I errors (rejection of a true null hypothesis) (Nunn et al. 2006). Importantly, a tiny amount of horizontal transmission is sufficient to cause serious problems. This parallels recent empirical work in biology which shows that trying to correct for phylogeny when working with rapidly evolving traits such as bird song can introduce serious error (Rheindt et al. 2004). More to the point, how can we claim that methods developed for analyzing genetical evolution work “equally well” for culture when we know, for example, how sensitive phylogenetic contrast analyses are to topological inaccuracies (Symonds 2002)?

4. The authors scrupulously differentiate macroevolutionary from microevolutionary questions, but others they cite have been less careful. Cavalli-Sforza and Feldman (1981) adopted the terms vertical and horizontal transmission from the field of epidemiology to denote, respectively, parent-offspring transmission and transmission between any two (usually unrelated) people. Soon these terms were adopted for use at the intergroup level, referring to traits that were spread from parent to daughter populations and between neighboring populations. Is an extrapolation from micro- to macroevolutionary processes legitimate? For example, from a study of Aka pygmies showing vertical transmission (parent-to-child) to account for a large majority of skills learned by children (80% of skills studied), is it appropriate to infer that Aka culture *as a whole* is highly conservative (Hewlett & Cavalli-Sforza 1986, p. 933)? The unstated assumption here is that the transmission patterns that occur within populations are the same as those that occur between populations. This, however, is untested because we have no measure of the extent of horizontal transmission between different populations, for example, between Aka and other pygmy populations, or between Aka and non-pygmy populations. Furthermore, even if all transmission is vertical, if there is any intermarriage between groups (or other kinds of immigration), vertical transmission within groups will not preserve variation between groups. A particularly clear example of the mismatch between transmission modes within and between populations, specifically inferring micro from macro patterns, comes from language. There is good reason to believe that portions of language are highly conserved within cultural lineages (Cavalli-Sforza et al. 1992), and yet we know that parents have limited influence on the language of their children after an early age; immigrant children do not speak their new national languages with their parents’ accents.

To be clear, we are not arguing that cultural evolution, because of horizontal transmission, invalidates an evolutionary approach, only that it requires novel treatment within a general evolutionary framework. More specifically, we think that some tree-based approaches are highly flawed (Borgerhoff Mulder et al. 2006) and need more thought (Eerikens et al. 2006). Analogies are powerful things. But returning to first principles and considering how cultural evolution functions in its own right are, in the long run, more powerful yet.

More generally, we think that this is a fabulous article – a wide-ranging and truly creative review, bristling with insight

and offering an inspirational glimpse into a very new kind of social science that may exist in the future. Our only concern is that readers may run with the ideas without thinking carefully about each step.

Evolutionary theory and the riddle of the universe

Denny Borsboom

Department of Psychology, University of Amsterdam, 1018 WB Amsterdam, The Netherlands.

d.borsboom@uva.nl <http://users.fmg.uva.nl/dborsboom>

Abstract: An effective restructuring of the social sciences around the evolutionary model requires that evolutionary theory has explanatory power with respect to the spread of cultural traits: The causal mechanisms involved should be structurally analogous to those of biological evolution. I argue that this is implausible because phenotypical consequences of cultural traits are not causally relevant to their chances of “survival.”

That there exists a certain likeness between the evolution of species and the manner in which cultural traits are propagated, stands beyond doubt. Before we jump to conclusions and start remodeling the social sciences according to the evolutionary blueprint that biology provides, however, it is important to have a clear indication that the evolution of cultural traits is not merely similar to biological evolution, but structurally analogous to it. Therefore, the important question is not whether models based on evolutionary theory are roughly *descriptive* of the spread of cultural traits, but whether the evolutionary model has *explanatory power* with respect to the process by which that spread occurs. And for this to be the case, the model has to get the causal mechanisms of the process right.

In the story “The Riddle of the Universe and Its Solution,” Czerniak (1981) describes a situation that would allow for a positive verdict on this score. It is useful to examine this situation, because it rather glaringly differs from the situation that we find ourselves in with respect to the propagation of ideas and other cultural traits. Czerniak imagines that, for humans, there exists an idea analogous to a Gödel sentence for computers. People who have this idea go into a catatonic state from which they are unable to recover. The propagation of such an idea (or rather, the process by which it goes extinct) would be truly analogous to biological evolution. The reason for this is that the causal system at work would be structurally analogous to selection of genes by biological evolution: A phenotypical consequence of having the Gödel idea (namely, going into catatonic state) is itself responsible for its lower chances of being propagated – just as the phenotypical properties associated with genes may cause their bearers to go extinct.

The fact that this story strikes us as science fiction suggests that, in reality, it does not work like this. At least on the face of it, the propagation of ideas and other cultural traits does not involve selection on their phenotypical properties (if that term is at all well defined). Ideas, artifacts, and other cultural traits are subject to changing levels of popularity, sometimes as a result of their becoming more or less useful over time, sometimes because of other factors. But surely the decline in popularity of, say, Dixieland music is not due to any phenotypical consequences of liking Dixieland music. In point of fact, liking Dixieland music does not prevent one from giving away Dixieland records for free, however much the decline in popularity of such records in the human population may resemble the evolutionary process by which genes become infrequent in a population of animals. In contrast, such a connection does exist between having a gene and being able to propagate it (namely, if the gene is bad for you, you die before you get the chance to propagate).

Mesoudi et al. attempt to anticipate the problem of identifying such causal mechanisms by stating that “just as Darwin formulated his theory of evolution with little understanding of genes or Mendelian inheritance, a theory of cultural evolution likewise does not necessarily have to rest on the existence of memes or particulate cultural transmission” (sect. 1, para. 12). But this confuses an ontological condition with an epistemological one. The relevant issue here is not whether Darwin *knew* about the mechanisms of inheritance via genetics; the relevant issue is that such mechanisms *exist* and are *causally relevant* to the biological phenomena that we want to explain. In other words, what convinces us of the usefulness of the evolutionary framework in biology has nothing to do with the epistemological position Darwin was in when working out the principles of evolutionary theory; it has to do with the fact that his theory, by and large, appears to be true.

The biological sciences are organized around evolutionary theory because evolution has causal relevance for each of the disciplines involved. For a similar organization of the social sciences to be an effective restructuring, rather than a case of plastic surgery, it is important to show that such causal relevance also exists for the various disciplines that make up the social sciences. Hence, the mechanisms by which cultural traits are propagated cannot be sidestepped as easily as Mesoudi et al. suggest, and they would, therefore, do well to offer some convincing arguments for the existence of such mechanisms. Otherwise our restructured social science, modeled after the biological plan, will be like a toy model of a Boeing 747. It will look just the same, but it won't fly.

It is not evolutionary models, but models in general that social science needs

Bruce Bridgeman

Department of Psychology, University of California, Santa Cruz, Santa Cruz, CA 95064.

bruceb@ucsc.edu <http://psych.ucsc.edu/faculty/bruceb/>

Abstract: Mathematical models are potentially as useful for culture as for evolution, but cultural models must have different designs from genetic models. Social sciences must borrow from biology the idea of modeling, rather than the structure of models, because copying the product is fundamentally different from copying the design. Transfer of most cultural information from brains to artificial media increases the differences between cultural and biological information.

Mesoudi et al. make a plea for the use of evolutionary models, developed for analyzing genetic evolution, in analyzing cultural influence and change. Indeed, they provide many illuminating examples of the usefulness of modeling in social sciences, but the connection to mathematical models of biological evolution is often indirect, sometimes only metaphorical. For example, in section 2.1.2 the authors cite Mace and Pagel (1994), who treat cultural traits as equivalent to biological characters, with independent instances of cultural change occurring when a cultural trait is invented, acquired from another culture, changed, or lost. This situation is very different from biological evolution, though, where “acquired” is not a possibility. Further, cultural traits are not like Mendelian units, independent of one another – they influence one another, they have different sizes and different nestings, and, as Mesoudi et al. note, they are frustratingly difficult to define.

Under these conditions, it is surprising that models developed to analyze biological evolution are also useful for looking at cultural development. But the value of the models may stem not so much from their link to evolutionary theory as from the way that they force investigators to define terms, use consistent categories, and in general discipline their data. Mathematical

models are also useful to identify ill-defined concepts or relationships, and to find unsuspected relationships among variables.

A particularly useful function of modeling is to uncover hidden assumptions in a discipline. A ground assumption of cultural anthropology, for example, might be that cultures are coherent, independent entities, and that a given person belongs to only one of them. Perhaps it was inevitable that many anthropologists came to think in this way, because our evolved capabilities for social reasoning revolve around individual people who have distinct traits and personalities; we use this capability to assign characteristics to groups, using the mental machinery that evolved in us to understand individuals (Bridgeman 2003, pp. 178–79). The pioneering modeling of Boyd and Richerson (1985), done without the concept of culture as a critical variable, showed the value of modeling social interactions but also showed how different the resulting models were from mathematical descriptions of biological evolution. In short, what social sciences must borrow from biology is not the models themselves, but a commitment to mathematical description of phenomena and modeling of the processes in which they engage.

The studies of cultural selection reviewed in section 3.3.3 highlight the structural differences between models of biological evolution and models of cultural change. The “selection” of cultural traits is different from selection of genes in a way that Susan Blackmore (1999) colorfully and effectively explained in her example of copying a pumpkin soup. I can ask for the recipe, and reproduce the soup according to a constant set of instructions, so that the similarity of my soup to hers is limited only by the similarity of available ingredients (the environment). If I change the soup, most of the recipe remains the same. Copying the recipe is analogous to genetic inheritance. Alternatively, I could go home and try to reproduce the soup by guessing at the ingredients, basing my guesses on the flavor and texture of the soup that I had experienced. This copy-the-product strategy is the pattern of cultural inheritance, which Blackmore points out is fundamentally different from copy-the-plan structures.

Another questionable assumption about the informational contents of culture appears in section 3.5.3, where Mesoudi et al. assume that cultural information is represented primarily in the brain. Merlin Donald (1991) has pointed out that this was once the case, before reading and writing made it possible to store information outside the brain. Today not only books but a vast array of technical aids store information and move it around the world, making much of the content of our culture so accessible that it is no longer necessary or even advantageous to store content in the head. Our minds are filled largely with pointers to the information we need, rather than the information itself. The transfer of cultural information to film, video, books, and other media vastly increases the richness and magnitude as well as the accessibility of the information, potentially enhancing cultural change even while making brain-based models of it obsolete.

In conclusion, I will stick with Plotkin (2002a): Differences between genetic evolution and cultural change are fundamental. They follow different rules and should be kept distinct even while both are modeled mathematically.

Intelligent design in cultural evolution

Lee Cronk

*Department of Anthropology and Center for Human Evolutionary Studies,
Rutgers University, New Brunswick, NJ 08901-1414.*

lcronk@anthropology.rutgers.edu

<http://anthro.rutgers.edu/faculty/cronk.shtml>

Abstract: Intelligent design, though unnecessary in the study of biological evolution, is essential to the study of cultural evolution. However, the intelligent designers in question are not deities or aliens but rather humans going about their lives. The role of intentionality in

cultural evolution can be elucidated through the addition of signaling theory to the framework outlined in the target article.

Darwinian aspects of cultural evolution were first identified long ago (e.g., Schleicher 1863). Mesoudi et al. update this analogy and make a convincing case for a unified science of cultural evolution that parallels the science of evolutionary biology. However, as Mesoudi et al. acknowledge, such a science must differ from evolutionary biology in a number of ways. One important difference, which they deal with quickly, is the active, often intentional role that humans play in cultural transmission and, thus, in cultural evolution. Although the notion of intelligent design is unnecessary in the study of biological evolution, it is essential to the study of cultural evolution. The intelligent designers in question, however, are not deities or aliens but rather humans going about their lives.

When they do address the active role that individuals play in cultural transmission, Mesoudi et al.’s interest in long-term cultural evolutionary trends leads them to focus on technological innovation and creativity. They are correct that the impact of human intentionality on long-term cultural change in those realms is an empirical question and that recognition of intentionality does not undermine the approach they advocate. But those of us who live, work, and study in the here-and-now, minute-by-minute, day-by-day, down-and-dirty, nitty-gritty reality of everyday human social life are constantly faced with the fact that the cultural pools in which we swim are at least stirred, if not created, by human intentions. When we study cultural change and other human phenomena on the short timescales of everyday life, grand analogies between biological and cultural evolution tend to become less interesting than the question of how our evolved psychological and behavioral propensities play themselves out in the things we say and do.

Furthermore, even very drastic cultural change is possible on short timescales, and even if such episodes can be phrased in the language of cultural evolution, it is not clear what is gained by doing so. For example, I have documented a brief episode of extreme culture change among the Mukogodo of Kenya (Cronk 1989; 2002; 2004). In the space of little more than a decade, the Mukogodo shifted from speaking a language called Yaaku, living in caves, hunting, and keeping bees to speaking Maa, living in houses, and keeping livestock. This was surely an instance in which a particular meme pool was drained and refilled in short order, but pointing that out seems much less interesting than exploring the reasons why Mukogodo individuals chose to make such a swift and radical change. Those reasons certainly do involve the question of what memes they had available to them – they adopted those of their new neighbors rather than inventing entirely new ones or adopting those of some more distant group – but they also concern the strategies Mukogodo individuals employed to obtain food, find mates, communicate, keep warm at night, stay dry when it rained, gain respect, and so on.

One interpretation of this argument might be that even if cultural evolutionary theories like those described by Mesoudi et al. are relevant to long timescales, human phenomena at shorter timescales are best studied using non-evolutionary methods. I reject that interpretation and seek instead a way to remain within an evolutionary framework while focusing on phenomena that people experience in their everyday lives. Elsewhere (Cronk 1991; 1994; 1995; 1999; 2005) I have argued that this can be accomplished by using animal signaling theory to study signals that humans construct primarily out of the cultural raw materials they have at hand.

With signaling theory, one can simultaneously acknowledge the role of intentionality in human affairs, remain within an evolutionary framework, and study human culture. Mukogodo ethnic signaling, for example, is better understood through an application of signaling theory (Cronk 2004). Since the early twentieth century, the Mukogodo have had limited success in raising their status by adopting the language, clothing, subsistence, religion,

and even stated offspring sex preferences of higher-status Maasai. Their difficulties in convincing anyone that they are real Maasai makes sense in light of signaling theory. Signals, including ones about ethnicity, are believable only if there is some guarantee of their truthfulness. One way to provide such a guarantee is to make a signal difficult to fake, and ethnic signals generally have that quality. Mukogodo awareness of this is shown by the fact that they chose to emulate the Maasai, who were removed from the area by the British in the early twentieth century, rather than the remaining high-status Maa speakers in the region, the Samburu. Whereas no Maasai were left to challenge Mukogodo claims to Maasai identity, any claims to Samburu identity could easily have been dismissed by the Samburu themselves. Other applications of signaling theory to human affairs include studies of fishing (Sosis 2000), hunting (Bliege Bird et al. 2001), dancing (Brown et al. 2005), cosmetics (Cronk et al. 2002), engagement rings (Cronk & Dunham 2003), political rhetoric (Johnson 1986; 1987; 1989; Salmon 1998), kin terms (Chagnon 1988; 2000), religion (Cronk 1994; Irons 1996; Sosis & Alcorta 2003), and interpersonal communication (Gerkey & Cronk 2005).

Signaling, which generally occurs at very short timescales, clearly belongs in the category of microevolutionary processes. The question arises, therefore, of how to relate it to other microevolutionary process and to cultural macroevolution. One approach to this problem is to emphasize the aspects of signaling theory that focus on receiver psychology (Guilford & Dawkins 1991). The basic idea is simple: Signals, whether they are designed by natural selection or by advertising executives, should be designed to fit the psychology of the intended receiver. Similarly, cultural traits may be more successful in persisting in the minds of individuals and in being replicated if they are memorable and attention-grabbing (e.g., Boyer 1994 on religious concepts). In this way, evolved human psychology becomes the link between the short life of an individual signal and the long life of a cultural tradition, and intentionality can be given the role it deserves in the unified science of cultural evolution outlined by Mesoudi et al.

A continuum of mindfulness

Daniel Dennett and Ryan McKay

Center for Cognitive Studies, Tufts University, Medford, MA 02155.

Daniel.Dennett@tufts.edu ryanmckay@mac.com

<http://ase.tufts.edu/cogstud/incbios/dennett/dennett.d.htm>

<http://homepage.mac.com/ryanmckay/>

Abstract: Mesoudi et al. overlook an illuminating parallel between cultural and biological evolution, namely, the existence in each realm of a continuum from intelligent, *mindful* evolution through to oblivious, *mindless* evolution. In addition, they underplay the independence of cultural fitness from biological fitness. The assumption that successful cultural traits enhance genetic fitness must be sidelined, as must the assumption that such traits will at least be considered worth having.

Mesoudi et al. provide a valuable survey of the parallels between biological and cultural evolution, but they ignore or underestimate several other parallels that go some way to explaining the intensity of the distaste with which many researchers in the humanities and social sciences view *any* attempt to introduce Darwinian thinking into their domains. When Darwin first proposed sexual selection as a significant factor in biological evolution, it was greeted with both dismay and delight: To some it was an ominous backslide from the mindless purity of natural selection, whereas to others it was a welcome relief, restoring cherished elements of “mind” into evolution (Cronin 1991; Dennett 1995). But Darwin had already shown us the continuum from foresighted attempts to redesign nature through to utter mindlessness in his trio of *methodological* selection (in deliberate

breeding and crossing), *unconscious* selection (in early domestication – which we might call domestication *without intent*), and *natural* selection proper, which invokes no minds or cognitive discriminations at all. It is important to avoid the common misconstrual that views methodical and unconscious selection as *alternatives* to natural selection, rather than as special *varieties* of natural selection, in which the selection pressure is focused through events in the nervous systems of the domesticating species. There is nothing counter-Darwinian, of course, in either phenomenon; intelligence *did* evolve by natural selection “proper” and thereupon became a potent selective force in the environment. Early domestication was thus an interspecific variation on sexual selection, in which the (cognitive) eye of the selector plays a crucial – but, of course, non-miraculous – role (Miller 2000). Neither the choosy females nor the early keepers of animals needed to understand their role in the “improvement of the breed.” To these selective phenomena we can add the more recent and still more mind-requiring tinkering of genetic engineering. The processes of generate-and-test that yield the would-be replicators come in all varieties of intelligence, but in the end, as Crick reminds us, Orgel’s Second Rule applies: Evolution is cleverer than you are (Dennett 1995).

What many thinkers in the humanities and social sciences find abhorrent in evolutionary perspectives is the imagined implication that any such model will replace the traditional freedom of will, rational authorship, and artistic genius imputed in their disciplines with mindless random mutation and mechanical selection. And indeed, in cultural evolution, as Mesoudi et al. make abundantly clear, there are undeniable cases of cultural features that evolve by Darwinian processes without any need to invoke authors, designers, or other intelligent creators. Most obviously, languages – words and pronunciations and grammatical features – evolve without any *need* for grammarians, deliberate coiners, or other foresighted guardians of these cultural items. But what Mesoudi et al. never properly acknowledge is that the traditional perspective of the humanities, in which intelligent authorship, foresighted, purposeful reasoning, and artistic judgment occupy center stage, also has a place in the evolutionary picture, so the dread of the humanists is misplaced. Again, there is a continuum, with many different levels of mindfulness or rational engagement to be discerned. There is unconscious selection (as Darwin would say) of musical styles, for instance, methodical selection (with much planning and debate) of political arrangements and elements of religious dogma, for example, and attempts at *memetic* engineering by advertisers and even scientists seeking the best – most vivid and unforgettable – acronym for their novel theory or investigative method. And here, as before, Orgel’s Second Rule applies. No matter how intelligent, foresighted, and purposeful the local process may be, most of the brainchildren of human cultural vectors fail to found long-lived lineages.

Another point that is underplayed in the target article is the extent to which cultural traits can flourish or perish independently of their effects on our genetic fitness. Because cultural evolution can occur in orders of magnitude faster than genetic evolution, many of its prominent patterns must be stabilized by forces that are only weakly related, at best, to the reproductive success of their vectors. The default presumption that all cultural traits that do evolve will be fitness-enhancing needs to be firmly set aside. Mesoudi et al. are right that this assumption is not uniformly made, but it is often tacitly implied or suggested by the way people write about cultural evolution. For example, the fact that some form of religion is found in every human group that has ever been studied leads many to conclude that religion *must* be enhancing to either individual or group fitness, but this is a serious non sequitur; the common cold also is found wherever there are people, but presumably it is not fitness-enhancing at all. It has evolved because it could evolve.

One may, of course, treat these shifting features of human culture as mere “noisy” variation around the few cultural traits

that do have a clear and measurable positive impact on genetic fitness, but this squanders the opportunity to see them as having their own fitness, as symbionts competing for rehearsal space and for opportunities to leap from host to host. The arms races that are conducted within each of us between our immune systems and our pathogens are themselves evolutionary phenomena, on a fast timescale, and they, too, have their parallels in cultural evolution. We certainly do not evaluate our ideas on the basis of their contribution to our *genetic fitness* – most of us do not care much about that goal – and the standards we do adopt are themselves products of cultural evolution. Even the presumption that any cultural item that spreads widely will at least be *deemed* (rightly or wrongly) to be worth having must be set aside, as it may instead be an unappreciated or even detested item that is just too well entrenched for the local coalition of cultural antibodies to remove. Advertising jingles are good examples.

We are largely in agreement with Mesoudi et al. about the parallels they describe, but think they have overlooked these further points that may prove equally fruitful in the project of studying culture with a unifying evolutionary framework.

Evolution is important but it is not simple: Defining cultural traits and incorporating complex evolutionary theory

Agustín Fuentes

Department of Anthropology, University of Notre Dame, Notre Dame, IN 46556.
afuentes@nd.edu

Abstract: Examining homology in biological and cultural evolution is of great importance in investigations of humanity. The proposal presented in the target article retains substantial methodological weaknesses in the identification and use of “cultural traits.” However, with refined toolkits and the incorporation of recent advances in evolutionary theory, this overall endeavor can result in substantial payoffs for biological and social scientists.

Mesoudi et al. present the premise that human culture undergoes Darwinian evolution and that key aspects of biological evolutionary patterns can be applied to the understanding of cultural change. The goal of this article is to promote a “more progressive and rigorous science of culture” (sect. 1, para. 3). However, as with the majority of treatments of this topic (cf. Richerson & Boyd 2005), the authors rely too heavily on psychological and linguistic examples. They do not attempt incorporation of a wide range of ethnographic data sets (the most overt nod to ethnography is a few paragraphs in sections 2.3.2 and 3.3.2) and they focus on uses of “culture” and “cultural traits” that most anthropologists will find problematic. Here I critique this key area and suggest a few additional evolutionary perspectives that could be useful in this project.

Simplifying assumptions have become a mainstay in biological theorizing. The immense complexity in genomic, developmental, and other biological systems has led to the use of simple models to create baseline parameters for assessing the mechanisms of said systems. Cultural systems, however, may not be as homologous to biological ones as is assumed by the authors of this article. They assert that one can overcome Galton’s problem by treating “cultural traits” as equivalent to biological characters. They also suggest that because vagaries in biological units (such as “gene”) do not inhibit the use of evolutionary models, the relatively vague “cultural trait” units are also amenable to similar applications (see sect/2.1). They state that the “apparent lack of discrete particles in culture equivalent to genes” (sect. 3.5.2) is not an inhibitor to the use of basic Darwinian models for cultural change. The authors do address the contention that there may be substantial differences between patterns of biological

and cultural change (see sect. 4), but do not incorporate these perspectives into their analyses of mechanisms in any central manner (sects. 2 and 3).

The authors use the term “cultural trait” at least 27 times without offering an explicit definition. In section 2.1.2 they suggest that cultural traits are things such as “language, tools, customs, or beliefs.” Of the many cultural traits mentioned in the article, the majority used in concrete examples supporting homology with biological systems are aspects of language or results from tests conducted by English-speaking experimental psychologists and economists. Others include patents, guns, teddy bears, stone tools, kinship patterns, behavioral rules, dairy farming, justice, money, the electric motor, the QWERTY keyboard, and religious beliefs, for example. A significant problem with this use of “cultural trait” is the lumping together of diverse elements that may not share common structural components or patterns of heritability.

If we are interested in modeling selection on cultural traits, we can look to two levels: phenotypic interactions with environments and other phenotypes, and trait-trait competition. That is, traits do not exist in a vacuum (biological or cultural), and therefore understanding of the phenotype (or the phenogenotype for bio-cultural contexts, sect. 3.1.2) in which they participate is core to modeling an evolutionary system. Alternatively, one can ignore the complexity at the phenotypic level and model trait-trait competition (usually seen as allelic competition in biology). However, any competition model must utilize similar “competing” units. Although section 3 of the article goes to great lengths to suggest that cultural and biological patterns of inheritance and change are roughly equivalent, the examples Mesoudi et al. provide often do not form compatible units for comparison. Psychological and economic experiments using two-choice option models may not be equivalent units to multiple chain event transmission sequences (sect. 3.2.2). Transmission of how to behave at a restaurant (a highly culturally contextual “unit”) may not break down into the same units as anagram-solving choice tests.

The biological examples provided in section 3 use overt behavioral and physiological measurements or assessments, whereas most psychological and anthropological research relies on perceptions, semantic exchanges, and culturally contingent decision processes. Measuring the constituent “traits” in cultural phenotypes can be a very different process with distinct results compared to biological systems and traits (however they are defined). A significant contribution to this endeavor would be the creation of specific definitions and measurement tools that can effectively represent diverse types of cultural patterns and elements. By moving these inquiries beyond an over-reliance on the most easily quantifiable cultural elements, such as those emerging from many language studies, we could achieve a more accurate comparison between systems of biological and cultural change.

It is possible that the landscape (environment or ecology) in which culture exists and changes may not be best, or primarily, amenable to modeling by standard neo-Darwinian approaches. However, recent enhancements of Darwinian perspectives such as developmental systems theory (Oyama et al. 2001) and niche construction theory (Odling-Smee et al. 2003) may offer more appropriate tools for the synthesis that Mesoudi et al. are proposing. Kevin Laland, an author of the target article, is also one of the major proponents of niche construction theory. I am surprised at the relative absence in the target article of this important addition to modern evolutionary perspectives. I suggest (echoing Odling-Smee et al. 2003) that niche construction may be a highly appropriate model for understanding patterns of human change. It may also be that developmental systems theory, with its emphasis on joint determination by multiple causes, extended inheritance, context sensitivity and contingency, and development as construction (Oyama et al. 2001), provides a more complex and contingent, but ultimately more satisfying, model for understanding homologies between

biological and cultural systems. The target article would have benefited from the inclusion of these theoretical perspectives as potential means for examining the homologies between cultural and biological evolutionary patterns.

I think that there is a great potential for collaboration between social and biological scientists in assessing the patterns and contexts of biocultural change. However, any such attempts (whoever initiates them) must make greater efforts to include multiple voices and perspectives, even if they make it increasingly difficult to rely on simple modeling as a major explanatory tool. Evolution is important, but it is not simple.

The role of psychology in the study of culture

Daniel Kelly,^a Edouard Machery,^b Ron Mallon,^c Kelby Mason,^a and Stephen P. Stich^a

^aDepartment of Philosophy, Rutgers University, New Brunswick, NJ 08901-2882; ^bDepartment of History and Philosophy of Science, University of Pittsburgh, Pittsburgh, PA 15260; ^cDepartment of Philosophy, University of Utah, Salt Lake City, UT 84112.

dankelly@rci.rutgers.edu machery@pitt.edu
rmallon@philosophy.utah.edu mason@philosophy.rutgers.edu
stich@rucss.rutgers.edu <http://www.pitt.edu/~machery/>
<http://www.philosophy.utah.edu/faculty/mallon/index.html/>
<http://www.rci.rutgers.edu/~stich/>

Abstract: Although we are enthusiastic about a Darwinian approach to culture, we argue that the overview presented in the target article does not sufficiently emphasize the crucial explanatory role that psychology plays in the study of culture. We use a number of examples to illustrate the variety of ways by which appeal to psychological factors can help explain cultural phenomena.

The target article makes three main claims. The first, a claim about culture itself, maintains that culture exhibits key Darwinian evolutionary properties. The second and third claims are about the study of culture. According to the second, research on culture can and should take a broadly Darwinian stance that borrows many of the theoretical assumptions, analytic tools, and experimental methods of evolutionary biology. The third claim is an account of a unifying framework within which that research should be organized: “the structure of a science of cultural evolution should broadly resemble the structure of evolutionary biology” (sect. 1, para. 2). Though we agree wholeheartedly with the first two claims, we find the third less convincing. For while the proposed account is useful, it is also importantly incomplete because it fails to clarify or sufficiently emphasize the central explanatory role that *psychology* is likely to play in the emerging science of culture.

Research has already shown that a number of features of the species-typical human psychological endowment influence cultural evolution along a variety of dimensions. For instance, the content of some cultural variants makes them more likely to be socially transmitted than others, and the increased frequency of such variants is often explained by the influence of *content biases* on social transmission processes. These content biases are, in turn, often explained by appeal to the operation and properties of psychological mechanisms. For example, Heath et al. (2001) showed how the psychology of disgust can influence the horizontal transmission of cultural variants. They found that the more likely an urban legend was to trigger disgust, the more likely it was to be passed along to peers and to appear on urban legend Web sites. Nichols (2002) showed that disgust can also bias the vertical transmission of cultural variants. He found that etiquette norms of the fifteenth and sixteenth centuries that prohibited actions likely to induce disgust were significantly more likely to have survived to the present than those that did not.

Appeal to psychological mechanisms can also help uncover and explain other important regularities relevant to the science of culture. Fessler and Navarrete (2003) showed that although details differ from one culture to the next, taboos regulating the consumption of meat were found in nearly all investigated cultures. The cross-cultural recurrence of meat taboos is explained, in part, by psychological factors, specifically the salience of meat to the human disgust mechanism. Machery and Faucher (2005; forthcoming) call attention to another instance of the pattern of local variations on a theme that is present in all or most cultures. Although races are conceptualized differently across cultures, a common theme is identifiable in the various conceptualizations: Races are cross-culturally conceptualized as biological entities. Following Gil-White (2001), Machery and Faucher argue that this puzzling regularity is explained by the character of the psychological mechanisms that underlie racial cognition: The observable cues associated with race mistakenly trigger a hypothesized system for *ethnic* cognition, and that system employs a folk biological mechanism as one of its constituent subsystems.

Other, more comprehensive projects, such as the recent work on religions and religious beliefs (Boyer 2001; Atran 2002), offer additional rich and suggestive examples of the substantive explanatory role psychology can play in the investigation of culture. Although the complex intersection of psychological and cultural phenomena is not yet completely understood, these examples begin to illustrate the range of ways in which psychological factors have already been shown to exert profound influence on social transmission and cultural evolution. This suggests to us that psychology should be deeply integrated into the foundations of a science of culture.

This perspective points to potentially fruitful lines of future inquiry as well. For instance, some of the most promising theoretic work on cultural evolution might be enhanced by more detailed psychological research. Theoretical models and experimental evidence show that the transmission of cultural variants is strongly influenced not just by their content, but also by the local social context of their transmission: Conformity and prestige biases lead people to adopt, respectively, cultural variants common among their peers, and variants adopted by prestigious members of their culture (Boyd & Richerson 1985; 2005). In much of that work, conformity and prestige are characterized behaviorally, and little is yet known about the nature of the psychological mechanisms underlying conformity and prestige biases (though see Henrich & Gil-White 2001; McElreath et al. 2005). Discovering more about those mechanisms' internal structure, the observable cues in the social environment to which they are sensitive, and the manner in which they process information about those cues promises to shed light on the cultural evolutionary dynamics that they influence. Perhaps more important, as in the case of racial cognition, idiosyncrasies uncovered in the functioning of the psychological mechanisms underlying conformity and prestige bias could provide resources for explaining the more puzzling aspects of the cultural phenomena they affect.

Despite the valuable overview provided by the target article, the organizational framework it proposes does little to emphasize or elucidate the significance of such psychological factors in explaining cultural phenomena, and thus leaves an important ingredient out of its account. Perhaps this indicates that the similarity to evolutionary biology is at best a partial one, and that nothing in evolutionary biology corresponds to the central role we maintain psychology will play in the study of cultural evolution. Alternatively, it could indicate that the analogy indeed holds, but the account of evolutionary biology is incomplete as well. Indeed, psychological factors such as sensory biases have been shown to have a powerful influence on biological evolution via the process of sexual selection (Miller 2000). Either way, we agree with the authors that such limitations do not “invalidate” an evolutionary approach to culture. Rather, they suggest that the account needs to be enriched to underscore the important role of psychology in the study of culture.

Evolutionary social science beyond culture

Harold Kincaid

Department of Philosophy, University of Alabama at Birmingham, Birmingham, AL 35294-1260.

kincaid@uab.edu <http://www.uab.edu/philosophy/kincaid>

Abstract: Mesoudi et al.'s case can be improved by expanding to compelling selectionist explanations elsewhere in the social sciences and by seeing that natural selection is an instance of general selectionist process. Obstacles include the common use of extreme idealizations and optimality evidence, the copresence of nonselectionist social processes, and the fact that selectionist explanations often presuppose other kinds of social explanations.

Mesoudi et al. do a nice job of arguing for the usefulness of evolutionary models in the social sciences. In what follows, I suggest that they both understate their case and underestimate some of the problems that evolutionary models face in the social sciences.¹

There are substantial bodies of social science research employing variation/selection/retention models that Mesoudi et al. do not cite, and some of that work is probably more rigorous than the work they do cite. One such area is organizational ecology in sociology (Hannan & Freeman 1989). This work develops large databases to show that different organizational strategies – generalist and specialist – cause differential survival and persistence of organizations in different kinds of environments (fine-grained, patchy, etc.). The arguments made parallel much of Endler's reasoning which Mesoudi et al. cite as a paradigm. In my view, this work is very well done and strongly supports Mesoudi et al.'s case.

Another important body of work comes from the enormous amount of work done in game theory in economics, political science, and history. The most obviously relevant is evolutionary game theory, which took its inspiration from Maynard Smith but has since been developed with considerably more mathematical rigor by economists (e.g., Gintis 2000). But even standard rational-choice game theory studies are relevant, since the Nash equilibrium they describe is unlikely to be reached by rational agents working out in their heads the relevant equilibrium but, instead, by a trial-and-error process where strategies are competing with each other and survive because of their payoffs. The work of Bates et al. (1998) is a particularly strong instance of this research program that combines detailed historical evidence with rigorous modeling.

Mesoudi et al. also understate their case at a theoretical level in several ways. First, they claim that borrowing of models and formalism across fields is unusual, when in fact it is standard practice in several areas. It is standard practice in physics, particularly in the search for what are called "universalities" (see Morgan & Morrison 1999; Batterman 2002). Applying the same formalism across multiple domains is a way of unifying different fields without reducing them to some more fundamental level. Advocates in evolutionary game theory explicitly invoke this rationale for their work (Gintis 2000).

Second, the authors' case could be made stronger by explicitly noting that evolutionary mechanisms can be described at various levels of abstraction in terms of details of the process. At the most abstract, selectionist mechanisms identify a causal effect of a character (strategy, practice, etc.) and show that having that effect causes the trait to persist. There are various ways to realize such causal processes, where direct copying and differential survival of genes is a paradigm case. But even in biology, literal copying is not essential (heritability can be achieved by other routes). So the common doubts about evolutionary accounts in the social sciences on the grounds that social selection is not analogous to the biological, miss the point. At one level, they are trivially analogous: As causal processes they are dynamical systems that we can trace through state space. The real question is whether there is differential survival and persistence, not whether there are social "genes." You can think the

memes idea hopelessly fuzzy and still think there are good selectionist explanations. The work of Hannan and Freeman (1989) is a case in point.

I would argue that Mesoudi et al. miss such support for their case because they restrict their discussion to explanations of culture. Obviously there is much more to the social sciences than cultural anthropology or the study of ideas, beliefs, and so on. Moreover, there are good reasons to think that culture as information in people's heads sets up an unnecessarily difficult situation. There are multiple problems here. Identifying units is hard, even if it can sometimes be done. Moreover, there is much cognitive science and social science research that suggests that "information in the head" is the wrong way to think about culture. From cognitive science the support comes from the idea that mental process are essentially tied up with an external "scaffold" that makes information processing possible in the first place (Clark 1997). From the social sciences, the argument is that knowledge and culture are distributed across individuals and embedded in institutions, social practices, and organizations (Hutchins 1995). These facts explain both why the narrow notion of culture may be hard to work with and why the social sciences gravitate toward selection mechanisms of practices, institutions, organizations, and so on.

On the downside, there are four important obstacles that Mesoudi et al. do not much discuss. (1) On their view, formal models are an important route to progress and should be in the social sciences as well. However, at least one social science – economics – uses formal models extensively; models based on idealizations that will make your head swim. So there is the big question of when and where evolutionary game theory is telling us something about the world. (2) Selectionist explanations in the social sciences are often supported by optimality arguments rather than direct evidence of selection, and the value of these arguments is an open question. (3) Selectionist causal processes are not incompatible with other, nonselectionist processes acting at the same time, as Mesoudi et al. acknowledge in the case of drift. A norm, for example, may promote coordination and persist in part because it does so, but may also exist in part because it furthers the interests of the powerful. This is not an inherent problem, but it may be a common one in the social case and it definitely does complicate things. (4) It is unclear how far selectionist stories can go in the social sciences, because frequently a selectionist account (cf. Bates et al. 1998) takes as given the organizational and institutional structures that determine payoffs and possible strategies. Perhaps these situations describe a social parallel to the kind of issues that worry advocates of niche construction and developmental systems in biology, and so these ought to be issues the authors are sensitive to, given their own work in this area.

NOTES

1. The comments that follow are based on Kincaid (1996, Ch. 4; 2006)

Cultural evolution is more than neurological evolution

Thorbjørn Knudsen^a and Geoffrey M. Hodgson^b

^aDepartment of Marketing and Management, Faculty of Social Sciences, University of Southern Denmark, DK-5230 Odense M, Denmark; ^bDepartment of Accounting, Finance, and Economics, The Business School, University of Hertfordshire, Hatfield, Hertfordshire AL10 9AB, United Kingdom.

tok@sam.sdu.dk <http://www.sam.sdu.dk/ansat/tok>

g.m.hodgson@herts.ac.uk <http://www.geoffrey-hodgson.info>

Abstract: Advancing a general Darwinian framework to explain culture is an exciting endeavor. It requires that we face up to the challenge of identifying the specific components that are effective in replication processes in culture. This challenge includes the unsolved problem of explaining cultural inheritance, both at the level of individuals and at the level of social organizations and institutions.

The central argument of this stimulating article is the need for a unifying evolutionary framework to span the social and biological sciences. We endorse the argument and also agree with Mesoudi et al. – against the views of some of our fellow social scientists – that such an evolutionary framework must essentially be Darwinian.

Arguments against extending the theory of evolution from the biological to the social domain are quite common. The critique of such arguments by Mesoudi et al. is considerably weakened by their neglect of an immense literature in the social sciences, particularly in evolutionary economics (e.g., Nelson & Winter 1982; Young 1998) and organizational ecology (e.g., Hannan & Freeman 1989), where Darwinian themes are central. Their stance is further weakened by its neglect of the recent development of general Darwinian concepts of replication and selection in the theory and philosophy of biology (e.g., Frank 1998; Hull 2001; Knudsen 2004; Price 1995). Even though David Hull's work is mentioned, one of its central messages is neglected: An adequate definition of selection processes where variety is replenished demands consideration of the causal relation between interaction and replication.

This neglect involves much more than inadequate referencing: It means the underdevelopment of a number of crucial themes concerning the units and mechanisms of cultural inheritance, which are highly relevant for a generalized Darwinian framework in the social domain (Hodgson & Knudsen, in press b). For example, refined concepts of replication and selection are essential to identify the *causes* of cultural change. Mesoudi et al. do not provide an explicit definition of cultural selection processes. Consequently, they overlook the fact that some of the most important cultural (and biological) selection processes are defined in terms of differential replication caused by environmental interaction (Hull et al. 2001). Crucially, without an adequate definition of selection processes and an identification of the entities involved in these processes (the interactors and replicators), there is no way of knowing whether cultural changes are outcomes of selection processes, drift, or something else.

Mesoudi et al. skip over these issues by loosely describing culture as information and referring to the literature on memes. They defend the meme concept against the criticism that it is vague and inadequately defined, by explaining that the concept of the gene also has changing and different meanings. But this ducks the fact that we know much more about the emergence and replication of genetic combinations than we do about the emergence and replication of cultural combinations. Furthermore, the genotype-phenotype distinction (or replicator-interactor distinction) is well established in biology, but largely unacknowledged in the literature on memetics. The status of a meme as a genotype (replicator) or phenotype (interactor) remains unresolved – a testimony to its inadequate definition.

Biology has a well-developed theory of inheritance but there has been little progress in explaining cultural inheritance, a problem that involves identification and empirical verification of the specific components that are effective in the replication of cultural combinations. Neither do studies of cultural inheritance compare to the empirical studies that helped establish Mendel's laws in biology, nor do models of cultural inheritance command explanatory power similar to Mendel's laws. The way in which cultural components combine and replicate is presently unknown.

Apart from pointing to possible future advances in neuroscience, Mesoudi et al. largely ignore these problems and many recent attempts to resolve them. Their message for social scientists is to wait for the neuroscientists to situate cultural inheritance in the human brain, ignoring the significant contributions that some social scientists have already made to the theory of social evolution.

Indeed, the authors make matters worse by suggesting that in the social domain the genotype-phenotype distinction is “speculative” and possibly “unproductive.” They go on to argue that further progress in this area will “also bear on whether cultural

inheritance can be described as ‘Darwinian’ or ‘Lamarckian’” (sect. 3.5.3, para. 5). Mesoudi et al. thus replicate the widespread but mistaken dichotomy that Darwinism and Lamarckism are mutually exclusive (Dawkins 1983; Hodgson & Knudsen, in press a), and provide an unwarranted excuse to dismiss the application of Darwinian principles in the social domain because of the common (but conceptually problematic; Hull 1982) assumption that acquired social characters can be inherited.

For a number of reasons, we need at least a preliminary understanding of cultural inheritance. First, we must explain continuity and stability in the social realm. Second, we must avoid the erroneous attribution of phenomena to absent or ineffective causes. It matters whether cultural changes are outcomes of selection processes, drift, or something else. Indeed, analyzing time-series of trait distributions without properly identifying the underlying causes is highly problematic; we must account for cultural inheritance, cultural fitness components, and more.

Inheritance at the level of individuals is very different from inheritance at the level of social organizations and institutions. For evolution to be truly social, it must involve social units. Social units are more than mere collections of individuals: They entail structured interaction. The idea that institutions or organizational routines can also be considered as organism-like or gene-like units in the evolutionary process has been around for more than 100 years (Hodgson 2004) but it is unmentioned by Mesoudi et al. Their vision is confined to “ideas” as evolutionary units, which they treat largely as neurological phenomena in the brain. It is necessary to consider social entities as well. Significantly, recent literature rehabilitates group selection in culture as a higher-level complement to individual-level selection (Henrich 2004a). Mesoudi et al. mention the issue of group selection once, but fail to elaborate on its significance. Institutions are mentioned only once in passing. There is no mention of social structure, one of the central concepts of the social sciences. They fail to elaborate on key differences between human and nonhuman culture, where the former involves a developed abstract language and capacities to attribute intentions and meanings (Bogdan 2000; Richerson & Boyd 2005; Tomasello 1999). This amounts to a neglect of critical aspects of culture that pose interesting challenges for the identification of the specific content of a general Darwinian framework applied to culture.

Overall, Mesoudi et al. make a commendable attempt to generalize Darwinism across the social and the biological sciences but engage inadequately with the nature of the social realm. Advancing a general Darwinian framework to explain culture is an exciting endeavor. It requires that we face up to the challenge of identifying the specific components that are effective in replication processes in culture. This challenge includes the unsolved problem of explaining cultural inheritance at the level of individuals, as well as social organizations and institutions. In essence, we submit that cultural evolution is more than neurological evolution. It involves social processes beyond those that can be situated in the human brain. An adequate theory of cultural evolution must therefore build on the combined efforts of neuroscience, psychology, and social science.

Cultural traits and cultural integration

R. Lee Lyman

Department of Anthropology, University of Missouri–Columbia, Columbia, MO 65211.

lymanr@missouri.edu

Abstract: Modern efforts to model cultural transmission have struggled to identify a unit of cultural transmission and particular transmission processes. Anthropologists of the early twentieth century discussed cultural traits as units of transmission equivalent to recipes (rules and ingredients) and identified integration as a signature process and effect of transmission.

I agree with Mesoudi et al. that much of value can be borrowed from what we know of Darwinian biological evolution and adapted (not just adopted) to cultural phenomena (e.g., Lyman & O'Brien 1998; O'Brien & Lyman 2002a). But I also think that Mesoudi et al. and those who hope to develop Darwinian social sciences have some significant work to do. Mesoudi et al. touch on one topic that is critical to the enterprise but that has, as yet, received limited attention from socio-behavioral scientists: What is the unit of cultural transmission? Mesoudi et al. mention memes, the still ambiguously and incompletely conceived unit of choice for many; I found Aunger's (2002) discussion of memes helpful to my own conceptualizing, but it focused largely on modern ideas about such units and ignored historically antecedent ones. The tendency today is to devote considerable attention to modern studies of the pathways of cultural transmission (e.g., Richerson & Boyd 2005 and references therein) and to ignore the deep history of studies of cultural transmission mechanisms, modes, and processes (see Lyman [in press] for a review of pertinent early ideas). Hence, many researchers seem unaware of the historical conceptualization of a unit of cultural transmission in anthropology (Lyman & O'Brien 2003). That unit is the "cultural trait," a term Mesoudi et al. use like many modern researchers in the social and behavioral sciences use it – without an explicit definition; though how Mesoudi et al. and others use it does imply that a cultural trait, whatever else it might be, is a unit of cultural transmission.

Those interested in developing Darwinian social science should study the history of their discipline, whether anthropology, sociology, or psychology, to learn what our intellectual ancestors thought about cultural transmission. From what I have read of their ancient writings (Lyman, in press; Lyman & O'Brien 2003), they had some good ideas that might help us build models of cultural transmission that include explicitly conceptualized units and processes of transmission. To illustrate, I summarize how a cultural trait was, and is still, conceived by many anthropologists, and I describe one key process of cultural transmission and its effects discussed more than 100 years ago.

To early twentieth-century anthropologists, cultural traits were units of cultural transmission that were diffused, learned, borrowed, and perpetuated (usually but not always) by face-to-face contact. A trait could vary in scale from the color of a decorative motif on a ceramic vessel to an entire behavioral complex such as the nineteenth-century Ghost Dance – a revitalization movement with elements of Christianity and indigenous religion and ritual that appeared and spread across portions of the western United States several times (DuBois 1939; Mooney 1896; Spier 1935). A modern conception of a cultural trait would be that of a recipe – how, when, where, and why to produce a behavior or an artifact (a behavioral by-product). A cultural trait (recipe) includes a set of ingredients, rules for acquiring ingredients, rules for preparing and measuring ingredients, rules for mixing and cooking (metaphorically) ingredients, and what to do with the finished product (Lyman & O'Brien 2003). Rules, ingredients, or both can be transmitted individually or as a more or less complete set, and can be mixed or altered to produce (metaphorically) a chocolate cake or a yellow cake, or a cookie or a pot roast.

Conceiving a cultural trait to be such a plastic entity is advantageous. A trait can vary in terms of its scale (inclusiveness), whether it is empirical or not, its mechanical constraints, and its tolerance limits (how closely must a recipe be followed to result in a suitable product?). With respect to transmission processes, can a cultural trait be integrated in a recipient culture or not? Integration was a process that seminal American anthropologist Franz Boas identified that allowed the tracking of cultural traits across time and space. Integration was the process by which a cultural trait was "adapted and changed in form according to the genius of the people who borrowed it" (Boas 1896, p. 5). The "adapting and changing" of a cultural trait comprises integration. Boas believed that in order for a newly

acquired cultural trait to be retained and replicated, it had to be modified to fit its new cultural context (Hatch 1973). Because many traits were acquired piecemeal from many and disparate sources, and such acquisition never stopped within a culture, integration was ongoing and resulted in a culture comprising a set of functionally and structurally interrelated traits that were modified to greater or lesser degrees from their original state. In Boas's view, integration was one of, if not *the*, "creative force" of culture. Thus, it was not only a process of transmission (on the receiving end), but it also had an effect on the general processes of cultural evolution and cultural transmission because it created new variants of cultural traits (which were subject to sorting processes such as natural selection, though Boas did not refer to sorting).

Mesoudi et al.'s effort is thoughtful, and it is also up-to-date conceptually. But to borrow a worn cliché, they and we ignore history at the peril of repeating old mistakes, and, I would add, at the peril of forgetting what our intellectual predecessors learned.

A long way to understanding cultural evolution

Werner Mende^a and Kathleen Wermke^b

^aBerlin-Brandenburg Academy of Science, 10117 Berlin, Germany; ^bCenter for Pre-Speech Development and Developmental Disorders, Julius-Maximilians-University Würzburg, 97070 Würzburg, Germany.

mende@bbaw.de wermke_k@klinik.uni-wuerzburg.de

Abstract: Understanding cultural evolution is one of the most challenging and indispensable scientific tasks for the survival of humankind on our planet. This task demands, besides an adoption of theories and models from biological evolution, theories for culture-specific processes as well. Language evolution and language acquisition offer interesting objects of study in this respect.

Mesoudi et al.'s review of concepts and models from biological evolution theory and their demonstration of numerous, amazing analogies and parallels between bio-evolution and cultural evolution is commendable. The long tradition, the generally high scientific level, and the wealth of reliable results of bio-evolution theory provide an excellent starting point for developing a scientific theory of cultural evolution. We strongly support the authors' view that it is a promising strategy to exploit these parallels and to apply the rich inventory of methods from biological evolution theory as far as possible. This should be done not only in terms of heuristics, but also in terms of mathematical modeling to the extent and depth as the necessary verifications allow.

Despite the fascinating parallels between biological and cultural evolution, however, which are mostly due to the structural similarity of certain interaction processes, there also exist certain essential differences between the two kinds of evolution processes. Complementing the examples given by Mesoudi et al., we would like to draw attention to the following: Traits in cultural evolution are more difficult to define and to identify; and they often have lower persistence and resilience. There is no stringent translation of the terms *individual*, *species*, *population*, *gene*, and so on, in corresponding analogs. Additional complications come up when we investigate cultural evolution as historical process: Often we find ourselves as acting a part on the stage. Decisions and valuations at all levels of society may act as selective forces. Expectations, beliefs, and predictions may become self-enforcing, even self-fulfilling, or self-defeating. Ecosystems are generally robust, resilient, and structurally stable against local impacts and disasters; cultural communities are, in contrast to this, much more vulnerable and manipulable. Local disturbances may have long-range and long-term consequences, and could become amplified violently and epidemically. In investigating

the cultural evolution of real historical communities, one has to consider economic subsystems, metabolism with the environment, corresponding energy flows, and information streams, as well as driving forces and constraints all the way down to the basic physical and thermodynamic laws. Otherwise we cannot understand the emergence, progression, and eventual collapse of these communities (see Diamond 1999; 2005). However, it should be possible to incorporate these culture-specific aspects in more advanced models of cultural evolution. The best-quality criteria are exhaustive tests of their predictive power.

Following Richerson and Boyd (2005), Mesoudi et al. adopt a rather wide definition of “culture” as “information capable of affecting individuals’ behaviour that they acquire from other members of their species” (target article, sect. 1, para. 10). According to this wide definition, language should get a high valuation because language qualifies as one of the most powerful tools affecting individuals and groups. We missed all the more a discussion of language beyond cladistics and learning. Language is such a primordial and fundamental constituent of culture that it deserves closer and specific attention. Moreover, language is also a unique motor of human cultural evolution, without any parallels in the history of nonhuman life. From the phylogenetic perspective, there is clearly a close coevolution of culture and language. This causes a deep impact of language on cultural evolution. Application of spoken or written language has dramatically shaped nearly all fields of culture, especially communication, on all scales and continuously creates new selective forces with sometimes high fluctuation amplitudes. Language is also responsible for fast-changing spiritual vogues, for intellectual fashions and ideologies, all unique to the human being – again, with no counterpart in the natural history of other biota.

Language evolution and language acquisition could therefore provide interesting objects of study for cultural evolution processes: The hereditary predisposition of an infant for the acquisition of any language is a clear vertical transmission process; the fast and seemingly effortless acquisition process itself is a maturation-controlled learning process with prevalent horizontal transmission. Both processes are coupled by the unique feature of testing and reshaping of coevolving language by a co-developing brain (Wermke & Mende 2006). Language acquisition is universal and at the same time highly flexible. The mastering of native languages is one of the necessary preconditions of cultural traditions.

To illustrate the growing gap between evolution of biota and cultural evolution, one should also consider the breathtaking acceleration made by the energy technology of the nineteenth century and even more so by contemporary information technology. The hyperlinked, interlocked global village has no counterpart in biological evolution. It is threatened by an intrinsic explosion of complexity, by the outbreak of good and evil fantasies, and urgently needs new strategies of stabilisation. Supreme effort is required to model and, most important, to understand these cultural evolution processes and to make reliable predictions and decisions. Modeling approaches have to take into account that far-reaching decisions are the result of the interaction of a large number of human brains and that even individual responses are generally the result of a huge potential for imagination and fantasy inside and outside of human brains. The progeny of Darwin, vertically and horizontally fairly well instructed, has to solve this puzzle as soon as possible. A deeper understanding of the underlying mechanisms of cultural evolution might be crucial for finding the trail toward a balanced and sustainable future of humankind.

Archaeology and cultural macroevolution

Michael J. O’Brien

Department of Anthropology, University of Missouri, Columbia, MO 65211.
obrienm@missouri.edu cladistics.coas.missouri.edu

Abstract: Given the numerous parallels between the archaeological and paleontological records, it is not surprising to find a considerable fit between macroevolutionary approaches and methods used in biology – for example, cladistics and clade-diversity measures – and some of those that have long been used in archaeology – for example, seriation. Key, however, is recognizing that this methodological congruence is illusory in terms of how evolution has traditionally been viewed in biology and archaeology.

Mesoudi et al.’s general premise is that human culture exhibits central Darwinian properties. They then ask a question that grows out of this premise: What sort of structural relationship might exist between a science of cultural evolution and the science of biological evolution? They divide biological evolution into macro- and microevolution and then align various methods and approaches used to examine each with corresponding methods and approaches used to examine cultural evolution. They find a considerable fit between macroevolutionary approaches in biology and some of the approaches used in anthropology and archaeology, and less fit between microevolutionary approaches. This is not surprising, given the numerous parallels between, say, the archaeological and paleontological records, which lend themselves to macroevolutionary methods such as cladistics, seriation, and clade-diversity measures. Likewise, the history of anthropology makes it clear that macroevolutionary approaches such as comparative anthropology are the backbone of the discipline.

Because of their focus, Mesoudi et al. necessarily bypass discussion of the “evolution” of these interests, approaches, and methods in anthropology and archaeology – a topic that Lyman and I have detailed elsewhere (e.g., Lyman & O’Brien 1997; 1998; Lyman et al. 1997; O’Brien & Lyman 2000). Here I point out that the considerable fit that Mesoudi et al. find between macroevolutionary approaches, methods, and issues in anthropology/archaeology and those in biology is a recent phenomenon rather than a long-standing tradition in the social sciences. The irony is that despite the parallels between subject matter, and despite the “naturalness” of traditional anthropological and archaeological methods for addressing cultural-evolutionary issues, social scientists have often been downright hostile toward even considering cultural evolution in Darwinian terms. Rather, they retreat to the cozy confines of nineteenth-century unilinear and progressive cultural evolutionism of Tylor (1871) and Morgan (1877).

Anthropologists and archaeologists have been encouraged in this retreat by several prominent biologists and paleobiologists such as Gould (e.g., 1987; 1996; 1997) and Mayr (1982; Angier 1997), who have done what countless anthropologists have done for more than a century – moved culture from the Darwinian realm into the Lamarckian realm. Note how Gould (1996, p. 222) viewed the situation:

[the] uniquely and distinctively Lamarckian style of human cultural inheritance gives our technological history a directional and cumulative character that no natural Darwinian evolution can possess. . . . [C]ultural change is potentially progressive or self-complexifying because Lamarckian inheritance accumulates favorable innovations by direct transmission, and amalgamation of traditions allows any culture to choose and join the most useful inventions of several separate societies.

This misguided gambit locates cause in the wrong place (O’Brien 1996). Although the mode and tempo of transmission are different when culture is involved, do these differences lead to the inescapable conclusion that humans have stopped evolving – that they somehow are beyond the reach of selection? The answer is an emphatic “no.” Humans today are no more immune to evolutionary processes than they were ten thousand or fifty thousand years ago.

All that is important in Darwinian terms – and it is difficult to overemphasize this point – is that variation, however it is generated, exists, and that transmission, however it is realized, takes

place. Reproductive success among variant forms of organisms will result primarily from selection and drift. Similarly, replicative success (Leonard & Jones 1987) among variant artifact forms will result from both selection and differences in transmission. Therefore, I cannot agree with Gould's (1996; 1997) plea that the phenomenon of cultural evolution be labeled "cultural development" rather than "evolution" because the latter carries too many biological connotations. It is precisely these connotations that it *should* carry.

Lyman and I have argued (Lyman & O'Brien 1997; O'Brien & Lyman 2000; 2002b) that archaeology today is in a period similar to that of the 1970s, when paleobiologists such as Eldredge and Gould (1972) proposed a new way of looking at the fossil record that involved some retooling of biological evolutionary theory. Despite more than a decade of squabbling, the success of their endeavors is abundantly clear. Evolutionary archaeology, too, is moving past the squabbling period, but challenges remain at both the macro- and the microevolutionary levels. Nonetheless, I suspect that within a decade we will see a modern synthesis in archaeology that will parallel what occurred in biology in the 1940s with the unification of the naturalists and the experimentalists (Huxley 1942). The basic theory requisite to archaeology, conceived of as an unabashedly historical science concerning people and their cultures, has been around since 1859, the year Darwin penned *On the Origin of Species*. The basic problem for archaeology is that Darwin did not write a theory that can be applied directly to the study of the archaeological record (O'Brien & Holland 1990). But we cannot, as Rindos (1989) put it, blame Darwin for not doing our work for us. Rather, we should heed the advice of one of the foremost archaeologists of the early twentieth century, who explained to his colleagues that:

the sooner we roll up our sleeves and begin comparative studies of axes and arrowheads and bone tools, make classifications, prepare accurate descriptions, draw distribution maps and, in general, persuade ourselves to do a vast deal of painstaking, unspectacular work, the sooner shall we be in position to approach the problems of cultural evolution, the solving of which is, I take it, our ultimate goal. (Kidder 1932, p. 8)

Sober (1992, p. 30) pointed out that "biologists interested in culture are often struck by the absence of viable general theories in the social sciences. All of biology is united by the theory of biological evolution. Perhaps progress in the social sciences is impeded because there is no general theory of cultural evolution." Sober is correct in noting that there is no general theory of cultural evolution, but if the survey by Mesoudi et al. is any indication of the analytical landscape, then it appears that help is indeed on the way.

Darwinian cultural evolution rivals genetic evolution

Mark Pagel

School of Biological Sciences, University of Reading, Whiteknights, Reading RG6 6AJ, United Kingdom.

m.pagel@rdg.ac.uk

Abstract: The study of culture from an evolutionary perspective has been slowed by resistance from some quarters of anthropology, a poor appreciation of the fidelity of cultural transmission, and misunderstandings about human intentionality.

Why is it so easy to accept that Darwinian evolution characterises genetic systems but not elements of culture? Mesoudi et al. begin their welcome and thoughtful article by suggesting that biology's success relative to anthropology as a scientific discipline derives from a willingness to simplify and from the synthetic nature of the theory of evolution. An additional problem that Ruth Mace and I alluded to in 1994 is that large branches of post-war anthropology adopted the view that "facts themselves should be

considered as social constructs ... and much of anthropology redefined itself as an interpretive humanity rather than a science, concerned with cultural *specificity* rather than comparison across cultures" (Mace & Pagel 1994, p. 549, emphasis added).

This belief in specificity – that particular human cultural elements are each *sui generis* – suggests a reluctance to adopt functional explanations for many aspects of culture: that cultural elements serve purposes, and those purposes may promote well-being, standing, reputation, or other important social attributes that could be related to fitness. Not all elements of culture will be amenable to functional analysis, but it is a useful gambit to assume they are until shown otherwise, and to search for the common link among apparently homologous or analogous traits across cultures. Elsewhere (Pagel 1994), I have called this gambit "the adaptationist wager."

There may also be an under-appreciation and misunderstanding of the fidelity of cultural transmission. Because cultural elements can, in principle, change every generation, they are often not seen as serious candidates for study as replicators. However, language is one part of the dual-inheritance system of culture and genes that is so prominent in humans. Among the Indo-European languages, the words for *two*, *three*, *five*, *I*, and *who* each form a single cognate set across the entire language family: Every Indo-European language speaker has used a related sound for each of these meanings. Given that Indo-European probably arose as a language family about 8,000 years ago (Gray & Atkinson 2003), this translates into rates of evolution (Pagel 2000) as low as that of some genetic elements.

Because cultural elements can be transmitted with high fidelity, then perhaps where they are not, fidelity may be unimportant and not just inherently noisy. For example, we might not expect the fidelity of linguistic transmission to exceed that required for three generations to talk to each other: There is no need to invest in the replication machinery to improve on this. What we observe is that even the most rapidly evolving parts of the fundamental vocabulary of languages change slowly enough to allow communication among generations (Pagel 2000). Biologists have come to treat replication fidelity as a variable of interest in its own right. The human immunodeficiency virus has some of the highest rates of mutation (lowest fidelity) observed in a functioning replicator. Its poor fidelity may allow it to escape detection by the human immune system.

The human capacity for intentionality or goal-directedness is thought by some to undermine the study of culture from within the framework of natural selection. Mesoudi et al. demur (see also Mesoudi et al. 2004), and I would like to add that this criticism may conflate intentionality with omniscience or omnipotence. Late *Homo erectus* may have frequently wished to make fire but could not work out how to produce matches. What matters is that attempts at solving problems, whether or not underpinned by intention or goal-direction, can be placed in a list ordered along a continuum of success. If success matters, those who find their way to the top of this list will outcompete those who do not.

The existence of intentionality makes plausible the argument that horizontally transferred elements of culture can be used to study cultural adaptation. Horizontal transmission or borrowing of cultural elements is often used as a stick with which to beat those who use cultural phylogenies to study the coevolution of cultural elements. But intentionality makes it plausible to apply the research gambit mentioned at the outset: the belief that horizontally transmitted elements of culture are adopted because they serve some function. This gambit will not always pay off, such as when the element of culture has been forced upon a society, but without intentionality the gambit would be fanciful.

Human cultures seem to divide up the world as if they were so many biological species (Pagel & Mace 2004). There is every reason to believe that studying variation among these cultural groups from an adaptationist perspective will yield the same sorts of insights as it has for nonhuman organisms.

Cultural evolution is not equivalent to Darwinian evolution

Dwight W. Read

Department of Anthropology, University of California at Los Angeles,
Los Angeles, CA 90095.

dread@anthro.ucla.edu

<http://www.sscnet.ucla.edu/anthro/faculty/read/>

Abstract: Darwinian evolution, defined as evolution arising from selection based directly on the properties of individuals, does not account for cultural constructs providing the organizational basis of human societies. The difficulty with linking Darwinian evolution to structural properties of cultural constructs is exemplified with kinship terminologies, a cultural construct that structures and delineates the domain of kin in human societies.

Cultural anthropologists, according to Mesoudi et al., are concerned with the same kind of issues and questions as evolutionary biologists. Because variability, inheritance, and selection also apply to cultural phenomena, then cultural anthropology, they suggest, could benefit by taking advantage of the theoretical and methodological advances made by evolutionary biologists. The only barrier, they note, is the unwarranted refusal by cultural anthropologists to drop their assumption that evolution (read: Darwinian evolution) is not relevant to understanding culture change. Yet cultural evolution, though not in the form of Darwinian evolution, has long been a central concept in anthropology: “Cultural selection . . . operates not on individuals but on cultural traits and on societies” (Carneiro 1985, p. 77, emphasis in the original). However, despite championing Darwinian evolution for understanding cultural evolution, the authors admit in the end that the matter may be more complex: “‘social constructions’ . . . have no real equivalent in the biological domain . . . [and this] requires a different evolutionary treatment from the one developed within biology” (target article, sect. 4, para. 5). So can we account for change within “culture as a kind of mental phenomenon” (D’Andrade 2001, p. 243) by reference to Darwinian evolution, where selection is based on properties of individuals? The answer is no (Read 2003). To see why, consider a universal cultural construct fundamental to human social systems, namely kinship, as it is expressed through a kinship terminology.

By a kinship terminology, I mean the terms that identify one’s (cultural) kin; for example, mother, aunt, cousin, and so on, for English speakers. The terms are culture-specific (e.g., unlike some kinship terminologies, English speakers do not have separate terms for mother’s sister versus father’s sister); hence, there is a problem translating the terms from one language/culture to the terms of another language/culture. Analytically the translation problem is circumvented by mapping kin terms to a common genealogical domain that makes possible genealogical definitions of kin terms regardless of language, such as aunt = {parent’s sister, parent’s brother’s wife} for English speakers.

We can see the social importance of kinship terminologies by considering the role of kinship in small-scale societies. Typically, societal membership is determined through kinship. Hunter-gatherers in the Kalahari Desert of Botswana, for example, refer to themselves as the *ju/wasi*, which means, roughly, “we, the real people” (Marshall 1976, p. 17). Real persons are one’s kin, and one’s kin are those persons included in the scope of reference of kin terms. The distinction between kin and non-kin is nontrivial, and for some groups, such as the Waorani of Ecuador, it meant the difference between being able to engage in social interaction or being killed on sight (Wilson & Yost 2001).

Terminological knowledge is located in individuals and hence can be considered to be part of the phenotype of individuals. Yet individual benefit does not arise, unlike for many biological traits, simply from having terminological knowledge as a trait. Instead, individual benefit arises from the properties of the social group formed of persons sharing the same terminology and who thereby are mutually kin.

How do we account for the macro-level phenomena of social relations and individual benefit structured through a kinship terminology? Mesoudi et al. consider that evolution occurs at the trait level because they accept uncritically the idea that macro-evolution is Darwinian microevolution writ large (but see Erwin 2000; Carroll 2001; Simons 2002; among others, for some of the issues involved). However, their argument does not work for kinship terminologies.

A terminology is not just a collection of terms, as it has a structural form (in the algebraic sense) determined by the way we compute kin relations using kin terms (Read 1984; 2001; 2005). If John, Mary, and Jim are English speakers and John refers to Mary by the kin term *aunt* and Mary refers to Jim by the kin term *son*, then when John refers to Jim by the kin term *cousin*, *cousin* is the product of the kin terms *aunt* and *son*. More generally, if person A (properly) refers to person B using the kin term *K* and person B (properly) refers to person C using the kin term *L*, then the product of *K* and *L* is the kin term *M* (if any) that A properly uses for person C. Through ethnographic elicitation of this kind of kin term usage, we can make evident a conceptual structure that expresses the manner in which the kin terms forming a particular terminology constitute a structured set of symbols (=terms).

The form of the structure is highly constrained. It can be constructed algorithmically by expanding a core structure so as to structurally introduce two basic properties of kinship terminologies: (1) reciprocity of kin terms, and (2) sex marking of kin terms. The core structure is generated algebraically by applying repeatedly the kin term product to the generating term(s), such as the kin term *parent* for the American kinship terminology.

Terminologies differ from one another with respect to the set of generating kin terms and the algorithms for introducing the above two terminological properties but share commonality by having structures that can be generated in this manner. Even more, the generative logic leads to 100% correct predictions of the genealogical definitions of kin terms, even though seemingly simple changes to a terminology (such as introducing the terms *aunt-in-law* and *uncle-in-law* into the American kinship terminology) would negate the ability to correctly predict genealogical definitions of kin terms.

The generative logic of terminologies would not arise from historically contingent selection based on phenotypic properties of individuals acting at the level of individual kin terms. Further, though terminologies are mental constructs transmitted in a social context through a developing child’s enculturation, knowing in more detail the mapping of individual kin terms – seemingly good candidates for memes – onto neurological location(s) will not tell us much either about the structural arrangement of kin terms or about the processes used by the brain to infer the implicit organizational structure of a kinship terminology. The structural logic of kinship terminologies appears to be inferred, much as the brain infers the implicit organizational structure of a language. The selection acting on kinship terminologies occurs at the level of structural properties and their consequences for the social organization of kin determined through the kinship terminology.

Evo-devo, modularity, and evolvability: Insights for cultural evolution

Simon M. Reader

Department of Behavioural Biology and Helmholtz Institute, Utrecht University,
Utrecht 3508 TB, The Netherlands.

s.m.reader@bio.uu.nl

<http://www.bio.uu.nl/behaviour/Reader/>

Abstract: Evolutionary developmental biology (“evo-devo”) may provide insights and new methods for studies of cognition and cultural evolution. For example, I propose using cultural selection and individual learning to examine constraints on cultural evolution. Modularity, the idea that traits

vary independently, can facilitate evolution (increase “evolvability”), because evolution can act on one trait without disrupting another. I explore links between cognitive modularity, evolutionary modularity, and cultural evolvability.

Mesoudi et al. argue that the methods and tools used to study biological evolution can profitably be applied to the evolution of culture, particularly human culture. Evolutionary developmental biology (“evo-devo”) is a major research axis of evolutionary biology, given little attention in the target article. Evo-devo studies the mechanisms that generate the phenotype, and whether these channel, bias, or limit evolution (Brakefield 2003). Issues studied include the evolutionary origins of phenotypic novelty, how fitness improvements are made without compromising past adaptation, influences and constraints on the rate and course of evolution, and whether evolvability, evolutionary adaptability, can itself evolve (Kirschner & Gerhart 1998; Wagner & Altenberg 1996; West-Eberhard 2003). Parallel issues are key to understanding cultural evolution, so there is potential for cross-fertilisation of ideas.

Of particular relevance is the notion that modularity can favour evolvability, the capacity to generate heritable, selectable phenotypic variation (Hansen 2003; Kirschner & Gerhart 1998; Wagner & Altenberg 1996; West-Eberhard 2003). In evo-devo, “modular” describes traits that have some degree of genetic and developmental independence: they are semiautonomous units. Such independence is argued to facilitate biological evolution, allowing traits to change without interfering with other traits’ functions (Hansen 2003). For example, a common theme in biological evolution is differentiation of repeated modules, such as teeth along a jaw or segments of an insect body. Replication, and the resulting redundancy, facilitates evolutionary change without the disadvantage of loss of original function. Cultural evolution may provide similar examples. During language evolution, single words might be duplicated to form several words of similar meaning. This could facilitate subsequent cultural evolution, because some of these duplicated words can diverge in meaning without loss of the original word’s meaning.

Cognition may also have a modular structure, although the extent and developmental causes of cognitive modularity are hotly debated (Fodor 1983; 2000; Panksepp & Panksepp 2000; Sperber 2002). This modular structure could influence the tempo and course of both cognitive evolution and cultural evolution. Critical defining characters of cognitive modules, such as computational distinctiveness and informational encapsulation, imply independence between modules (Fodor 1983; Shettleworth 2000). Independence could facilitate cognitive evolution, because selection can act on one cognitive module without affecting the function of others. Hence, although the Fodorian and evo-devo modularity literatures have generally developed separately (but see, e.g., Sperber 2002), Fodorian cognitive modules may be modular in the evo-devo sense. Cognitive structure and processes are essential in supporting and moulding culture (Mesoudi et al. 2006; Sperber & Hirschfeld 2004). Now, the question is: are the cognitive processes that support cultural evolution modular, do cultural traits themselves form modules, and does this influence cultural evolution?

Culturally transmitted traits often occur in clusters. For example, speaking French is associated with religious, dietary, technological, and societal preferences and norms. Causes of trait clustering and consequences for cultural evolution are important issues: How and why are these stable clusters maintained? Do they act as modules? And does clustering limit or facilitate cultural evolution? Traits may occur together because each trait is an independent adaptation to a shared physical or socio-cultural environment, and/or because of cognitive, historical, or phylogenetic constraints. In addition, trait acquisition may facilitate acquisition of other traits. Evo-devo can inspire empirical methods to address these issues. For example, across-species comparison of butterfly wing patterns revealed that posterior and anterior forewing spots varied in size, and that some size

combinations were observed in nature (e.g., both eyespots large or both small), whereas others (e.g., posterior eyespots large, anterior small) were not (Brakefield 2003). This would be equivalent to finding only particular combinations of *cultural* traits in comparative studies of natural populations (e.g., reliance on tools A and B is observed, as is reliance on neither tool, but reliance on A without B is never observed). Such a pattern of inter-group differences could suggest an evolutionary constraint: particular trait combinations evolve readily, and others, rarely.

Evo-devo can go beyond comparative investigation of whether traits are separable and modular. One can artificially select one trait (e.g., posterior eyespot size) and observe effects on other traits (e.g., anterior eyespot size). Moreover, by selecting for combinations of traits, constraints on evolution can be examined (Brakefield 2003). Such studies may produce counterintuitive results. For example, the natural distribution of eyespot patterns suggested an evolutionary constraint. However, under artificial selection, pattern combinations not observed in natural species evolved as readily as combinations observed in the field (Brakefield 2003). This suggests that other reasons beyond developmental or genetic constraints, such as ecological demands, are responsible for the natural distribution of these trait combinations. Thus, artificial selection experiments can help address why particular traits co-occur.

Similarly, artificial *cultural* selection could be used to identify and pull apart clusters of cultural traits. For example, the coevolution of culturally transmitted traits could be studied using laboratory microsocieties and transmission chain approaches (e.g., Baum et al. 2004). Another possibility would be examination of learning within individuals to assess the stability and integrity of culturally acquired trait clusters. If reinforcement of one trait facilitates or impedes production of another, cultural coevolution of the two traits will be affected. For instance, learning one tool technique (e.g., termite fishing; Whiten et al. 1999) may facilitate acquisition of another technique (e.g., nut-cracking) if common skills are involved, but may hinder acquisition if training in one skill reduces competence in another.

Finally, can evolvability itself evolve? Within biology, it is controversial as to whether architectures that favour evolvability are themselves adaptations (Earl & Deem 2004; Kirschner & Gerhart 1998; Radman et al. 1999). There is evidence that, for example, mammalian immunological systems are designed to favour the production of variability, on which selection can act. Furthermore, these variation-generating mechanisms are not general but targeted to the immunoglobulin genes (Radman et al. 1999; Weill & Reynaud 1996). The evolvability question is relevant to cultural evolution: Are there cognitive structures, artefacts, or societal designs that favour or hinder cultural evolution, do they target particular domains of cultural evolution, and have these structures evolved *because* of their optimising effect on rates of cultural evolution? If the production of cultural variants is too fast, beneficial variants may be lost, and if too slow, adaptability may be compromised. In conclusion, the evo-devo viewpoint suggests important questions for cultural evolution, but also provides a body of theory and methods that could help provide answers.

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A unified science of cultural evolution should incorporate choice

Barry Sopher

Department of Economics, Rutgers University, New Brunswick, NJ 08901.
sopher@econ.rutgers.edu

Abstract: Analogies between biological and cultural evolution may be illuminating and suggest methods to pursue in the quest for a unified

science of cultural evolution. Significant progress, however, is unlikely to be made by trying to fit cultural evolution neatly into a biological evolution schema. A key element defining and differentiating cultural evolution may be the role of conscious human choices.

The very extensive review of Mesoudi et al., and their proposed taxonomy of a theory of cultural evolution parallel to biological evolution, is useful insofar as it identifies a wide range of approaches to use in analyzing cultural evolution and in identifying possible underlying processes by which cultural evolutionary change may be explained. I have some doubts, however, that this is the way in which the goal of a unified theory of cultural evolution will be achieved.

When Charles Darwin proposed his theory of natural selection, he had only the evident (living and fossil) results of a process, but essentially no clue as to the precise mechanics of that process. Mendelian genetics was the process; it came to light years later, and further refinements and deeper understanding (e.g., the fundamental biochemistry of genetics) followed on from this initial discovery. Moreover, the genetic process, the mechanics of which accomplish the natural selection Darwin posited, is not the only process at work in biological evolution. We now know that there is non-adaptive genetic change, genetic drift, which accounts for some of what we see today in the living world. More recently, the synthesis of evolutionary thinking with developmental biology, popularly known as “evo-devo,” is suggesting yet other processes, either to augment or to replace those processes that biologists believed to be the basis for evolution as recently as 20 years ago.

The point of this (coming from a non-expert in biology) for what I want to say here is that the discovery of these processes was not necessarily the outcome of an explicit search for a unifying theory of biological evolution, but rather the outcome of a search to understand very specific mechanisms. I believe that progress in achieving a unified theory of cultural evolution will similarly be composed of findings in a number of specific research programs that are not obviously or mainly targeted at an overarching unified theory of evolution (although some may be), but rather, more typically, are targeted at understanding a specific mechanism, such as how people use natural language to persuade others that one course of action is superior to another.

The authors’ treatment of research in anthropology is quite detailed, and I will not presume to add anything of substance to what they have said about the many fascinating research avenues along which anthropologists are working. In this connection, though, work by writers such as Richerson and Boyd (2005) provides a challenge to their approach. Richerson and Boyd adopt the view that cultural evolution is an aspect of evolution generally and cannot or should not be separated from things biological. I do not know if Richerson and Boyd have had the final word on the question, but they have stated a compelling counterpoint to that of Mesoudi et al.

A treatment of economic phenomena is largely absent in the article, and I would like to draw attention to a number of strands in the literature that I believe to be relevant and, perhaps, even central to the project the authors propose. Though some people may conduct their economic lives more or less instinctively, it is clear that much economic behavior is quite purposeful and goal-oriented, even if it is not always clear to the actors what the ultimate impact of their actions on others or on society as a whole will be. The ability to organize themselves in complex ways and to transmit information and knowledge to others, even others who are far removed, must be the defining characteristic of humans vis-à-vis other mammals. Indeed, our ability to consciously manipulate symbols and to communicate across time and space is unparalleled in the biological world.

Schumpeter (1934) asserted that economic history evolves according to a process of “creative destruction.” In this we have, analogous to what Darwin did, an observation that

economic institutions and activities do evolve, and a conjectured process to explain that evolution, but the detailed mechanics of how that process operates are not really uncovered. The “new institutional economics” (e.g., Nelson & Winter 1982; North 1978; Schotter 1981; Williamson 2000) organize our thinking about economic life by the conjecture that economic institutions arise and evolve as a way of solving a variety of coordination problems that arise in organizing economic interaction.

Recent work on the role of networks in economic activity (e.g. Goyal 2005; Jackson & Watts 2002) add a bit more detail and suggest specific processes whereby economic activity might evolve. Research on social learning (e.g., Anderson & Holt 1997; Banerjee 2002; Bikhchandani et al. 1992; Gale & Kariv 2003; Young 1993; 1998) treats the important role of information transfer in the learning process. Research that explicitly makes use of natural language in social learning (e.g., Chaudhuri et al. 2005; Nyarko et al., forthcoming; Schotter & Sopher 2003; 2006; forthcoming; Weber & Camerer 2003) is beginning to show that communication with natural language, and not just observations of others, may play a critical role in solving problems in economic life.

In all of these cited works, conscious, or at least deliberate, actions by economic agents are involved. Multinational conglomerates are not formed by accident. Someone has to make a decision to put all of his or her money into high-risk assets rather than into safer but lower-yielding government bonds. The processes that biologists use to organize their thinking about biological evolution, though, are largely unconscious processes. Whether we will ultimately find, as Richerson and Boyd (2005) suggest, that cultural evolution is just part of one big theory of evolution, or that there is a distinct theory that organizes the data on cultural evolution as such, there clearly is a need to investigate those distinct processes in cultural evolution that involve conscious human choices.

The uses of ethnography in the science of cultural evolution

Jamshid Tehrani

Centre for the Evolution of Cultural Diversity, Institute of Archaeology, University College London, London, WC1H 0PY, United Kingdom.

j.tehrani@ucl.ac.uk

Abstract: There is considerable scope for developing a more explicit role for ethnography within the research program proposed in the article. Ethnographic studies of cultural micro-evolution would complement experimental approaches by providing insights into the “natural” settings in which cultural behaviours occur. Ethnography can also contribute to the study of cultural macro-evolution by shedding light on the conditions that generate and maintain cultural lineages.

In this insightful and thought-provoking article, Mesoudi et al. build a convincing case for modelling the study of cultural evolution on the disciplinary structure of evolutionary biology. Their use of this framework succeeds on two levels, producing a wide-ranging and coherent survey of the current state of the field while also making an important and timely contribution to its further development. Although in recent years evolutionary approaches to culture have proliferated and grown in popularity, there has been surprisingly little (e.g., Shennan 2002) explicit theorising over how different approaches such as memetics, dual inheritance theory, and cultural phylogenetics might actually fit together. The evidence presented here demonstrates that a cultural equivalent to the “evolutionary synthesis” in biology is both possible and necessary: It is possible because of the progress that has been made in so many different areas of study, and necessary in order to prevent the development of

serious ontological divergences like those which have split the traditional social sciences.

In support of a unified theoretical framework that is conceptually flexible and inclusive, Mesoudi et al. propose a program of research that is methodologically pluralistic, incorporating techniques imported from evolutionary biology as well as ones that are better established in the social sciences. Unfortunately though, it appears that the authors take such a dismal view of social anthropology that they rather downplay the role that ethnography could play in this enterprise by subsuming it within ethnology – the synthesis of ethnographic case studies into cross-cultural databases (e.g., Murdock 1967) – and a more generic and less well-defined category of “anthropological field studies.” The latter encompasses a wide range of research styles, some of which differ markedly from ethnographic fieldwork – particularly in the degree to which they employ a “top-down” rather than a “bottom-up” approach. Thus, questionnaire-based studies (e.g., Hewlett & Cavalli-Sforza 1986), psychological experiments (e.g., Barrett 2004), and economic games (Henrich et al. 2005) in small-scale societies are designed to investigate specific anthropological problems using highly structured data-collection strategies that are implemented over relatively short periods of time. The time frame of ethnographic research is much greater, requiring months and often years of fieldwork, the aims and outcomes of which are only loosely contained within the parameters set by a predetermined research question. Compared to other approaches, ethnographic methods are more informal and typically consist of unstructured or semi-structured interview techniques and “participant-observation,” which involves immersing oneself in the lifeways of a community and learning the language and habits of its members firsthand (e.g., Bradburd 1998).

Rather than focusing on isolated subsets of cultural complexes, ethnographers attempt to situate behaviours within wider contexts of cultural meaning, event histories, and social relationships. For example, whereas an economic game experiment (e.g., Henrich et al. 2005) would investigate norms of reciprocity and punishment through performance in a money allocation task, an ethnographer might focus instead on different orders and currencies of exchange within a particular culture. Thus, an ethnographic analysis might compare and contrast the sorts of expectations that individuals have of monetary transactions with strangers, with the social and moral obligations implied by the giving and receiving of gifts among kin, friends, and allies (Bloch & Parry 1989). Moreover, ethnographic accounts of the “natural” settings in which cultural behaviours are expressed and evaluated are certainly compatible with more structured experimental studies (e.g., Astuti et al. 2004; Henrich et al. 2004). Using the framework developed by Mesoudi et al., these approaches could be combined to investigate cultural micro-evolution within populations in exactly the same way as field-based studies of animal behaviour in the wild complement studies carried out in captivity and in laboratory conditions.

Ethnographic studies can also make a useful contribution to our understanding of cultural macro-evolution. Although studies indicate that cladistic methods can be as useful for reconstructing cultural histories as they are for recovering and classifying the relationships among species (e.g., Collard et al. 2005; 2006), the underlying mechanisms responsible for generating and maintaining cultural lineages remain poorly understood. Using evidence from the ethnographic record, Durham (1990; 1992a) has proposed that the apparent prevalence of warfare, language barriers, endogamy, and ethnocentrism in human societies may act in a similar way to reproductive isolating mechanisms that restrict gene flow among biological populations and which are believed to be important in speciation. Collard and I found evidence of these mechanisms in the phylogenesis of Turkmen textile designs, which, we argued, might be explained by ethnographic reports relating to the extent of intertribal warfare and endogamous marriage practices (Tehrani & Collard

2002). However, it should be noted that the presence and influence of these mechanisms cannot be assumed to be universal (e.g., Jordan & Shennan [2003] found branching processes to be much less dominant in Californian basketry traditions) and nor can they be assumed to be constant: Blending among Turkmen textile traditions increased in importance following the pacification of the Turkmen tribes in the late nineteenth century and the introduction of commercial craft production (although branching continued to dominate). Thus, as well as varying from case to case, the processes responsible for generating patterns of cultural diversity can change significantly within a few generations. Ethnographic studies can advance our understanding in this area by shedding more light on the specific social, economic, and political conditions that cause groups to become isolated from one another or encourage them to interact. Moreover, long-term participant-observation studies of cultural learning can help to establish which traditions are likely to be strongly affected by social change and rates of inter-group contact, and which ones are more stable and long-lasting (e.g., Pétrequin & Pétrequin 1999).

Unfortunately, in recent decades there have been relatively few ethnographic studies that have directly addressed the issues that I have raised here. This can largely be accounted for by the rise of so-called hermeneutic approaches (e.g., Clifford & Marcus 1986; Geertz 1973) which focus on the problems of interpreting meaning and experience in different cultures, and which are inspired more by movements in literary criticism and philosophy than by the social or biological sciences. However, while the idea of a science of culture has fallen out of fashion in mainstream social anthropology, I have attempted to show that there is considerable potential for developing an ethnographic research agenda within the framework proposed by Mesoudi et al. The starting point for this agenda is recognising that by carrying out long-term fieldwork in a single community and observing the interactions and behaviours of its members in the absence of experimental controls, ethnographers can provide important insights into the evolution of culture that would complement – or possibly challenge – those obtained by the approaches discussed in the article.

Generative entrenchment and an evolutionary developmental biology for culture

William C. Wimsatt

Philosophy and Committee on Evolutionary Biology, University of Chicago, Chicago, IL 60637.

wwim@midway.uchicago.edu

Abstract: Mesoudi et al.’s new synthesis for cultural evolution closely parallels the evolutionary synthesis of Neo-Darwinism. It too draws inspiration from population genetics, recruits other fields, and, unfortunately, also ignores development. Enculturation involves many serially acquired skills and dependencies that allow us to build a rich cumulative culture. The newer synthesis, evolutionary developmental biology, provides a key tool, *generative entrenchment*, to analyze them.

In 1982, Mayr and Provine celebrated the evolutionary synthesis, the articulation of disciplines into a population genetic – driven theory of evolution (Mayr & Provine 1980). Sewall Wright’s absence was widely felt (Mayr did not invite him). His place and that of mathematical theory had to await Provine’s (1986) masterful biography. Present but *not* felt was Viktor Hamburger, representing embryology, the disenfranchised mother of evolution (Richards 1992). But not disenfranchised for long: Discoverers of HOX genes, phylogeneticists, embryologists, and renaissance paleontologists recruited partners to a fusion as evolutionary developmental biology became the *newer* synthesis, one increasingly overreaching the original. Raff (1996), Arthur

(1997), Davidson (2001), Schlosser and Wagner (2004), Carroll (2005), and others drive an expansive adaptive radiation of the new theory that even reaches culture, with Oyama et al. (2001), Jablonka and Lamb (2005), and Odling-Smee et al. (2003). This list could have been quadrupled (Maienschein & Laublicher 2006).

Mesoudi et al. survey and inform a synthesis increasingly stimulating research throughout the human sciences. They embrace the mathematics that Mayr avoided but reproduce the other mistake: development is far too central to be ignored in an account of cultural change, even more so than for biological evolution. Crucial to the architecture of the theory, development also gives handles on classes of phenomena not addressed effectively by any part of their new synthesis (Wimsatt & Griesemer 2006).

Biological life cycles begin with zygotic genomes, complete at birth, participating on cue in rich downstream interactions with their embodying and embedding contexts. Surviving organisms differentially become parents to make new zygotes. In this framework, one can abstract and separate out heredity, development, and selection (Wimsatt 1999), simplifying components not being directly studied or modeled, often treating problems as “nearly decomposable” without major distortions of evolutionary dynamics. In this problematic limit (Griesemer 2005), development is commonly lumped with selection as a black-box scalar multiplier for gene frequencies, and then ignored.

By contrast, transmission of cultural information is *not* complete at birth: it has barely begun. As the authors note, cultural transmission is commonly horizontal, generating different dynamics from those possible for biology. As they fail to note, individual enculturation is most often sequentially dependent: We *must* learn arithmetic (and many other things) well before calculus. Agents accumulate, coadapt, and construct contents and practices throughout the life cycle. Earlier assimilations potentiate, filter, and amplify, selecting and often transforming (Sperber 1996) later acquisitions. New contents may transform agents’ connections in the social network mediating reception and transmission. Such sequential dependencies are not modeled in any extant theory. Furthermore, in development, selection and heredity are almost impossibly confounded and path-dependent, and details of individual history matter (Wimsatt 1999). Evolutionists and creationists taking the same curriculum in population genetics and developmental biology would draw, systematically, quite different lessons from it.

Why are some elements of a different culture readily diffusible, others rejected, and others transformed nearly unrecognizably? Epidemiological models of infectibility and resistance can utilize networks to model contacts but ignore cultural contents. Conformity bias and broad categories of “content-based bias” do not have the structure to deal with sequence-dependent skill acquisition or model the specificity and relatedness of ideas or technologies. One needs structures capable of dealing with the content.

One way looks promising. Developmental dependency of elements in the life cycle characterizes both biological and cultural evolution: You generate what comes later from what you have earlier. Inferential structures (including scientific theories and legal codes) have dependencies too. Biological, cognitive, and cultural architectures are all constrained by and tuned to creatively elaborating these dependencies. We can use them to build theory.

To Lewontin’s (1970) three requirements for evolution (heritable variance in fitness) add two more: (4) developmental trajectories show sequential dependencies (*generativity*), and (5) systemic elements differ in downstream consequences and magnitude of effect (*differential generative entrenchment*). These provide a minimal but absolutely general account of development. All nontrivial evolutionary systems satisfy all five assumptions (Wimsatt 2001). And much more follows. Differential generative entrenchment yields a robust evolutionary dynamics

and many new consequences (B. Arthur 1994; Schank & Wimsatt 1988; 2000; Wimsatt & Schank 1988; 2004). The key is neo-Darwinian: Larger mutations give more places for something to go wrong and so are exponentially less likely to be adaptive. So they are also less likely to be incorporated in evolution, generating a differential conservatism. An evolutionary dynamics arises simply from differential dependency, a general feature of organizational structure.

Here are some of the new consequences:

1. Features earlier in development that are more generatively entrenched should tend to be more evolutionarily conservative.
 - 1a. This yields von Baer’s “laws,” roughly, that earlier developmental stages tend to look more alike than later stages (Gould 1977).
 - 1b. Generative entrenchment in early development also predicts life *cycles*: Successive generations must start in places like their parents, however much they diverge later, until reproduction “closes” the cycle (Wimsatt 2001).
2. New population-genetics models of entrenchment (Schank & Wimsatt 1988) give purchase on “complexity catastrophes” and the evolution of modularity (Wimsatt & Schank 1988; 2004) that are also suggestive for culture.
3. An entrenchment account of phenomena spoken of as “innate” captures the maximal consistent subset of criteria for innateness and predicts new ones (Wimsatt 1986; 2003).
4. For culture, as things get more deeply entrenched, we resist changing them, suggesting how things become conventional, standardized, and acquire a normative loading.
5. Standardization is crucial to technological progress when further developments require common components, a more general feature of the truly *cumulative* culture sought by Richerson and Boyd (2005).
6. In literary theory, Turner (1991) employs entrenchment to explain differences between literal and figurative meaning.
7. Differences between biology and culture in how we can generate and deal with deeply entrenched changes are crucial to the rapidity and sometimes revolutionary character of cultural change (Wimsatt & Griesemer 2006).

Evolutionarily recent changes in deep structures provide apparent exceptions worth closer study (Raff 1996). Some changes (e.g., *bicoid*; Schmitt-Ott & Wimmer 2004) first appear as fine-tuning for a control structure, then co-opting and amplifying the role of that control structure to become deeply entrenched (like our information technologies). Other organizational features matter in determining entrenchment. Selection in evolutionary genetics is modulated by linkage, drift, and population structure and makes a richer theory for that. Similarly, a mature theory of generative entrenchment should articulate with other systematic organizational factors, such as redundancy, sequestration, modularity, and canalization. All decrease entrenchment in diverse ways with further implications. There are other fruitful complications for biology and many more for culture (Wimsatt & Griesemer 2006).

Differential dependencies – what remains invariant, and what changes with what – can produce organizational information from comparative data. In 1987 Rasmussen proposed a tentative architecture for *Drosophila* development inferred from 22 developmental mutations (Rasmussen 1987) – still often correct despite massive amounts of new data. Still key in evolutionary developmental biology, analyses of relative stasis and dependency help to unravel developmental programs and predict phylogenetic relationships (Arthur 1997; Davidson 2001). They can be used to good advantage in studying cultural change: Dependency relations are often more readily discovered and analyzed than is selection, and complement other methods in the powerful new paradigm.

Population structure is crucial for biological evolution (Wade & Goodnight 1998), but the breeding population for one trait does for all. Enculturated individuals getting traits piecemeal have as

many breeding populations as reference groups and the salience of these groups shifts over time. Acquisition of sequential skills organizes many of these transitions (Wimsatt 2001). Divergent specialties and values midwife heterogeneous societies and sub-cultures as we bootstrap institutions, technologies, and material cultures to maintain and elaborate them (Basalla 1988). Molar structures – settlements, schools, governments, legal codes, religions, firms, and markets that scaffold our enculturation – organize, regulate, and contribute to its content. Entrenchments organize contingencies of practice into more stable structures, only to be modulated by the next round of contingencies. This produces for history and culture a fractal organization of relevant detail on many size and time scales (Gaddis 2002). Entrenchments thereby help to generate a qualitative understanding of the organization and richness of even “thick” culture through the development of individuals and the more stable superindividual structures (Wimsatt & Griesemer 2006).

Authors' Response

A science of culture: Clarifications and extensions

Alex Mesoudi,^{a,c} Andrew Whiten,^a and Kevin N. Laland^b

^aCentre for Social Learning and Cognitive Evolution and School of Psychology, University of St. Andrews, St. Andrews, Fife KY16 9JP, Scotland, United Kingdom; ^bCentre for Social Learning and Cognitive Evolution and School of Biology, University of St. Andrews, St. Andrews, Fife KY16 9TS, Scotland, United Kingdom; ^cDepartment of Anthropology, University of Missouri–Columbia, Columbia, MO 65211; and W. Maurice Young Centre for Applied Ethics, University of British Columbia, Vancouver, British Columbia V6T 1Z2, Canada.

MesoudiA@missouri.edu
www.missouri.edu/~mesoudia/ aw2@st-and.ac.uk
www.st-and.ac.uk/~aw2/ kn11@st-and.ac.uk
www.st-andrews.ac.uk/~seal

Abstract: We are encouraged that the majority of commentators endorse our evolutionary framework for studying culture, and several suggest extensions. Here we clarify our position, dwelling on misunderstandings and requests for exposition. We reiterate that using evolutionary biology as a model for unifying the social sciences within a single synthetic framework can stimulate a more progressive and rigorous science of culture.

R1. Introduction

We are pleased and encouraged by the generally positive tenor of the commentaries. The majority of commentators (**Barkow; Borgerhoff Mulder, McElreath, & Schroeder [Borgerhoff Mulder et al.], Cronk, Dennett & McKay; Kincaid; Lyman; Mende & Wermke; O'Brien; Pagel; Reader; Tehrani; Wimsatt**) accept the core features of our evolutionary framework, and many of them go on to recommend additions or extensions to our approach. These additions are discussed in more detail in section R2.

Several other commentators (**Aunger; Blackmore; Fuentes; Kelly, Machery, Mallon, Mason, & Stich [Kelly et al.]; Knudsen & Hodgson; Sopher**) agree with the need for an evolutionary approach to culture, but take issue with our particular framework or appear to reserve judgement until certain key issues are dealt with. Finally, **Borsboom, Bridgeman, and Read** appear to reject the

premise that any (Darwinian) evolutionary approach can be applied to culture. The objections of all of these commentators are dealt with in section R3.

R2. Suggested extensions

We are very encouraged that the commentators have already proposed new branches to the synthetic evolutionary framework for studying culture that we illustrated in Figure 1, either by drawing new parallels with subfields of evolutionary biology that we omitted, or by drawing our attention to existing subfields of the social sciences that might appropriately fit into a unified science of cultural evolution. We do not see this as a failing of our original proposal and are broadly receptive to their suggestions. On the contrary, a significant test for our synthetic framework is whether it can usefully accommodate such additions, which we believe it can and does. After all, the modern synthesis that unified evolutionary biology (Huxley 1942) was far from complete when it was first outlined in the 1930s and 1940s, and evolutionary biology continues to incorporate new subdisciplines to this day (Carroll 2000; Kutschera & Niklas 2004).

R2.1. Omitted social science literatures

Kincaid, Knudsen & Hodgson, and Sopher point to areas of the social sciences that have already adopted evolutionary methods with some success, but which we failed to acknowledge in the target article. Kincaid and Knudsen & Hodgson cite “organisational ecology” in sociology (Hannan & Freeman 1989), whereas Knudsen & Hodgson and Sopher reference “evolutionary economics” (Nelson & Winter 1982). We welcome this opportunity to draw attention to such work and encourage its integration with our broader evolutionary framework. Given these fields' emphasis on large-scale and long-term interactions between entire organisations, this might require a new branch of the macroevolution section of Figure 1, perhaps drawing a parallel between population or community ecology (biology) and organisational ecology (culture).

Kincaid also mentions evolutionary game theory (Danielson 2004; Gintis 2000), which, although currently used extensively within economics, in fact represents a methodological tool that can be used to model cultural evolution more generally. This would complement the methods derived from population genetics discussed in section 3.1.2, and although game-theoretic methods are already used extensively within gene-culture coevolutionary theory (e.g., Boyd & Richerson 1985), there are clear opportunities to broaden their application to cultural phenomena.

Agent-based modelling (Axelrod 1997; Epstein & Axtell 1996; Kohler & Gummerman 2000) represents yet another means to model cultural evolution, and we are happy to highlight the potential utility of this within our framework. Indeed, this is a methodology that we ourselves have used to explore the coevolution of paternity beliefs and genetic variation underlying human mating behaviour (Mesoudi 2005). All of these mathematical tools have strengths and weaknesses, and each can be applied, in a “horses

for courses” manner, to address a broad range of issues related to cultural evolution.

R2.2. Further parallels with evolutionary biology

Reader, Wimsatt, Fuentes, and **Cronk** point to other theories, tools, and concepts from evolutionary biology that may also apply to the study of culture. Although we restricted our schematic of the structure of evolutionary biology to that given by Futuyama (1998: left side of our Figure 1), we are happy to explore the applicability of other areas which have not yet been fully integrated into mainstream biology.

Cronk proposes that signalling theory (Krebs & Dawkins 1984), originally developed within biology, might be used to solve a problem that he perceives with evolutionary approaches to culture: that human culture is directed by intelligent action or foresight. We agree that this approach has great potential within the human sciences and discuss this further in section R3.6. Here we focus on two other parallels, “evo-devo” and “niche construction.”

R2.2.1. Evo-devo. **Reader** and **Wimsatt** explore how the emerging findings of evolutionary developmental biology (“evo-devo”) might be applied to culture. We agree that evo-devo is having increasing influence within evolutionary biology and subscribe to the view that it will soon be integrated fully into the mainstream of that discipline. We also accept that evo-devo may contribute important concepts to the study of cultural evolution, such as **Reader’s** proposal that cultural traits may occur in clusters because of cognitive constraints on learning.

However, before rushing to apply concepts and findings from evo-devo to cultural evolution, it needs to be carefully and explicitly stated exactly *what* is developing. In biology, development is the process through which interaction between a genotype (together with various extragenetic sources of hereditary material) and various environmental factors generates and maintains a phenotype. If we treat the semantic information that is stored in brains and in external storage devices (e.g., books or computer memory) as the cultural equivalent of the genotype and the expression of that culturally acquired information (e.g., motor behaviour, spoken language, material artifacts, or social organisations) to be the equivalent of the phenotype, or extended phenotype (see sects. R3.1 and R3.2), then cultural evo-devo would therefore describe how this transition shapes and constrains subsequent cultural evolution. This would, therefore, require an understanding of how neural structures generate behaviour, how artifacts are constructed, and how organisations are formed.

Neither **Reader** nor **Wimsatt** appear to take this approach, in which development is seen from the perspective of the transmitted information (the “meme’s-eye-view,” as Blackmore [1999] puts it), although we suspect they might be sympathetic to it. They instead appear to see development from the point of view of the individual in both biological *and* cultural evolution. Hence, **Reader** talks of clusters of multiple traits within an individual brain or within a group (“speaking French is associated with religious, dietary, technological, and societal preferences and norms”), while **Wimsatt** discusses changes in cultural traits during an individual’s development

(“individual enculturation is most often sequentially dependent: We *must* learn arithmetic well before calculus. . . . You generate what comes later from what you have earlier”).

We are not saying that the first of the views of cultural evo-devo outlined above is correct and those of **Reader** and **Wimsatt** are wrong, simply that we need to avoid confusion by stating exactly what is developing from what and into what. This is particularly important given that simplistic ideas about relationships between evolution and development have in the past caused considerable harm within the social sciences and are among the reasons why Darwinian evolution is misunderstood and rejected by many social scientists. Early practitioners of cultural “evolution” such as Tylor (1871) and Morgan (1877), continuing to White (1959), Steward (1955), and Sahlins and Service (1960), saw cultural change not in terms of Darwinian evolution but as a process of linear development, resulting in attempts to fit entire contemporary societies into fixed and inevitable developmental stages. It is important to emphasise that this is a gross distortion of Darwinian evolution. **O’Brien** reminds us that Gould (1996; 1997) wished cultural evolution to be relabelled as “cultural development” to disavow the parallels that we are highlighting and thus maintain the separation of the biological and social sciences. As **Lyman** notes, “we ignore history at the peril of repeating old mistakes.”

R2.2.2. Niche construction. **Aunger, Fuentes, Kincaid, Knudsen & Hodgson,** and **Wimsatt,** explicitly or implicitly, place emphasis on a role in the cultural evolutionary framework for niche construction, in which organisms actively modify sources of natural and/or cultural selection in their environments (Laland et al. 2000; Odling Smee et al. 2003). We welcome this suggestion, which concords fully with our views, and below we discuss the specific application of niche construction to the issue of external storage of cultural information (sect. R3.2) and intentionality (sect. R3.6).

Here we note that niche construction affects developmental environments as well as selective environments, as stressed by **Wimsatt**. Human mental processes build on an “external scaffold” (**Kincaid**), which is itself a product of the niche-constructing activities of the members of a society. Niche-constructing organisms modulate flows not only of energy and matter but of information, because they are, advertently or inadvertently, constructing the learning environment for other individuals. Several commentaries stress that knowledge and culture are distributed across individuals and embedded in institutions, social practices, and organisations. This, in turn, determines payoffs and possible strategies (**Kincaid**). **Knudsen & Hodgson** refer to the unsolved problem of explaining cultural inheritance at the levels of social organisations and institutions, whereas **Mende & Wermke** refer to the challenge of understanding the emergence of “the hyperlinked, interlocked global village.” Related issues concern **Read**. The challenge is to explain how such group-level phenomena can come into existence.

One possibility is through group-level selection (see sect. R3.4), but it is not the only possibility. The collective social niche construction of individuals may create institutions and conventions (evocative of generative

entrenchment: **Wimsatt**), where they construct a learning environment biased towards the currently performed behaviour, or enhance the payoffs of that behaviour. For example, circumstantial evidence suggests that wild chimpanzees (Whiten et al. 1999) and orang-utans (van Schaik et al. 2003) possess local cultures defined by extensive suites of different kinds of tradition (e.g., foraging techniques, tool use, grooming customs) that extensively shape the repertoire of successive generations. Recent experimental evidence indicates a conformity bias that has the potential to strengthen the effect of the culturally shaped niche to which each developing individual is exposed (Whiten et al. 2005). Among both human and nonhuman societies, such culturally constructed niches may be instantiated not only materially, as in the case of accumulations of useful tools at chimpanzee termite sites (Sanz et al. 2004), but in social conventions. For example, Perry et al. (2003a; 2003b) have described several types of intimate social interactions and games, including bizarre actions like resting one's fingers deep in companions' mouths and noses, that have the hallmarks of local conventions among different communities of wild capuchin monkeys. Variation in such conventions is not obviously attributable to differences in ecological resource distribution or genetic differences across sites, and the monkeys may use group-specific social conventions to test the quality of their social relationships. Their activity creates a social niche within which such otherwise improbable actions become readily acquired and may further adapt and evolve.

Conventions may also be important in circumstances where it is costly for individuals to acquire information about resources, such as food or mates, or to solve problems alone. For instance, many fishes exhibit traditions for feeding, resting, and mating in particular places and for traditional routes to and from such sites (Helfman & Schultz 1984; Warner 1990). Experimental studies suggest these traditions are stable because individuals would be more vulnerable to predation without the protection of being in a group (Laland & Williams 1998). In game-theoretic terms, the traditions are Nash equilibria, in which it never pays any individual to abandon the tradition unilaterally, leaving populations locked into conventions. Here members of the population performing the tradition construct a social niche that biases both the optimal behaviour and the learning environment of naïve individuals to leave it more likely that they, too, will adopt the same behaviour. There are many examples among humans, for instance, language learning: If most individuals in a child's region speak English, not only is it optimal for the child also to become an English speaker, but there will be many more opportunities for the child to learn English than an alternative language. As **Wimsatt** notes, socially constructed institutions scaffold human enculturation.

R2.3. Additional methodologies

Fuentes and **Tehrani** both argue that we failed to acknowledge that ethnography can play an important role in an evolutionary science of culture, and **Tehrani** presents a number of potentially relevant lines of investigation using ethnographic methods. We are largely in agreement

with these researchers over the need for long-term observational studies of cultural evolution in natural settings.

Tehrani notes that to date there has been a general lack of interest from social anthropologists in the kinds of issues raised by evolutionary approaches, such as who learns what from whom and how. We also note that ethnographers seldom make a set of clear theoretical predictions that they then test by collecting quantitative data and using comparative methods. This may be due to the anti-science position that **Barkow** suggests is held by many cultural anthropologists, and a tendency, remarked on by **Pagel**, to see societies as specific and unique rather than subject to more general principles. Ethnologists and behavioural ecologists who study animal behaviour face similar problems to ethnographers, yet have reacted not by abandoning the scientific method but by employing sophisticated methodological and statistical techniques to deal with the complexity of their subject matter (e.g., Krebs & Davies 1997). The facts that proposals for such practices to be adopted in ethnography (e.g., Aunger 1995) have gone largely unheeded, and that studies which apply such techniques (e.g., Aunger 2000a) remain in a minority, are unfortunate reflections on the current state of socio-cultural anthropology. Hopefully some of the scientific alternatives outlined in this paper, along with positive proposals like those of the ethnographer **Tehrani** and the work he cites, will stimulate more such work.

Finally, **Barkow** argues that another, complementary way to stimulate a more scientific study of culture is by following his principle of vertical integration, which he hopes will "salvage the bulk of humanities-oriented anthropology." We agree with **Barkow** that our framework and his methodology are "entirely compatible," and we encourage its application.

R3. Points of contention

A number of commentators took issue with how we defined key terms and with our position on certain theoretical matters. Although we feel that some of these criticisms were actually dealt with in the target article, some points bear repeating. For example, **Bridgeman** argued that cultural change is not like biological evolution because in biology there is no equivalent of traits being acquired across societies, and "cultural traits are not like Mendelian units, independent of one another." In section 2.1.2 we highlighted the presence of horizontal gene transfer in biology (migration of individuals into new groups is also an example of genetic material being transferred between groups), and section 3.5.2 was devoted to illustrating, on the basis of findings from molecular biology, how genes can neither be accurately described as neat discrete units nor as independent of one another. In spite of these complications within the biological domain, simple models still have considerable utility.

Other commentators raised issues and criticisms that we did not address, and we deal with these below. In the target article we tried to avoid certain thorny theoretical issues that we feel have sidetracked previous debates regarding cultural evolution, preferring to draw together the growing number of compatible empirical studies that

have emerged in recent years. However, this response is an appropriate place to further clarify and expand our theoretical position.

R3.1. Culture as semantic information

Blackmore expresses reservations regarding our definition of culture as “semantic information” that is “represented primarily in the brain,” whereas **Knudsen & Hodgson** argue that we have inadequately identified replicators and interactors in cultural evolution. We reiterate our position that culture is most usefully regarded as semantic information that is transmitted from individual to individual via social learning and expressed in behaviour and artifacts. This information is what is replicated and is the counterpart to genetic information in biology. This follows Williams’ (1966) and Dawkins’ (1995) conception of genes (biological replicators) as information in an abstract sense, independent of its physical instantiation in molecules of DNA.

This replicating cultural information may be encoded in the brain, or it may be stored externally in artifacts, from the hammerstones of chimpanzees and early hominins, to the Internet. **Aunger, Bridgeman, Blackmore, and Kincaid** take issue with our original statement that “cultural information is represented primarily in the brain” and argue that we did not sufficiently acknowledge the role that artifacts play in cultural transmission. We did, in fact, also state that “cultural knowledge does not exist solely in human brains and does not rely exclusively on face-to-face communication for transmission” (target article, sect. 3.4.2, para. 6), and cited numerous studies of archaeological and technological artifacts in section 2.2.2 and elsewhere. Nevertheless, let us clarify our belief that cultural information is also located in external memory stores in the environment (Donald’s [1991] “exograms”), explicitly, such as written text in books or digital code in computer memory, or more implicitly in the structure of manufactured items such as tools, and that this route of information transmission is important, perhaps increasingly so. There is also growing evidence that artifacts, tools, and other constructions are important to some nonhuman species as well as ourselves (van Schaik et al. 2003; Whiten 2005b). Terkel (1996), for example, offered elegant experimental evidence that young black rats learned how to manipulate and extract seeds from pine cones via the incompletely but expertly processed cones abandoned by their mothers.

However, while acknowledging the possibility that culturally transmitted information may be stored in artifacts, we maintain that the brain plays a central role in cultural transmission. Semantic information is useless unless there is a brain capable of decoding it. For those of us unfamiliar with the language, a text written in ancient Greek contains only configural information and precious little meaning. Contrary to **Blackmore’s** claims, we believe our definition is perfectly consistent with Dawkins’ original definition of a meme: “A meme should be regarded as a unit of information residing in a brain” (Dawkins 1982, p. 109). We also disagree with Blackmore when she states that “skills and fashions” are not caused by semantic information stored in the brain, because this would imply that humans typically have no knowledge of, say, what clothes they buy or choose to wear.

Her assertion that “memes might continue to thrive and evolve even if all humans died” would be plausible only if there were another form of intelligent life with a brain-like, information-processing organ akin to the human brain. Brains are not empty vessels that simply store (or are “infected by”) memes: rather, there are rich, biologically evolved, developmentally generated cognitive structures in the brain that shape cultural transmission, as noted by **Cronk and Kelly et al.** (see sect. R3.7).

R3.2. Cultural traits

Culturally transmitted semantic information, whether it is stored in brains or in external memory stores, may be *expressed* in a variety of forms, including motor behaviour, material artifacts, and social organisations (**Knudsen & Hodgson** highlight the latter). These expressed forms, which can be considered the cultural equivalents of the phenotype, can also be seen as synonymous with the term “cultural trait.” Again, this echoes Dawkins: “The phenotypic effects of a meme may be in the form of words, music, visual images, styles of clothes, facial or hand gestures, skills such as opening milk bottles in tits, or panning wheat in Japanese macaques. They are the outward and visible (audible etc.) manifestations of the memes within the brain” (Dawkins 1982, p. 109).

Fuentes argues that it may be unproductive to lump all cultural traits together in this way. If “cultural traits” are seen as phenotypic cultural expressions, however, this diversity is not necessarily problematic (although it is important to distinguish between the information and its expression and to acknowledge, as in biology, that there is no one-to-one correspondence between the two). The traits are simply different ways in which semantic information is expressed. Indeed, biological traits (i.e., the phenotypic expression of biologically inherited genetic information) are similarly diverse and range from behaviour to morphology to artifacts (“extended phenotypes”), interlinked in a complex manner and differentially expressed. Indeed, it may be useful to consider cultural traits in a similar way, with artifacts as equivalent to extended phenotypes, behaviour as equivalent to phenotypes, and information as equivalent to genes (Laland & Brown 2002). The niche-construction perspective in evolutionary biology similarly stresses the importance of living organisms in constructing artifacts and other features of their environments, thereby modifying selection pressures and codirecting evolution. Individuals inherit not only genes but also a legacy of modified selection pressures, manifest in a developmental environment part-constructed by their ancestors. Human cultural artifacts and constructions are merely a special case of a more general process. In cultural organisms, such niche construction is as likely to affect cultural selection as natural selection.

Lyman proposes that cultural traits can be seen as “recipes” (seemingly independently of **Blackmore’s** recipe example, which we discuss below), interrelated conceptual structures that link physical characteristics, behavioural rules and raw materials that, combined, comprise the knowledge required to construct an artifact. This may be a good way of capturing the interrelated structure of cultural traits noted above, as well as bringing in the

evo-devo approach discussed earlier (indeed, recipes are also a common metaphor for how genes operate: Dalton 2000; Ridley 2003). Cognitive psychologists (Weber et al. 1993; Weber & Perkins 1989) have independently arrived at a similar concept to the recipe using schema theory, where an artifact is seen as a “frame” which has variable “slots” (representing the ingredients or physical characteristics of the artifact) and which is associated with “action scripts” (the behavioural rules required to make or use the artifact). Plotkin (1999; 2000) makes a similar point that cultural traits are best conceived of as hierarchically organised knowledge structures such as schemas, scripts, or frames (although it remains to be seen whether these concepts apply to other aspects of culture, such as organisations: **Knudsen & Hodgson**). What is needed now is an integration of psychological data and theory regarding how information is represented in the brain (e.g., as scripts and frames) with ethnographic data regarding how that information is expressed as artifacts (i.e., how the artifacts are manufactured and used, equivalent to their “development”) and an exploration within a “cultural evo-devo” framework of how that developmental process affects macroevolutionary changes in artifact forms, as studied by evolutionary archaeologists.

R3.3. Cultural inheritance

The distinction between cultural information (or replicators) and cultural traits (or interactors) allows us to discuss inheritance. In **Blackmore’s** recipe example (also mentioned by **Bridgeman**), the written recipe constitutes an external memory store that contains the information required to bake a cake, while the cake itself is the physical expression of that information. Information can be acquired directly from the external information store – the recipe – in what Blackmore calls copy-the-instructions (although, as noted above, a recipe is useless without a brain to understand it). Information can also be acquired indirectly from the expression of the information – the cake – in what Blackmore calls copy-the-product. Laland and Brown (2002) also proposed “copy-the-process,” in which the behaviour required to bake a cake is imitated. We stress that all of these forms of transmission – copy-the-instructions, copy-the-product, and copy-the-process – are consistent with an evolutionary approach to culture. In the words of **O’Brien**, “[a]ll that is important in Darwinian terms is . . . that transmission, however it is realized, takes place.”

One common source of confusion is that the term “Darwinian” has two different uses in this context. “Darwinian” is used to describe the general theory of biological *evolution* that is accepted by modern biologists and which we are arguing in this paper can be applied to culture. However, “Darwinian” is also used to describe a theory of biological *inheritance* in which Weissman’s barrier separates the replicator and the interactor (resembling “copy-the-instructions”: **Blackmore**), in contrast to “Lamarckian” inheritance in which acquired phenotypic characteristics are inherited genetically (resembling “copy-the-product”: **Blackmore**). Somewhat confusingly, Charles Darwin himself held Lamarckian views regarding biological inheritance (Darwin 1859/1968), so we might more accurately talk here of “Weissmanian” inheritance rather than “Darwinian” inheritance. To clarify, in the last paragraph of section

3.5.3 in the target article, our use of “Darwinian” referred to Darwinian *inheritance*, or, as we should have called it, Weissmanian inheritance. A Darwinian theory of cultural *evolution* is therefore perfectly compatible with either a Lamarckian or a Weissmanian theory of cultural inheritance (or both, at different times for different traits). We were not arguing that the issue of inheritance (whether Weissmanian or Lamarckian) could ever “dismiss the application of Darwinian principles in the social domain” (**Knudsen & Hodgson**), as we also made clear in a previous paper (Mesoudi et al. 2004).

R3.4. Cultural selection

Knudsen & Hodgson complain that we “do not provide an explicit definition of cultural selection processes,” which is a fair point and one we address now. As noted above, culturally transmitted semantic information may be expressed at multiple levels, from individual-level traits such as motor behaviour or some material artifacts, to group-level traits such as social organisations and other complex artifacts. In principle, it is possible to conceive of group-level cultural traits being aggregated together into higher-order group-level traits. Hence, we anticipate that it may be useful to regard culture as a multi-layered phenomenon, with these different levels linked together through recipes and schemas. Cultural selection refers to any case in which there is differential replication of cultural variants relative to their alternatives, as a consequence of differences in their longevity, transmission fidelity, and probability of spreading. Cultural selection may act on any of the aforementioned levels, as helpfully highlighted by Knudsen & Hodgson.

Contrary to **Read’s** claim that in Darwinian evolution “selection is based on properties of individuals,” in the past few decades multilevel models of selection have become widely accepted within evolutionary biology, as we note in section 4 of the target article. Hence, biologists frequently model natural selection acting not only on the individual (Darwin 1859/1968), but at any level that exhibits variation, differential fitness, and inheritance of fitness-related characters (Lewontin 1970). This may include levels below the individual, such as the case of selfish DNA (Orgel & Crick 1980) which is selected within the genome but which does not directly affect selection at the phenotypic level, or above the individual, as in the case of group selection (Sober & Wilson 1998; Wilson & Sober 1994), species selection (Stanley 1975), or clade selection (Vermeij 1996). We see no difficulty envisaging similar multilevel selection occurring in cultural evolution, negating much of Read’s criticism that Darwinian evolution cannot deal with selection operating at the social level, as with kin terminology (“The selection acting on kinship terminologies occurs at the level of structural properties”). However, we are not convinced that multilevel selection is necessary to explain the phenomena to which Read refers. We note that kinship terminology is an example of language use, and as **Pagel** and **Mende & Wormke** emphasise, language is a prime example of cultural evolution, several examples of which we used to illustrate sections of our target article. We also note that many of the properties of kinship terminology that Read regards as problematic for Darwinian evolution can be found in animal communication, a topic for which there are

well-established Darwinian theoretical foundations (e.g., Hauser 1996).

Selection above the level of the individual means that macroevolutionary change cannot always be explained exclusively through microevolutionary principles, leading to a partial uncoupling of micro- and macroevolution. This is possible for both biological and, we would argue, cultural evolution. Contrary to **Read**, therefore, we do not “accept uncritically the idea that macroevolution is Darwinian microevolution writ large.” However, we acknowledge that our statement in section 3 is a little misleading and perhaps should have read “large-scale macroevolutionary patterns of change are *often* the result of small-scale microevolutionary changes in gene frequencies within populations.” Nevertheless, our original point still stands – that the connection between micro- and macroevolution was hugely important in the unification of biology (Mayr 1982; Mayr & Provine 1980), notwithstanding more recent models of multilevel selection. A similar connection between cultural micro- and macroevolution, although occasionally proposed (e.g., Schwartz & Mead 1961), has not yet occurred.

R3.5. Mechanisms of cultural transmission

Knudsen & Hodgson argue that there is currently little understanding of cultural transmission (“Biology has a well-developed theory of inheritance but there has been little progress in explaining cultural inheritance. . . . The way in which cultural components combine and replicate is presently unknown”), as does **Borsboom** (“the mechanisms by which cultural traits are propagated cannot be sidestepped as easily as Mesoudi et al. suggest, and they would, therefore, do well to offer some convincing arguments for the existence of such mechanisms”). **Aunger** goes further and takes the somewhat extreme position that social scientists have yet to determine whether behavioural distributions are due to cultural transmission, as opposed to the evoked responses to immediate environmental conditions that are already present because of biological evolution or individual learning, citing Tooby and Cosmides’ (1992) “jukebox model.” We note that Tooby and Cosmides (1992) never argued that the jukebox model could explain *all* human behavioural variation (“complex shared patterns that differ from group to group may be evoked by circumstances or may be produced by differential transmission . . . the jukebox thought experiment is an unrealistically extreme case”; Tooby & Cosmides 1992, pp. 116–17), and that they also acknowledge a transmitted “epidemiological culture” (p. 121).

We believe that there is solid evidence against the extreme position that all human culture is evoked and none is transmitted, and we maintain that very much more is known regarding cultural transmission than is often realised. Although understanding of cultural inheritance is far from complete, we take issue with the claims by **Borsboom** and **Knudsen & Hodgson** that little progress has been made in this area. Moreover, we reiterate the fact that the principles of biological inheritance are also far from fully understood – indeed, they have changed dramatically over the last decade (Gilbert 2000; Mousseau & Fox 1998; Wolf et al. 2000). It is therefore a distortion to portray biological and cultural inheritance at opposite

poles of a spectrum representing scientific understanding. We have discussed some of the available evidence that demonstrates cultural transmission and the mechanisms that underlie it in a previous paper (Mesoudi et al. 2004), and Richerson and Boyd (2005) have recently made a parallel case. However, this evidence is perhaps worth summarising here.

First, there are many cross-cultural studies that demonstrate a double dissociation between culture and the environment. For example, Hallpike (1986) describes how East African and Indo-Iranian pastoralists, who live in the same ecological environment and have the same means of subsistence, differ in social organisation and religious beliefs, whereas two Ethiopian societies that inhabit very different environments have essentially identical social institutions, religious beliefs, and cultural values. Many other cross-cultural comparisons demonstrate evidence for cultural inheritance (e.g., Guglielmino et al. 1995; Hewlett et al. 2002), as do phylogenetic analyses of present cultural diversity (e.g., Collard et al. 2005; Mace & Pagel 1994; Tehrani & Collard 2002). Ethnographic studies provide evidence of cultural transmission within these societies (e.g., Aunger 2000a; Hewlett & Cavalli-Sforza 1986; Ohmagari & Berkes 1997).

Second, longitudinal studies demonstrate how cultural traits persist over long periods of time even when the bearers of those traits migrate large distances into novel environments. One such study, Rice and Feldman (1997), found that variation across the United States in behaviour relating to civic responsibility (e.g., voting or donating to charity) can be predicted from similar variation in their parent European populations. For example, both Scandinavian countries in Europe and U.S. communities founded by Scandinavians have high levels of civic responsibility relative to other European countries and other areas of the United States respectively. This implies that the strong civic-responsibility values of the colonists have persisted via cultural transmission over the last few hundred years through to present day U.S. populations. Rice and Arnett (2001) further document this persistence over the last 100 years.

Third, extensive archaeological, historical, and sociological studies have shown that when culture *does* change, it frequently does so independently of the ecological environment and too rapidly to be explained by genes. Hence, there are (a) archaeological seriations that constitute lineages of artifacts causally linked by cultural transmission (O’Brien & Lyman 2000); (b) detailed historical studies of the cumulative evolution of technological artifacts (Basalla 1988; Petroski 1994; Ziman 2000), documenting how inventors have built on previous inventions and borrowed components from different lineages of inventions, such as Carlson’s (2000) reconstruction of the invention of the telephone through a detailed analysis of Thomas Edison’s notebooks; and (c) sociological studies that have documented the rapid horizontal diffusion of technological or behavioural innovations within single biological generations, not plausibly explained by population-genetic or demographic changes, as summarised in Rogers (1995). More generally, it is unclear that psychological adaptations, supposedly favoured in the ancestral Pleistocene environment labelled by Tooby and Cosmides (1992) and others as the “Environment of Evolutionary Adaptedness,” would necessarily evoke successful and functional

behavioural responses in contemporary human populations that are living in quite different ecological and social environments. It is yet more difficult to envisage that responses that are merely evoked can account for construction of novel cultural phenomena ranging from space travel to the Internet. We find it difficult to conceive how culture can change and accumulate in the new, diverse, and often progressive ways it has in postindustrial societies without some form of cultural transmission.

Fourth, as highlighted by **Pagel** and **Mende & Wermke**, scientific approaches to culture have already made headway on the evolution of languages, and there is a large existing literature on language acquisition that has documented how children readily acquire the language spoken by people around them (Bloom 2001; Pinker 1995; Tomasello et al. 1993). This vast literature provides detailed studies of cultural transmission that counter **Knudsen & Hodgson's** claims that the mechanisms of cultural transmission are presently unknown. Here we will simply make the following observations that counter **Aunger's** "evoked culture" argument: There is no sense in which the English or Chinese languages fit in any significant way with the environments of England or China respectively; languages such as English or Chinese are spoken by people in many different physical environments; languages spoken in the same environment change over time; and children of English-speaking parents who are brought up by Chinese parents acquire Chinese, not English. In short, children raised in China culturally inherit the lexicon and grammar of the language their parents and others speak there. Such observations significantly count against the notion that the specific languages that people speak are either tied to the environment or fully specified genetically.

Fifth, experimental studies have demonstrated and elucidated the cultural transmission of information under controlled settings in the laboratory. Developmental psychologists have demonstrated high-fidelity imitation by subjects of the behaviour of a model, from Bandura's classic studies on aggression (e.g., Bandura et al. 1961) through to comparative studies of observational learning in children and chimpanzees (Horner & Whiten 2005; Nagell et al. 1993; Whiten 1998; Whiten et al. 1996; Whiten et al., in press), and the role of pedagogy in cultural transmission (Csibra & Gergely 2005; Gergely & Csibra 2006; Wood et al. 1976). Other studies have tracked the transmission of text along linear chains of participants (Bangerter 2000; Kashima 2000; Mesoudi & Whiten 2004; Mesoudi et al., 2006). Finally, studies have demonstrated the cultural transmission of behavioural strategies within small groups of participants (Baum et al. 2004; Insko et al. 1980; McElreath et al. 2005).

Taken together, these studies provide strong converging evidence against **Aunger's** claim that "genetic evolution may be able to account for the phenomena we consider to be cultural." At the very least, the case for cultural transmission is stronger than the evidence supporting any exclusively genetic explanation. We agree with **Aunger** that genetic evolution has shaped our capacity for the acquisition, storage, and expression of cultural knowledge and that this will impose biases on the content of culture (see sect. R3.7). However, it does not follow from this that the content of culture is fully specified by genes, or even by gene-(ecological) environment interactions. We

are satisfied that there is sufficient empirical evidence to be able to state with some confidence that a theory of culture that denies cultural transmission is untenable. More generally, we believe that **Aunger**, **Borsboom**, and **Knudsen & Hodgson** are underestimating the evidence amassed by countless studies from psychology, anthropology, sociology, history, and linguistics. Ultimately, this may be because these strands of research are often developing independently of one another. Perhaps if the social sciences were more integrated, as we hope to facilitate with this article, more social scientists would be aware of these different studies, the connections between them, and the coherent collective message they impart.

Although **Aunger** may be correct that the tools of neuroscience are not currently advanced enough to be able to observe changes in brain states corresponding to the cultural transmission of information (although see Iacoboni 2005; Williams et al. 2006), we refer him to **Barkow's** notion of vertical integration, which implies that valuable studies of cultural transmission can be performed without a full understanding of that phenomenon at the neural level. Although an understanding of the neural basis of cultural information is desirable, what is necessary at this stage is for these studies to be consistent with the findings of neuroscience, which appears to be the case for the studies cited above.

R3.6. The role of "intentionality"

Cronk, Dennett & McKay, **Pagel**, and **Sopher** raise the issue of what they variously describe as "the active, often intentional role that humans play in cultural transmission and, thus, in cultural evolution" (Cronk), "intelligent authorship, foresighted, purposeful reasoning, and artistic judgment" (Dennett & McKay), "the human capacity for intentionality or goal-directedness" (Pagel), and "those distinct processes in cultural evolution that involve conscious human choices" (Sopher).

The notion that human action is often intentional, goal-directed, conscious, teleological, mindful, intelligent, directed, purposeful, guided, or designed is a common argument against adopting an evolutionary approach to culture (see commentaries on Rindos 1985). However, **Dennett & McKay** and **Pagel** both make the valuable point that there is a continuum of "intentionality," from blind, unconscious, undirected selection to goal-directed, conscious, directed selection, and the full range of this continuum is likely present in both biological and cultural evolution. Elsewhere (Laland et al. 2000; Mesoudi et al. 2004) we have referred to the acquisition of "smart" variants, cultural traits that have been tried and tested by other individuals. Once again, we believe it is important to stress that the existence of such variants does not invalidate the concept of cultural evolution or the use of evolutionary models and methods (although it may affect the characteristics of such models).

Cronk also rejects the notion that intentionality invalidates a science of cultural evolution, and proposes the use of signalling theory and receiver psychology to understand how and why people produce signals that fit and shape the psychology of the intended receiver. This has parallels with Sperber and Wilson's (1986) relevance theory of language use, in which utterances are tailored to be maximally relevant to the intended target, and also

Gergely and Csibra's (2006) studies of pedagogical learning, in which human infants and adults have been found to exhibit species-specific cognitive adaptations to facilitate high-fidelity cultural transmission of behaviour when the efficacy or functional relevance of the behaviour is unclear. Chimpanzees have been found to have a contrasting tendency to preferentially acquire only those modelled actions that are functionally relevant to solving a task (Horner & Whiten 2005).

We suspect that one of the motivations behind these kinds of criticisms of cultural evolution is the desire to separate humans from other species. **Knudsen & Hodgson** similarly argue that we "fail to elaborate on key differences between human and nonhuman culture, where the former involves a developed abstract language and capacities to attribute intentions and meanings." Although the widespread use of symbolic language does seem to be specific to humans, a capacity to use symbols and attribute intentions and meanings is to some extent shared with other species (Tomasello et al. 2005). Indeed, one of the benefits of the evolutionary approach that we advocate is the use of the comparative method, where the approaches outlined in section 5 can be used to identify homologous or convergent cognitive adaptations in other species that may underpin the biologically evolved capacity for culture in humans.

Niche construction offers another way of integrating both human and nonhuman agency with a biological and cultural evolutionary framework (Laland et al. 2000). **Fuentes** states that "most psychological and anthropological research relies on perceptions, semantic exchanges, and culturally contingent decision processes." One characteristic of the niche-construction perspective that potentially makes it more palatable to the human sciences than the conventional view of evolutionary biology, is that it stresses the active role of organisms in evolution and development. Moreover, because niche construction can result from learned and socially transmitted behaviour, some organisms are able to modify selection processes in a manner that is "goal directed," "intentional," and "intelligent" (Odling Smee et al. 2003). We note that other researchers have already started to use this niche-construction perspective to explore how culturally transmitted "expectancies" – the mind-shaping effects of our mind-reading dispositions – can become an important developmental resource for humans, and critically affect the evolution of cognition (Mameli 2001).

R3.7. The relationship between biological and cultural evolution

Blackmore and **Dennett & McKay** argue that it should not be assumed that culture is always biologically adaptive. Their position contrasts with **Pagel's** "adaptationist wager" that it is often useful to assume culture is adaptive. These both contrast, again, with the work of **Neiman** (1995), **Bentley and Shennan** (2003), and others who use the neutral-drift model of cultural change as a null hypothesis. Although these different approaches seem inherently contradictory, they can potentially complement each other, given that different elements of culture may be biologically adaptive, biologically maladaptive, and biologically neutral at different times and in different contexts. Ultimately, however, it should be an empirical issue

whether a specific cultural trait is biologically adaptive, maladaptive, or neutral for its carriers, to be tested on a case-by-case basis. Although we acknowledge the power and utility of adaptationist reasoning, we prefer to adopt an "open-minded" stance rather than taking an a priori position that the entire contents of culture are always biologically adaptive or always biologically maladaptive. It is also important to clarify each use of the term "adaptive" and "maladaptive" as to what entity is benefiting in each case (e.g., genes, memes, individuals, or groups).

We stress the importance in this context of distinguishing between the *capacity* for culture and the *contents* of culture. **Richerson and Boyd** (2005) make a convincing argument, supported by extensive mathematical theory (**Boyd & Richerson** 2005), that the capacity for culture is a biological adaptation. At the same time, however, features of that biological adaptation, such as "fast and frugal" social learning strategies like conformist or indirect bias (**Boyd & Richerson** 1985), may in certain circumstances lead to the spread of biologically maladaptive cultural contents. We think **Blackmore** misunderstands this distinction when she claims that **Richerson and Boyd's** (2005) "culture is an adaptation" position implies that the contents of culture will be biologically adaptive. **Boyd and Richerson** would no doubt agree with **Blackmore**, as would we, that some cultural traits spread parasitically in spite of imposing fitness costs on their human carriers. Presumably, **Blackmore** would agree with **Boyd and Richerson**, and us, that some cultural traits confer fitness benefits on their carriers.

We find puzzling **Blackmore's** claim that "culture is not and never was an adaptation. It began as a by-product of the evolved capacity for imitation." If her use of the term *culture* here refers to the *capacity* for culture, then for what function did the ability to imitate initially evolve if not the acquisition of knowledge and skills (i.e., culture)? Most researchers in this field, ourselves included, would regard the ability to imitate as a key component of the capacity for culture. Although in principle one could argue that imitation is necessary but not sufficient for culture, to our knowledge **Blackmore** has not adopted this position. Conversely, if (as we suspect) **Blackmore's** use of the term refers to the *content* of culture, there is no major difference between her position and that of **Boyd and Richerson** or ourselves. A biological adaptation is a character favoured by natural selection for its effectiveness in a particular role, and none of us believes that pepperoni pizza or baseball exists primarily because of natural selection on genes. The content of culture is rarely itself a biological adaptation: rather, it is the product of more general adaptations, such as the capacity to learn, to acquire information from others, to conform, and so forth. Although we might differ from **Blackmore** with respect to our intuitions as to the proportion of cultural phenomena that are parasitic, we see no fundamental disagreement here.

The relationship between culture and biological fitness also relates to **Borsboom's** argument that culture can be said to evolve only if cultural traits have the ability to kill individuals (i.e., reduce their biological fitness to zero). Although biologically lethal cultural traits will have a dramatic effect on both cultural and biological evolution, it is long established that the contents of culture may spread independently of biological fitness (**Cavalli-Sforza &**

Feldman 1981; Boyd & Richerson 1985), as **Dennett & McKay** helpfully reiterate. Borsboom's argument is also predicated on a distorted view of biological evolution in which single genes "cause their bearers to go extinct" in a single generation, and gene frequencies change because of their lethal effects ("if the gene is bad for you, you die before you get the chance to propagate"). In reality, biological evolution commonly involves small differences in fitness causing gradual changes in relative gene frequencies over multiple generations. Moreover, these are usually genetic differences in rates of reproduction that are not necessarily tied to survival.

Kelly et al. discuss various content biases (e.g., disgust) and context biases (e.g., conformity) that have been shown to affect the cultural transmission of information, as we acknowledge in section 3.4.2. Many of these psychological biases appear to serve biologically adaptive functions, representing an interaction between biological and cultural evolution. We therefore wholeheartedly agree with Kelly et al. that psychology should play an important role in any science of cultural evolution. We also share **Barkow's** lament that sociocultural anthropology is non-psychological or even anti-psychological. Evolutionary psychologists have not always been sympathetic to the idea of cultural evolution (e.g., Daly 1982). However, the two perspectives are perfectly compatible, and evolutionary psychology can valuably contribute to the cultural evolutionary synthesis by specifying and delineating biologically evolved biases that affect cultural transmission.

However, while agreeing that psychology will be important, we maintain that no single discipline should be given a "central explanatory role" (**Kelly et al.**) in preference to any other branch of Figure 1. This is highlighted by recent work in cross-cultural psychology (Choi et al. 1999; Nisbett et al. 2001) which has found cultural differences in the psychological dispositions of East Asians and Westerners, and by Henrich et al.'s (2005) studies showing that cultural differences influence how different societies interact in various experimental economic games. Such work emphasises that psychological processes may not be biologically evolved universals, and that cultural differences uncovered by anthropologists may influence psychology and the transmission of cultural knowledge.

R3.8. Assumptions underlying cultural phylogenies

Borgerhoff Mulder et al. provide a valuable contribution to our article by raising for debate some of the key underlying assumptions in the use of phylogenetic methods to analyse cultural data, as employed by many of the studies that we cite in section 2.1.2. We agree that the details of cultural transmission (horizontal or vertical, individual- or group-level) will affect such methods in important ways and that it is essential that practitioners consider whether the data in hand are appropriate to the method's assumptions. Simulation studies that explore the effects of non-vertical cultural transmission on phylogenies (e.g., Eerkens et al. 2006; Nunn et al. 2006) are extremely helpful, as are better ethnographic data regarding actual cultural transmission, echoing **Tehrani**. We also agree that cultures are "made up of multiple traits, each of which may have a different phylogeny" and that it is typically necessary to treat cultural elements on a trait-by-trait basis.

However, we reiterate the point we made in section 2.1.2, that biologists face the same problem, for example, with horizontal gene transfer in bacteria (Doolittle 1999; Rivera & Lake 2004) and plants (Abbott et al. 2003). Although we agree with **Borgerhoff Mulder et al.** that it is vital that the parallels between biological and cultural evolution should not blind researchers to the differences, the significance of horizontal transfer to the two disciplines is a matter of degree, not kind. Indeed, there have been almost identical arguments in biology for the use of alternative methods more sensitive to horizontal cross-lineage transmission (Ragan 2001). Such methods might include reticulated phylogenetic networks (Bandelt et al. 1999), which have already been used to analyse the Indo-European language family (Forster & Toth 2003) and North European Mesolithic fishing spear data (Riede, in press). Such methods might yet be used to detect a "core phylogeny" resulting from vertical cultural transmission, for example of the common words noted by **Pagel** to change very slowly (e.g., "two," "three," "five"), surrounded by a reticulated network generated by horizontal cultural transmission, as highlighted by Borgerhoff Mulder et al. This parallels recent proposals that prokaryotes feature a core phylogeny resulting from vertical genetic inheritance surrounded by a reticulated network generated by horizontal gene transfer (Philippe & Douady 2003).

In sum, we hope that **Borgerhoff Mulder et al.**'s analyses will lead to a healthy debate and ultimately to the development of improved methodological tools for studying evolutionary systems subject to horizontal transfer, be they biological or cultural. We believe that such debates and refinements are a sign of strength within any productive science. However, we do not think it necessary to return to "first principles," given that many of their criticisms can also apply to biological phylogenies and that methods are beginning to be developed to deal with these issues. Phylogenetic methods will be an important set of tools in the developing evolutionary science of culture irrespective of whether there is more horizontal transmission in cultural than in biological systems.

R3.9. Other theories of cultural evolution

There have been many different theories of "cultural evolution" in the past. **O'Brien** helpfully restates the distinction between the "unilinear and progressive cultural evolutionism of Tylor (1871) and Morgan (1877)" and the modern Darwinian theory of evolution that we advocate here. Other commentators, however, see differences where none exist. For example, **Sopher** describes Boyd and Richerson's (1985) work as a "compelling counterpoint" to our evolutionary framework, and states that Boyd and Richerson (1985) "adopt the view that cultural evolution is an aspect of evolution generally and cannot or should not be separated from things biological." This again confuses the capacity for culture (a biological adaptation) and the contents of culture (a separate evolutionary process that may interact with biological inheritance, within what Boyd and Richerson [1985] themselves refer to as "dual-inheritance theory"), as discussed in section R3.7.

We would like to clarify that our position is in no way counter to Boyd and Richerson's, who, along with

Cavalli-Sforza and Feldman (1981), have made probably the most important contribution to the evolutionary framework proposed here by establishing that a rigorous and conceptually accurate version of Darwinian evolution can be successfully applied to culture. And in a related aside, we were slightly puzzled by **Bridgeman's** assertion that Boyd and Richerson's (1985) modelling was "done without the concept of culture as a critical variable," given that their 1985 book almost exclusively focussed on transmitted culture (they even called it *Culture and the Evolutionary Process*). As we have made clear in earlier sections and writings (Mesoudi et al. 2004), biological and cultural evolution are inextricably interwoven processes.

Bridgeman also sets up a false dichotomy between our position and that of Plotkin (2002b). According to Bridgeman, Plotkin argues that "differences between genetic evolution and cultural change are fundamental. They follow different rules and should be kept distinct even while both are modeled mathematically." Plotkin (2002b) actually stated with regard to the mathematical modelling of culture:

Perhaps the best image to take from gene-culture co-evolutionary modelling is of two parallel tracks of evolving processes, the biological and the cultural. The forms of evolution of the tracks may or may not be identical in terms of process. What is certain is that quite different mechanisms underlie each track. But the tracks are not independent of one another: they interact and influence one another. They do this through lines of force, through causal connections, that link them and mediate the interactions between them, and these lines of force are the mechanisms of human intelligence. (Plotkin 2002b, p.140)

Furthermore, it is clear from Plotkin's earlier writings (Plotkin 1995; 1997) that he is fully committed to evolutionary explanations for culture.

Blackmore repeatedly argues that "memetics" provides a superior alternative to our evolutionary framework (e.g., "Memetics can handle this far better than other theories of cultural evolution," and "Memetics alone makes sense of this"). "Memetics," however, does not seem to be an alternative to our framework. To the extent that memetics can be characterised as a body of empirical research or a set of methodologies for studying culture, it is reliant on a subset of the kinds of data and methods that we emphasise. We view memetics as a set of conceptual tools (e.g., taking the "meme's eye view") and concepts (the meme itself) that, as we showed in section 3.5, have a potentially valuable place within a larger evolutionary science of culture. Unlike others (e.g., Boyd & Richerson 2000; Richerson & Boyd 2005), we have attempted to accommodate these tools and concepts into our framework. However, in our view, it is neither accurate nor useful to regard "memetics" as a competing alternative, nor is memetics sufficient to provide a satisfactory evolutionary framework for the social sciences. After all, genetics is not an alternative to evolutionary biology; it is but one branch of a larger evolutionary science.

R4. Concluding remarks

In section 1 of the target article we state that our primary aim in this paper is "to stimulate a more progressive and rigorous science of culture." In the following sections we

have argued that this can be achieved by placing the social sciences within a unified evolutionary framework modelled after the structure of evolutionary biology, and by borrowing and adapting various tools, theories, and methods that have been developed by evolutionary biologists in order to solve similar problems facing researchers studying culture.

Although the majority of commentators here are receptive to our argument, we share **Barkow's** suspicion that had the paper appeared in *Current Anthropology* rather than *Behavioral and Brain Sciences*, then the responses might have been less positive. **O'Brien** similarly notes that "social scientists have often been downright hostile toward even considering cultural evolution in Darwinian terms." Nonetheless, given that social scientists regularly read and contribute to this journal, we are tempted to interpret the absence of criticism as signifying that the cultural evolutionary framework is no longer *easily* dismissed. Perhaps the modern theory of cultural evolution has now reached the stage where it has shed the historical baggage acquired by (inappropriate) associations with erroneous nineteenth-century progressive conceptualisations, or twentieth-century human sociobiological arguments. Hopefully, social scientists will now accept that cultural evolution is not synonymous with genetic or biological determinism, that it does not foster prejudice or support political or ideological arguments, that biology is not simple and well-understood relative to culture, and that, while there are differences between the processes that underpin biological and cultural change, the parallels are sufficiently real to be worth taking seriously.

The problem, however, may be broader than a hostility to Darwinian evolution. **Barkow** remarks that we "pay scant attention to the likelihood that very few [anthropologists] are interested in modeling their endeavor on *any science*" (his italics), let alone evolutionary biology. While this may be true, we hope that the body of work that we have reviewed in this target article sends the message that there is now a clear, vibrant, productive, and rapidly growing alternative to this hostile-to-evolution, hostile-to-science tradition in the social sciences. This alternative is also culture-friendly and conversant with other social science findings and methods. We invite social scientists frustrated with the negativity of post-modernist, deconstructivist, and other anti-scientific movements within their discipline to join us in building a scientific theory of culture.

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[The letters "a" and "r" before author's initials stand for target article and response references, respectively.]

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