POPULATION GENETICS AND CULTURAL HISTORY.

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Abstract

Three major questions must be resolved before the theory of natural selection can be fruitfully applied to cultural systems. The questions are, what are the units of selection, what is the fitness currency and what is the long term pattern of relationship among cultural elements. In this thesis I define units of selection as the largest repeatably, reliably replicating units in a cultural system and demonstrate a simple method for detecting such units in a model system. I argue that meme copy rate is a satisfactory fitness currency and show how this perspective encourages us to test hypotheses of selfish cultural adaptation. I propose a method for the detection of long term patterns of cultural transmission using population level genetic differences.

As Darwin (1859) predicted, evolutionary trees based on linguistic information are similar to trees constructed from genetic distance measurements (Cavalli-Sforza et al. 1989, Cavalli-Sforza et al. 1992, Chen et al. 1995). It is as yet unknown to what degree cultural history in areas other than language follows population history. I examined the degree to which the distributions of 47 cultural characteristics paralleled the history of 32 African populations. A multiple regression model based on the Mantel matrix correlation test (Mantel 1967, Smouse et al. 1986) was used to examine the fit of seven cultural dissimilarity matrices to genetic and geographic distance matrices. The partial regression of cultural distance on genetic distance was significant for two of the seven sets of characters: social hierarchy and kinship

organization. These correlations suggest that over thousands of years, some cultural characteristics have been inherited in parallel with genetic lineages (Sokal et al. 1991, Cavalli-Sforza et al. 1993, Guglielmino et al. 1995) producing an 'historical signature'. However, most cultural changes appear to occur at a rate fast enough to obscure the signatures left by gene frequency changes detected through these methods.

Dedication

This thesis is dedicated to all those people whose complex lives have been condensed down into a few distance matrices.

Acknowledgments

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"One of the most interesting things about Darwin's explanation of the origin of species is that scarcely anything need be assumed about the actual nature of species, as evidence that natural selection occurs; the same process is in progress with respect to languages, religions, habits, customs, rocks, beliefs, chemical elements, nations, and everything else to which the terms stable and unstable can be applied. The only things required of a species are the capacities of variation and inheritance." RA Fisher, 1912.

Introduction

In this thesis I will examine the theory of natural selection as it is applied to problems of cultural change. In chapter one, I describe three basic problems, each representing a fundamental issue that must be addressed before models from evolutionary biology can be usefully applied to the study of culture. These three problems are, what are the units of selection, what is the appropriate fitness currency and what is the long term pattern of relationship among the units. In chapter two, I examine the long term patterns of relationship among cultural elements and their human hosts. Through a comparison between gene frequency differences and cultural differences at the population level, I estimate the degree to which various traits are transmitted in parallel with the genes.

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Cultural replicator theory, reviewed in Durham (1990, 1992), emerged in the 1970's (Cavalli-Sforza and Feldman 1973, Cavalli-Sforza and Feldman 1978, Richerson and Boyd 1978) as an attempt to provide evolutionary sound alternatives to the emerging sociobiological model (Wilson 1975). Instead of retreating from the problems inherent in using evolutionary theory to better understand human behaviour, they attempted to use some of the tools from population genetics to model the process of cultural evolution.

The cultural replicator approach is clearly distinguished from the long tradition of 'social evolution' theory, its roots found in Tylor (1865, 1871) and recently championed by Hallpike (1986). Stage based social evolution theories, focusing on universal 'laws' of progressive development from one evolutionary level to another (White 1959, Sahlins and Service 1960) are distinct from the population based thinking (Mayr 1982) and replicator focused perspective (Dawkins 1976) found in the body of theory in which a modern cultural evolution will be grounded.

Sociobiology (Wilson 1975) differs substantially from cultural replicator theory. While some of the modeling techniques may be similar, the emphasis is shifted away from a focus on reproductive success (Alexander 1979) to the parallel currencies of biological and cultural success (Boyd and Richerson 1985).

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Ties between the ideas of 'genetically determined' behaviour and evolution are strong in the popular presentation of evolutionary theory (Gould 1991). Cultural replicator theory stresses the socially learned factors which contribute to between group variation in human behaviour. Neither deterministic links between genes and behaviour nor simplistic racial typology (Rushton 1995) are a part of cultural replicator theory.

Cultural replicator theory is an elaboration of contemporary neo-Darwinian theory with a focus on natural selection as a process that can occur on many levels simultaneously, both in the biological and cultural realm. It is an attempt to synthesize the long term effects of the evolution of the human mind through a process of organic evolution and the rapid evolution of culturally transmitted traits which takes place within populations of those minds.

Natural selection is a general principle

Dawkins (1976, 1982) has convincingly argued what evolutionary biologists have claimed since the inception of the field (Darwin 1859, Fisher 1912), the theory of natural selection is not limited to genetic systems. Change due to selection is not a property of a particular mode of inheritance, it is a universal principle of self-replicating systems (Holland 1975, Schuster and Sigmund 1983). In this thesis I will address the application of natural selection theory to the differential propagation of cultural characters through human social networks. While many authors

have investigated the similarities between human culture and self-replicating biological systems (Cloak 1973, Ruyle 1973, Campbell 1976, Mundinger 1980, Ball 1984, Artigiani 1987, Csanyi 1987, Hull 1988, Dennett 1990, Plotkin 1994, Lynch 1996) fewer have taken the steps to construct an explicit model of cultural transmission (Cavalli-Sforza and Feldman 1981, Lumsden and Wilson 1981, Boyd and Richerson 1985, Findlay, Lumsden et al. 1989, Laland 1993, Gabora 1993, Bura 1994), and fewer still have attempted to test these models (Cavalli-Sforza, Feldman et al. 1982, Hewlett and Cavalli-Sforza 1986, Lynch, Plunkett et al. 1989).

In chapter one I outline the conditions necessary for change due to selection to occur. I then define units of selection and review my recent work involved in the detection of such units. In section two I elaborate on the concept of selection at the level of the replicator in a cultural system and outline some of the situations in which replicator level selection is expected to be a strong force. In the third section I discuss problems involved in describing the historical relationships among cultural elements and their human hosts. This problem is a stumbling block in two important areas of cultural replicator theory. First, our ability to perform a statistically rigorous comparative test is inhibited by confounding historical effects and second, our understanding of the degree to which cultural and biological inheritance are transmitted in parallel depends upon an understanding of long

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term patterns of association between cultural characters and their hosts. In the second chapter of the thesis I go into a more detailed explanation of the third problem (long term patterns of association) and its relevance to the study of cultural evolution. I then develop a methodology for assaying the transmission mode of cultural characters and apply the method to a broad sample of cultures in Africa.

Chapter One

Three fundamental problems in cultural replicator theory

The theory of natural selection, although it is primarily applied to organic systems, is framed in a generic manner that allows it to be applied to many different systems. Any system which exhibits a few basic properties will be expected to undergo change due to selection. The minimal properties which are necessary for change due to selection to occur are imperfect replication and trait/fitness covariance (Lewontin 1974). I state this principle in the following manner.

Change due to selection is expected in any non-homogeneous population of imperfectly replicating entities which have heritable traits that contribute to their replication success.

Large amounts of theoretical formalism can be used to examine any system under selection. However, before we can make use of this conceptual apparatus we must investigate several key assumptions. Until it has been successfully demonstrated that cultural processes have the properties of imperfect replication and trait/fitness covariance, further theoretical development in models of cultural evolution is left with inadequate foundation.

The purpose of this chapter is to outline cultural replicator theory and address the three key problems which must be resolved to allow further development. To this end I have divided the chapter into three sections, each of which addressees one of the primary questions which must be answered to better ground cultural replicator theory.

The three questions

Three primary questions facing the application of the theory of natural selection to cultural evolution, are:

I) What are the **units of selection**.

II) What is the appropriate **fitness currency**

III) What is the long term **pattern of relationship** among cultural and genetic elements

At the onset I phrase these questions as if there are units of selection, fitness currencies and tractable historical patterns in cultural evolution. However, if any of these three fundamental assumptions could be demonstrated to be unfounded, then the theory of cultural replicators would be substantially weakened, further development in the area might be described as fruitless, and research effort would be better directed elsewhere.

I) Units of selection

Units of selection are essential to any evolutionary model. Without differentially replicating units, natural selection cannot take place. While some transmission based approaches to cultural change may be workable without the assumption of any sort of cultural particle (Boyd and Richerson 1985), recent works in modeling cultural evolution assume that some sort of units exist (Findlay 1992, Laland, et al. 1995). I argue that attention to the problem of the units of selection is an essential element in an understanding of the process of cultural evolution. Much confusion in evolutionary biology has been caused by a vague conception of the units of selection (Williams 1966), and much of the literature on the topic is more philosophical than empirical (Lloyd 1989, Walter 1991, Sober 1992, Sober and Wilson 1994, Hill 1994). While I agree that a philosophical analysis can help direct us towards asking the right questions, the description of appropriate units of selection is primarily an empirical question.

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We must stress that as natural selection is an hierarchical theory I cannot claim to address the problem of what is the sole unit of selection, but I look for a unit (or set of units) of selection at an appropriate level. Under different circumstances and in different systems, the units of selection may change or operate in parallel. In evolving systems selection may simultaneously favor different replicators at different interacting levels of selection (Breden and Wade 1989, Breden and Hausfater 1990).

The primary approaches to modeling cultural evolution skirt the issue of units of selection and go on to develop models of the process assuming that there are units in the systems they discuss. Dawkins (1976) introduces the term "meme" and claims that they are "tunes, ideas, catch-phrases, clothes fashions, ways of making pots or of building arches". This throws many things into the definition and does not focus on any particular unit of selection. Cavalli-Sforza and Feldman (1981) describe cultural characters as "second order organisms" focussing primarily on material culture. Boyd and Richerson (1985), while they primarily make use of particulate models, argue that particles are not a necessary part of their theory. Durham (1991: p420) addresses the problem of units of selection most clearly, "I have therefore assumed (1) that both systems [biological and cultural] can be divided into recognizable subunits of transmission and inheritance; (2) that within all populations there are sources of variation in these units, sources that create alternative forms at least occasionally; and (3)

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that there exist one or more mechanisms of transmission through which these units are conveyed among the individuals of a population ... Assumption 1 is probably the most important and most controversial of the set.". Lumsden and Wilson (1981) make an attempt at defining the culturegen, the closest equivalent to a unit of selection in their work. They claim that culturegens are sets of cultural traits that are measureably similar in many aspects. They suggest multivariate cluster analysis as a tool for the description of culturegens, which leads the way for the numerical taxonomic based approach that I will introduce at the end of this section.

Having a clear concept of the units of selection is essential for any study of an evolutionary process. Unclear perspectives on the locus of selection can cause us to waste time looking for adaptations where none are likely to exist. The process of adaptation depends upon units of selection which possess variable properties that can be modified. As these units become smaller we assume they will provide less raw substrate on which selection can act. As units become larger, they will fall prey to two problems, both of which will cause them to be less likely to generate adaptations. First they will become less likely to reproduce with sufficient fidelity, due to the larger number of external contingencies involved in their replication process. Second, they will be subject to fewer sorting events. Sorting

events are instances where one alternative versus another is differentially replicated.

Thus larger units (presumably replicating less frequently) will be subject to selection as a weaker force (as they undergo fewer sorting events) as well as being ineffective at responding to selection when it does occur (due to their lower replicative integrity). The size of different units will represent a trade-off between increased substrate on which selection can act, and the twin problems of reduced selection pressure (due to fewer sorting events) and reduced effective response to selection (due to contingencies). Size in this case is broadly defined and may be measured on different scales for different systems. Implicit in this discussion of the size of units of selection is the assumption that whatever the large units may be, they are comprised of the smaller units. Thus we assume some sort of hierarchical organization. For a discussion and review of hierarchical organization schemes of cultural replicators and their parallels in biological systems see Sereno (1991).

When we measure the fitness of a given cultural replicator, we can break down the factors that influence replication success into categories based upon the degree to which the property is the result of characters of the replicator itself or interactions with the characteristics of other replicators or the environment. Using quantitative genetics terminology, (Falconer 1989) we can

describe the cultural analogs to additive, epistatic and environmental effects. Additive effects are those elements of fitness that are properties of the replicator itself. Epistatic effects are the result of interactions with other replicators. In the cultural system there are not well defined cultural loci or cultural alleles. Epistatic in this case is meant to describe interactions between independent replicators. Environmental factors signify a host of external forces that can influence replication success. Splitting fitness into additive, epistatic and environmental components will allow to estimate how important the individual properties of a particular meme are to its replication success in comparison to other factors. One important test of replicator integrity is the determination of a minimal additive fitness component (Wimsatt 1980), representing a core of functional continuity across both interactions with other memes and different environments. I expect that most memes will have one or a few robust functions, and that contingent function will be extremely important. One possible criticism of cultural replicator theory is that the fitness of a cultural character may be entirely a product of contingency. If the replication success of memes is determined entirely by environmental circumstance and not by factors that are properties of the memes themselves, then it is impossible for meme level adaptations to arise. Similarly, without some sort of population structure it is difficult for natural selection to take advantage of epistatic fitness effects (Wright 1980).

Levels of Selection

A meme perspective should not be considered to be an analysis of only the smallest possible units within a cultural system. While this sort of reductionism is often a productive route, when it comes to addressing the function of cultural elements we must not abandon a multi-leveled approach. A focus on units of selection may provide building blocks that guide theory at higher levels of organization. By focusing on fundamental units of selection instead of particular vehicles of selection (Hull 1980) such as individual humans we find that different levels of organization can be addressed simultaneously. Societies may be held together by assemblages of adaptations that function at different levels. Cultural traits that do not necessarily have the same replicative output may result in tension and conflict across the levels. However, a multi-leveled approach must always keep track of replicator level success or failure. If we abandon an 'individual' centered perspective we find that a replicator level approach lends itself not only to studies examining within individual conflict (Hurst 1992), but also kin based (Hamilton 1964) and structured group (Breden and Wade 1989, Wilson and Sober 1994) approaches. Similarly, in cultural evolution a meme based perspective does not always mean an exclusive focus on the smallest possible unit. While there are many scales on which meme-influenced constructs interact, (just as genes interact within cells, among gametes carrying alleles,

between organisms and kin groups and so on) keeping track of the replicating pattern itself is necessary.

Wright (1980) summarizes the process of the 'shifting balance' model of evolution, whereby locally inbreeding sub-populations may act as vehicles of selection (Hull 1980). We can consider that one effect of the shifting balance process is an increase in the size of the units of selection. Inbreeding reduces the local variation of the genetic environment thus maintaining the replicative integrity of groups of alleles that would be broken apart in non-subdivided population. The shifting balance process provides a mechanism for the fixation of alleles with epistatic effects that could never increase in frequency in a large panmictic population. Groups of interacting alleles can come to fixation in smaller populations where many of the contingencies that they depend upon to provide their fitness advantage are guaranteed due to the lack of genetic variability at other loci.

Social structure and other barriers to communication may act in such a way as to produce population structure among cultural replicators, allowing complex adaptations to arise. Particularly large memes may only be able to replicate within 'intellectually inbred' groups. Increases in within-population hierarchy and social differentiation may create a positive feedback loop that results in large amounts of population subdivision. First, population differentiation allows the invasion of larger more coherent memes that can evolve complex adaptations. These adaptations may then further influence

processes of social differentiation, feeding back into the process and again increasing population structure. The limits of this potentially unstable process may be the maximum cultural capacity of individuals within society. The island model of Lumsden and Wilson (1981) adapted from MacArthur (1967) could perhaps be extended to social islands within a geographically bounded society.

Entire societies are not likely effective units of selection. They may not be well integrated enough to be replicated with the high fidelity necessary for an effective response to selection. More importantly, they suffer from inadequate sorting events. Hallpike (1986) proposes a model whereby he describes each society as an array of traits (t) each with a number of states (s). The number of possible conformations of this array is s^t. He claims that given reasonable estimates of the parameters s and t (he uses s=10, t=143 based on (Murdock 1967)) and an estimate of 10^4 societies, exploring 10^4 conformations each, over human history there have been 10^8 out of 10^{143} possible societies (assuming every society was distinct in some way from all others). He claims that given any reasonable estimate of selective coefficients simple neo-Darwinian selection is insufficient to account for the extraordinary amount of convergent evolution found in the structure of observed societies. This argument suggests that either some force other than 'simple' neo-Darwinian evolution may be at work structuring the organization of societies, or societies are the wrong level of analysis and natural selection at

levels below the society are responsible for the social organization observed.

Phlogiston, enteleechy, protoplasm and culture.

The concept of 'culture' is an imprecise descriptor. Attempts to define culture (Kroeber and Kluckhorn 1952) fail to achieve consensus and seem to lump so many phenomena into the definition that the word has become so inclusive that its use sometimes obfuscates more than it reveals. Phlogiston, enteleechy and protoplasm are now gone from our vocabulary, replaced with a host of new terms that are more accurate labels of the myriad of phenomena that were at one time tossed together in the aforementioned categories. The word culture itself may be identified to be a classification term that has little meaning. The word 'meme', however, does hold some promise. I have chosen to adopt it in this discourse, while leaving a plethora of alternative terms used to describe units of cultural inheritance to the wayside ('memory image' (Blum 1963), 'idea' (Boulding 1970), 'instruction' or 'cultural corpuscle' (Cloak 1973), 'concept' (Hill 1978), 'culturgen' (Lumsden and Wilson 1981), 'cultural entity' (Cavalli-Sforza and Feldman 1981), 'cultural variant' (Boyd and Richerson 1985)). I argue that meme should become a commonly used descriptor for the specific type of cultural phenomena defined above. At this point, due to its distribution in popular culture, 'meme' is, in a self referential manner, a successful replicator. It is perhaps not too fanciful to imagine that Dawkins (1976) may

have explicitly crafted this word in the hopes that it would come to rise in usage, carrying everywhere it goes the cry of ME ME, representing the selfishness that he argued underlies all replicating patterns. Provisionally, I will make use of Boyd and Richerson's (1985, p33) definition of culture as: "information acquired capable of affecting individuals' phenotypes which they acquire from other conspecifics by teaching or imitation." I shall use the phrases 'cultural trait' and 'cultural element' more or less interchangeably throughout this document to refer to any socially transmitted character. Meme will refer specifically to cultural characters that fit the following definition.

The Definition of Meme

Following Williams' (1966) definition of the gene as "that which segregates and recombines with appreciable frequency" and Dawkins' descriptions (Dawkins 1976, 1982) of cultural replicators, I argue that the appropriate units of selection will be the largest units of socially transmitted information that reliably and repeatedly withstand transmission intact. This definition of meme describes a unit that is most likely to come under selection and thus respond through the production of adaptations While genes are perhaps sometimes more appropriately defined as an open reading frame in the DNA, or a section of DNA that create a single protein transcript (Watson et al. 1987), William's definition of a gene still has utility. The two important characteristics that this definition encompasses are that a unit be large enough to

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exhibit properties that may covary with replication success and still be small enough to have robustly developing characteristics that reappear from host to host. At this point we have little information about any putative units of cultural inheritance.

Are memes particulate?

The claim that ideas are not particulate may be raised against the cultural replicator argument. While it may be true that ideas are not always best represented as particles (Hallpike 1986), there are many types of ideas that do seem to fit the replicative unit model. While we may find aspects of culture that are best described as gradients of non-particulate information, the existence of easily repeated and remembered cultural elements, such as choruses, tunes, recipes, expressions, figures of speech and religious rites suggests that at least some elements of culture can be described as discrete cultural particles with tractable phylogenetic histories. At this point, the field of cultural evolution is in such a primitive state of development that even simple cultural patterns such as bird song choruses (Payne, Payne et al. 1988; Shackell, Lemon et al. 1988; Lynch, Plunkett et al. 1989; Gibbs 1990; Laland 1992) could be much better understood. It is not a refutation of the theory that larger bodies of culture such as economic and religious systems may presently reside outside our purview. Simple replicating patterns are the units of analysis for this preliminary foray into the empirical basis of cultural replicator theory.

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Eigen-text: A System for the Detection of Textual Replicators

Pocklington and Best (1996)(see also Best 1996) have developed a system for the detection of units of selection within a model cultural system. They study the NetNews system of the Internet where individual posts on various topics follow threads as one poster responds to another. Many posts are isolated messages that generate no follow up, while some posts generate 10's or even 100's of responses. Pocklington and Best (1996)(see also Best 1996) attempt to detect the largest units of culture that reliably and repeatedly replicate throughout this textual system. Their system for the detection of cultural replicators, eigen-text, can be briefly outlined as follows.

A large body of text, broken down into individual posts, is converted into a matrix of posts by terms. The most common words in the English language (and, if, or etc.) are removed, as are all suffixes, stemming the words down to their core meaning (e.g. computers becomes computer). A post/term matrix is generated by examining the frequency with which each word is found in each post relative to the overall frequency of the word across all posts. The post/term matrix is then decomposed into three matrices using singular value decomposition (Berry 1992). Two of these matrices represent terms by post subspaces and posts by term subspaces. A term-subspace element is that value which represents the strength with which a collection of individual term

elements are found within a particular post. A high value for a particular term-subspace represents a collection of words that are found together much more frequently than is expected by chance within that particular post. Sample term-subspaces from their analysis include the word clusters [japan, pearl, harbor], [algorithm, fuzzy, genetic, inference, neural] and [chlorine, depletion, ozone, stratosphere]. These term-subspaces are the putative cultural replicators, units of selection, in their analysis of the system.

Term-subspaces generated through the eigen-text procedure are used in a variety of evolutionary/ecological investigations (Pocklington and Best 1996). One of their tests is particularly important to the cultural replicator argument. They measure the degree to which a particular term-subspace influences the reproductive success of a given post. Reproductive success in their system is measured as the number of posts within a single NetNews thread over time. They find that there are cases where there is a strong term-subspace/post fitness covariance. This demonstrates that these putative units of selection not only replicate reliably and repeatably, but also vary in their fitness consequences.

This is the first attempt to define explicit units of selection in a cultural system and then track their reproductive success. I argue that it is this bottom up approach that treats the cultural units as the focus of the analysis and the human hosts as a part of

the environment that will lead to a fruitful paradigm in cultural replicator theory.

In a critical review of what he calls "cultural selectionism" (cultural replicator theory), Hallpike (1986, p46) suggests: "theories of basic units of culture do not rest on any evidence, or on any sociological theory at all, but are simply proposed because if one is trying to explain culture on the basis of a neo-Darwinian theory of natural selection, it is highly inconvenient not to have a 'unit' like the meme or culturgen". While his proposition that there is no evidence for units of culture is unsubstantiated, his claim that the lack of units is inconvenient is understated. I argue that some unit of cultural evolution is essential for further progress in the field and until the units of selection in cultural evolution are adequately described the entire body of theory lies in a precarious situation.

II) Fitness currency

In this section I present the argument that natural selection on cultural variation is expected to produce many traits that appear to be maladaptive from the point of view of the humans hosting the cultural traits. From a purely biological perspective, this makes little sense. However, from an evolutionary perspective, when we take into account all the potential selective forces, a different conclusion is reached. The finding that over

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evolutionary time scales most cultural transmission is not vertical (chapter two) provides a situation where memes and genes are expected to be in conflict. Due to the tremendous potential rate of change of cultural characters, these conflicts may often be settled to the memes advantage.

One of the main controversies surrounding the application of evolutionary theory to human culture may be considered to be phrased as a question of 'currency'. While sociobiological models stress the biological fitness consequences of culture (Alexander 1979), more traditional social scientists appeal to other cultural forces as the determinants of cultural character adoption (Sahlins and Service 1960). This dichotomy can be phrased as an argument over which currency is optimized in cultural evolution, biological or cultural success. The relative importance of biological reproductive success over cultural transmission rate appears to be a fundamental dichotomy. However, these two perspectives need not be seen as polar alternatives. The identification of memes as the units of selection (section I) points us towards the use of meme copy rate as the appropriate fitness currency for studies of cultural evolution. However, the criteria under which humans judge the value of cultural characters is influenced by biological predispositions.

A simple experiment to demonstrate selfish cultural adaptation.

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A simple experiment demonstrates how one might test for cultural adaptation at the level of the meme. We remove from a population of birds one adult male and a number of eggs. Young males are allowed to develop their song based on the template of the single male. The learners are exposed to the template male's song in a noisy environment. We then propagate lineages of male to male transmission of song in the noisy environment. Each male should be exposed to the ancestral song and all other versions that have occurred earlier in the serial propagation. Cultural adaptation (change in the song that increases its rate of copy number increase) is demonstrated if we find that the song propagated in the noisy environment is preferentially learned over the ancestral song in that environment. We can test this by exposing a group of naive males to both the ancestral song and the terminal serially propagated song in the noisy environment. Cultural adaptation is demonstrated if the young males learn the serially propagated song more often than the ancestral song when in the noisy environment. This would demonstrate that the serially propagated song had changed in such a way that males in the noisy environment were more likely to hear and learn it. We can consider this selfish cultural adaptation if the sisters of the males we test for song learning are less attracted to the modified song than the ancestral song. In this case, the changes to the song would have a 'cost' in terms of their utility to the birds. Selfish adaptation in this sense is demonstrated by a change in the culturally transmitted character which increases its fitness at a

cost to the hosts fitness. These experimental results would demonstrate that the song evolved a transmission bias in the new environment, yet that this adaptation interferes with the genetic function of the behaviour. Thus the modified song has a selfish cultural adaptation, one that aids its transmission through the population at the expense of the reproductive success of those males who adopt it. This example suggests that any analysis of signaling systems, involving culturally transmitted signals, should keep track of costs and benefits not only for the signaler and receiver, but also for the signal itself. This example demonstrates that under certain conditions, cultural evolution can act as a force that does not necessarily work to increase the reproductive success of the hosts for the cultural character.

Transmission Mode and Gene/Culture Conflict of Interest

Cultural characters that do not follow strict patterns of vertical inheritance have an evolutionary fate that is decoupled from that of their hosts. The replicative success of a cultural character does not depend upon its hosts' reproductive success, (except indirectly). Instead, it is a function of the probability that the host acts as an effective vehicle for further cultural transmission. Reproductive success is only relevant to the cultural characters' fitness when a large proportion of the transmission is from parent to offspring. Under conditions of non-vertical transmission (also referred to as asymmetric transmission (Boyd and Richerson 1985)) the success of a cultural trait is determined

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by both the reproductive and the cultural success of its hosts (Boyd and Richerson 1985). The degree of asymmetry in transmission is related to the degree of potential conflict of interest between the reproductive success of the host and replication of the cultural trait. Boyd and Richerson's (1985) parent teacher/model shows that a trait that makes an individual more likely to be a teacher and less likely to be a parent can proliferate under circumstances of asymmetric transmission given that the cultural selection advantage for the trait and the degree of asymmetric transmission outweigh the genetic fitness cost. The more asymmetric the cultural transmission is, the more important cultural success is relative to biological reproduction. This situation is analogous to parasite virulence models, where horizontally transmitted elements are generally more virulent than vertically transmitted elements (Bull et al. 1991, Ewald 1991, Bull 1994, Ewald 1994, Frank 1996). To expand on the parent/teacher model, we expect that traits that do not modify the chance that their bearer becomes a teacher in general, but modify the chance that the host re-transmits the essential information necessary for the propagation of that cultural character, have an advantage.

In order to know how important gene/culture conflict of interest is, we need to estimate the degree of transmission asymmetry over evolutionarily relevant time scales. We can estimate the predominant transmission mode for a character over

the long term in the following manner. For a given trait under strict vertical inheritance (non-asymmetric transmission) two cultural groups with genetically similar populations should exhibit similarity in culture regardless of geographic distance. In chapter two I demonstrate that genetic similarity among populations is usually a poor predictor of cultural similarity. Thus, while on short time scales parental models may be important (Hewlett and Cavalli-Sforza 1986), over longer time scales vertical transmission represents a small proportion of cultural transmission. Thus if the bulk of cultural transmission is asymmetrical, we expect that conflict of interest between genes and culture will be the rule rather than the exception. Given such a conflict, differences in the rate of evolution between genes and culture will resolve the issue of the relative prevalence of genetic or cultural adaptation. Adaptation, here refers to traits that are effective replicators, not traits that are necessarily psychologically pleasant or 'morally good'. While cultural replicator theory may eventually have important contributions to moral theory, the trite conflation of adaptive with positive, beneficial, good or right is an oversimplification.

From the perspective of a cultural trait, one transmission from host to host is a generation. Characters that are vertically transmitted have generation times similar to those of their hosts. Horizontally transmitted characters can have much shorter generation times. Thus over the same period of time they may

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respond to selection much more rapidly than vertically inherited traits under equivalent selection pressure in a similar sized population. Thus the transmission mode difference not only provides for a gene/culture conflict of interest, but also accelerates the rate of evolution in cultural parasites (which are expected to be horizontally transmitted) as the rate of sorting events is much higher.

Given that humans constantly strive to perform behaviour that in their ancestral environments would have achieved reproductive success, cultural transmission is not predominantly vertical (see chapter two) and the rate of evolution in horizontally inherited characters is more rapid than in vertically inherited characters, we make the following conclusion. Many behaviours that hosts 'intend' to replicate genes may instead act to replicate parasitic cultural practices, most of which are spread among non-genetic relatives. This conclusion implies that instead of seeing culture as if it were a part of the human who practices it, a parasite/host situation may often be the closest ecological parallel to the relationship between our culture and our genes. Assuming that cultural practices always act as adaptations for the people who practice them is an error akin to the trite group-selection fallacy. The arguments are analogous. Selection at the level of the individual is more rapid than selection between groups (in many but not all cases), just as selection in culturally transmitted

practices will cause vertical/genetic response to be swamped due to their relatively slower rate of evolution.

An example of parasite exploitation of host behaviour: Natural History of Rhabdovirus

The disease rabies has a natural history that illustrates the parallel between biological pathogens and memes. Rabies is a devastating disease caused by infection with a *Rhabdovirus* (Burnet and White 1972). Infection usually occurs through bite wounds, as the virus particles are shed in saliva. After infection, the viri do not incubate directly in the hosts' salivary glands. While in the blood stream rabies particles bind to acetylcholine receptors facilitating avoidance of an effective immune response (Nesse and Williams 1994). The virus spreads through nervous tissue, entering the brain and concentrating in the thalamus, hypothalamus and pons (Huang 1986). The build up of particles in these areas of the brain produces excessive salivary activity, excitation, confusion, anxiety and aggressive behaviour. These changes in turn lead to infection of other animals through bite wounds. An essential portion of the life history of the virus is its ability to modify the behaviour of its mammalian host. In the terms of Dawkins (1982) the behaviour of the mammal is an extension of the phenotype of the virus. The mammals' genes produce a complex structure, including a neurological system, which the virus exploits to influence behaviour that results in its

own replication. The behaviour of the mammalian host has been sculpted by natural selection on genes in the virus. Just as any other mammal has no way of knowing when it should be angry, other than its internal state, we rely upon states which may be triggered by cultural constructs. While humans may have evolved psychological adaptations that function to increase the probability that they adopt cultural practices that are adaptive, they cannot measure the fitness costs and benefits of any given cultural practice directly but must do so through the assessment of proximal fitness tokens (Barkow et al. 1992). Cultural traits are expected to deliver stimuli that mimic the proximate fitness tokens that ancestral humans used to estimate the fitness consequences of their behaviour.

When we observe an individual performing a behaviour it is sometimes an unwarranted assumption that the behaviour is motivated by the genotype which was responsible for constructing the body which performs the behaviour. There is a long chain of contingencies between selection acting on genes and the outward behaviour of an organism. At any of the steps along the way control over the phenotype can be usurped (Dawkins 1982). This does not invalidate the evolutionary perspective as a tool to understand behaviour, it complicates it. We must always be aware that there is the possibility of manipulation by another replicator.

The meme hypothesis directs us to investigate cultural traits to see if they possess self-referential adaptations which increase their fecundity, transmission fidelity or competitive ability. While we may make reference to the potential benefits a given person may receive for practicing a cultural trait, the meme hypothesis suggests that culture need not always have a function that refers to the carrier of that culture, but could have a function solely with reference to the trait itself. From a meme perspective we make use of optimality based calculations to help understand the evolution and function of cultural traits with respect to their self-referential fitness effects. Thus the currency being optimized is not human utility, nor host inclusive fitness, nor overall social stability. It is change in meme copy rate. Individual utility, reproductive success/inclusive fitness and social stability may well be important parameters that bear on the replicate success of a given cultural trait. While economic, sociobiological and sociological forces are all key to understanding cultural change, the meme hypothesis attempts to provide a currency with which we can analyze arguments regarding cultural function. When we are attempting to understand the function of a cultural character, its route to replication success is always important.

Culture vs Individual Decision Making

It is important to be clear about the definition of culture (see section I). Similarity in behaviour among individuals or between group differences in behavior may be due to parallel

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individual choices. Thus a group of humans may all make one choice rather than another because each one individually decides to make that choice. Unless this decision is mediated by socially transmitted information then it is not behaviour that the meme/replicator perspective will help elucidate. Many sociobiological hypotheses are based on explaining human behaviour that is the result of individual decision making (Smith and Winterhalder 1992). Under these situations maladaptation should be much rarer.

Parasitic Cultural Practices

When current environments differ substantially from the environments under which particular adaptations arose, we may find that ancestral mechanisms produce currently maladaptive or nonadaptive behaviour (review in Crawford 1996). This argument can be considered the point where sociobiology and evolutionary psychology differ the most. A main premise of evolutionary psychology (Cosmides and Tooby 1991) is that current fitness consequences of behaviour are not relevant to an evolutionary analysis. Environmental mismatch theory (Bailey 1987) argues that the past environments that sculpted our genetic make up are now so far removed from our present environment that we should not expect our ancient adaptations to function effectively. Foley (in press) reviews the evolutionary psychologists use of the concept of the 'environment of evolutionary adaptedness', (EEA) (Bowlby 1969). A realistic

approach to evolutionary psychology will not concentrate on gatherer-hunter lifestyles in the Pleistocene, but should examine human behaviour as a composite of ancestral and derived traits at many different taxonomic depths. Paleohistory, primatology, mammology and comparative biology in general are all essential tools in understanding the historical origin of our adaptations.

The change in environment over time assures us that all organisms, not just humans, are adapted to past environments. Humans, however, are expected to exhibit more frequent maladaptive behaviour because of their reliance upon a system of sociocultural transmission which itself can evolve in ways that are not always adaptive for its host. Thus while the increased rate of cultural change over genetic change makes the time lag/environment mismatch problem less important in humans than in other organisms, maladaptive behaviour should be more frequent due to the conflict of interest between the genetic and cultural inheritance systems.

Above and beyond the caveat that the 'environment' has changed since the Pleistocene, cultural replicator theory makes predictions about what sort of decision processes are more likely to be exploited by cultural parasites. Here I examine a few processes that illustrate the replicator perspective. The cost of errors, the relationship between behaviour and payoff and the ease of testing the hypothesis are three parameters that likely influence the opportunity for cultural parasitism.

The Cost of Error

Parasitic cultural traits are more likely to develop around decisions where the cost of type II (wrongly rejecting a true hypothesis) error is more important than that of type I error (wrongly supporting a false hypothesis). I assume that socially transmitted information will be more likely to be accepted when it is deemed important. As a given decision is perceived to be more important to fitness, evolved predispositions may create increased sensitivity to any observed correlations. Under these circumstances people may be more likely to accept socially transmitted information without sufficient evidence to demonstrate the efficacy of the belief.

Type I error will be more costly for frequently repeated behaviour, behaviour that must be performed rapidly, and complex sequences of contingent behaviours. In these circumstances, cultural parasitism will be less likely. Type II error is more costly when there are large negative consequence of a mistake, the prior investment in the behaviour is large, it is a difficult decision to make correctly or the decision is urgent. These are the types of decisions where we expect cultural parasites to attach themselves. Note that all of the above parameters may be amenable to further cultural manipulation. The development of adjunct beliefs may increase the persistence of a parasitic cultural character by falsely escalating the cost of type II errors. Traits that stress the dire consequences of a mistake or the urgency of a decision (both stressing the cost of

type II error) are examples of common culturally transmitted characters that may be the result of selfish cultural adaptation. Lynch (1996) advances the meme-centered argument that fear of hellfire (large type II error, made explicit in Pascal's wager (Richerson and Boyd 1989)) and the immanent day of judgment, are both meme level selfish adaptations of Christianity. Chain letters frequently stress the large potential cost of a mistake and also create urgency by presenting time limits for the completion of the chain.

The Relationship Between Behaviour and Payoff

The longer the time lag between the performance of a given behaviour and the supposed result the more likely cultural parasites may invade. As time passes more contingent events occur and individuals are less likely to accurately measure the relationship between behaviour and effects. A convoluted relationship between behaviour and payoff involving confounding variables may produce a similar effect. This observation generates the prediction that cultural parasites are expected to promise benefits in future, rather than immediate rewards.

Spurious correlations between behaviour and results may be more easily generated under situations where the base payoff of the behaviour is highly stochastic. Cultural parasites are less likely able to attach to decisions made regarding completely deterministic phenomena. The most extreme case is the situation where the cultural trait adopted has absolutely no effect on the

process that it supposedly influences (myriad types of 'divination' may fall into this category). In this case no individual learning can stabilize the culturally transmitted trait and rates of copy error may be large. In many circumstances, while cultural transmission may be involved in influencing a given decision, each practitioner of the trait has an opportunity to guide the trait towards some stable form through individual learning. Any cultural trait that has no effect on the real world events that it supposedly influences cannot be stabilized through individual learning. The increased rate of change in a trait that is freed from this stabilization force allows it to change rapidly and explore more of the adaptive landscape. This increases the probability that it will eventually exist in a conformation that gives it a transmission advantage, either through the discovery of some function for its hosts or through the production of a selfish adaptation.

Hypothesis Testing

Cultural traits that express an hypothesis that is expensive for any individual to test will likely have increased tenacity. Food taboos are an example where no one likely has the inclination to pay the potentially lethal cost of doing the individual learning experiment that would disprove the taboo. Here we have the interesting situation that individual selfishness reinforces a group norm that produces a restraint on the consumption of a resource that may be valuable.

The inherent untestability of an hypothesis may protect a parasitic trait from being discarded. Generating a situation where the data necessary to falsify the hypothesis is not likely available could be a selfish cultural adaptation. Mythic creature hypotheses may be adapted in this way through their physical crypticity. A story predicting a dozen huge, bright red creatures performing a specific dance step while trumpeting loudly at noon in the village square may be easily refuted. However a story involving a small number of tiny green creatures performing some cryptic ritual at an unspecified time in an unspecified location deep in a foreboding wood may be more likely to persist. I expect that mythical creatures become more cryptic as populations become more and more aware of their environment. The outcome of this process may be complete invisibility. Some mythical beings are more than invisible, they are intangible or are said to inhabit realms that are impossible to explore. The invisible, intangible, unknowable being is a fine example of an hypothesis that may have come to the end of its rope in terms of that particular anti-hypothesis testing adaptation. Beings that start 'way over there' may eventually begin to live up on a hill, then on a mountain, then in the sky and finally retreat to the 'beyond'.

Resistance to Parasitic Culture

Durham (1991, p317) argues that the view that cultural elements may frequently be maladaptive "must be challenged if

we are also to accept the argument that our 'capacity for culture' evolved under the influence of genetic selection". Alexander (1979) and Symons (1979) have made similar arguments, and claim that maladaptive variants will primarily be prevalent in a group due to manipulation of one person by another. Their argument against the parasitic nature of cultural traits is that if such traits existed they would prosper in undefended human hosts and there would be strong selection against non-resistant individuals. I challenge the assertion that culture must be genetically adaptive because "in environments containing pathogenic viruses, [genetic] selection favors the most resistant individuals [and genotypes]" (Symons 1979, p 308). Humans may have evolved mechanisms to prevent contamination with parasitic culture. However, due to the relative rates of cultural vs biological change as discussed above, these mechanisms are more likely cultural themselves. Given that the rate of cultural change can be so rapid as to swamp out potential genetic change (Chapter Two) it is not clear if biological evolution is fast enough to effectively respond to repeated cultural changes. In Durham's (1991) terminology, secondary value systems (values based on culturally transmitted knowledge and not directly linked to any biological predispositions) arise to protect against cultural exploitation. If parasitic memes abound, the selection against those with no resistance to parasitic exploitation is likely strong. The process of the evolution of a system of protection against parasitic culture most likely results in an arms-race-like

escalation of cultural innovations. The result of this conflict is expected to be rigid vertically transmitted cultural patterns that resist masses of horizontally transmitted parasites. Due to the increased rate of evolution in horizontally transmitted traits, we expect that they will be able to flourish even when other cultural mechanisms to resist them have evolved.

While cultural evolution is primarily likely to be responsible for any resistance we have against parasitic culture, there are some possible genetic responses to exploitation by maladaptive cultural practices, most notably the presence of menopause (Hill and Hurtado 1991). Adopting cultural traits from one's mother is a strategy that guarantees both the minimal amount of between individual exploitation (although there is some conflict of interest between a mother and her child (Trivers 1985), maternal guidance is likely to be the least exploitative information available) and that the model exhibiting the culture is at least competent enough to successfully reproduce. Unfortunately, serial propagation along long chains of individuals leads to degradation without some error checking mechanism. Contact with multiple copies of culturally transmitted information can increase the fidelity of transmission. However learning from anyone who is not part of ones matriline opens up the possibility of transmission asymmetry and thus parasitic culture exploitation. A grandmother, however, allows for a second vertically transmitted copy of any culturally transmitted information. Grandmothers not

only have greater realms of experience on which to draw from than mothers, but when combined with maternal transmission they provide an error checking mechanism that can generate high fidelity, vertically inherited culture. Menopause, through reduction of mortality rates in older women allowing them to act as culture carriers for longer, may be a result of ancient competition between memes and genes.

III) Patterns of relationship

Williams (1966) went to great lengths to argue that optimality and adaptation were not to be assumed when one examined an organic structure. Facile adaptationism (reiterated eloquently by Gould and Lewontin (1979)), is a typical error made by those who misunderstand the processes of evolution. The complex and adaptive behaviour around us arose through a process of natural selection among variation that results from the fundamental imperfection in the replicating systems that underlay all living processes (Darwin 1859). When we observe human behaviour we must be careful about our attribution of function and adaptation. Some anthropologists assume that every aspect of a culture must have some function; "every custom, material object, idea and belief fulfills some vital function" (Malinowski 1926, p133), "sociocultural systems are largely if not exclusively composed of positive-functioned, that is, useful traits" (Harris 1960, p60), "no cultural forms survive unless they

constitute responses which are adjustive or adaptive, in some sense, for the members of the society or for the society considered as a perduring unit" (Kluckhorn 1967, p79). Kluckhorn's perspective displays both hyper-adaptationism and a focus on the function a trait has for the good of the social group. This type of argument is typical of the naive group-selection thinking that still plagues many sociologists and anthropologists.

Function cannot be assumed, it must be carefully demonstrated, primarily through the detection of convergent evolution. Multiple examples of convergent evolution is strong evidence of adaptation (Pagel 1994). In order to detect this convergence we must use cross-cultural data. Unfortunately, the comparative analysis of cross cultural data poses statistical problems that are as yet unsolved (Dow 1991). The historical correlations among elements of the cultures we study can compromise our understanding of their functional relationship. Before we can test any hypothesis, we must have some way of assuring the independence of our data points. Cultures which share elements due to a common history can not be considered independent sources of data.

Mace and Pagel (1994) have presented a method which they claim could be used to circumvent the problem of the non-independence of cultural traits due to shared ancestry. Their method can be summarized as follows. (1): They produce a dendrogram (tree diagram) that represents historical relationships

among a group of cultures based upon linguistic relationships. They suggest that any other evidence we can gather regarding the historical relationships among cultures would be useful to help construct what they call the "true phylogeny". (2): The cultural character states are then mapped onto the tips of the cultural phylogeny. Ancestral states can be found through historical or archaeological evidence or they may be inferred through the process of parsimony, a method that infers ancestral character states that produce the tree that has the smallest possible number of character changes. (3): The tree is then examined to see if any trait changes occur together more often than expected by chance.

This method is inadequate to control for many cases of non-independence. Since the cultural phylogeny drawn does not represent the history of all the traits, there may be historical associations which are undetected by the simple tree, thus changes in state on the branches are not always independent. The problem lies in what trees are used to infer independent events.

Figures 1.1, 1.2 and 1.3 show three trees representing genetic, cultural and linguistic relationships among 20 African populations. While each pair of trees shows similarities, the substantial differences among them implies that there may be no single "general cultural phylogeny". A strict consensus of the three trees generates a completely unresolved star polytomy.

Figure 1.1   Genetic Similarity Among 13 African Populations.
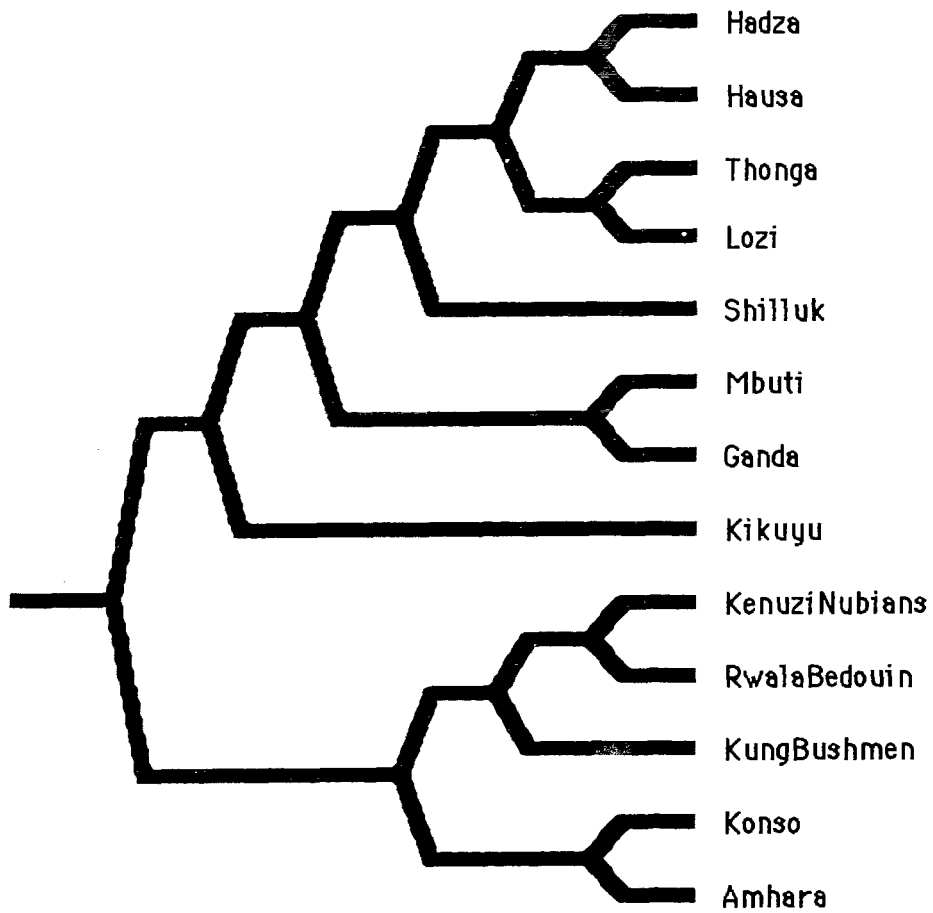
Figure 1.1.   This tree is constructed using the neighbor joining (Saitou and Nei 1987) algorithm of Phylip (Felsenstein 1993), it is based on a matrix of Fst genetic distances using 20 loci per population.   Genetic Data from Cavalli-Sforza, Piazza et al. (1994).

Figure 1.2.   Linguistic Similarity Among 13 African Populations.

Mbuti
Kikuyu
Ganda
Lozi
Thonga
Shilluk
KenuziNubians
Hausa
Konso
Amhara
RwalaBedouin
Hadza
KungBushmen
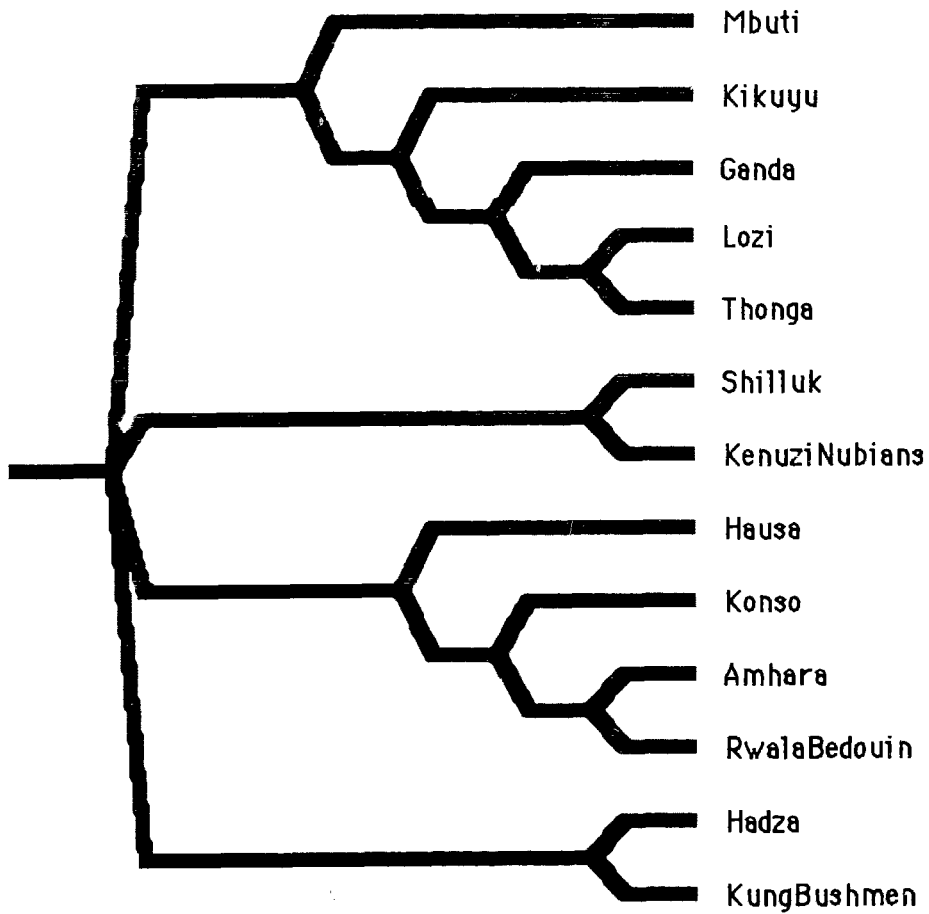
Figure 1.2.   This tree is a dendrogram representing language relationships, adapted from Ruhlen (1987).

Figure 1.3
Cultural Similarity Among 13 African Populations.
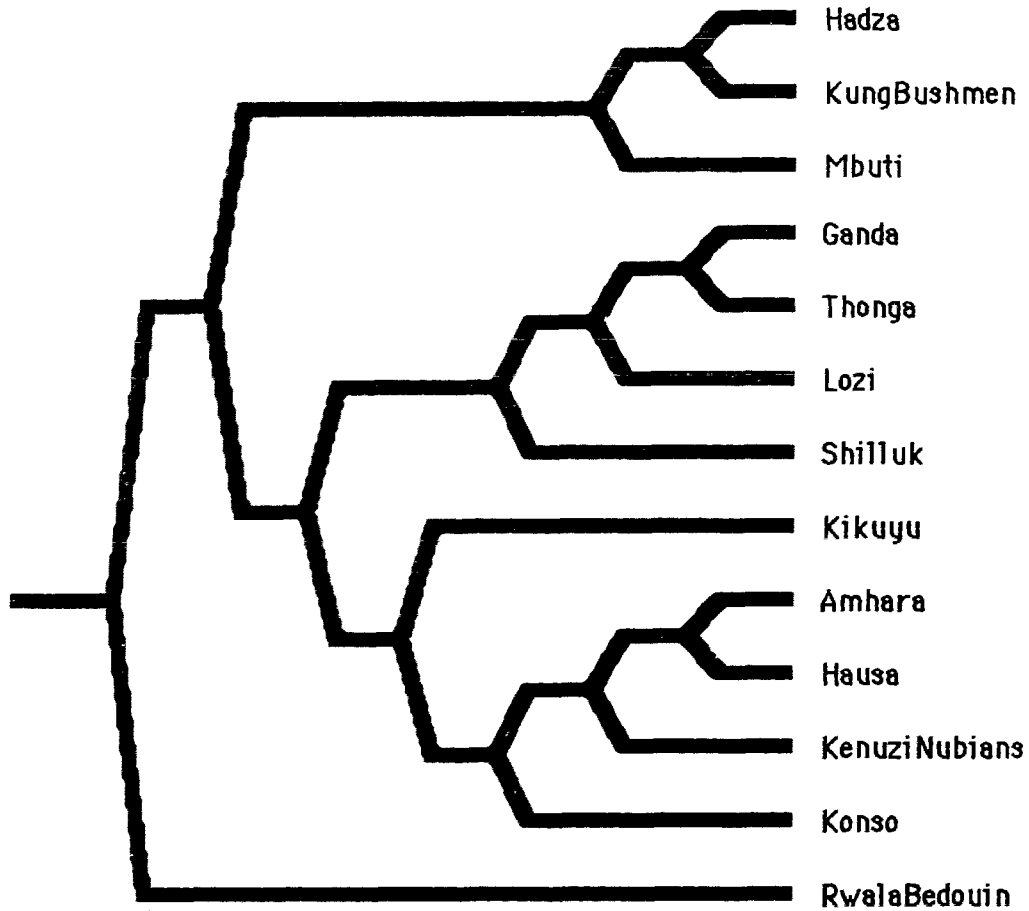
Figure 1.3. A maximum parsimony tree generated with PAUP (Swofford 1991), using 1623 cultural characters (unordered) found in the Standard Cross Cultural Sample (Murdock and White 1980). Australian aboriginal people are used as the outgroup.

The problem with this use of cladistic comparative methodology for the study of cultural evolution is that it relies on a model of cultural change that is unrealistic. Mace and Pagel (1994, p563) assert that "cultures ... persist through time, and occasionally give rise to daughter cultures.". While this likely describes an important class of cultural changes it is by no means a comprehensive description of the processes which produce cultural diversity. More importantly, it is not the only process that could result in non-random distributions of traits due to shared history. There are types of cultural changes which involve groups of elements moving from culture to culture. Examples include religions, modes of production and technology clusters (Rogers 1983). Some sets of cultural elements may be specialized for active propagation through cultures as a unit; thus, scoring their presence in multiple cultures would be akin to counting the presence of attributes in a single species in multiple habitats as multiple incidence of the same association of characters. Clearly this method falls prey to potential non-independence of the data due to historical interactions.

The aim of cross cultural tests should be to remove the effects of common ancestry, providing an analysis which treats as data only independent changes in the relationships between cultural elements. It is not enough to look for changes within cultural groups because they may change without there being an independent incidence of the association between the traits in

which we are interested. Thus to demonstrate a relationship between two cultural elements we must find that they appear together more often than by chance, while controlling for their own history. This history may or may not parallel the history of the language or the genes of the people involved. If we map specific elements onto a general culture phylogeny we may ignore the actual historical relationship between traits.

When performing comparative analysis, we should focus on the detection of historically independent associations among traits. In the absence of a single phylogeny which can explicitly show the history of the traits of interest, the independence of the data points must be supported in some other manner. Using the wrong phylogeny may be worse than using no phylogeny at all.

Davis and Nixon (1992) make it clear that we should be careful what we place in a phylogenetic framework when they state that "the ability to generate a resolved cladogram of attributes ... does not demonstrate that the terminals of the analysis are elements of a hierarchic descent system.".

Evolving systems involve constantly changing patterns of relationship due to both current interactions and historical ties. Several major innovations have allowed us to better investigate the historical connections among organisms; the detection of protein polymorphisms, reading of DNA sequence, and computer based statistical analysis tools. These techniques combine to produce the growing field of molecular systematics (Hillis, Moritz

et al. 1996). The use of molecular tools not only provides us with information regarding our connection to other organisms, but it allows us to develop a fine grained picture of the demographic history of our species (Cavalli-Sforza, Piazza et al. 1994). This population genetic data provides an historical skeleton on which we can overlay information regarding cultural history. Through the fusion of genetic history and ethnographic data we can begin to produce a dynamic model of cultural change.

The non-isolated nature of pools of cultural information makes patterns of cultural evolution appear to be completely distinct from the discrete phylogenetic bifurcations we expect in biology. In fact, memes and genes may not be so different in this respect as not all 'species' maintain genetic barriers between their gene pools and those of other species. The lack of horizontal genetic transmission between animal taxa may not be representative of all biological evolutionary processes (Dreiseikelmann 1994). Prokaryote evolution, for example, may be better represented by a constantly reticulating network than a branching tree (Mindell 1992).

Patterns of reticulate evolution may have important consequences for theories of cultural evolution. When two animal species interact with one another over evolutionary time, they influence each others' evolution but cannot trade adaptations. When a small granivorous rodent and a small granivorous

passerine begin to occupy the same habitat we do not expect to see the birds gain cheek pouches, or the rodents start to fly. In cases of cultural contact, we see adaptations flowing both ways across boundaries between previously isolated groups. When two cultural systems collide, individuals in each group are provided with a great pool of new information upon which they can draw. Cultural contact between groups that are genetically distinct (and have been culturally isolated) may be an important event culturally as they represent the opportunity for very different cultural systems to interact. I predict that the more genetically dissimilar two groups are when they contact, the more cultural elaboration will take place if they begin to reticulate. Hybrid systems that contain many of the elements of both parent cultures may arise. Cultures that are the result of this process will have complex histories that are not easily traced. Recent developments in the history of western thought suggest that incidences of contact between genetically distinct people may be an important historical force (Bernal 1987, Lefkowitz and Rogers 1996) .

Distributions of cultural elements may be represented as matrices of populations by elements. These matrices can be analyzed in two fashions, the distribution of cultures across elements (clustering populations based on distributions of elements) or the distribution of elements across cultures (clustering elements into suites based upon their distribution across populations) (Jorgensen 1981). This type of data and the

known historical and geographical nature of the associations among cultures and among elements provides us with a circular problem. How can we examine functional associations among elements across cultures if the element by culture data is used to cluster the cultures into groups? A solution may be achieved through the use of an outside source of information that resolves one of the two sets of relationships. Genetic information is a useful tool for tracing these inter-population relationships. We can estimate historical relationships among populations genetically, and thus with an external set of data resolving one of the two sets of relationships we can go about examining relationships among elements.

Summary of chapter one

In this chapter I have discussed three problems that must be resolved for a theory of cultural replicators to be further advanced. These issues, the units of selection, the fitness currency and the pattern of historical relationships are addressed in the following manner. Units of selection are the largest reliably and repeatably replicating patterns within a given cultural system. Before the start of any investigation in cultural evolution we need to clearly define these units. Term-subspaces are introduced as an appropriate unit of selection in one model cultural system. Relative cultural element copy rate is the appropriate currency for investigations of cultural evolution. In situations where there is a

large amount of vertical transmission, the biological reproductive success of the hosts may enter as a relevant factor, but only through the correlation between fertility and vertical transmission. In chapter two I demonstrate that the bulk of cultural traits are not primarily vertically transmitted. Historical patterns of relationship between cultural elements are not always reducible to a simple cultural phylogeny. Without an understanding of the mode of transmission of a cultural trait, it is not possible to develop a model that takes into account the multiple correlations between variables expected to result from purely historical associations.

This chapter points us directly towards key empirical investigations that will be discussed in the next chapter. Cultural replicator theory identifies as important relatively large coherent units of culture which have tractable histories in populations that are genetically well studied. This data is essential to determine the degree of conflict of interest between genes and memes over evolutionary time scales. It is also an essential first step in the development of a rigorous comparative test of cultural adaptation. The next step in advancing our knowledge of cultural evolution involves careful study of the historical relationships between populations and an examination of the distribution of cultural elements within and between these groups. This historical perspective is facilitated through the use of gene frequency data. This data allows us to generate an historical structure on which

cultural changes may be superimposed. Once we better understand the transmission patterns of the important cultural characters, we can begin to search for multiple independent incidences of cultural change. These events, when correlated with changes in other cultural elements or environmental shifts, provide for us the raw material with which we may generate a theory of cultural evolution.

Chapter Two

A Method for the Estimation of Transmission Mode of Cultural Elements.

Gene frequency information provides a tool through which we can reconstruct historical relationships among extant human populations. These historical relationships, estimates of time since any pair of populations were once a single interbreeding group, can produce an historical structure on which change in language and culture can be superimposed. These reconstructions allow us to add a temporal depth to our investigations of patterns of cultural change from the pool of information gathered in the ethnographic record. Thus the combination of contemporary (synchronic) investigation and genetic markers allows us to attempt an historical (diachronic) reconstruction of cultural change.

Before we can make effective use of genetic information to help build historical models of cultural change, we must better understand the transmission properties of cultural characters (Cavalli-Sforza and Feldman 1981). The degree to which transmission of culture parallels the transmission of genetic information is an essential parameter for any model that attempts to make use of both sources of data. Through a comparison of the

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fit of a cultural character's distribution to both an historical and a geographic model, we can estimate its mode of transmission. Table 2.1 shows four transmission mode inferences based on comparisons of a given character's distribution with genetic and geographic data. Cultural similarity and genetic similarity in the absence of geographical proximity suggests that historical forces and vertical transmission are important. Cultural similarity and geographic proximity without genetic similarity suggests horizontal transmission or diffusion processes as explanatory factors. Cultural similarity without genetic similarity or geographic proximity suggests independent cultural change.

The degree to which a given cultural character parallels the transmission patterns of genetic information has important evolutionary consequences (Cavalli-Sforza and Feldman 1981, Boyd and Richerson 1985). Differences in micro evolutionary patterns of transmission (along genetic lineages vs. across genetic lineages) will be reflected in longer term patterns of cultural differentiation. Thus cultural groups that are more closely related genetically should also be similar in aspects of vertically transmitted culture, while cultural groups that are geographically close should be similar in elements of horizontally transmitted culture (Figure 2.1).

Figure 2.1

Four Cultures and an Outgroup
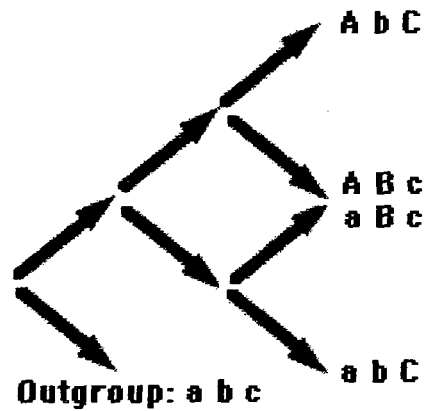
Figure 2.1 shows historical and geographical relationships among four populations and an outgroup. The y axis can be considered a measure of geographic distance, while the x axis represents time. The arrows represent the past movements of the populations. Terminal points represent the current position of the group and their score for three culturally transmitted characters. Character A supports a vertical transmission model, character B supports a horizontal transmission model and character C likely arose twice independently.

Table 2.1

For a given trait shared by two groups:	**Genetic Relationship**	
	Close	**Distant**
Geographic Relationship **Close**	Confounding Effects Equivocal Result	Horizontal Transmission Diffusion of Innovation
Distant	Vertical Transmission Historical Forces	Independent Origin Convergent Evolution

Table 2.1. The predominant transmission mode for a given cultural trait can be assayed through the comparison of its distribution in cultural groups that are genetically and geographically described.

Individuals migrate a limited distance and both mate and communicate more frequently with individuals that are near to them in space. This pattern of behaviour confounds historical and geographic relationships. In order to test for an historical signal in the distribution of any character we must first partial out the effect of spatial proximity. Only the degree to which culture corresponds with history while controlling for geographic proximity is evidence for a vertical transmission mechanism. Similarly if we wish to test the hypothesis that a given character fits a horizontal transmission/geographic diffusion model then we must first partial out historical similarity. Any statistical analysis that demonstrates that language or other culturally inherited factors fit historical or geographic models is flawed unless it explicitly controls for the correlation of history and geography (cf. Smouse et al. 1986, Smouse and Long 1992, Welsch et al. 1992, Roberts et al. 1995).

The classification of cultural elements according to predominant transmission mode bears on several key issues in evolutionary anthropology (Cavalli-Sforza and Feldman 1981, Boyd and Richerson 1985, Hewlett and Cavalli-Sforza 1986). Understanding the transmission dynamics of cultural characters is important for both cross cultural comparative tests (Mace and Pagel 1994) and resolving issues of gene/culture conflict (Lumsden and Wilson 1981). In both of these areas,

distinguishing between vertical and horizontal transmission is essential.

Comparative Tests

In the comparative analyses of cross cultural diversity, it is essential that we make use of historically controlled comparisons (Boas 1940). When attempting to test hypotheses regarding the function of cultural elements we must recognize that not all observed correlations among traits signify functional connections among those elements. Some correlations among variables are the result of common history or spatial proximity. Mace and Pagel (1994) have stressed the point that instead of developing sampling schemes, or attempting to deal with a historical non-independance problem statistically, we should attempt to identify independent incidences of change along cultural lineages. Due to the reticulate nature of the connections among human populations, it is difficult to produce a simple representation of the appropriate historical connections among cultural characteristics. We may use gene frequency data and other measures of shared genetic history as indices of shared cultural history only if we are examining traits that have been vertically inherited. In contrast, horizontally transmitted traits are not amenable to such a comparative test. If the phylogeny used for the comparison represents the genetic history of the populations, it tells us little about previous historical connections among horizontally inherited traits. The history of such traits may lie in

cultures genetically unrelated to the cultures under examination. Performing a comparative test on horizontally inherited traits using a phylogeny generated using genetic information will produce misleading results. Before we can apply a comparative test to any set of characters we must first assay them for their transmission properties. Those that fit a primarily historical model may then be analyzed using a gene based phylogeny. Those that have a better fit to a geographic diffusion model must be subjected to alternative methods.

Gene/Culture Conflict

Discriminating between patterns of horizontal and vertical transmission is essential for addressing the potential conflict of interest between genetically and culturally influenced behaviour. Vertical transmission, however, should not be mistaken for evidence of genetic transmission. There are mechanisms through which 'hereditary' traits may be culturally transmitted (Cavalli-Sforza and Feldman 1981). Estimates of transmission mode are unlikely to adequately address this issue, which is best left to the realm of behavioural genetics. When we seek to address gene/culture conflict through the use of genetic data, we do so because knowledge of the transmission pattern regardless of the physiological mechanism of transmission (genetic/biochemical vs cultural/neurological) is important.

Strictly vertically transmitted patterns of behaviour have similar evolutionary dynamics regardless of their nature as culturally or genetically transmitted elements. When cultural transmission no longer parallels genetic lineages the same sort of conflict of interest that exists among a parasite and host can occur between the biological host and the cultural information itself. Thus, cultural traits that are not handed down along family lines may exist in forms that do not necessarily contribute to the hosts' fitness (Cavalli-Sforza and Feldman 1981, Boyd and Richerson 1985, Findlay et al. 1989, Findlay et al. 1989b). They may be, in effect, cultural parasites (Dawkins 1976, p192). Cultural characters that have previously been described as adaptations for the people that practice them may be parasitic forms that exploit humans as a resource and have evolved adaptations to increase their own tenacity within hosts or their ability to spread among hosts. While there is no guarantee that all vertically transmitted culture is genetically adaptive (Edgerton 1992), we predict that horizontally transmitted characters are more likely to exist as parasitic forms (Bull et al. 1991, Bull 1994).

Study System

In this paper I derive a pattern of historical relations among a group of populations based on genetic data. This historical distance matrix, combined with a matrix of geographic distances between each pair of populations, is used as a predictor of cultural differences. A wide variety of cultural characters are transformed

into sets of cultural distances. These cultural distance matrices are assayed for their fit to the historical and geographic distances. Characters that fit the historical distribution significantly better than they fit the geographic distribution are considered to indicate vertical transmission. Those that fit the geographic distance matrix better are considered to indicate horizontal transmission.

Thirty-two African populations, from above and below the Sahara, were used. Their historical/genetic relationships are assayed through the use of allele frequency data on forty-seven loci. Forty-seven cultural characters representing a wide variety of variables were used to construct seven cultural dissimilarity matrices.

Methods

The study sample is made up of 32 African cultural groups (Table 2.2) that have been identified ethnographically, geographically, linguistically and genetically. Groups were selected for which both coded ethnographic data and gene frequency data were available. DNAbase, the human population genetics database maintained by Eric Minch in L.L. Cavalli-Sforza's laboratory was used as the source of population level genetic data. The Ethnographic Atlas (Murdock 1967) was the source of coded ethnographic data. There is not always a simple one to one correspondence among the populations identified in the genetic

database and the cultural groups defined in the Ethnographic Atlas. Different investigators have used various written terms to describe the same people. Table 2.3 shows correspondences among names drawn from the population genetic database and those used in the ethnographic record. Geographic information, linguistic information (Rhulen 1987, Ethnologue 1992) and ethnic descriptions (Murdock and White 1980) were used in the identification of correspondences among genetic and culturally defined populations.

Table 2.2

32 African Populations Sampled

amhara	fulani	kung	shilluk
ashanti	ganda	lozi	somali
bambara	hadza	masai	tallensi
bedouin	hausa	mbundu	teda
bemba	ibo	mbuti	thonga
bogo	khoi	mende	tiv
egyptian	kikuyu	nubian	tuareg
fon	konso	riffian	wolof

Table 2.2. Thirty-two populations described ethnographically, geographically, linguistically and genetically.

Table 2.3

Genetically identified population	Culturally identified population	Subpopulations supplying genetic data
Khoi	nama	Khoisan Dama Denasena G//Ana G/Wi Giana Griqua Heiom Hottentot Kede Nama Topnaar Khoi Khoikhoi Korana Kwadi Kwengo
San	kung	Kaukau Naron Kung Kwisi
Shangana	thonga	Bitonga Changana Ronga Shangaan
Sotho	lozi	Barotse Basuto Kgalagadi Koni Lozi Mangwe Pedi Rotse Sotho Tswana
Ganguela	mbundu	Lunda Mbunda Quioco
Tonga	bemba	Bemba Bisa Ila Lamba Lenje Luano
Hadza	hadza	Hadza
Akamba	kikuyu	Digo Embu Giriama Gusii Ikoma Kamba Kikuyu Meru Taita Wakamba
Ganda	ganda	Kiga Nkole Nyoro Soga Toro
Mbuti	mbuti	Pygmy Aka Bambuti Efe
Ibo	ibo	Ibo
Ewe	fon	Andagbe Fon
Volta	ashanti	Baoule Akim Akposso Akwapim Ashanti Brong Buem Fanti Ghanadian Kwahu Nzima
Mande	mende	Bambara Bokabo Gagu Gbah Gbandi Kpelle Loma Malinke Mandingo Mandinka Mano Mende Mona N'Da Gagu Soninke Yacouba Yaoure
Ouoloff	wolof	Ouoloff
Gur	tallensi	Nankani Kurumba Mossi Tiefo Zara
Foulah	fulani	Foulbe Fula Fulani
Hausa	hausa	Hausa
Nilosaharan	shilluk	Acholi Alur Bari Dinka Etesot Kakwa Karamojo Lango Luo Mabaan Masai Hamitic Nilotic Nuer Samburu Shilluk Teso Turkana Walur
Cushitic	konso	Afar Billen Borana Falasha Galla Sidamo
Somali	somali	Darod Gadaboursi Ishaak Issa Midgaan Rendille Somali
Amhara	amhara	Amhara
Nubian	nubian	Egyptian Kounouz
Tubo	teda	Tebu Teda Toubou
Tuareg	tuareg	Touareg
Moroccan	riffian	Rif Bahloula Beni Brane Chiadma Dkhissa Doukkala Exnaga Guerrouane Guich Haha Hayana Tanan Zik Imaziren Marrakchi Mejjat Menasra Mesfioua Meghraoua Mezraoua Mokhtar Moulay Mtioua Oudaia Oulad Sais Sefiane Senhaja Shluh Souassa Soussi Zaer Zaian Zemmour Zrahna
Egyptian	egyptian	Fedikyaee Gaafra
Bedouin	bedouin	Jebeliya Towara Chaamba Chorfa Reguibat Shaigiya

Table 2.3. List of correspondance between genetically identified and ethnographically identified populations.

Of the 32 sample populations found to have adequate coded ethnographic information and sufficient gene frequency information, 4 pairs: ibo:tiv, masai:shilluk, konso:bogo and mende:bambara were not genetically distinguishable with the available data. These pairs were represented as one data point each for genetic analyses, while they were scored independently for all other measurements. It is important to recognize that populations genetically indistinguishable through these methods can be geographically distant or culturally distinct.

Genetic Distance

A total of 47 loci (Table 2.4) were used in genetic distance measurements. Each population has been scored for between 3 and 28 loci, (mean 16). TopoTreeMatch (Minch 1996) was used to convert the raw allele frequency data into a matrix of Fst genetic distances (Wright 1951). These distance measures are the Fst values averaged across all loci for each pair of populations. Fst is a measure of population substructure. Fst is calculated as the observed variance in gene frequencies divided by the maximum variance in gene frequencies. If there is restricted gene flow between a pair of populations then Fst increases with time. We can estimate the amount of time, in generations, since any two populations began to diverge genetically (and culturally with respect to vertically transmitted traits) as:

$$t = -2N \ln(1\text{-}Fst)$$

Where t is the divergence time in generations and N is the effective population size (Hartl 1989).

Thus, Fst is an index of the 'historical distance' between two populations. This distance measure assumes that population size remains constant, there is no natural selection and no migration. However it is satisfactory as a first approximation of 'historical' distance.

Table 2.4

47 Loci Used *

A2M	ABO	ACP1	ADA	AG	AK
BF	C3	CHE1	CHE2	CP	DI
DIA	ESD	FUT2	FY	G6PD	GC
GLO	GPT	HLAA	HLAB	HP	IGHG1G3
IGKC	JK	KEL	LDH	LE	LP
LU	MDH1	MNS	P	PEPA	PEPB
PEPC	PEPD	PGD	PGM1	PGM2	PHI
PI	PTC	RH	SOD	TF	

Table 2.4. List of all loci used to generate Fst genetic distance among 32 African populations. * For more information see "The History and Geography of Human Genes" (Cavalli-Sforza et al. 1994)

Geographic Distance

I constructed a matrix of pairwise distances between cultures using sets of longitude and latitude coordinates. While the groups themselves span ranges of different sizes, I used the location of peak ethnographic observation to represent the position of each cultural group.

Variables Used

I analyzed 47 key variables from the Ethnographic Atlas (Murdock 1967), listed in Figure 2.2. The character correlation matrix from Guglielmino et al. (1995) was converted into a distance matrix representing the degree to which each of the 47 variables covaried across 277 African societies. From this distance matrix I reconstructed a dendrogram (Figure 2.2) using a neighbor joining cluster analysis (Manley 1986). This split the data into seven categories each composed of five to nine variables. Each category became the basis for a cultural distance matrix.

Cultural Distance Matrices

Sets of variables from each of the seven cultural categories were used to construct distance matrices. Cultural distance is a measure of how dissimilar two groups are for all those characters within a given category. For each pair of taxa the cultural distance measure is defined as the sum of number of steps between the character states for each character over all characters

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for which both taxa had been measured, divided by the total number of comparisons. When all characters are unordered (changes among any two states are assumed to be equiprobable), the cultural distance is equal to the proportion of characters shared between the two groups. Since the distance matrices themselves are difficult to interpret, I constructed maps of cultural similarity using a multidimensional scaling (MDS) algorithm (Manly 1986). MDS is a technique used to distill a high dimensional problem down to an arbitrary number dimensions. In our case the two dimensional MDS maps are those sets of co-ordinates that minimize the discrepancy between measured distances between points on the 2D map and the distances in the matrix from which the map was constructed.

Linguistic Distance

In order to represent linguistic association as a distance measure I make the crude approximation that the distance within a language phylum is 0 and the distance between phyla is 1. This approximation allows ns to test to see if language groups are more geographically or historically clustered.

Multiple Distance Matrix Comparisons

We compared the distance matrices using an extension of the Mantel matrix correspondence test (Smouse et al. 1986). This test allowed direct comparisons of the degree of correspondence among distance matrices composed of geographic, genetic and

cultural data. The Mantel test produces a score which estimates the similarity of two matrices by computing the sum of their element by element products. The observed score for a matrix pair is compared against the distribution of scores for many matrix pairs created by holding one matrix constant and randomly permuting the order of the elements in the other matrix. The test can be extended to more than two matrices using a multiple regression model. In this form, it provides an estimate of the degree to which one matrix (common history or shared geographic proximity) corresponds with another (variation in cultural similarity) while holding similarity in a third (geography or history) constant. The test assumes that we can model cultural dissimilarity as a linear combination of geographic and genetic distances. The two distance measures are considered fixed predictors of the third matrix of cultural differences.

Results

Distance Matrices

Table 2.5 shows the genetic and geographic distances among the 32 taxa. The lower left diagonal shows the Fst genetic distance between each pair of populations while the upper right diagonal shows the distance between the sampling locations in kilometers. Four rows and columns in the lower left are identical because some pairs of populations were genetically indistinguishable.

Table 2.5

Pop		khoi	kung	thong	lozi	mbund	bemba	hadza	kikuy	ganda	mbuti	tiv	ibo	fon	ashan	mende	wolof	mende	talle	fulan	hausa	shill	masai	konso	somal	amhar	konso	nubia	teda	tuare	riffia	egypt	bedou
1	khoi	0	927	1534	1443	1697	2359	3270	3678	3510	3445	3959	3814	4186	4322	5017	5761	5146	4646	4836	4427	3394	4255	5204	4979	5351	6082	5338	5728	7260	6058	7126	
2	kung	0.055	0	1376	526	949	1486	2388	2793	2591	2518	3267	3168	3635	3839	4709	5420	4695	4106	4129	3664	3500	3525	4427	4196	4303	5204	5351	5338	6588	5136	6202	
3	thonga	0.03	0.126	0	1426	973	1716	2474	2846	2793	2591	2518	3070	4460	4406	4929	5165	6078	6780	5398	5276	4722	5400	4615	3975	2996	2008	2821	3816	3535	3907	4111	
4	lozi	0.019	0.084	0.039	0	862	973	1867	1716	2474	2846	2910	3070	4460	4406	4929	5165	6078	6780	5398	5276	5400	4615	3975	3869	2923	2698	2321	2219	3038	2980	3508	
5	mbundu	0.04	0.114	0.073	0.043	0	1538	2262	2618	2253	2011	2321	2067	2910	3070	4460	4929	5398	6024	5276	5400	4615	3781	3169	2718	2955	2431	3029	4139	3615	3535	3907	
6	bemba	0.024	0.073	0.036	0.019	0.02	0	911	1319	1225	1356	3092	3122	3727	4042	5127	5730	4867	4163	3803	3453	2955	2431	3029	3615	3961	4608	3643	4111	4714	6327	4647	
7	hadza	0.047	0.122	0.108	0.04	0.066	0.047	0	408	1319	1225	1356	3092	3727	4042	5127	5730	4867	4163	3803	3453	1040	176	659	318	779	1896	1846	2609	2773	3774	4234	
8	kikuyu	0.042	0.08	0.063	0.045	0.036	0.04	0.047	0	531	543	959	3152	3888	4243	5390	5901	4998	4269	3693	3450	1556	318	659	779	1053	636	1472	1846	2609	3181	4234	
9	ganda	0.047	0.119	0.114	0.049	0.005	0.03	0.081	0.067	0	481	1011	3246	3383	4007	5532	5999	5088	4358	3698	3508	1317	1556	659	318	779	1053	1466	1834	2637	3181	4205	
10	mbuti	0.05	0.098	0.079	0.059	0.058	0.043	0.105	0.039	0.048	0	2236	2372	2996	3363	4522	4990	4080	3350	2735	2509	982	1088	636	779	1100	2253	1953	2642	2418	3356	4948	
11	tiv	0.039	0.066	0.07	0.032	0.008	0.013	0.049	0.044	0.012	0.045	0	268	782	1159	2316	2755	1847	1117	877	397	2489	3303	3158	3201	1604	2642	3629	3372	1734	1772	3322	
12	ibo	0.039	0.066	0.07	0.032	0.008	0.013	0.049	0.044	0.012	0.045	0	0	628	990	2151	2646	1755	1042	1057	556	2704	3417	3339	3427	3612	3372	3889	1997	1948	3447	3475	
13	fon	0.033	0.066	0.07	0.032	0.008	0.013	0.049	0.044	0.012	0.045	0	0	0	377	1535	2020	1140	471	1060	715	3266	4045	3939	4418	4213	3201	3629	4309	1824	3127	3837	
14	ashanti	0.044	0.106	0.035	0.043	0.064	0.023	0.05	0.063	0.029	0.064	0.023	0.013	0.004	0	1161	1688	859	420	1325	1063	3642	4403	4315	5369	4992	3967	4119	2237	1974	3109	3837	
15	mende	0.039	0.102	0.032	0.071	0.044	0.053	0.058	0.037	0.044	0.034	0.053	0.058	0.037	0.095	0	752	913	1641	2462	2507	4782	5553	5473	6512	6826	5804	5768	3562	2519	2648	5192	
16	wolof	0.064	0.101	0.081	0.077	0.101	0.063	0.078	0.057	0.037	0.073	0.037	0.017	0.009	0.016	0	730	1590	2268	2161	4782	5110	6056	5859	6826	5738	5664	3469	2597	3141	5128	5830	
17	bambara	0.039	0.102	0.032	0.071	0.044	0.034	0.053	0.058	0.037	0.077	0.068	0.073	0.037	0.059	0.047	0.016	0	999	882	500	4208	5150	4948	5930	4852	4963	4938	2755	1844	2521	4410	
18	tallensi	0.059	0.098	0.05	0.061	0.058	0.033	0.131	0.037	0.083	0.046	0.059	0.052	0.017	0.017	0.009	0	500	2669	882	1595	4208	5150	4315	5553	5473	5581	5664	2711	1564	2711	4705	
19	fulani	0.053	0.124	0.077	0.038	0.061	0.031	0.022	0.083	0.082	0.046	0.038	0.076	0.038	0.095	0	0	2669	3822	1595	2669	3509	4420	4232	5237	4176	4288	4387	2220	1222	896	2462	
20	hausa	0.058	0.101	0.091	0.026	0.03	0.017	0.021	0.04	0.062	0.058	0.017	0.042	0.077	0.042	0.071	0.017	0	2628	500	882	3509	4420	4232	5110	5859	4420	4948	2755	1844	3123	4049	
21	shilluk	0.038	0.097	0.043	0.041	0.012	0.013	0.046	0.019	0.035	0.051	0.01	0.01	0.024	0.03	0.033	0.077	0.033	0.034	0	1584	3593	3822	3354	4357	3302	3431	3595	1543	1394	2926	3123	
22	masai	0.038	0.097	0.043	0.041	0.012	0.013	0.046	0.019	0.035	0.051	0.01	0.01	0.024	0.03	0.033	0.077	0.033	0.049	0.034	0	829	3593	4357	3277	3431	3349	3396	1222	896	2462	2872	
23	konso	0.065	0.134	0.055	0.088	0.073	0.042	0.069	0.042	0.073	0.041	0.034	0.067	0.083	0.049	0.043	0.034	0	977	1154	1813	829	0	1584	3453	3277	3349	3396	896	2462	2872	3720	
24	somali	0.055	0.038	0.116	0.045	0.068	0.04	0.055	0.041	0.041	0.041	0.055	0.037	0.037	0.1	0.112	0.107	0.078	0.052	0.031	0	1730	1813	977	0	1108	3277	3349	896	2462	5870	3720	
25	amhara	0.06	0.089	0.117	0.076	0.04	0.073	0.076	0.043	0.069	0.108	0.049	0.049	0.071	0.042	0.115	0.135	0.135	0.11	0.053	0.002	747	1730	829	1108	0	377	3431	4606	5870	2312	2842	
26	togo	0.065	0.098	0.134	0.04	0.089	0.073	0.076	0.049	0.049	0.04	0.062	0.083	0.083	0.049	0.053	0.092	0.052	0.002	0.031	0.02	0	807	1176	1189	377	0	806	1772	1801	2332	3500	
27	nubian	0.079	0.083	0.108	0.074	0.084	0.059	0.095	0.034	0.067	0.083	0.108	0.153	0.108	0.111	0.083	0.092	0.052	0.052	0.096	0	977	2152	1176	1189	806	0	2210	2305	3470	4683	2332	
28	teda	0.006	0.041	0.012	0.043	0.024	0.02	0.137	0.019	0.017	0.037	0.026	0.026	0.021	0.02	0.042	0.042	0.036	0.065	0.073	0.046	0.034	0.03	0.012	0.04	0.033	0.096	0	1169	2587	3294	3396	
29	tuareg	0.049	0.084	0.049	0.069	0.056	0.064	0.083	0.028	0.089	0.038	0.036	0.02	0.02	0.127	0.067	0.014	0.033	0.012	0.04	0.033	0.096	0.055	0.088	0.003	0	1628	2697	1658	616	1166	4812	
30	riffian	0.08	0.115	0.074	0.064	0.069	0.058	0.1	0.05	0.093	0.048	0.076	0.038	0.09	0.067	0.014	0.033	0.012	0.04	0.033	0.096	0.046	0.096	0.091	0.05	0.09	0.087	0.047	0	3652	2697	1140	
31	egyptian	0.081	0.086	0.11	0.075	0.064	0.087	0.107	0.093	0.141	0.102	0.096	0.064	0.038	0.042	0.042	0.076	0.105	0.13	0.092	0.073	0.046	0.034	0.003	0.088	0.031	0.053	0	3823	3323	2511	1946	
32	bedouin	0.106	0.108	0.138	0.131	0.162	0.076	0.087	0.059	0.108	0.159	0.12	0.12	0.104	0.114	0.116	0.169	0.18	0.122	0.21	0.12	0.146	0.147	0.059	0.051	0.082	0.059	0.05	0.073	0.088	0.031	0.053	0

Table 2.5. Above diagonal entries show the distance between pairs of populations in kilometers. Below diagonals show Fst genetic distances.

Character Clusters

Figure 2.2 shows a dendrogram of the seven clusters of variables used to construct the cultural distance matrices that were compared against genetic and geographic distances.

Figure 2.2

Economic System

- Gathering
- Hunting
- Animal Husbandry
- Agriculture
- Fishing
- Agricultural Intensity
- Settlement
- Div Labour:Fishing
- Div Labour:Animal Husb

Domestic Organization

- Domesticated Animals
- Settlement Size
- Div Labour:Agriculture
- Ground Plan
- Floor Material
- Wall Material
- Roof Shape
- Roof Material

Gender Issues

- Div Labour:Leatherworking
- Div Labour:Pottery
- Div Labour:Boatbuilding
- Div Labour:Housebuilding
- Div Labour:Gathering

Religious Practices

- High Gods
- Games
- Sexual Taboos
- Genital Mutilations
- Segregation of Boys

Family Structure

- Sexual Restraints on Girls
- Marriage Type
- Family Structure
- Community Organization
- Residence
- Patrilineal Groups
- Matrilineal Groups
- Cognatic Kin Groups

Familial Organization

- Cousin Marriage
- Cousin Terminology
- Headman
- Property Inheritance
- Mobile Property Inheritance

Social Heirarchy

- Within Group Hierarchy
- Between Group Hierarchy
- Class Structure
- Caste Structure
- Slavery
- Div Labour:Metal Working
- Div Labour:Weaving

Figure 2.2. Dendrograms representing the relationships among 47 cultural variables.

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Cultural Distance

As distance matrices of cultural dissimilarity are difficult to interpret, I present Figures 2.3-2.11 instead of a table of distance measurements. Each figure is a map constructed using a multi-dimensional scaling algorithm. Thus the distance matrix is condensed into a 2D map that minimizes the discrepancy between the observed distances between the points on the map and the distances in the matrix.

Figure 2.3: Geographic Position

Legend

khoi	A	kung	B	thonga	C	lozi	D
mbundu	E	bemba	F	hadza	G	kikuyu	H
ganda	I	mbuti	J	tiv	K	ibo	L
fon	M	ashanti	N	mende	O	wolof	P
bambara	Q	tallensi	R	fulani	S	hausa	T
shilluk	U	masai	V	konso	W	somali	X
amhara	Y	bogo	Z	nubian	a	teda	b
tuareg	c	riffian	d	egyptian	e	bedouin	f

Linguistic Affiliation:

- Khoisan: A, B, G
- Niger-Kordofanian
  - Bantoid: C, D, E, F, H, I, J, K, L
  - Non-Bantoid: M, N, O, P, Q, R, S
- Nilosaharan: U, V, a, b
- AfroAsiatic: W, X, Y, Z, c, d, e, f

Figure 2.3 shows the 2-D representation of pairwise geographic distances. It roughly regenerates a map of Africa.

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Figure 2.4: Historical Separation


```
         -+-----------+-----------+-----------+-----------+-----------+-
    1.0 +               WZ          G  I                              +
        |                Y                                            |
        |                            LK   E                           |
    0.5 +                               D                            +
        |                      C      H  V     A                      |
        |          f        B            U       T                    |
    0.0 +                   X        b          F                    +
        |       a                                                     |
        |       e                                                     |
   -0.5 +            d            J    M                             +
        |                         N         S                         |
        |                         Q O C                               |
   -1.0 +                         R                                  +
        |                         P                                   |
        |                                                             |
   -1.5 +                                                            +
         -+-----------+-----------+-----------+-----------+-----------+-
         -3          -2          -1           0           1           2
```

Legend

khoi	A	kung	B	thonga	C	lozi	D
mbundu	E	bemba	F	hadza	G	kikuyu	H
ganda	I	mbuti	J	tiv	K	ibo	L
fon	M	ashanti	N	mende	O	wolof	P
bambara	Q	tallensi	R	fulani	S	hausa	T
shilluk	U	masai	V	konso	W	somali	X
amhara	Y	bogo	Z	nubian	a	teda	b
tuareg	c	riffian	d	egyptian	e	bedouin	f

Linguistic Affiliation:

- Khoisan: A, B, G
- Niger-Kordofanian
    - Bantoid: C, D, E, F, H, I, J, K, L
    - Non-Bantoid: M, N, O, P, Q, R, S
- Nilosaharan: U, V, a, b
- AfroAsiatic: W, X, Y, Z, c, d, e, f

Figure 2.4 shows a 2-D representation of the pairwise Fst genetic distances between all 32 populations.

Figure 2.5: Domestic Organization

```
   -+-------------+-------------+-------------+-------------+-
 2 +                                                         +
   |
   |
   |
 1 +                 F     O  C      Y                       +
   |                  D E      W
   |      G J              Z      P                    e
   |      B      X   S     I RU  T          L        d
 0 +            A           K                               +
   |                                 H        Q
   |                                        N
   |              b                 M   a
-1 +         V       c                                       +
   |                          f
   |
   |
-2 +                                                         +
   -+-------------+-------------+-------------+-------------+-
   -2            -1             0             1             2
```

Legend

khoi	A	kung	B	thonga	C	lozi	D
mbundu	E	bemba	F	hadza	G	kikuyu	H
ganda	I	mbuti	J	tiv	K	ibo	L
fon	M	ashanti	N	mende	O	wolof	P
bambara	Q	tallensi	R	fulani	S	hausa	T
shilluk	U	masai	V	konso	W	somali	X
amhara	Y	bogo	Z	nubian	a	teda	b
tuareg	c	riffian	d	egyptian	e	bedouin	f

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- AfroAsiatic: W, X, Y, Z, c, d, e, f

Figure 2.5 shows a 2-D representation of pairwise cultural distances.

Figure 2.6: Economic System

```
    -+---------------+---------------+---------------+---------------+--
  2 +                                                                 +
    |                                                                 |
    |                                                                 |
  1 +              S X                                                +
    |            V   Z    c    b         L HW                         |
    |              f                                                  |
    |                                   U    QRPYTea                  |
  0 +                                        CEI                      +
    |                        A            D    dM                     |
    |                                     K    O  N                   |
    |          BG                         F                           |
 -1 +           J                                                     +
    |                                                                 |
    |                                                                 |
    |                                                                 |
 -2 +                                                                 +
    -+---------------+---------------+---------------+---------------+--
       -2             -1              0              1              2
```

Legend

khoi	A	kung	B	thonga	C	lozi	D
mbundu	E	bemba	F	hadza	G	kikuyu	H
ganda	I	mbuti	J	tiv	K	ibo	L
fon	M	ashanti	N	mende	O	wolof	P
bambara	Q	tallensi	R	fulani	S	hausa	T
shilluk	U	masai	V	konso	W	somali	X
amhara	Y	bogo	Z	nubian	a	teda	b
tuareg	c	riffian	d	egyptian	e	bedouin	f

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- Nilosaharan: U, V, a, b
- AfroAsiatic: W, X, Y, Z, c, d, e, f

Figure 2.6 shows a 2-D representation of pairwise cultural distances.

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Figure 2.7: Familial Organization

```
    -+--------------+--------------+--------------+--------------+-
 2 +                                                              +
   |
   |
   |                                  U         d
 1 +                     X                          L V           +
   |            e                          W
   |          a N              b M         I      H Z  Y
   |                                              D  R
 0 +          f           E Q                                     +
   |            T                              O
   |          cF          A          C              JK
   |                     P
-1 +                   S                 G                        +
   |                        B
   |
   |
-2 +                                                              +
    -+--------------+--------------+--------------+--------------+-
    -2            -1              0              1              2
```

Legend

khoi	A	kung	B	thonga	C	lozi	D
mbundu	E	bemba	F	hadza	G	kikuyu	H
ganda	I	mbuti	J	tiv	K	ibo	L
fon	M	ashanti	N	mende	O	wolof	P
bambara	Q	tallensi	R	fulani	S	hausa	T
shilluk	U	masai	V	konso	W	somali	X
amhara	Y	bogo	Z	nubian	a	teda	b
tuareg	c	riffian	d	egyptian	e	bedouin	f

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- Nilosaharan: U, V, a, b
- AfroAsiatic: W, X, Y, Z, c, d, e, f

Figure 2.7 shows a 2-D representation of pairwise cultural distances.

Figure 2.8: Family Structure
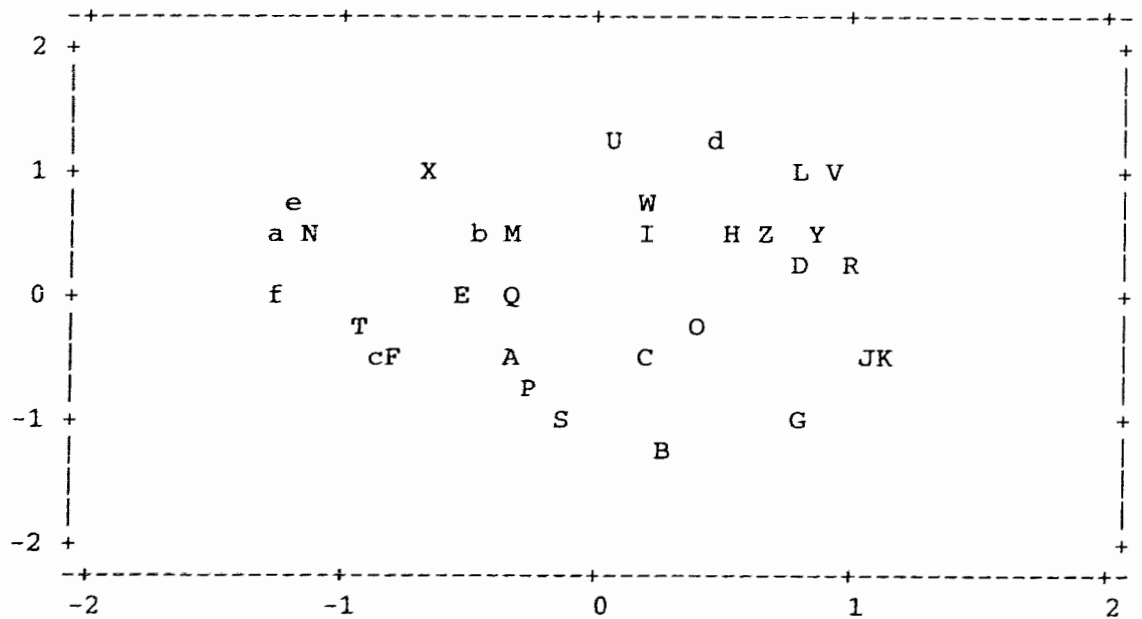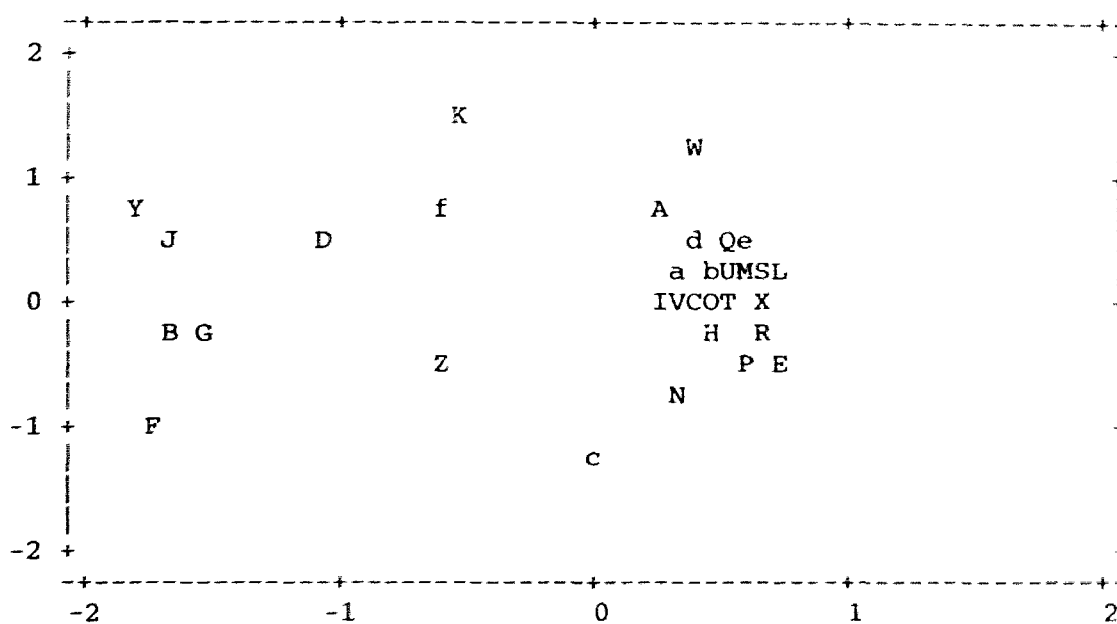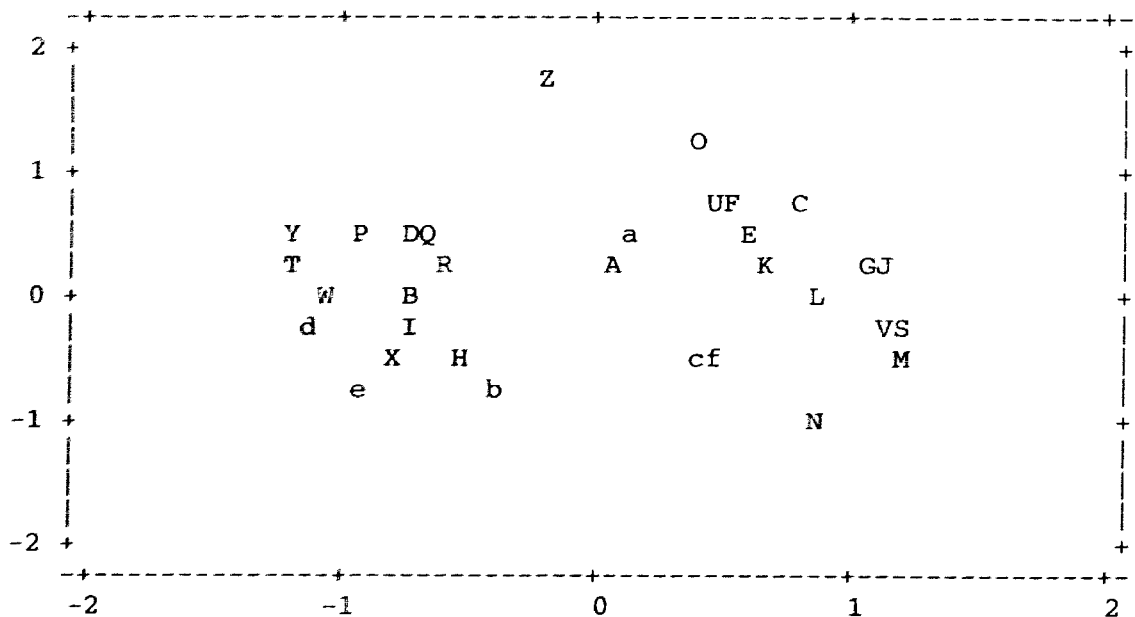
```
   -+-----------+-----------+-----------+-----------+--
 2 +                                                     +
   |
   |               K
   |                          W
 1 +                                                     +
   |   Y            f           A
   |     J       D                 d Qe
   |                               a bUMSL
 0 +                               IVCOT X              +
   |     B G                       H   R
   |               Z                  P E
   |                               N
-1 +   F                                               +
   |               c
   |
   |
-2 +                                                     +
   -+-----------+-----------+-----------+-----------+--
   -2          -1           0           1           2
```

Legend

khoi	A	kung	B	thonga	C	lozi	D
mbundu	E	bemba	F	hadza	G	kikuyu	H
ganda	I	mbuti	J	tiv	K	ibo	L
fon	M	ashanti	N	mende	O	wolof	P
bambara	Q	tallensi	R	fulani	S	hausa	T
shilluk	U	masai	V	konso	W	somali	X
amhara	Y	bogo	Z	nubian	a	teda	b
tuareg	c	riffian	d	egyptian	e	bedouin	f

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- Nilosaharan: U, V, a, b
- AfroAsiatic: W, X, Y, Z, c, d, e, f

Figure 2.8 shows a 2-D representation of pairwise cultural distances.
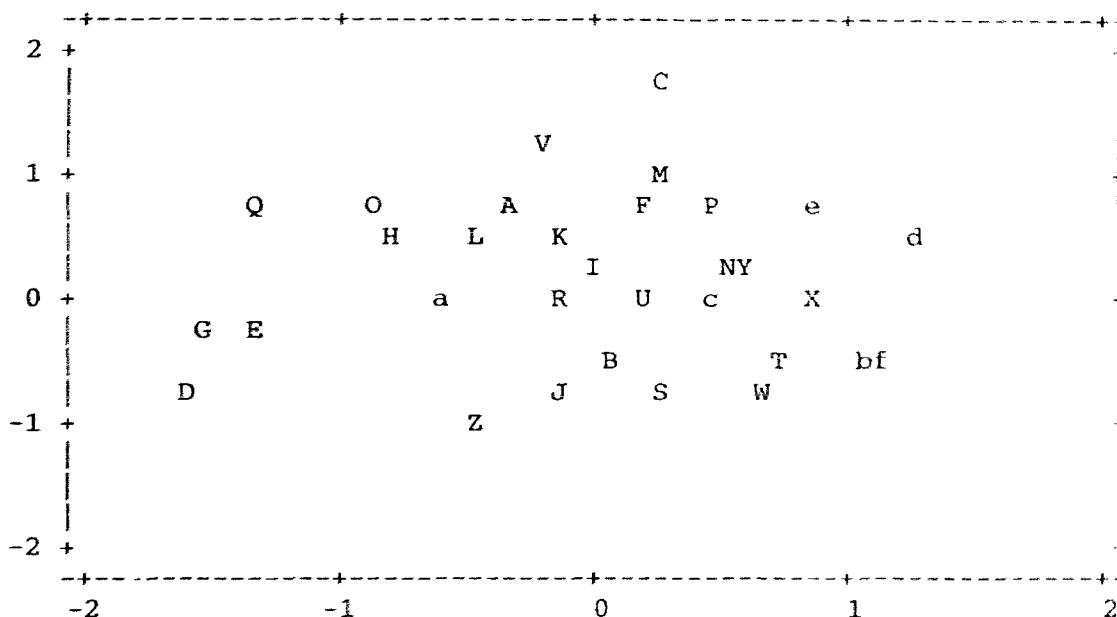
78

Figure 2.9: Gender Issues

```
    -+-------------+-------------+-------------+-------------+-
  2 +                                                             +
    |                         Z
    |
    |                                  O
  1 +                                                             +
    |                               UF    C
    |         Y    P   DQ          a      E
    |         T         R          A      K      GJ
  0 +            W    B                   L                       +
    |         d     I                            VS
    |            X   H              cf           M
    |          e        b
 -1 +                                  N                          +
    |
    |
    |
 -2 +                                                             +
    -+-------------+-------------+-------------+-------------+-
    -2           -1            0             1             2
```

Legend

khoi	A	kung	B	thonga	C	lozi	D
mbundu	E	bemba	F	hadza	G	kikuyu	H
ganda	I	mbuti	J	tiv	K	ibo	L
fon	M	ashanti	N	mende	O	wolof	P
bambara	Q	tallensi	R	fulani	S	hausa	T
shilluk	U	masai	V	konso	W	somali	X
amhara	Y	bogo	Z	nubian	a	teda	b
tuareg	c	riffian	d	egyptian	e	bedouin	f

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- Nilosaharan: U, V, a, b
- AfroAsiatic: W, X, Y, Z, c, d, e, f

Figure 2.10 shows a 2-D representation of pairwise cultural distances.
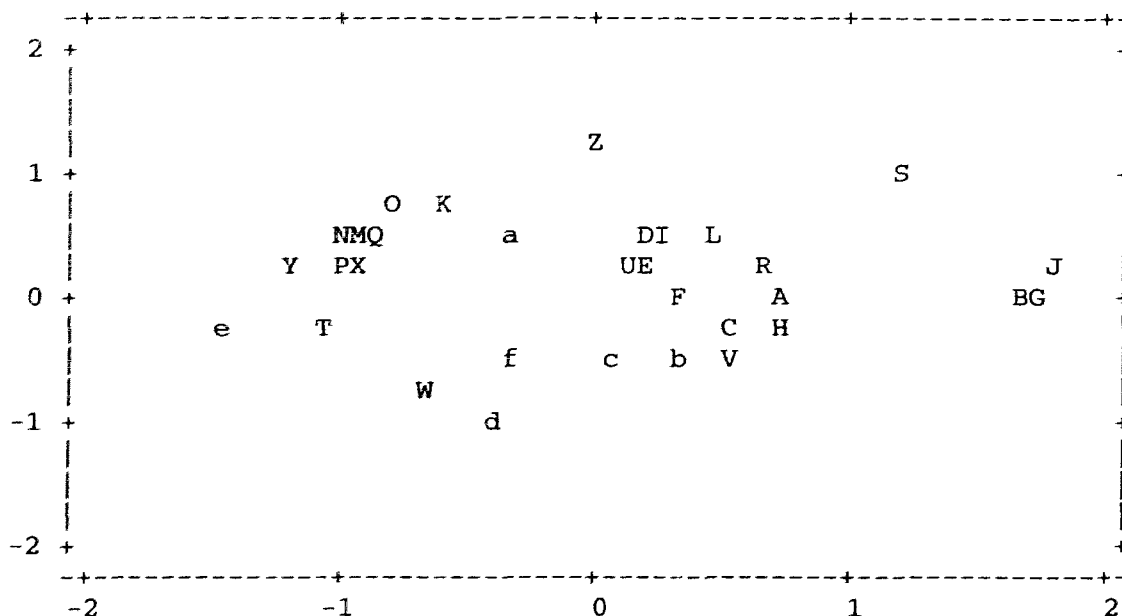
79

Figure 2.10: Religious Behaviour

Legend

khoi	A	kung	B	thonga	C	lozi	D
mbundu	E	bemba	F	hadza	G	kikuyu	H
ganda	I	mbuti	J	tiv	K	ibo	L
fon	M	ashanti	N	mende	O	wolof	P
bambara	Q	tallensi	R	fulani	S	hausa	T
shilluk	U	masai	V	konso	W	somali	X
amhara	Y	bogo	Z	nubian	a	teda	b
tuareg	c	riffian	d	egyptian	e	bedouin	f

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    - Non-Bantoid: M, N, O, P, Q, R, S
- Nilosaharan: U, V, a, b
- AfroAsiatic: W, X, Y, Z, c, d, e, f

Figure 2.10 shows a 2-D representation of pairwise cultural distances.

Figure 2.11: Social Hierarchy

```
   -+-------------+---------------+---------------+--------------+-
 2 +                                                              +
   |
   |
   |                            Z
 1 +                                          S                   +
   |             O  K
   |           NMQ        a          DI  L
   |         Y PX                    UE       R              J
 0 +                                     F    A           BG      +
   |     e      T                         C  H
   |                          f     c   b V
   |             W
-1 +                         d                                    +
   |
   |
   |
-2 +                                                              +
   -+-------------+---------------+---------------+--------------+-
   -2           -1              0               1              2
```

Legend

khoi	A	kung	B	thonga	C	lozi	D
mbundu	E	bemba	F	hadza	G	kikuyu	H
ganda	I	mbuti	J	tiv	K	ibo	L
fon	M	ashanti	N	mende	O	wolof	P
bambara	Q	tallensi	R	fulani	S	hausa	T
shilluk	U	masai	V	konso	W	somali	X
amhara	Y	bogo	Z	nubian	a	teda	b
tuareg	c	riffian	d	egyptian	e	bedouin	f

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    o Non-Bantoid: M, N, O, P, Q, R, S
- Nilosaharan: U, V, a, b
- AfroAsiatic: W, X, Y, Z, c, d, e, f

Figure 2.11 shows a 2-D representation of pairwise cultural distances.

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Historical, Geographical and Linguistic Confounds

Matrices representing genetic history and geographic distance are positively correlated (two matrix Mantel test, $r = 0.31274$, $P < 0.0001$). As geographic and genetic distances are confounded, a multiple regression technique is necessary to examine independent historical or geographic influences on cultural dissimilarity.

Matrix Permutation Tests

Table 2.6 shows the results of the Mantel tests for all seven clusters of cultural characteristics. The table shows the correlations with both the historical and geographical distance matrices for each of the seven character clusters. The partial correlation of culture on history controlling for geography, and the partial correlation of culture on geography controlling for history are also shown. Correlations represent the proportion of the variance in the cultural distance matrices explained by each of the two predictor matrices (history or geography). Partial correlations represent the effect of history on culture while controlling for common geography and then geography on culture while controlling for common history. P values are from 49999 matrix permutations.

Table 2.6

Mantel Tests of History, Geography and Culture

	Correlations				Partial Correlations			
	Genetic History	P	Geography	P	Genetic History	P	Geography	P
Religious Practices	0.02	0.39	0.12	0.03	-0.02	0.58	0.12	0.03
Domestic Organization	0.10	0.10	0.12	0.02	0.06	0.20	0.10	0.06
Gender Issues	0.07	0.13	0.02	0.35	0.07	0.14	-0.00	0.52
Family Structure	0.10	0.15	-0.02	0.61	0.11	0.12	-0.05	0.77
Economic System	0.10	0.11	0.017	0.40	0.10	0.11	-0.02	0.60
Familial Organization	0.17	0.002	0.08	0.06	0.15	0.005	0.03	0.27
Social Hierarchy	0.20	0.002	0.05	0.18	0.19	0.003	-0.01	0.57
Language Phylum	0.26	0.0001	0.20	0.0002	0.21	0.001	0.13	0.01

Mantel tests of matrices representing genetic similarity, geographic distance and eight indices cultural and linguistic similarity.
The four leftmost columns show correlations of genetic history and geographic distance measures against cultural distances. The four rightmost columns show partial correlations, first genetic history controlling for geographic distance and then geography controlling for genetic distance. P values from 49999 random matrix permutations.

Discussion

In summary, I find that two of seven indices of cultural similarity significantly follow patterns of genetic differentiation. This finding implies that for these characters vertical transmission has likely played an important role over many generations. Only one character had a significant correlation with geographic distance. Only in the case of religious behaviour is mere geographic distance between cultural groups a good predictor of cultural similarity (Table 2.7). This implies that in the long term, mere proximity may be a necessary and sufficient condition for cultural change in this area.

Table 2.7

Confounded Effects Equivocal Result	Horizontal Transmisison
● Linguistic Phyla	● Religious Practices

Vertical Transmission	No Strong Correlations Independent Origin
● Social Hierarchy ● Familial Organization	● Gender Issues ● Family Structure ● Economic System ● Domestic Organization

Table 2.7 tabulates the results showing how each of the eight cultural dissimilarity matrices fit into the scheema presented in table 2.1.

Characters, Clusters and Cultural Distance

Our empirically derived character clusters were similar to the a priori categories used in Guglielmino et al. (1995). The two grouping schemes of cultural elements differ primarily in the division of 'family and kinship' into two subcategories and the dispersion of many of the 'division of labour by sex' variables into other categories. While half of the gender characteristics fall together, associated most closely with religious behaviour, the other half are found scattered among three other character clusters, suggesting that some divisions of labour may be the result of specific gender issues, while others are related to economic, domestic or hierarchic organization. The character "Division of labour by sex: metal working" provides an illustrative example. In all the societies in our sample, metal working, if it is practiced, is a predominantly male activity. Thus the code "Division of labour by sex: metal working" is showing us the distribution of metal working (which is related to the degree of hierarchical organization), it does not provide information about gender issues.

Just because a given variable is measured by an ethnographer does not guarantee that it is an important, independent, cultural variable. In order to remove some of the observation/attention bias, and to help cope with a plethora of missing data, I clustered the characters into 7 cultural similarity

indices. For example, many of the domestic organization variables are different aspects of house construction. These are replaced with a single measure of domestic organization which subsumes individual aspects of house shape. In order to determine relatively independent cultural variables for these tests, I would ideally attempt to create a variance-covariance matrix using variability within cultures, in order to cluster and weight the measured traits into characters for study. Unfortunately, within population variation is not available in the Ethnographic Atlas. As a surrogate for within population variability, I used data collected at a temporally shallower depth of separation (the 277 population sample) to cluster the characters. The 32 populations in my sample represent groups that are more culturally distinct (from one another) than the 277 populations of the Ethnographic Atlas. Thus I use correlations among the 277 groups in the same way I would use within population variation if it were available.

This clustering scheme avoids the potential circularity in using the same data matrix to both construct factors that link variables together and then to examine the relationships among cultures based on those factors.

State Transition Matrices and Character Ordering

Each of the cultural distance matrices I produced was based on the dissimilarity among populations for five to nine cultural traits. Cultural distance was calculated as the number of steps

between the character states, summed over the characters, divided by the number of comparisons. Unfortunately, it is difficult to determine how different any two character states are. Subjective decisions concerning the differences among cultures are often based on an implicit ordering of characters in a sequence leading from lower to higher. This 'unilineal' evolutionist thinking is the antithesis of modern evolutionary theory. The production of character transition matrices, an important concern in phylogenetics, is particularly difficult in studies of cultural change.

I left most of the characters in this study unordered. For unordered comparisons, each state is assumed to be equally likely to change into any other state and no state is assumed to precede any other state. The main exceptions to this practice are for those characters which are already quantitative variables. For example, Dependence on Gathering is considered to be an ordered character, as it represents the percentage of food that is obtained through gathering. Similarly, Jurisdictional Hierarchy of Local Community is also ordered, as it is already a numerical variable (2, 3 or 4 steps). Even though these characters are ordered, I have assumed that they are not polarized. (Character polarization implies a knowledge of the order in which characters change) A change from two to four levels of social hierarchy is equivalent to a change from four levels of social hierarchy to two. No assumptions of 'higher' or 'lower' character states are made. For most of the analyses, ordering the characters may change the magnitude of the results but does not modify them qualitatively.

The only important exception is the case of Familial Organization. Analysis of these characters supports a geographical explanation if they are all considered ordered, while an historical model is supported if all unordered characters are used. I display results (Table 2.6) using four unordered and one ordered character.

Building transition matrices is a complex processes and until a good model of historical connections between groups is developed it is difficult to estimate transition probabilities. Archaeological data is likely the perfect source of information to use to build state to state transition probabilities. For now I have left the majority of the characters unordered, although I recognize that this choice itself is an assumption of a transition matrix.

Transmission mode is variable

I argue that attempting to determine if language is associated with 'culture' in general (Welsch et al. 1992; Roberts et al. 1995), is not a particularly useful question. My results suggest that there is great variability in the mode of transmission of the different trait classes studied. Using genetic markers as indices of shared history I am able to measure the magnitude of historical cultural inertia and begin to estimate rates of cultural change for particular characters. Table 2.7 shows how indices of cultural change, fit into the schema presented in Figure 2.1.

While traits in the vertical transmission category show clear correspondence between genetic and cultural differences among

groups, this should not be misconstrued as representing any causative link between the genetic differences and the cultural differences.

It is interesting that Religious Practices are the only group that strongly support a diffusion model (although Domestic Organization produces a similar, but statistically borderline result). Characters with this type of contagion-like spread, where contact may be a necessary and sufficient condition for cultural change, are most likely to exhibit parasitic adaptations due to the potential conflict of interest between the host and a horizontally transmitted character.

While there are cases where the confounding effects of historical association and geographical proximity obscure our understanding of transmission mode I found that only Language Phylum has significant association with both historical and geographical distances. None of the cultural distance matrices supported both transmission models. Most of the characters fit the historical and geographic distance matrices equally poorly, suggesting that adaptation/innovation may be a strong force, erasing both historical associations and the effects of cultural diffusion.

Previous Approaches

Quantitative investigations into estimations of historical effects on distributions of cultural elements are rare in the literature. Jorgensen (1969) pioneered work in this area by examining correlations of culture with measures of historical association. He examined correspondences among similarity matrices representing geographic, religious, technological and social variables. Among the Salish peoples Jorgensen found that social organization, religion and technology all showed strong relationships with language and weak correlations with geography. He concludes that for some aspects of culture, linguistic affiliation (used as a measure of historical forces) is more important than the present physical or social environment.

Chakraborty et al. (1976) compared the distribution of multiple cultural characters to genetic distances among South American Amerindians. They failed to find any influence of history on culture above and beyond the effect of geographical proximity. However they used only seven alleles and scored a single measure of total cultural dissimilarity. Sokal et al. (1991) examined the fit of the distribution of agriculture across Europe to a genetic expansion model and found strong support for a vertical transmission/demic expansion model of cultural change for this character in this area.

Guglielmino et al. (1995) have investigated the transmission mode of the same 47 traits I used across 277 African societies

9 1

from Murdock's "Ethnographic Atlas" (1967). Correlations with linguistic grouping were assumed to represent evidence of vertical transmission. Spatial clustering of the distribution of a character was taken as evidence of horizontal transmission. They found that most of the traits they examined had some association with linguistic history and that family and kinship traits showed strong associations with language groupings. 'Division of labour by sex' and 'Various' traits both showed spatial clustering.

Our estimate of the transmission mode of agriculture did not demonstrate an important role for vertical transmission. This does not necessarily conflict with the demic expansion model for agriculture throughout Europe (Sokal et al. 1991), as such regional non-replication may indicate that the same cultural trait has different transmission properties in different social or physical environments.

Our approach is complementary to that of Guglielmino et al. (1995), although it differs in two important aspects. First, I made a direct comparison of cultural character distributions with genetic distances. Second, I used a partial regression model in an attempt to place each group of cultural traits into one of the four categories outlined in Table 2.1. Thus I specifically address and attempt to control for the confounding influences of correlated historical and geographical distances.

History, Geography and Language

Correlations between language phylum and cultural characters distributions are important, but they are not equivalent to correlations between genetic distances and cultural distances. While we have a detailed understanding of the mechanism of transmission of genes and models to explain how they change over time, unfortunately the same does not hold for language. Although gene trees and language trees are clearly more similar than expected by chance (Cavalli-Sforza et al. 1988, Cavalli-Sforza et al. 1992, Penny et al. 1993, Chen et al. 1995), it is essential to recognize that genetic history, linguistic history and cultural history are three independent inheritance systems. As Boas (1940) argued since the beginning of this century, there is no known causal connection among race, language and culture. Correspondence among genetic and linguistic trees, while statistically significant, by no means demonstrate that linguistic history is identical to population genetic history. I note that these results suggest that geographic proximity has a strong statistically significant effect independent of shared genetic history in explaining the distribution of language phyla. It is the only character that falls into the confounding factors class. At this point there is still enough uncertainty about correlations between language and history that any examination of cultural variables correspondence with linguistic variables should be taken as an examination of correspondences among cultural elements, not between culture and population history.

Figure 2.4 diagrams the relationship between the genetic/historical dissimilarity among the 32 populations and the linguistic groups. While there are parallels, it is clear that genetic history and linguistic history may deviate. In several cases, (Nubians, Hausa and Kung) populations are found to cluster genetically with people who speak a language dissimilar at the phylum level. These results suggest substantial disparity between linguistic and genetic histories. For example, the Hausa are genetically similar to speakers of Niger-Kordofanian languages yet speak an Afro-Asiatic language. The Nubians speak a Nilo-Saharan language yet cluster with Afro-Asiatic speakers. As these data show, it is premature to use linguistic similarity as a measure of population genetic history. In order to test hypotheses of vertical transmission we must directly examine the correspondence between the distribution of cultural and genetic traits. As language phylum falls into the confounded situation where both history and geography are important independent explanatory variables, I stress that correlations between cultural trait and language group do not necessarily represent 'historical' effects.

Limitations of the Genetic Data

We have used as much allele frequency information to estimate historical distances as is available, however more specific polymorphisms such as microsattelite loci (Bowcock et al. 1994, Tishkoff et al. 1996) will eventually permit much better

estimates of population structure and history. There is a trade off between the breadth of populations studied and the amount of detailed genetic information available. In this study, I avoided the construction of phylogenetic tree diagrams for the populations because it is not clear that representation as a non-reticulating tree is a legitimate method of diagramming population history within a species (Batemen et al. 1990, Moore 1994).

Characteristics of the Populations sampled

Our results differ substantially from those of Guglielmino et al. (1995). It is likely that the particular populations I used, rather than the number of populations, has an important effect on the results. The 32 populations I used were spread unevenly throughout the 277 populations used by Guglielmino et al. (1995). Many of the smaller and rarer ethnic groups in the SCCS, (e.g. Mao and Fur) are not represented in our study as there has not yet been adequate genetic data collected from them. Unfortunately, if these rare ethnic groups represent populations that have been isolated for long periods of time we may lose considerable information in their exclusion. Weng and Sokal (1995) found that when analyzing the relationship between gene frequency clines and hypotheses of Indo-European expansion, deep language relations and shallow language relations gave contradictory results. Some of the correlations found in the 277 population Ethnographic Atlas sample may be due to the correlations within shallow groupings (such as the Bantu) while at the deeper levels

of structure (between West African and Bantu groups for example) alternative patterns may predominate. This points out a potentially serious scaling problem that necessitates careful selection of cross cultural samples. The current Standard Cross Cultural Sample (Murdock and White 1980) includes a sample drawn to represent all geographic regions. While this makes sense in some ways, it distinctly over-represents members of recent population expansions. For example, South America has as many cultural groups in the sample as does Africa while the American lineages have been diversifying for perhaps as little as one tenth as long as African groups. As an alternative to such a geographically based sample we might choose a cross cultural sample of populations that are equally historically distinct (as measured through genetic differentiation).

Null Model

Once we have a fair understanding of the modes of transmission of various cultural characters we can begin to produce a null model of cultural change against which adaptive hypotheses can be tested. The development of a comparative method for detecting instances of convergent cultural evolution could provide a valuable theory testing tool for many disciplines within anthropology. The phylogenetic problem in anthropology is considerably complex, due to the reticulate nature of the historical connections among human populations and the horizontal transmission of many elements. These problems,

however should not be considered to be insurmountable. Careful historical examinations at the regional level may be expanded to include much larger areas and longer time scales through the use of genetic data as a tool to trace population histories.

Through the use of genetic data I are able to compare cultural data directly with our best estimate of population genetic history. I do not wish to give the impression that genetic data should be considered to be somehow superior to linguistic or cultural data. Genetic data is valuable because it has properties that permit the use of relatively robust historical reconstructions. If comparative anthropology is to thrive as a scientific discipline, it must adapt to the plethora of population genetic tools that are arising. I argue that the development of detailed population level genetic histories will open a whole new era of comparative research where both cultural anthropology and archaeology can become intermingled through the use of genetic markers, ethnography and statistical methods for the reconstruction of historical change.

Through the use of genetic markers we will be able to probe the deeper historical ties among cultural groups and eventually will have as accurate a map of ancient human population movements as we can afford. Unlike most historical/archaeological data sources, the population genetic information available to us at this point seems virtually limitless.

Each and every person alive on the planet holds in their body a huge storehouse of historical information in the sequence of their DNA. We need now only implement a worldwide tissue sampling program and develop our statistical techniques and we will have access to a virtually limitless fountain of information about our history.

Eventually we may reconstruct the culture of our most ancient ancestors through a combination of archaeology, population genetics and cross cultural data. We must abandon 'unilineal' evolutionary theories that treat any extant group as if they were 'living ancestors'. No contemporary group of people represent the condition in which our common ancestors lived. All cultural groups are mosaics of ancestral and derived traits. Through broad cross cultural comparison, extensive genetic investigations and methodically rigorous reconstructions of ancestral character states can we determine how our common cultural ancestors likely behaved. The tools and data of molecular biology and population genetics may become one of the most valuable sources of data we have ever had regarding the mystery of our past and questions dealing with the evolution of human culture.

Conclusion

I summarize the central thesis of the cultural replicator hypothesis as follows:

As memes are independent replicating entities which have the properties of heritability, variability and covariance among their content and replication success, we expect that over time those memes with conformations which improve their replication success will become more prevalent relative to those without such adaptive conformations.

Evolutionary theory lends us two main sets of tools with which we can better understand human culture. First, connections between population genetics and cultural transmission allow us to make use of certain aspects of evolutionary theory in understanding the dynamics of cultural change. Of special importance may be the importance of the force of natural selection on cultural variation that can produce adaptations that benefit the culture itself and not its human host. Second, the environment in which memes replicate is the human mind, itself a product of natural selection. Understanding the evolutionary history and functional organization of the capacities of the human mind allows us to better understand the environment in which culture grows and reproduces.

A better understanding of historically bounded blind optimization through the differential propagation of randomly varying replicating patterns, (natural selection) will help us understand aspects of human culture on both planes: its own optimization trajectory and the substrate in which it replicates.

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