

**COMPARATIVE CULTURAL PHYLOGENETICS AND
THE TRANSMISSION OF BELIEF
IN AN ORAL SOCIETY**

Robert Aunger
Department of Biological Anthropology,
University of Cambridge
CB2 3DZ
ENGLAND
bob@robertaunger.net
<http://www.robertaunger.net>

RUNNING HEAD: Comparative Cultural Phylogenetics

KEYWORDS: comparative method, cultural transmission, phylogenetic reconstruction, food taboos, belief systems

Abstract

Cultural transmission typically results in a network of connections between cultural units (such as individuals or social groups), not the branching patterns of descent seen in genetic inheritance. As a consequence, the application of phylogenetic (or evolutionary clustering) methods to cultural history faces methodological problems. Most importantly, the history of relationships inferred through phylogenetic reconstruction, and manifested in the tree's topology, cannot be trusted. In this paper, I suggest a novel use of phylogenetics which does not depend on the correct identification of ancestral relationships. In this method, alternative models of how information can be culturally transmitted are implemented on the same population, and the resulting trees compared. The model which better extracts "phylogenetic signal" or descent relations from the cultural data is preferred. The virtue of this method is that it relies only the general features of phylogenetic trees to make inferences about cultural history. An empirical case study concerning the social learning of food avoidances in a rural African population demonstrates that this comparative use of phylogenetics can effectively identify aspects of cultural inheritance. Such results could not be readily obtained using standard statistical procedures. Thus, by using phylogenetics comparatively, interesting things about cultural transmission can be learned.

1. The Problem of Reticulation in Cultural History

Evolution is an historical process, but is typically studied by looking at patterns of variation within contemporary species or populations of individuals. But analytical units -- whether social groups or individuals or genes -- are related through common descent from ancestors to whom they are linked through a chain of transmission events. While this shared parentage is the basic consequence of any evolutionary process, it coincidentally invalidates an important assumption of standard statistical analysis: that the data-points in a sample be independent of one another. So when investigators attempt to formally analyse the variation they find among contemporary analytical units, they are confounded by the problem of common ancestry. The obvious solution -- to somehow extract this interdependence from the data statistically -- has been advocated in various forms by a number of workers (Dow et al. 1984; Grafen 1989). The basic goal is to "correct for" history, thereby making standard statistical procedures valid again.

For example, evolutionary biologists might be interested in "controlling" for history to understand the variation in genes or morphology they see. Alternatively, they can be interested in that history itself, in discovering the course through which evolving players travelled to reach their current relationships. For example, perhaps an ecologist wishes to know the correlation between body size and territory size among passerine birds. This investigator will always find that the set of species to be included in the statistical test are more or less similar to one another morphologically and share more or less similar niches, suggesting the possibility of interbreeding between these species in the past. Indeed, some species might be descendants of the same ancestor. But to the ecologist, this evolutionary history is largely an annoyance. The possibility of shared descent contradicts an important assumption of standard statistical methods -- that data points be independent of one another. Ignoring a history of interdependence when conducting parametric statistical analysis can be problematic, potentially leading to false conclusions. Realization of this problem has prompted the development of new methods which take into account branching relationships of common descent (Brooks and McLennan 1991; Harvey and Pagel 1991; Ridley 1986).

The same dilemma is faced by social scientists. In testing for a relationship between patrilocality and bridewealth in cultures across the world, for example, an investigator will always find that the relevant cultural groups are more or less close to one another geographically and speak more or less similar languages. This suggests a degree of contact between these groups in the past. Indeed, one group might have been socially or culturally "parented" by the ancestor of another. Since becoming aware that comparative studies of cultural groups involve "cultural heritability" (called by them Galton's problem), social scientists have adapted phylogenetic methods (or evolutionary cluster analysis) in various ways for the study of cultural problems (Guglielmino et al. 1995; Mace and Pagel 1994; Pocklington 1997).

However, an obvious consequence of using "phylogenetically correct" methods is that effective sample size is reduced. This means that such tests on a given dataset have lower statistical power than standard ones. The question therefore arises: is the need for phylogenetically-aware statistical tests truly general in the evolutionary sciences? If history is largely irrelevant compared to current selection pressures, standard methods are both appropriate and more powerful.

Whether controlling for history is relevant depends on two things: first, what kind of evolutionary process is generating the observed variation in traits, and second, the time scale over which the test is being conducted. Standard methods for phylogenetic reconstruction assume randomized errors in the traits, which is equivalent to a neutralist evolutionary model -- that is, Brownian motion or a flat fitness functions (Martins and Hansen 1996). However, it is commonly believed that most traits of interest are subject to "biased" selection, in which certain variants are consistently favored in transmission from generation to generation. The result of such selection is the non-random obliteration of historical relationships as each descendant group adapts to its new circumstances. From a statistical point of view, this will lead to a relatively quick recovery of independence between data-points. This implies that the amount of dependence between observations will generally be overestimated by phylogenetic analysis and the relative statistical power of the test used unnecessarily weakened. Further, existing

phylogenetic-based statistics also assume tree topology is known with certainty, so that the statistical power of such tests is artificially inflated. It may therefore be that the universal application of phylogenetic correction is unnecessary (Rogers and Cashdan 1997). But since the past history of selection on the traits of interest is typically unknown, whether phylogenetically-informed methods are appropriate in a given case remains an open question. Therefore a conservative approach is probably warranted, implying that phylogenetic relationships should be considered -- at least when the time period is long relative to the rate of mutation in the traits being investigated.

What about the alternative case, when history is actually the focus of a researcher's attention? Unfortunately, the application of phylogenetics to the reconstruction of that history itself can present another, more fundamental problem. Phylogenetic methods were originally developed to describe speciation, a process in which groups become reproductively isolated from one another, and therefore no longer exchange genetic information. Hence, applications of phylogenetics assume strict bifurcation in descent; that each member of a descendant generation is related to only a single member of the ancestral generation. The assumption of informational isolation following the split from a common ancestor is generally appropriate for genetic comparisons of populations, since population division implies a speciation event and reproductive isolation is the defining feature of the predominant "biological species concept" (Mayr 1969). Single parentage is also true for haploid traits -- a fact exploited by those searching for relationships between populations in haploid organisms, such as some viruses (e.g., Louwagie et al. 1993), or for the origins of a mammalian species, using their mitochondrial DNA, where inheritance is largely maternal (e.g., Vigilant et al. 1991).

However, if one looks at evolution within a single population, multiple copies of the same gene or cultural trait often exist. A mutation affecting one copy does not necessarily result in extinction of the ancestral form -- which remains behind in other bodies. Each copy of a trait can therefore mutate to different forms, producing many descendant types. This is represented as a multifurcation in a population or gene tree. If no root is assumed, such multifurcations produce network structures, not branching diagrams. This can make the use of phylogenetic trees for intra-population evolution problematic (Crandall and Templeton 1996).

This difficulty seems exaggerated in the case of cultural evolution. It is commonly assumed that cultural traits may be learned at different points in an individual's life, and from a variety of people. Thus, cultural transmission often violates the primary assumption of phylogenetics --- that units acquire their inheritance from one source, their evolutionary ancestor. This "single linkage" assumption is valid in the case for which it was derived, since (nuclear) genes necessarily come from one or the other biological parent. This possibility -- indeed likelihood -- of multiple cultural links between individuals or groups has spawned an anti-phylogenetic movement, the so-called ethnogenesis approach (Moore 1994), which advocates the application of methods appropriate to "reticulate," or inter-woven, rather than tree-like descent relationships for the study of cultural evolution. Of course, a cultural trait with a consistently uniparental pattern of inheritance may be found, or sufficient historical signal may be preserved over the relevant temporal and spatial scales to make the phylogenetic approach useful in particular cases (Boyd et al. 1997). However, generally speaking, the probable cross-lineage borrowing of socially-acquired information places considerable limits on the utility of phylogenetics to cultural evolution, despite the increasing sophistication of some recent applications (e.g., Sellen and Mace 1997).

We therefore have a conundrum: we probably should allow for dependency relationships in cultural data, but we don't have a well-grounded method for doing so. The relatively poor fit of most cultural datasets to phylogenetic assumptions means that phylogenetics cannot be expected to produce trees which accurately represent the cultural history of a population.

1.1 Hope for cultural phylogenetics?

These profound difficulties would seem to effectively preclude the development of a cultural phylogenetics. The only possible course of action seems to be to ignore history and to hope that cultural selection pressures are sufficiently strong to blur the effects of history on contemporary variation. But in fact we still desperately need phylogeny to study culture. Why?

First, because it is the method most clearly suited to the study of hierarchical branching processes like evolution. Thus, if culture evolves, we had better find a way to make phylogeny

relevant. No other technique makes the transmission of information its core question. Certainly, appropriate methods for studying information transmission have not been developed in the social sciences. Indeed, standard social scientific theory altogether ignores the fact that information is a scarce resource. Instead, the distribution of requisite competencies for social interaction and the socializing of new generations into the prevailing cultural milieu are accomplished through magical processes outside of time and space (Thompson 1995).

Second, phylogenetics has well-developed methods with a large associated empirical literature. There is also an earnest, vigorous and wide-spread movement afoot to improve the available methods in response to any critique which arises, so that hope of rapid improvement of available methods for cultural analysis is realistic. Methods specific to reticulated processes, to the extent that they exist,¹ are at present rudimentary, and are not being pursued by such a large pool of talented researchers as in systematics. So viable alternative methods to analyze transmission processes are presently unavailable.

But I have just argued that phylogenetics is generally inappropriate when applied to cultural processes, due to significant reticulation in cultural transmission patterns. This means that the relative placement of individual evolutionary units in a tree will generally be unreliable. How can we move toward a legitimate cultural phylogenetics, given such stringent constraints on our potential use of this important method?

Happily, we are in the situation of having only weakly applicable methods at hand, but finding that weak results are all that is required to say something interesting about cultural evolution. This is because cultural evolution doesn't obey Mendelian rules of inheritance, so general questions about underlying evolutionary processes remain unanswered. Despite over one hundred years of social scientific activity, we still don't know who tends to serve as cultural "parents" to whom, nor what kind of information they transmit. As a result, gross features of the cultural process remain of considerable interest. Such questions can best be answered by a method which can compare explicit models of the evolutionary process, and with respect to individual domains in a given population (because the pattern of transmission may vary in each case). Such a method is phylogenetics.

Thus, being able to distinguish between alternative models of inheritance is all that is required at present to make substantive advances in the study of cultural evolution. This appears to provide us with a window of opportunity for applying phylogenetic methods to the case of culture traits. But how are we to implement this collection of methods? We still face the likelihood of falsely accepting propositions about cultural evolutionary processes based on analyses with low powers of resolution.

1.2 Comparing cultural histories

I argue the trick is to use phylogenetics *comparatively*, focusing on the gross, relatively reliable features of phylogenetic analysis. The solution relies on comparing trees generated by alternative models of evolutionary change in cultural traits. Essentially, different assumptions are made about how cultural information is transmitted through a population, and these assumptions are considered to be validated if they perform relatively better at extracting the phylogenetic signal out of necessarily "messy" cultural data. Such comparisons deal only with the most general aspects of trees -- in particular, they use tests which do not depend on the correct inference of historical relationships between individual units, nor the particular branching sequences in the topology of the tree. This method therefore remain valid, despite the general misbehavior of cultural transmission patterns, because it does not assume that phylogenetics can accurately model the specific sequence of events in a cultural history. The objective of these comparative tests is derivative, requiring only appropriately weak assumptions: to ascertain which model of transmission is more consistent with the assumption of branching descent. While it is doubtless true that non-phylogenetic patterns will also be present in cultural data, there must still be descent with modification present in any cultural evolutionary history. Comparative

¹ Moore (1994) argues that methods developed to predict the qualities of metal alloys and for describing river-channel morphology could be applied to the analogous case of cultural evolution, but does not elaborate on how he expects the transfer of these methods to proceed.

phylogenetic analysis can determine which kind of inheritance is most consistent with that part of the evolutionary process.²

This is of course not standard procedure in genetics, where the one best set of branching relationships (or tree topology) is sought, given the tight, well-known constraints on the transmission of genetic information. But a more fault-tolerant procedure is of value in the case of cultural traits, where no equivalent of the Mendelian process is currently established. Nor is such a universal law likely to be found. Each cultural domain will probably exhibit a unique pattern of transmission, depending on the composition of the population, the preferences or psychological biases for favoring particular teachers over others, and the technologies for information transfer. Thus, the need for comparative cultural phylogenetics will remain for some time to come.

Here's how the comparative method works.³ Phylogenetic methods aim to reconstruct the history of descent with modification that produced the variation in some current set of taxonomic units, such as mammalian species. It achieves this goal by making assumptions about the kinds of mutations allowed to trait values during the reconstruction of this history. These constraints on how information can be inherited constitute a model of trait evolution. For example, one can assume an order to trait changes. In essence, certain states are considered to be necessarily ancestral to, or more primitive than, others, and should therefore occur earlier in any hypothesized lineage of descent (Mickey 1982). Models reflecting detailed, even asymmetric, probabilities of change can be accommodated in the form of a "step-matrix" which specifies the costs of each possible transition from one state to another. Different models of trait evolution, given the same basic set of information about contemporary patterns of variation, will lead to the history of a population being reconstructed in distinct ways, producing trees with divergent topologies. Once these branching hierarchies have been created, their characteristics can be compared with respect to various criteria. Darwin advocated a similar comparison of hypotheses about inheritance for the study of biological traits before the rules of genetic transmission were known.

The reconstruction of evolutionary history depends, however, on the use of an algorithm for inferring phylogenetic structures. These algorithms take the information about variation in traits and, given a set of constraints on trait change, piece together branches and nodes one by one. Although there are several classes of phylogenetic algorithms, I will focus here on the two most popular ones. Maximum parsimony methods (Sober 1988) attempt to minimize the total number of changes in traits required to place all taxonomic units into a branching hierarchy. On the other hand, various "minimum evolution" algorithms, such as least squares (Fitch and Margoliash 1967) or neighbor joining (Saitou and Nei 1987), are designed to minimize the spanning distance in a tree -- that is, the sum of all branch lengths combined. This may sound the same as minimizing the number of trait changes, but is not necessarily. Maximum parsimony deals directly with the states of the traits under consideration. However, branch lengths in minimum evolution algorithms are not measured in terms of trait changes, but as quantitative distances gauging the degree of similarity between taxonomic units. It is these distances, rather than trait-states themselves, which are used in assembling trees. By including different information in the calculation of inter-unit distances -- for example, by varying the number or kind of characteristics combined in the calculation, or the weight given to specific changes in

² Why not just use network analysis (Wasserman and Strauss 1994) if a network is the best characterization of cultural relationships? Because network analysis doesn't *find* the network; it assumes one and then analyzes its characteristics. Phylogenetics is the only well-established method for finding a "good" network. Admittedly, phylogenetic methods significantly constrain this search to hierarchically nested networks (or trees), and this search nevertheless rapidly exceeds the ability of most algorithms to find the best tree as the number of units rises. But as such transmission chains remain a significant part of any evolutionary story, it is worth knowing something about.

³ The comparative approach outlined here is not the same as the "comparative methods" used to "correct for" history, such as Grafen's (1989) "phylogenetic regression" or Harvey and Pagel's (1991) ANCOVA-based approach. The method I advocate compares models of the evolutionary process; it is not designed to remove the phylogenetic signal from a given dataset, thus allowing the use of standard statistical techniques.

trait-states -- specific evolutionary models can be tested using minimum evolutionary algorithms, just as in the case of maximum parsimony.

Some models of trait change are easier to implement with a particular algorithm. For example, assumptions about the order of trait changes are more facile with the maximum parsimony method, which can explicitly consider the sequence of states along a lineage. Distances do not retain information about the constituent states in taxonomic units, so distance-based methods have trouble conforming to order assumptions.

Parsimony-based and minimum-evolution algorithms will often produce the same topology given the same model of evolutionary change, but the sample of taxonomic units has to be "well-behaved" in various ways -- a fact ascertained through computer simulations (Huelsenbeck 1995; Saitou and Imanishi 1989). It is therefore important to make sure that when trees from different algorithms are compared, allowance is made for possible biases in reconstruction due strictly to the algorithms themselves. Either the evolutionary models being compared must be sufficiently similar, or redundancy must be introduced into the comparative test to guard against peculiar interactions between a given population and algorithm.

Even when the same algorithm is used, comparisons of the topologies or data structures resulting from different evolutionary models depend significantly on the availability of tests which are insensitive to the specifics of phylogenetic reconstruction. This is because -- as I argued earlier -- cultural traits are unlikely to obey the standard phylogenetic assumption of bifurcating descent. As another bit of luck, such tests -- which depend only on the general features of trees -- have recently been developed.

In the rest of this paper, I establish the feasibility of this comparative approach to cultural phylogenetics through an empirical investigation. This case study involves the application of two different phylogenetic models on two related populations, and compares the resulting trees between populations. This redundancy in the research design provides an important control for the unknown level of phylogenetic noise in the data, and secures against idiosyncracies in the use of different algorithms for phylogenetic reconstruction. This investigation, conducted on a standard ethnographic population living in central Africa, shows that several aspects of cultural transmission can indeed be isolated by comparative phylogenetic tests. I conclude from this study that *comparative* cultural phylogenetics is valuable, and awaits further use.

2. Background

The case study concerns a population consisting of a variety of ethnic groups from both Sudanic and Bantu backgrounds who live intermingled in the Ituri Forest of northeast Democratic Republic of Congo (formerly Zaire). They practice either shifting horticulture or foraging as their primary subsistence activity. Horticulturalists live in villages identified by shallow patriline, while a more flexible system of residence in mobile camps characterizes the forager lifestyle. For much of the year, a forager camp will associate itself with a particular village to exchange game for garden produce. Social ties between specific pygmy foragers and villagers are extensive and obligatory, creating a complex social system (Bailey 1991; Grinker 1994; Wilkie 1988; Wilkie and Curran 1993).

People in the Ituri -- like people everywhere -- avoid the consumption of a variety of foods for cultural reasons. The avoided foods are primarily wild animals of the forest. I will classify the wide range of beliefs about food into three general categories. First, "ancestral taboos" are very dangerous restrictions which threaten death to the violator. They are linked to a folk "blood theory" which suggests some special relationship between those who share a certain kind of human blood (effectively, a clan), and those animals which share that kind of blood (a species). Second, as in most other populations, many food taboos surround liminal periods in the life-history, such as pregnancy and child-birth or adolescent rites of passage. These I call "homeopathic taboos" because they depend on recognition of a relationship between some anomalous feature of the animal and the act of consumption (e.g., a fetus develops a long nose because its mother ate elephant meat during her pregnancy). Finally, there are idiosyncratic disgust reactions to the look or taste of particular animals. These more individualized beliefs are not culturally sanctioned and hence not true taboos; I call them simply "other avoidances" (Aunger 1994a, 1996).

Local people also believe they should learn their food taboos from a specific individual. This norm identifies their same-gender parent as the individual responsible for their cultural

upbringing in this respect. The primary characteristics of this indigenous view, for our purposes, are the following:

(1) Transmission is strictly “vertical” since food avoidances are passed from biological parent to offspring -- cultural and biological parents are synonymous, according to this view.

(2) Because a given individual uses only a single teacher (the same-gender parent), each gender constitutes a separate cultural lineage, making the transmission process similar to biological reproduction. An obvious consequence of such a model is that no significant correlation in trait values should be found between associated individuals of opposite gender, including opposite-gender sibs or spouses.

(3) Transmission occurs at a single point early in life. Cultural generations are therefore of the same length as biological ones, only offset in time by some delay.

(4) There is no natural selection on food avoidances. They have no “proximate” or “ultimate” effects on nutritional level or biological fitness. (This is an emic belief which I have already determined is false; see Auger 1994a).

(5) No change in the value of a trait occurs as a result of transmission, or at any other time in life after official transmission, due to personal experiences. (This belief is also empirically false; see Auger 2000). This implies a complete lack of mutation, and hence perfect inheritance from generation to generation.

This norm for learning food taboos will serve as our Null Model of transmission. Note that the features of this Model, when combined, imply that cultural traits are perfectly replicated through generations, producing independent same-gender lineages which maintain belief in the original ancestral values. Graphically, this would appear not as a branching tree of descent with modification, but as a set of parallel tracks through time.

3. Methods

“The current state of our understanding of cultural evolution is analogous to that of natural selection in Darwin’s time: that transmissible variation occurs is hardly doubted by those who have given serious thought to the topic, but the mechanism giving rise to this variation is unknown” (Buss 1987:176). It is therefore necessary to be explicit about the evolutionary process underlying any analysis purporting to reconstruct cultural history. In this paper, two different models of cultural trait change are implemented on two Populations which, although very similar, differ in known ways that might influence the estimated pattern of transmission. Comparison of the trees representing different evolutionary histories based on these assumptions provide tests which should favor one or the other evolutionary process for these cultural traits.

3.1 Evolutionary Models

The traditional method for representing the evolutionary history of descent with modification is a phylogenetic tree. Unlike traditional clustering methods, certain assumptions are made about the process underlying the transformation of characters when analyzing the relationships between individuals using phylogenetics. The characteristic assumption is that all existing copies of a trait are inherited from a single common ancestor. Current similarity therefore reflects the degree of shared ancestry. The objective of evolutionary clustering algorithms is to minimize the spanning distance, or the number of inferred differences between individuals, required to account for all the variation observed in the population (a minimum evolution assumption).⁴

⁴ Implementing a phylogenetic approach with respect to cultural traits involves other considerations. In particular, I will consider cultural traits to be haploid, or inherited from a single cultural “parent.” This does not necessarily imply that a cultural trait is learned only once. However if there are subsequent transmission events to an individual, the newly-learned trait is presumed to overwrite the earlier one -- in effect, it is assumed there is no blending of knowledge.

The importance of this distinction is that a pedigree based on diploid traits exhibits an expansion in the number of relevant individuals as one progresses backward in time. With haploid traits, this geometric increase in the size of the relevant population does not occur

In studying an evolutionary process, constraints must be applied on the material of evolution -- in this case, cultural traits. In biological evolution, the replication of genetic material occurs through well-known (Mendelian) processes within cells. In the case of cultural traits, replication involves two poorly-understood processes: first, social learning (i.e., receiving information from outside sources such as other people or artifacts -- e.g., through verbal interaction or reading), and second, information storage (involving equally opaque changes to neural substrates). Only the grossest kinds of assumptions will be made here about cultural transmission, but they are sufficient for the analysis of variation at the population level.

In particular, I assume that food avoidances are learned, remembered and recalled in the context of consuming particular animals. This implies that the appropriate unit of cultural analysis is an individual's belief about the edibility of a particular food. I argue further that these beliefs can be represented as rules with the following general form: "I/We don't eat X because Y." X, the animal, I will call the *referent*, while Y, the rationale of the rule, determines what I will call its *type*. For example, "I don't eat [X:] mice, because [Y:] they stink." I will call the two parts of rules (referent and type) *components*. I will assume that each component is mentally represented as a separate "locus" that can vary independently, and that an individual's set of food avoidances can therefore be treated as a sequence of codes analogous to an individual's DNA (although these assumptions are not crucial to the analysis).

However, there may be psychological constraints on the ways in which this two-part rule can vary, with implications for the evolutionary process that produces the observed pattern of variation in belief. In the first Evolutionary Model of trait change to be considered here, the Type Mutation Model, the referent of the food avoidance rule is considered fixed, while the avoidance type can vary. I use independent information, derived from 67 interviews that were repeated on the same individuals, to determine the probability of transformations from one rule type to another during transmission (see Aunger 1994b). These transition probabilities (which need not be symmetric) reflect the likelihood that informants will change their report of a particular avoidance from one type to another (e.g., if 30 percent of avoidance type A reports during first interviews changed by informants to type B reports in a second interview, the transition probability from avoidance type A to B is estimated as 0.3).⁵ In effect, I assume that transitions (or mutations) can occur from any given type to any other in a single step (i.e., in phylogenetic parlance, these traits are "unordered"), but occur with different probabilities, defined by the transition matrix.

An alternative Model, the Referent Mutation Model, suggests that individuals tend to acquire a certain number of beliefs of each type which can be applied to different animals, depending on cultural inputs. In effect, this is the opposite way of limiting the evolution of

(Hudson 1990:1). The number of coalescent events (i.e., nodes) instead decreases as one moves backward in time, resulting in a cladistic tree such as observed with species trees. For example, mitochondrial DNA is haploid, being inherited strictly from mothers (at least in higher organisms); mitochondrial DNA is also considered to be a single gene. Thus, mitochondrial DNA-based trees are "gene trees" (Nei 1987).

In the present case, the data consists of sequences from individuals in a single population like a gene tree, but each value or code in an individual's sequence represents a meaningful, independent unit, the equivalent of a gene -- as in a species tree. I will call this a "population tree," to indicate that, strictly speaking, it has characteristics that fall between a species or gene tree. These differences are important in interpreting the topology of the resulting phylogeny, because the underlying model of evolutionary change is different in each case.

⁵ Are such transition probabilities good measures of the likelihood of transmission/mutation changes? After all, they represent *intra*-individual mutation rates that have been applied to the estimation of *inter*-individual mutation probabilities. These are obviously not the same, since inter-individual variation is partly a function of the transmission process itself, not just the cognitive "mistakes" which arise during recall. Thus the intra-individual rates of response change probably underestimate transmission error probabilities, since they involve only changes originating with the sender of a message, not those involved in its interpretation by the receiver. Nevertheless, there is probably a linear relationship between intra- and inter-individual mutation rates, because the medium for all avoidance transmission is the same: verbal reports.

avoidance rules from the previous: during transmission from person to person, the type of rule does not change, but the particular animal to which it refers might (while remaining within the same general ethnofaunal clade). What varies in this case is the number of avoidances of a given type within an animal group. Thus, individuals can be characterized by a set of numbers which reflect the number of avoidances of each type they report within each family of animals (e.g., three Ancestral Taboos against primates and so on).

Trees produced using these different Models can then be compared against each other with respect to their degree of “fit.” Fit measures the consistency of an evolutionary model with the assumptions of phylogenetic analysis, and is generally considered to be the proximity of an actual tree to some ideal, such as a theoretically minimum length (Farris 1989). Fit is thus relatively independent of ancestral state assignments or specific relationships among taxonomic units, and hence is an example of what we are calling a general feature of a tree. Cultural evolution necessarily exhibits descent with modification, so fit can be considered a measure of the “goodness” of the evolutionary model producing a tree. Evolutionary models with a greater ability to extract the phylogenetic signal from a given set of data -- that is, with higher measured fit -- can therefore be preferred.⁶

3.2 Sample populations

Two geographically separate Populations were identified, A (N = 112) and B (N = 107), on which identical Evolutionary Models will be applied. These Populations are arranged side-by-side along the major road through the eastern Ituri, and have been intensively sampled (90% of individuals over age 10) (Aunger 1994a, 1996). As a result, the sampled individuals constitute effectively the entire population along a three-mile stretch of road, separated by six largely unpopulated miles. They are: geographically contingent; naturally bounded by environmental features; predominantly derived from a single ethnic group (79.5/75.7% are Lese-Dese; 91.1/91.6% are Sudanic), with balanced gender-ratios (52.7/53.3% male), and demographically characteristic age structures (27.7/42.1% are under 26; 74.1/86.9% are under 51); are acculturated to roughly the same degree (72.3/73.1% with less than four years of schooling; 82.1/87.9 have never worked for wages); and share the same “vocabulary” of avoidances (described above). Finally, on a methodological note, the author interviewed over eighty percent of the informants in both Populations, while a single Sudanic assistant from the local population was responsible for the rest.

3.3 Rooting trees

There is no consensus about the relative merits of outgroup comparison, paleontological or ontogenetic criteria for rooting genetic trees (Sober 1989:229). Similarly, all phylogenetic methods for reconstructing cultural history (parsimony, maximum likelihood or distance-based methods) must depend on psychological and historical assumptions. As a result, independent information must typically be used to root cultural trees, either through inclusion of an explicit outgroup, or through use of von Baer’s principle that heterogenous structures arise from more homogeneous ones during ontogenetic development (Maddison et al. 1984).

⁶ There are other methods which compare trees. For example, one can calculate “tree-to-tree” distances, as in the partition metric of Penny and Hendy (31). These distances are the number of nearest neighbor shifts required to transform the topology of one tree into another. The patterns of distance with respect to the variables of interest are then analyzed using ANOVA.

Alternatively, standard statistical methods such as regression models could be used to see if being in the same cluster or not is a function of other characteristics of the taxonomic units concerned. But again, the results from such tests depend on how being in the same cluster is defined. This in turn depends on whether the topologies used are correct. But I have argued that the specific placements of taxonomic units cannot be trusted in the case of cultural phylogenies. So no method which depends on comparing specific relationships in topologies is appropriate in my view.

I use this second strategy to root trees deriving from both Evolutionary Models.⁷ The interpretation of the von Baer approach is different for each Model, however. The Type Mutation Model trees are rooted *post-facto* by assuming the ancestral state for all traits is no avoidance. In effect, I deem that all individuals begin life without cultural beliefs, because an individual's natural attitude toward a food is to consider it perfectly edible. However, cultural inputs can modify this belief to some type of restriction on consumption, with such beliefs accumulating over the course of an individual's lifespan. This assumption gives the Type Mutation Model a distinctly ontogenetic feel. The lack of historical constraint is evident in that the Model makes no explicit reference to earlier states, allowing any change between states to occur in a single jump. In effect, the constitution of the avoidance system is supposed to re-establish itself with every generation. Those who exhibit the greatest number and widest variety of avoidances should therefore be in the most derived positions, from multiple social contacts with others. Those relatively early in their career of social learning (presumably younger people) should, in contrast, have relatively long terminal branches.

The Referent Mutation Model, on the other hand, implements the von Baer strategy by including an explicit assumption concerning the polarity of evolutionary change in trait states.⁸ This represents an assumption that the "state of nature" is no culturally-transmitted avoidances in a population; avoidances must therefore have accreted over time, with a tendency for rules to accumulate in specific cultural lineages. This should lead some groups to specialize animals in particular ways.

In effect, the Referent Mutation Model is related to the Type Mutation Model in just the same way as Haeckel's "biogenetic law" that "phylogeny recapitulates ontogeny" is related to von Baer's rule governing ontological development: in both cases, relatively complex structures (here cultural belief systems) typically derive from simpler ones. Only the temporal scale at which development is supposed to occur has been changed. The rooting assumption in the Referent Mutation Model is that descendants exhibit more derived features than ancestors. The inclusion of phylogenetic constraints leads to an expectation of some phylogenetic inertia, or hold-overs from the cultural history of previous generations, in determining relationships among current members of the population. So where the Type Mutation Model is the cultural equivalent of von Baer, the Referent Mutation Model is "cultural Haeckel." The common strategy of rooting using von Baer-like assumptions makes trees from both Models more comparable.

3.4 A final precondition for phylogenetic analysis

Before proceeding to phylogenetic analysis, we must first ask whether the assumption that present-day variation is produced by a hierarchical branching process is reasonable for these cultural beliefs. Otherwise, the application of phylogenetics would construct a spurious tree from data having no such underlying structure (Lyons-Weiler et al. 1996:751). Fortunately, a quite general test of this assumption is available. Relative apparent synapomorphy analysis (RASA) provides a deterministic measure of "phylogenetic signal," or the degree to which similarities calculated from a two-mode data matrix are consistent with representation as a nested hierarchical structure -- that is, as a tree (Lyons-Weiler et al. 1996).⁹ For Population A, the

⁷ I resorted to this less-preferred method because outgroup rooting proved to be problematic: the inclusion of individuals from other ethnicities with historical roots in the same region did not consistently create "monophyletic" in-groups in the resulting trees. In effect, variation within the Populations studied was so great as to absorb these intended "outgroup" individuals -- evidence that cultural traits do not obey ethnic boundaries.

⁸ This is implemented by defining all numeric characters as ordered with polarity (or "Dollo up" in phylogeny-speak), with higher values considered to be more derived states. A phylogenetic reconstruction satisfies the Dollo constraint if a pathway can be traced between any pair of nodes possessing the same character state without passing through a node with a less derived state (Swofford and Olson 1990:460).

⁹ The test is not dependent on comparison to a particular, presumably optimal tree (e.g., the maximum parsimony tree), and so does not rely on assumptions about tree topology, ancestral character states or the mode of evolution (e.g., maximum parsimony or minimal spanning

relevant statistic, $t_{\text{RASA}} = 10.0352$, $df = 6101$.¹⁰ For Population B, $t_{\text{RASA}} = 35.27213$, $df = 5561$. Both values are considerably larger than the critical value of 3.291 for large samples at $p = .001$. These results suggest that there is a highly significant phylogenetic signal in these cultural data: relationships of descent appear to hold between individuals with respect to their cultural beliefs (especially in Population B). I can therefore safely proceed with the phylogenetic analysis of this belief system.

4. Comparing Evolutionary Models: Fit

The first Evolutionary Model suggests that each animal-specific rule is transmitted in roughly independent fashion, with an occasional mutation to the part of the rule which determines its avoidance type. Implementing this Type Mutation Model involves estimating a phylogeny from a weighted distance matrix using the neighbor-joining method (Saitou and Nei 1986) on Populations A and B.¹¹

As the first resulting tree diagram shows (see Figure 1a), Population A is divided into major clusters by age and gender. The first groups to bud off from the root are mostly individuals born into a neighboring group of Sudanic horticulturalists (ethnicity down to family membership is not shown in the Figures, but is known to the author). Despite this major ethnic distinction, clan-level clustering is not obvious overall. These neighboring adults are followed by most of the children in the population, and then adult males and females, consecutively.

distance). Generally speaking, t_{RASA} has been found in simulation to reliably measure the amount of phylogenetic signal in data in an unbiased fashion (Lyons-Weiler et al. 1996:752). It is sensitive to changes in the mutation rate, the number of characters and number of variant states per character (Lyons-Weiler et al. 1996:753-4), and preliminary results suggest that there is an appropriate decrease in the measure of signal when the proportion of long branches increase (Lyons-Weiler et al. 1996:755). RASA first calculates RAS_{ijk} , the number of times any taxon other than i and j takes some other state when i and j share a state for character k . When summed over all characters, the various RAS_{ij} can be plotted against their respective E_{ij} , the number of informative characters (i.e., phenetic distance) between i and j , a baseline similarity value or null hypothesis for the test. t_{RASA} , the test statistic for homogeneity of the two slopes derived from linear regression of the RAS_{ij} and E_{ij} , is distributed as Student's t . To test for the presence of phylogenetic signal, the value of t_{RASA} can then be compared with the critical value for the appropriate number of degrees of freedom (equal in this case to the number of taxon pairs minus the number of taxa minus three; Lyons-Weiler et al. 1996:756). RASA 2.1 (Lyons-Weiler, 1997) was used to calculate t_{RASA} .

¹⁰ Since the Population A sample contains missing data, I used the modal states for the relevant trait in the appropriate ethnic group as the best information available to replace missing values.

¹¹ While there are philosophical reasons to prefer cladistic methods, which concentrate on shared derived traits during reconstruction (e.g., deQueiroz and Good 1997), neighbor-joining has been found in simulation studies to perform as well as or better than parsimony in the recovery of known topologies (Huelsenbeck 1995; Hillis et al. 1992; Saitou and Imanishi 1989). This is especially true when, as here, distances include information about substitution biases (Hillis et al. 1994). Since neighbor-joining adds together all pairwise discrepancies in codings as weighted by the probability of the observed type of discrepancy, its distance measures include all the information available to parsimony analysis that is not position-sensitive. Constraining the pathways of character evolution in this way limits the number of topologies consistent with the more likely transitions; tree resolution is thus improved (Martins and Hansen, 1996). Further, since all traits (as opposed to state-changes) are weighed equally, no information has been lost by use of this distance- rather than character-based method. The NEIGHBOR program from Felsenstein's (1993) PHYLIP package (version 3.572) was used to calculate neighbor-joining trees. All tree diagrams were produced using PAUP* 4.0 (Swofford in press).

The Population B phylogeny (Figure 1b) exhibits two root-level groupings of children (with subclusters by gender), the second (counting from the left of the diagram) then followed by two clusters each of adult men and adult women. The overall similarity in structure with Population A is striking: obviously, age and then gender are the most important structuring elements under this Evolutionary Model. There is, however, greater division by clan in Population B, perhaps due to the greater diversity in kinship present in this Population.

I next implement the second Evolutionary Model, which argues that animal referents can change during transmission, but only within animal groups. In this case, phylogenetic analysis requires the explicit comparison of trait values between individuals when reconstructing the evolution of beliefs in the population (i.e., a cladistic analysis [Henning, 1966]). Parsimony analysis uses an algorithm with this characteristic. It is a method that infers phylogenies from discrete character data by searching for trees which minimize the amount of evolutionary change required to explain the observed data, given a set of constraints on permissible character changes (Swofford and Olson 1990:451).¹²

The resulting trees for Population A and B (see Figure 2) exhibit some interesting divergences from the previous set. Where the Type Mutation Model trees were primarily clustered by gender and then age, the Referent Mutation Model trees (especially that for Population B) put considerably greater emphasis on distinguishing clans. This is reflected in the greater hierarchical structure inside the “backbone” (or primary clusters) exhibited by the Referent Mutation Model trees: clans define secondary clusters (missing from the Type Mutation Model trees), with age and sex forming groups within these distinctions. This structuring may arise because the Referent Mutation Model essentially compares individuals by their “cultural histograms”: the number of traits within a clade are simply counted up and the sequence of these numbers contrasted between individuals. This appears to place greater weight on a particular profile of avoidances characteristic of a clan. The Type Mutation Model, in contrast, weighs specific kinds of discrepancies in belief during pair-wise comparisons. This probably emphasizes sex-based differences in avoidance types, as well as the general cultural naivete of younger members of the Population.

As I noted before, more detailed comparison of the trees, and particularly the placement of particular taxonomic units (individuals), is unadvised. Nevertheless, several questions about our Evolutionary Models can be answered on the basis of these results. First: Do the trees conform with the Null Transmission Model? Second: Is the ontogenetic assumption of the Type Mutation Model correct? Third: Is there significant variation in the degree to which individual traits used to construct the trees are consistent with phylogenetic assumptions?

4.1 Do the trees conform with the null model?

¹² One-hundred runs of PAUP* 4.0 (Swofford in press) were performed for each analysis, using quick swapping and heuristic search (with tree bisection-reconnection swapping), and starting trees found by the random addition of sequences. The maximum possible number of trees held at any stage during a run was effectively unlimited (7500 trees, which did not constrain search). All characters were weighed equally. For Population B, only a single tree with the shortest overall distance resulted, and is used here; for Population A, two such trees were produced (in a single run); the first one was randomly chosen. This procedure does not guarantee that the most parsimonious tree was found, but should be sufficient to find a tree comparable in quality to that determined by the neighbor-joining method in the previous analysis.

Since my concern is with emic cognitive categories, I group the animals for this analysis according to available supra-species-level ethnolinguistic markers. Such locally-named guilds include: *tepe* (primates), *ura-mani* (Bovids and Suids), *kou-kou* (Insectivores, Pholidots, and Vivverids), *sio* (rodents), *kufu* (fish), *keli* (birds), and “other” (an unnamed group, primarily reptiles and insects). Further subdivisions were identified by a heuristic process of consensus-building based on animal phylogenies elicited in the field from four expert Sudanic male informants (Aunger unpub. data). Distinctions were drawn at a level to make an effective number of classes for statistical analysis. This level varied from class to class, depending on the level of subjective importance of such animals, resulting in a higher Linnean level for, e.g., insects than mammals (see Table 1 for a full listing).

The transmission norm, which can be glossed as same-gender parent-to-offspring transmission, specifies a transmission mode equivalent to haploid genetic transmission. As a result, it is consistent with the foundational assumptions of phylogenetic analysis. The primary expectation from this norm-based Null Model is that trees will consist of male kin clusters, and non-kin-based lineages of females (since female clan alliance changes with each generation through marriage into new groups). But clustering by kin of either sex is not conspicuous in any of the trees (although it is more characteristic of the parsimony-based trees than those derived from the neighbor-joining method). Family group members often appear at quite disparate points, suggesting that they share more avoidances in common with non-family members than with others in their own family. Tree topology therefore suggests little conformity to the transmission norm. Apparently, people in the Ituri do not follow normative prescriptions about from whom to learn these beliefs. If the same-gender parent is not solely responsible for the transmission of food avoidances, and people with other genealogical relationships to the focal individual are consulted, then strictly vertical transmission can also no longer be true, and the separation of genders into independent cultural lineages is also likely to be false. Further, it allows the possibility of choice among transmitted trait values by individuals, and hence allows various forms of transmission bias. This suspicion is confirmed by the interpretation in the next section.

4.2 Von Baer or Haeckel in the interpretation of cultural history?

The Type Mutation Model trees (especially that for Population B) generally exhibit the pattern expected by von Baer's principle of increased differentiation during development: younger individuals branch off early, due to their lack of cultural experience, while those with many avoidances -- particularly adult women -- are those with the most recent ancestral nodes.¹³ However, state reconstructions for internal nodes on these trees¹⁴ do not reach back to an inferred ancestor who has no avoidances, the "cultural Eve" or "original innocent." Since root nodes do not represent the primordial state of nature, the trees are not phylogenetic in depth. Rather, these trees should be interpreted ontogenetically: individuals with the largest numbers of avoidances tend to have the most cultural ancestors, and so appear in the most derived positions. Thus, it is incorrect to interpret the Type Mutation Model trees as suggesting that adult males tend to be the descendants of children, or adult females of adult males.

The interior nodes in these cultural trees represent when two individuals last had an identical set of food avoidances (the cultural analogue of a common ancestor). Internal nodes can therefore be taken to represent social contacts resulting in the transmission of cultural information. If the entire phylogeny is supposed to represent a period of time reflecting the lifespan of the oldest current member of the population, the length of a branch between two individuals represents the amount of time since divergence of their beliefs (assuming that cultural time is the same along all branches of the tree). From this perspective, it is not unexpected that children diverge relatively early: they have spent a smaller proportion of their lives under the sway of adult beliefs.

By contrast, the general kin-based structuring of the Referent Mutation Model trees is consistent with the expectation that earlier generations continue to influence contemporary patterns of variation in belief: the structuring by kin-groups, and within kin-groups by sex, suggest powerful phylogenetic constraints on what is learned by today's individuals.

The ontogenetic interpretation of the Type Mutation Model trees suggests, however, that most learning takes place *after* the individual's last transmission event, since the terminal branches (those leading to the individuals themselves) are typically long. This indicates that a significant proportion of each individual's avoidances are not shared with those who are most

¹³ Use of von Baer's principle to choose the root node does not necessarily determine the overall pattern of cultural complexity seen in tree clusters.

¹⁴ This involves treating a neighbor-joining tree as if it were constructed using parsimony analysis; inferring putative states for the Referent Mutation Model trees using PAUP* 4.0 leads to the same conclusion.

similar to them in belief, which suggests that most of the avoidances reported by individuals are unique to them, and therefore cannot be culturally transmitted. The implication is that individuals are making up most of their avoidances themselves. For example, the Population A Type Mutation Model tree (Figure 1a) exhibits 4150 changes along branches in the tree, or 37 on average for each individual.¹⁵ This represents 25.6% of animal-specific responses per informant: in effect, one-quarter of an individual's beliefs are being argued to be original with them. Thus, the implication is that there has been considerable independent evolution of belief after the transmission events enculturating each individual -- even in the case of a high-density sample from a single phratry.

This is surely false: food avoidances are expensive, complex rules which individuals are unlikely to invent and adopt for themselves. It is more likely that the primary assumption of the analysis -- that all the information related to food edibility is acquired by an individual from a single cultural lineage -- has been violated. In addition, *since nearly all terminal branches are long, this violation must be true of everyone in the population: everyone picks and chooses their cultural beliefs about food from a variety of others in the group; further, these others belong to separate cultural descent groups.* Only a method which both explicitly represents each individual in its output and defines descent relationships could exclude the possibility that each individual learned all of their avoidances from a single teacher (or from members of a single lineage), but that the choice of this teacher (or lineage) varied between individuals. This is a significant conclusion dependent on the particular assumptions of phylogenetics.

Consistent with this interpretation is the generally shorter lengths of terminal branches in the Referent Mutation Model trees. Because the Type Mutation Model results in the "descent" of adults from children and suggests that individuals engage in significant individual learning of avoidances, it seems that Referent Mutation is a more reasonable model of how cultural evolution actually proceeds in the Ituri.

As a final point, this interpretation also explains how generally poor indications of fit to the minimum evolution assumption¹⁶ -- and in particular high measures of homoplasy -- can be reconciled with the RASA statistics presented earlier, which suggested strong phylogenetic signals in these data. The most likely reason is that there is inheritance, but the transmission pattern is significantly different between traits.¹⁷ Assuming a single mode of inheritance for the entire suite of 145 traits used to calculate the trees -- although legitimate for genetic characteristics -- is apparently inappropriate for these cultural beliefs. In the extreme, each

¹⁵ This analysis again treats the tree estimated via neighbor-joining as the result of trait-specific evolution, and uses unweighted characters. A figure of 42 changes in the number of clade-specific avoidances (or 70 percent of clades) per informant is reached for the same Population by using the Referent Mutation Model tree.

¹⁶ Population A: Tree Length = 4694; Consistency Index = 0.064; Rescaled Consistency Index = 0.0510; Retention Index = 0.795; Homoplasy Index = 0.936; f-ratio = 2.799. Population B: Tree Length = 5173; Consistency Index = 0.058; Rescaled Consistency Index = 0.0428; Retention Index = 0.743; Homoplasy Index = 0.942; f-ratio = 2.620. All these statistics are from PAUP* 4.0.

¹⁷ One possible remedy is to weight characters. In particular, characters which fit a tree well can be rewarded and those which do not penalized *a posteriori* by weighting them according to some measure of fit (Swofford and Olson 1990:465). The objective is to minimize the impact of characters which dilute the phylogenetic signal and hence reach a stable topology which should provide a better picture of evolution in those characters which share a common pattern of transmission (are less homoplastic). An extreme form of character weighting is the iterated parsimony technique (McElreath 1997), which assigns a weight of zero to characters not achieving some minimum value of fit. After excluding characters which fail to exhibit some critical value, parsimony analysis is repeated. However, choice of the fit index (consistency index or retention index) and criterion of fit (best or mean fit to the tree) is somewhat arbitrary, and can lead to very different trees (Swofford and Begle 1993:55). For these reasons, and because nothing more than general features of the trees seem to be stable, this option is not pursued here. A more principled technique, however, is pursued in the next section.

cultural trait may be independently acquired -- that is, food avoidances may be remembered with specific animal referents, and learned during separate transmission events. This suggests there is significant reticulation in the pattern of transmission, as expected by the ethnogenetic school (Moore 1994). Whether there is differentiation in the transmission pattern at the level of individual traits is addressed next.

4.3 Variation in the “fit” of traits to phylogenetic reconstruction

The parsimony method, used to estimate the Referent Mutation Model, permits an examination of how well individual traits fit the assumptions of this tree reconstruction algorithm. This may allow us to isolate subsets of traits which have different transmission modes than the dominant one, or ascertain that individuals tend to acquire certain kinds of avoidances from particular teachers. This again provides information about details of the evolutionary process.

The retention index (RI; Farris 1989), my measure of fit, ranges from 0 to 1; higher values indicate better fit (i.e., lower homoplasy or parallel evolution in that character -- that is, fewer multiple changes to the same character in different branches of the tree).¹⁸ The results are presented in Table 1 for the Population A and B trees, respectively.

There is considerable similarity in the pattern of RI values between the two trees. For example, felids and crabs have the lowest average RI in both trees; plants the highest. The number of belief states per animal group is also consistent between Populations. However, Population A fits somewhat better than Population B (average RI for Population A = .7954; for Population B = .7433). Also, average RI by category varies between the two Populations. Homeopathic taboos fit least well in Population A, while this distinction goes to Other Avoidances in Population B. Ancestral taboos fit best in Population A, where there is relatively little ethnic variation; where this variation is higher, Homeopathic Taboos fit better. This is consistent with Ancestral Taboos being concentrated within kin-groups, and Homeopathic Taboos more readily traversing kin boundaries. The more varied Population B also shows an inconsistent pattern of transmission of Other Avoidances.

Examination of the pattern within each Population indicates that variation in the degree of fit exists along all possible dimensions. This suggests, as did the Type Mutation Model results, that the underlying mode of transmission is not the same for all of the traits being considered. In general, those traits with high RI are those which are coded “consistently” throughout the tree -- they “fit” the tree by having relatively few inferred changes in value since the root ancestor. By implication, they are more consistent with the assumption of linear descent with modification. The question then is how does a cultural trait get from tree root to terminal branch in the fewest

¹⁸ Parsimony methods permit one to estimate how close the resulting maximum parsimony tree comes to a minimum evolution tree. This is considered a measure of fit. However, all available indices of fit to trees are imperfect measures of the desired quantity: consistency with the assumption of decent-with-modification. For example, all indices must take cognizance of the number of states a character takes, but the larger such a number is, the greater its impact on tree length (and hence measures of fit) because at least 1-N steps (where N = the number of observed states in the population) are required to deal with the observed variation in each trait (Swofford and Begle 1993:85-6). Thus, equal weighting does not necessarily mean equal influence on tree topology. However, compared to its primary alternative, the consistency index, RI is generally less sensitive to missing data, the number of character states, and the distribution of states within the dataset (e.g., Hauser and Boyajian 1997; Poe 1998). RI is defined as

$$\frac{g - s}{g - m}$$

where g = the maximum number of steps a character could require on any conceivable tree (i.e., its length on a “star” phylogeny), s = the number of changes in character state calculated from the reconstructed tree, and m = the minimum number of changes the character could possibly require (i.e., 1- N, as defined above) (Swofford and Begle 1993:54).

possible steps (given the logical minimum required to encompass the variants observed)? RI seems little influenced by the number of belief states. For example, while variation in belief is concentrated in the primates and Vivverids, their average RIs do not suffer. Indeed, a strong pattern of avoidance seems to improve RI. For example, catfish are implicated in many Homeopathic Taboos, but exhibit the highest RI in that category; similarly for raptors with respect to Other Avoidances. This is demonstrated by the fact that higher average RI values by avoidance category are strongly correlated with a greatest range of variation in RI between animal groups: specialization of avoidances within particular animal groups improves fit.

It thus seems that if a particular category of animal is avoided for the same reason by a significant proportion of the population, phylogenetic algorithms are generally able to cluster them together, with few changes in states assigned. Thus, what seems primarily responsible for high RI values is clustered belief: some group of people that have the same beliefs across a wide number of species. Belief clusters, involving animals from a variety of categories which remain relatively constant, can thus pass relatively unchanged from the root to terminal branches. However, if there is incompatibility in transmission between such belief clusters (that is, individuals tend to adopt only one cluster from a given other person, so that their suite of clustered beliefs is derived from multiple sources, with whom they only share one cluster), then the overall RI will be reduced. While average RI values are not particularly low, they do suggest some degree of incompatibility between belief clusters.

Thus, we appear to see here some viability for a larger unit of transmission: a belief cluster that refers to a constellation of animal species (perhaps from several different faunal clades). In effect, there may be hierarchical structure to the avoidances maintained by individuals. Transmission events may still involve specific rules, but either the accumulation of avoidances forces people to organize them into larger cognitive categories, or these avoidance clusters are naturally grouped because they derive from a particular teacher.

5. Comparing Evolutionary Models: Tree Shape

Although we have already learned several significant points about the evolutionary process which must underly the transmission of food avoidances in the Ituri, more information can yet be drawn out of the data using phylogenetics. In particular, the same method, phylogenetic reconstruction, has now been implemented in two different ways on the same Populations. It is therefore possible to determine which of the two Evolutionary Models is more consistent with the process that generates the cultural similarity data. Determining which method produces better trees provides greater justification for the underlying Model. Since each Model is associated with a number of specific hypotheses, this in turn provides important clues about how the cultural transmission of these beliefs actually proceeds.

However, to compare trees produced using different reconstruction methods we require a test that measures some general feature of tree structure, since I argued above that cultural phylogenetic analysis generally cannot be trusted beyond that level of detail. In particular, the method cannot depend on comparing estimated distances between taxonomic units (in this case individuals).

Tree shape has recently been advocated as a feature of phylogenetic topologies which can be used to study a variety of interesting evolutionary phenomena, including extinction rates and adaptive radiations in both genetic and cell lineages (Mooers and Heard, 1997). As the name suggests, shape relates to the overall “branchiness” of a tree. Two characteristics have been considered diagnostic of tree shape: tree balance and the distribution of branch lengths. I discuss each in turn.

5.1 Tree balance

Tests of tree balance look for significant differences in the proportion of taxonomic units partitioned to either side of a node. Imbalance is generally considered to be unlikely, with the standard assumption being that each extant lineage has an equal probability of producing a variant (such as a new species in the case of species trees) in the next unit of time. The goal is to find the tree which exhibits greater symmetry, and hence less disfiguring bias due to violations of phylogenetic assumptions. The model of trait change producing that tree is favored.

More specifically, tree balance measures the degree to which nodes at a given temporal level in the tree define subgroups of equal size (Mooers and Heard 1997:34). Any number of indices measuring balance have been advocated (reviewed in Shao and Sokal 1990; Kirkpatrick and Slatkin 1993). However, the most widely used, computationally simple, and statistically powerful measure is Colless' (1982) index of imbalance, I_C , which is the absolute difference in the number of tips subtended by the right- and left-hand branches defining each node, summed for all internal nodes, and normalized by dividing by the largest possible score.¹⁹ The index thus ranges from 0 for perfect balance, to 1 for complete imbalance. Note that this index depends only on the distribution of tips across nodes, and makes no reference to estimated branch lengths.

For robust trees, there is generally little difference in estimates of tree balance between cladistic and phenetic methods (Mooers and Heard 1997:40). This would suggest that trees reconstructed using each of these methods, as here, can generally be compared.²⁰ The usual evolutionary assumption is that "better" trees have greater balance, because all lineages extant at a given time have an equal probability of speciating during the next interval (the Markovian null model for evolution) (Simberloff et al. 1981).

Visual inspection of Figures 1 and 2 strongly suggests that the Referent Mutation Model trees are much better balanced than their Type Mutation Model counterparts; in fact, the degree of imbalance in the former case is generally only one-half that for the latter (see Table 2). Before discussing the implications of this test, I proceed to an analysis of the second aspect of tree shape, the distribution of branch lengths.

5.2 The distribution of branch lengths

Whereas the shape of a tree is a timeless quality, its branch lengths are all about time. The histogram of branch lengths in a tree should follow a particular distribution if the size of the population represented by that tree has remained constant since the original, or root, ancestor. If this population size has increased or decreased significantly over this period, then the distribution should take on another shape. Since it is difficult to produce statistical tests comparing the shapes of distributions themselves, these curves can be transformed into lineage-through-time plots, where the slope of the plot at any point is the average rate at which branches produce new branches at that time (Nee et al. 1994 a,b). Because the number of new lineages would grow hyperbolically as one approaches the present, this plot should be linear in logarithms if population size has not changed (Nee et al. 1996). A simple statistical test can determine whether there is significant deviation from linearity in this plot, and therefore whether population size can be said to have remained constant or to have significantly increased or decreased (Rambaut et al., in press). Some expectation concerning the history of population size must be derived from an independent source of information to make use of this test. In the case of

¹⁹ That is,

$$I_C = \frac{\sum_{(\text{internal nodes})} |R - L|}{\frac{(n-1)(n-2)}{2}},$$

where R and L are the number of tips subtended by the right and left branches of a node, respectively.

²⁰ Mooers et al. (1995) have shown that cladograms with high degrees of homoplasy tend to be more unbalanced than well-supported trees. Further, Huelsenbeck and Kirkpatrick (1996) show that, even when their assumptions are met, both parsimony and neighbor-joining methods produce significantly biased (more asymmetric) estimates of tree shape -- especially when rates of evolution are high, as here. However, these caveats do not present a problem when the objective, as here, is to qualitatively compare Evolutionary Models using balance measures, rather than to produce a good estimate of tree balance for a specific tree.

cultural evolution, one might rely on demographic records, for example. Used comparatively on questions of cultural evolution, the test is about which tree is more consistent with the expected cultural history of the population. Hopefully, the result from the branch length distribution test will be consistent with the evolutionary model preferred by the tree shape investigation.

The basic idea is to use the distribution of intervals between nodes derived from tree structure to determine whether the population producing the observed variation has been of constant size over the relevant period. Branch length distributions can be represented as lineages-through-time plots, where the slope of the plot at any point is the average rate at which branches produce new branches in the phylogeny at that time (Nee et al. 1994a,b). Transformations of the data can be performed which control for differing assumptions about the underlying rate of population growth and allow statistical tests of linearity on the resulting plot (Nee et al. 1995). For example, traits drawn from a population that has been of constant size over the period covered by the inferred history are expected to be related by a genealogical tree that grows hyperbolically in the number of branches as it approaches the present, since trees get bushier near the top (Nee et al. 1996:69).

Looking at that history in reverse, nodes can be seen as points at which divergent lines of evolution coalesce. If one makes the Markovian assumption that there is a constant probability of coalescence across lineages and time-frames, then the likelihood of such an event is a constant function of the number of lineages existing at that point in the past (Hudson 1990). This provides a direct translation from evidence of a constant population size to the conclusion that transmission has been endemic in that population (due to a constant rate of lineage births and deaths). Thus, under the endemic transformation, the estimated production rate for branches will appear to be a linear function of time if the population has been at a constant size. Other transformations will produce a linear plot if either epidemic (exponential) or logarithmic growth has characterized a population's history (Nee et al. 1995).

Based on this coalescent theory, the "endemic-epidemic" test (Rambaut, 1994; Rambaut et al. in press) has been developed to determine whether an epidemic or endemic transmission process underlies a given distribution of variation in a population, based on the distribution of branch lengths. Since this test examines only gross features of topology, it makes no reference to the means by which topology was reconstructed, and so can be used to compare trees produced using different methods. The test therefore does not require information that we know cultural phylogenetics cannot provide. It simply asks whether the constant population size assumption is likely by comparing the empirical distribution of branch lengths to that expected from coalescent theory. Although less attention has been devoted to the statistical investigation of these distributions and their measurement than tree balance, estimates of the rate of growth in the number of lineages through time may be more robust than other features of tree topology (Harvey and Nee 1996:4), and so provide a reasonable measure for comparing cultural trees.

To use this test here on a cultural tree, we need to know how consistent tree structure is with some independently known fact about the cultural evolution of food avoidances in the Ituri. Since food avoidances are characteristic of every human population, and have been since recorded history, it would be surprising to find there has been a significant increase in the rate of new beliefs appearing in recent times: the pattern of transmission should be closer to the endemic than the epidemic end of the transmission spectrum. Further, previous work has suggested that, if anything, there has been a slight decrease in the robusticity of the Ituri avoidance system in recent days, with the advent of acculturating influences introduced by missionaries (Aunger 1996). Applying the "endemic-epidemic" test to the trees previously constructed using the Type and Referent Mutation Models permits us to determine which Model produces a tree having higher values for measures of endemism.²¹

In fact, the epidemic model is the best fit to the trees actually produced under the phylogenetic assumptions of the two Evolutionary Models (see Table 2).²² This provides a

²¹ Although, as in the case of tree balance, there are caveats concerning the accuracy of branch length measurements using different estimation procedures (e.g., Huelsenbeck and Kirkpatrick 1996), these are largely irrelevant when the goal of analysis is grossly comparative, as here (see previous footnote).

²² The END-EPI software program (Rambaut 1994) was used for all tests concerning the number of lineages-through-time, and produced Figures 3 and 4.

strong indication that population size has *not* remained constant over the relevant period, as expected if new cultural mutants are produced at a relatively constant rate by individuals from a stable population. Visual inspection of the lineage plots (Figures 3 and 4) also suggests that the epidemic transformation is the best description of the rate of cultural lineage growth over time for both Populations and both Models, since they are roughly linear.

However, epidemic transmission is furthest from the “truth,” since it suggests the rate of new lineage appearance has been growing exponentially as we approach the ethnographic present (Nee et al. 1995). But I have argued from historical data that both the number of individuals and size of the “cultural population” (or pool of food-related beliefs) has declined in the recent past. What causes this mismatch of result to expectation? It is likely that the reticulation problem is again responsible, pushing changes into later nodes. This produces a tree which is bushier in the recent past than expected. This in turn suggests an increase in the rate of mutation, despite evolution in a steady-state population.

If we assume the endemic representation is correct, then the question is: which Model comes closer to representing an endemic process? The Referent Mutation Model again has less extreme values for a one-tailed Wilcoxon’s signed-ranks test for linearity in both Populations (see Table 2).²³ Note that this two-by-two research design (Population by Evolutionary Model) shows that the results are internally consistent, and not due to the selection of a particular subpopulation. Further, there is also agreement across the two different aspects of tree shape.²⁴

So, according to this second test on tree shape, the Referent Mutation Model is more consistent with the hypothesis that there have been no great changes in the system of avoidances with time, and hence is to be preferred. This is despite two apparent disadvantages of the Referent Mutation Model for phylogenetic reconstruction. First, its model of trait change is more strict than that of the Type Mutation Model (where any state is capable of transforming into any other in a single step), and second, there are many fewer traits than in the Type Mutation case because a single trait covers a class of animals rather than individual ones.

This leads to a number of important conclusions. Since both Evolutionary Models share the minimum evolution objective, it must be the Model-specific assumptions which are responsible for the varying performance of phylogenetics in the two cases. This implies, first, that changes to both parts of the avoidance rule are constrained -- in effect, *the two components which make up these cultural rules are cognitively linked*. This is because the Referent Mutation

²³ This test compares gradients from line segments defined by related nodes near the end of the plot with a sample from the middle of the endemic transformation (Rambaut et al. in press).

²⁴ However, one result is inconsistent with the overall indication in this paper that the Referent Mutation Model is a superior representation of the cultural evolutionary process: the Type Mutation Model is slightly more consistent with a constant population size assumption (as measured by Cramér’s U), even though it is less consistent with endemic diffusion (as measured by Z_C). Both of these tests for endemicism are based on the same endemic transformation plots. How can these conflicting results be reconciled? Where the Wilcoxon test only investigates changes in the right-hand tail of the plot, Cramér’s U -- which measures whether inter-node distances under the endemic transformation are consistent with a Poisson distribution (as expected under the null-hypothesis of constant population size) -- is based on the entire curve. The lack of significance for the Wilcoxon tests suggests the tails of these plots are effectively linear, whereas the highly significant uniform conditional test (rejected for both Populations for both Models with $p < .01$) indicates the Referent Mutation Model curves are slightly *more* nonlinear overall than the Type Mutation Model curves. That is, there is less evidence of epidemic differentiation in recent history, but a greater overall sense of population increase. In effect, the combination of test results on endemicism suggest that a higher proportion of trait changes takes place during early parts of the population history in the Referent Mutation Model trees. This indicates that the trait polarity assumption forces more trait changes to occur closer to the tree root, in the differentiation of clans, rather than later. So the constant population size statistic probably reflects the greater degree of structure in the middle of the Referent Model trees.

Model constrains mutations in both parts of the cultural rule (since it allows changes to the animal referent, but only within clades).

This mirrors the earlier evidence (from the variation in fit by trait) of hierarchical organization in individuals' food avoidance sets. This may arise because the animal referents of some rules are linked by membership in the same ethnobiological clade or because rule types are of the same general class. This in turn probably results in variable patterns of transmission between subsets of rules because they will be learned from the same source if categorized as an ensemble by such criteria. For example, if fathers are primarily responsible for the transmission of Ancestral Taboos, they will tend to follow one kind of pathway through a population, while lineages linked through mothers will form for Homeopathic Taboos (if the above conclusions are correct). It is important to note that these variable patterns arise because particular transmission pathways are socially legitimated by reference to other belief systems (e.g., what I have called the "blood" theory). Thus, links to other belief systems are vital to understanding the functions of the avoidance system, which cannot easily be divorced from this larger context. For this reason, the proper object of study must be cultural complexes.

A second implication can be derived from the difference in performance between Evolutionary Models. The relatively better fit of the Referent Mutation Model indicates that, within cultural lineages, *losses of avoidances within animal groups over time are less likely than the gradual accumulation of avoidances*. In this Model, each trait is assumed to pass through a specific sequence of values (in this case, lower to higher values). In essence, this requires that each derived character state (in this case, more avoidances within an animal group) arise only once in a tree; the same change is not supposed to occur in parallel lineages. However, mutations within cultural lineages may sometimes bleed between the borders of animal clades, leading to loss. A reduction in avoidance number may also result from a lack of opportunity to transmit the relevant information, due to peoples' inability to get into physical proximity (e.g., thanks to residential patterns).

Third, the relatively better fit of the Referent Mutation Model is consistent with the earlier suggestions that the Type Mutation Model's ontogeny assumption is false. Rather, *phylogenetic history structures population-level variation in cultural belief, although there are also ontogenetic changes undergone by individuals as they mature into cultural competence*. The clustering by kinship in the Referent Mutation Model trees rather than by gender and age, as in the Type Mutation Model, also suggests this.

Finally, Population A exhibits more extreme measures of imbalance and branch-length distribution than Population B, even though the latter contains less variation in belief (a pattern consistent with the RASA test above). Why? Because in Population B changes in the state of cultural traits are assigned to earlier branches. In Population A there is greater sharing of beliefs, which can link a higher proportion of individuals before positing mutations becomes necessary. The result is that a higher proportion of trait changes are shunted toward terminal branches in Population A, making the process appear more epidemic-like.

6. Summary and Conclusion

Researchers interested in cultural evolution have increasingly turned to phylogenetic methods to "correctly" test propositions concerning the origin or diffusion of particular cultural traits. However, these intrepid scholars have had to face major *a priori* problems in applying techniques devised for genetic inheritance to the case of cultural traits. Foremost among these is that cultural transmission usually violates the primary assumption of phylogenetic analysis: reticulation or networks of relationships rather than single linkages between cultural units are more likely to characterize the typical population of individuals or groups. Nevertheless, this paper outlines a novel, comparative methodology for using phylogenetics with respect to cultural data. This method *can* provide useful information about the process of cultural transmission in a population because it avoids the inconsistencies between cultural transmission processes and the assumptions of phylogenetic reconstruction. It also allows the question of reticulation itself to be addressed. Phylogenetic methods can determine empirically how significant the reticulation problem is for a particular suite of cultural traits, so we need not simply argue that reticulation makes phylogenetic methods universally inappropriate.

The utility of comparative cultural phylogenetics has been empirically demonstrated through a case study. Two geographically-defined sample Populations drawn from a rural African society were investigated with respect to the cultural domain of food avoidances. A variety of comparative tests consistently suggests that one model of trait change reflects a greater proportion of the phylogenetic signal in the data. However, results also show that cultural descent is not purely tree-like in this case: the degree to which the methodological assumption of single parentage is violated by the actual transmission pattern is significant. Nevertheless, by comparing trees produced by algorithms making different evolutionary assumptions, substantive conclusions concerning aspects of the cultural evolutionary process can be derived. For example, the forcing of many trait changes into terminal branches indicates that individuals generally acquire their cultural beliefs from a variety of others belonging to different cultural lineages. In addition, the higher fit of the evolutionary model with a parity assumption suggests there is greater accumulation than loss of avoidances within most cultural lineages. The variation in fit between cultural traits also indicates a tendency for groups of animal-specific rules to be mentally linked or learned from specific others. This cognitive as well as social clustering of belief produces the observed intra-population variation in cultural traditions.

Measures of fit from phylogenetic analyses were relatively poor for both Populations, despite strong results from a test of phylogenetic signal (RASA; Lyons-Weiler et al. 1996). This is probably due to heterogeneity in the underlying process generating variation for individual traits. Attempting to infer evolutionary relationships between individuals using their entire set of food avoidances aggregates over what are in fact a number of different kinds of learning experiences: the clear message from phylogenetic analysis is that the great majority of individuals in the population learn their avoidances from a variety of others, acquiring some fraction of their knowledge from each of them. Further, these teachers tend to represent at least somewhat independent cultural lineages, so the result is a mixing of inherited beliefs in each new learner of food avoidances. Complex learning networks link each individual to a variety of other people in the local population. This pattern of social learning violates an emic norm about how such beliefs should be acquired, a norm of same-gender parental transmission (which by coincidence is consistent with the assumption of phylogenetic analysis that individuals acquire their information in a single bundle). Since this norm could potentially influence how individuals actually acquire their cultural beliefs, it was used as the Null Evolutionary Model against which to compare empirical results. However, it did not appear to characterize the pattern of transmission of these traits, so local people's own belief about how avoidances should be acquired does not fit the facts, at least when all traits are considered together: the cultural rule does not fully determine social practice (Aunger unpub. data).

The use of multiple mentors also constitutes a violation of the fundamental phylogenetic assumption of "single package transmission." Unfortunately -- and unlike single genetic traits, which can generally be coded as long sequences of nucleotides -- each cultural trait is typically composed of relatively few components (in the present case only two), which usually does not produce sufficient variation within a population for the estimation of statistical models. Alternative -- and more roundabout -- means of analysis therefore have to be pursued to determine the pattern of transmission (Aunger, unpub. data). It has certainly been found here that applying phylogenetic methods to the study of intra-population cultural relationships is inappropriate: one cannot infer the history of cultural descent using only cultural similarity as a foundation, due to cross-lineage transmission. In effect, you can't believe that two individuals are close cultural cousins simply because they wind up next to each other on a phylogenetic tree. This conclusion should provide succor to those who advocate the abandonment of such methods, such as the ethnogenesisists (e.g., Moore 1994).

Nevertheless, the use of phylogenetics to test more general propositions about transmission patterns has led to a number of substantive conclusions concerning the ways in which people learn these socially significant beliefs -- including their reliance on multiple teachers. In particular, relationships of cultural descent *do* characterize the sets of beliefs that people report. Although the entire belief system must be re-created anew each generation as individuals mature, there is also an element of continuity or tradition between generations. Even though previous generations of individuals are not present in the sample population, their influence is nevertheless felt in the reconstruction of relationships between living individuals. This is consistent with independent analyses suggesting that there is strong inter-generational

transmission (Aunger unpub. data) and a slow rate of change in these beliefs in response to the primary forces of acculturation (Aunger 1996).

Second, analysis shows that people acquire their avoidances in episodes where rules involving specific foods are transferred. Nevertheless, there is also evidence of some higher-level organization in the beliefs that individuals acquire, or at least remember: similar kinds of animals tend to be avoided for similar kinds of reasons. This is reflected both in the pattern of variation between traits for measures of fit and by the fact that the Evolutionary Model was preferred which allows changes both in rule type and the animal to which it refers. This organization of belief may arise either from cognitive or social causes. For example, individuals may react in the same way to animals which resemble each other (and hence share classification). Alternatively, teachers may specialize in the transmission of particular categories of avoidance (e.g., males on avoidances related to carnivores).

Finally, most previous work in cultural phylogenetics has been at the cross-cultural level (Guglielmino et al. 1995; Pocklington 1997; Sellen and Mace 1997), including the advocated work in ethnogenetics (Moore 1994). In contrast, the present case study has focused on the application of phylogenetics to intra-population cultural variation. However, the same tests of general tree qualities would hold at other scales, since the logic of comparison does not depend on whether the taxonomic units represent individuals or groups. Thus, the methods should translate directly to the case of cross-cultural comparison. This makes the uses of phylogenetics outlined here generally applicable for comparative work in cultural evolutionary studies. The ability to apply a body of sophisticated, well-known methods able to favor one model of the evolutionary process over another should constitute a considerable boon to this fledgling science.

Acknowledgements

David Swofford permitted me to use PAUP* 4.0 beta versions. Stephen Sherry and Koichiro Tamura helped with software problems in the early stages of working on cultural phylogenies. James Lyons-Weiler kindly responded to questions about RASA. Discussions with Alan Rogers, Anna DiRienzo, and Robert Ballard helped determine the early direction of the paper. Earlier versions were perceptively read by Gillian Bentley, Kevin Laland, and David Sloan Wilson. The fieldwork which provided the empirical data was supported by the National Science Foundation, Sigma Xi and the Graduate School, University of California, Los Angeles. The field site was developed by Robert Bailey and other members of the Ituri Project. The time to pursue this line of research was provided by fellowships from the National Institutes of Mental Health (to the Committee on Human Development, University of Chicago), and King's College, Cambridge.

References

- Aunger, R. (in prep a): "Exposure versus susceptibility in the epidemiology of everyday beliefs."
- Aunger, R. (2000): "The life history of culture learning in a face-to-face society." *Ethos* 28(2):1-38.
- Aunger, R. (1996): "Acculturation and the persistence of indigenous food avoidances in northeastern Zaire." *Human Organization* 55: 206-218.
- Aunger, R. (1994a): "Are food avoidances maladaptive in the Ituri Forest of Zaire?" *Journal of Anthropological Research* 50: 277-310.
- Aunger, R. (1994b): "Sources of variation in ethnographic interview data: Food avoidances in the Ituri Forest, Zaire." *Ethnology* 33: 65-99.
- Bailey, R.C. (1991): *The Behavioral Ecology of Efe Pygmy Men in the Ituri Forest, Zaire*, Anthropological Papers, 86. Ann Arbor, MI: Museum of Anthropology, University of Michigan.
- Boyd, R., Borgerhoff-Mulder, M., Durham, W. H. and Richerson, P. J. (1997): "Are cultural phylogenies possible?" In Weingart, P., Maasen, S., Mitchell, S. and Richerson, P. J., (eds.): *Human By Nature*, NJ: Erlbaum.
- Brooks, D. R., and McLennan, D. A. (1991): *Phylogeny, Ecology and Behavior: A Research Program in Comparative Biology*. Chicago: University of Chicago Press.
- Buss, L. (1987): *The Evolution of Individuality*. Princeton: Princeton University Press.
- Colless, D. H. (1982): "Review of: Phylogenetics: The Theory and Practice of Phylogenetic Systematics." *Systematic Zoology* 31: 100-104.
- Crandall, K. A. and Templeton, A. R. (1996): "Applications of intraspecific phylogenetics." In Harvey, P. H., Leigh Brown, A. J., Maynard Smith, J. and Nee, S., (eds.): *New Uses for New Phylogenies*, Oxford: Oxford University Press, pp. 81-99.
- deQueiroz, K., and Good, D. A. (1997): "Phenetic clustering in biology: A critique." *Quarterly Review of Biology* 72: 3-30.
- Dow, M., Burton, M., White, D., and Reitz, K. (1984): "Galton's problem as a network autocorrelation." *American Ethnologist* 11: 754-70.
- Farris, J. S. (1989): "The retention index and the rescaled consistency index." *Cladistics* 5: 417-419.
- Felsenstein, J. (1993): "PHYLIP (Phylogeny Inference Package) version 3.5c." *Distributed by the author. Department of Genetics, University of Washington, Seattle.*
- Fitch, W. M., and Margoliash, E. (1967): "Construction of phylogenetic trees." *Science* 155: 279-84.

- Grinker, R. R. (1994): *Houses in the Rainforest: Ethnicity and Inequality among Farmers and Foragers in Central Africa*. Berkeley, CA: University of California Press.
- Guglielmino, C., Viganotti, C., and Hewlett, B. (1995): "Cultural transmission in Africa: Role of mechanisms of transmission and adaptation." *Proceedings of the National Academy of Sciences*92: 7585-7589.
- Harvey, P. H., and Pagel, M. D. (1991): *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.
- Hauser, D. L., and Boyajian, G. (1997): "Proportional change and patterns of homoplasy: Sanderson and Donoghue revisited." *Cladistics* 13 (1-2): 97-100.
- Hennig, W. (1966): *Systematic Phylogenetics*. Urbana, IL: University of Illinois Press.
- Hillis, D. M., Bull, J. J., White, M. E., Badgett, M. R., and Molineux, I. J. (1992): "Experimental phylogenetics: Generation of a known phylogeny." *Science*255: 589-592.
- Hillis, D., Huelsenbeck, J. P., and Cunningham, C. (1994): "Application and accuracy of molecular phylogenies." *Science*264: 671-677.
- Hudson, R. R. (1990): "Gene genealogies and the coalescent process." In Futuyma, D. and Antonovics, J., (eds.): *Oxford Surveys in Evolutionary Biology*, Oxford: Oxford University Press, pp. 1-44.
- Huelsenbeck, J. P. (1995): "Performance of phylogenetic methods in simulation." *Systematic Biology*44: 17-48.
- Huelsenbeck, J. P., and Kirkpatrick, M. (1996): "Do phylogenetic methods produce trees with biased shapes." *Evolution*50 (4): 1418-1424.
- Kirkpatrick, M., and Slatkin, M. (1993): "Searching for evolutionary pattern in the shape of a phylogenetic tree." *Evolution*47: 1171-81.
- Louwagie, J., McCuthan, F. E., and Peeters, M. (1993): "Phylogenetic analysis of gag genes from 70 international HIV-1 isolates provides evidence for multiple genotypes." *AIDS*7: 769-80.
- Lyons-Weiler, J. (1997): "RASA 2.1 for the Mac."
<http://loco.biology.unr.edu/archives/rasa/rasa.html>
- Lyons-Weiler, J., Hoelzer, G. A., and Tausch, R. J. (1996): "Relative Apparent Synapomorphy Analysis (RASA) I: The statistical measurement of phylogenetic signal." *Molecular Biology and Evolution*13 (6): 749-757.
- Mace, R., and Pagel, M. (1994): "The comparative method in anthropology." *Current Anthropology*35: 549-564.
- Maddison, W. P., Donoghue, M. J., and Maddison, D. R. (1984): "Outgroup analysis and parsimony." *Systematic Zoology*33: 83-103.
- Maddison, W. P., and Maddison, D. R. (1992): *MacClade: Analysis of Phylogeny and Character Evolution*. Sunderland, MA: Sinauer Associates.

- Martins, E. P. and Hansen, T. F. (1996): "The statistical analysis of interspecific data: A review and evaluation of phylogenetic comparative methods." In Martins, E., (ed.): *Phylogenies and the Comparative Method in Animal Behavior*, Oxford: Oxford University Press, pp. 22-75.
- Mayr, E. (1969): *Principles of Systematic Zoology*. New York: McGraw-Hill.
- McElreath, R. (1997): *Iterated Parsimony: A Method for Reconstructing Cultural Histories*. Ph.D. diss., Department of Anthropology, University of California, Los Angeles.
- Mickevich, M. F. (1982): "Transformation series analysis." *Systematic Zoology*31: 461-78.
- Mooers, A. Ø., and Heard, S. B. (1997): "Evolutionary process from phylogenetic tree shape." *Quarterly Review of Biology*72 (1): 31-54.
- Mooers, A. Ø., Nee, S., Page, R. D. M., Purvis, A., and Harvey, P. H. (1995): "Character congruence and the balance of cladistic trees." *Systematic Biology*44: 332-42.
- Moore, J. H. (1994): "Putting anthropology back together again: The ethnogenetic critique of cladistic theory." *American Anthropologist*96: 928-948.
- Nee, S., Holmes, E. C., May, R. M., and Harvey, P. (1994): "Extinction rates can be estimated from molecular phylogenies." *Philosophical Transactions of the Royal Society of London, B344*: 77-82.
- Nee, S., Holmes, E. C., Rambaut, A., and Harvey, P. (1995): "Inferring population history from molecular phylogenies." *Philosophical Transactions of the Royal Society of London, B349*: 25-31.
- Nee, S., Holmes, E. C., Rambaut, A. and Harvey, P. (1996): "Inferring population history from molecular phylogenies." In Harvey, P. H., Leigh Brown, A. J., Maynard Smith, J. and Nee, S. (eds.): *New Uses for New Phylogenies*, Oxford: Oxford University Press, pp. 66-80.
- Nee, S., May, R. M., and Harvey, P. (1994): "The reconstructed evolutionary process." *Philosophical Transactions of the Royal Society of London, B344*: 305-11.
- Nei, M. (1987): *Molecular Evolutionary Genetics*. New York: Columbia University Press.
- Penny, D., and Hendy, M. D. (1985): "The use of tree comparison metrics." *Systematic Zoology*34: 75-82.
- Poe, S. (1998): "Sensitivity of phylogeny estimation to taxonomic sampling." *Systematic Biology*47 (1): 18-31.
- Rambaut, A. (1994): *Endemic-Epidemic: Phylogenetic Process Analysis*. Oxford: University of Oxford Department of Zoology.
- Rambaut, A., Harvey, P. H., and Nee, S. (in press): "END-EPI: An application for reconstructing population dynamic histories from phylogenies." *Computer Applications in Biological Sciences*.
- Ridley, M. (1986): *Evolution and Classification: The Reformation of Cladism*. London: Longman.

- Rogers, A. R., and Cashdan, E. (1997): "The phylogenetic approach to comparing human populations." *Evolution and Human Behavior*18: 353-58.
- Rogers, A., and Harpending, H. (1992): "Population growth makes waves in the distribution of pairwise differences." *Molecular Biology and Evolution*9: 552-69.
- Saitou, N., and Imanishi, T. (1989): "Parsimony, maximum-likelihood, minimum-evolution, and neighbor-joining methods of phylogenetic tree construction in obtaining the correct tree." *Molecular Biology and Evolution*6: 514-25.
- Saitou, N., and Nei, M. (1987): "The neighbor-joining method: A new method for reconstructing phylogenetic trees." *Molecular Biology and Evolution*4: 406-425.
- Sellen, D., and Mace, R. (1997): "Fertility and mode of subsistence: A phylogenetic analysis." *Current Anthropology*38 (5): 878-889.
- Shao, K., and Sokal, R. R. (1990): "Tree balance." *Systematic Zoology*39: 266-76.
- Simberloff, D., Hecht, K. L., McCoy, E. D. and Connor, E. F. (1981): "There have been no statistical tests of cladistic biogeographical hypotheses." In Nelson, G. and Rosen, D. E., (eds.): *Vicariance Biogeography: A Critique*, New York: Columbia University Press, pp. 40-63.
- Sober, E. (1988): *Reconstructing the Past: Parsimony, Evolution and Inference*. Cambridge, MA: MIT Press.
- Swofford, D. L. (in press): "PAUP* 4.0." *Smithsonian Institution*
- Swofford, D. L., and Begle, D. P. (1993): *PAUP: Phylogenetic Analysis Using Parsimony User's Manual*. Champaign, IL: Illinois Natural History Survey.
- Swofford, D. L. and Olsen, G. J. (1990): "Phylogeny reconstruction." In Hillis, D. M. and Moritz, C., (eds.): *Molecular Systematics*, Sunderland, MA: Sinauer, pp. 411-501.
- Thompson, J. B. (1995): *The Media and Modernity: A Social Theory of the Media*. Oxford: Polity Press.
- Vigilant, L., Stoneking, M., Harpending, H., Hawkes, K., and Wilson, A. (1991): "African populations and the evolution of human mitochondrial DNA." *Science*253: 1503-7.
- Wasserman, S., and Faust, K. (1994): *Social Network Analysis: Methods and Applications*. Cambridge: Cambridge University Press.
- Wilkie, D. S. (1988): "Hunters and farmers of the African forest." In Denslow, J. S. and Padoch, C., (eds.): *Peoples of the Tropical Rainforest*, Los Angeles: University of California Press, pp. 111-126.
- Wilkie, D. S., and Curran, B. (1993): "Historical trends in forager and farmer exchange in the Ituri rain forest of northeastern Zaire." *Human Ecology*21: 389-417.