

Evolution and Human Behavior 27 (2006) 169-184

Evolution and Human Behavior

Branching, blending, and the evolution of cultural similarities and differences among human populations

Mark Collard^{a,d,*}, Stephen J. Shennan^{b,d}, Jamshid J. Tehrani^{c,d}

^aDepartment of Anthropology and Sociology, University of British Columbia, Vancouver, Canada ^bInstitute of Archaeology, University College London, London, UK ^cDepartment of Anthropology, University College London, London, UK ^dAHRB Centre for the Evolutionary Analysis of Cultural Behaviour, University College London, Gower Street, London, UK

Initial receipt 12 August 2004; final revision received 6 July 2005

Abstract

It has been claimed that blending processes such as trade and exchange have always been more important in the evolution of cultural similarities and differences among human populations than the branching process of population fissioning. In this paper, we report the results of a novel comparative study designed to shed light on this claim. We fitted the bifurcating tree model that biologists use to represent the relationships of species to 21 biological data sets that have been used to reconstruct the relationships of species and/or higher level taxa and to 21 cultural data sets. We then compared the average fit between the biological data sets and the model with the average fit between the cultural data sets and the model. Given that the biological data sets can be confidently assumed to have been structured by speciation, which is a branching process, our assumption was that, if cultural evolution is dominated by blending processes, the fit between the bifurcating tree model and the cultural data sets should be significantly worse than the fit between the bifurcating tree model and the biological data sets. Conversely, if cultural evolution is dominated by branching processes, the fit between the bifurcating tree model and the cultural data sets should be no worse than the fit between the bifurcating tree model and the biological data sets. We found that the average fit between the cultural data sets and the bifurcating tree model was not significantly different from the fit between the biological data sets and the bifurcating tree model. This indicates that the cultural data sets are not less tree-like than are

^{*} Corresponding author. Department of Anthropology and Sociology, University of British Columbia, 6303 NW Marine Drive, Vancouver, Canada V6T 1Z1. Tel.: +1 604 822 4845.

E-mail address: mark.collard@ubc.ca (M. Collard).

^{1090-5138/06/\$ –} see front matter © 2006 Elsevier Inc. All rights reserved. doi:10.1016/j.evolhumbehav.2005.07.003

the biological data sets. As such, our analysis does not support the suggestion that blending processes have always been more important than branching processes in cultural evolution. We conclude from this that, rather than deciding how cultural evolution has proceeded a priori, researchers need to ascertain which model or combination of models is relevant in a particular case and why. © 2006 Elsevier Inc. All rights reserved.

Keywords: Cultural evolution; Branching; Blending; Demic diffusion; Cultural diffusion; Ethnogenesis; Phylogenesis; Cladistics; Homoplasy

1. Introduction

The processes responsible for producing the cultural similarities and differences among human populations have long been the focus of debate in the social sciences, as has the corollary issue of linking cultural data with the patterns reconstructed by historical linguists and by biologists working with human populations (e.g., Bellwood, 1996; Boas, 1940; Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Cavalli-Sforza, Piazza, Menozzi, & Mountain, 1988; Durham, 1991; Goodenough, 1999; Hurles, Matisoo-Smith, Gray, & Penny, 2003; Jones, 2003; Kirch & Green, 1987; Kroeber, 1948; Lumsden & Wilson, 1981; Mesoudi, Whiten, & Laland, 2004; Moore, 1994; Morgan, 1870; Petrie, 1939; Renfrew, 1987, 1992; Rivers, 1914; Romney, 1957; Schmidt, 1939; Smith, 2001; Smith, 1933; Terrell, 1988; Welsch, Terrell, & Nadolski, 1992; Whaley, 2001). Currently, debate is focused on two competing hypotheses, which have been termed the branching hypothesis (also known as the "genetic," "demic diffusion," or "phylogenesis" hypothesis) and the blending hypothesis (also known as the "cultural diffusion" or "ethnogenesis" hypothesis; Bellwood, 1996; Collard & Shennan, 2000; Guglielmino, Viganotti, Hewlett, & Cavalli-Sforza, 1995; Hewlett, de Silvestri, & Guglielmino, 2002; Kirch & Green, 1987; Moore, 1994, 2001; Romney, 1957; Tehrani & Collard, 2002). Other models have been proposed (e.g., Boyd, Borgerhoff Mulder, Durham, & Richerson, 1997), but to date, these have received little attention in the literature.

According to the branching hypothesis, cultural similarities and differences among human populations are primarily the result of a combination of within-group information transmission and population fissioning. The strong version of the hypothesis suggests that Transmission Isolating Mechanisms, or TRIMS (Durham, 1992), impede the transmission of cultural elements among contemporaneous communities. TRIMS are akin to the barriers to hybridisation that separate species and include language differences, ethnocentrism, and intercommunity violence (Durham, 1992). The branching hypothesis predicts that the similarities and differences among cultures can be best represented by the type of branching tree diagram that is used in biology to depict the relationships among species (Fig. 1). The hypothesis also predicts that there will be a strong association between cultural variation and linguistic and biological patterns (e.g., Ammerman & Cavalli-Sforza, 1984; Bellwood, 1996, 2001; Cavalli-Sforza, Menozzi, & Piazza, 1994; Cavalli-Sforza et al., 1988; Diamond & Bellwood, 2003; Kirch & Green, 1987, 2001; Renfrew, 1987).



Fig. 1. Example cladogram.

In contrast, supporters of the blending hypothesis (e.g., Dewar, 1995; Moore, 1994, 2001; Terrell, 1988, 2001; Terrell, Hunt, & Gosden, 1997, Terrell, Kelly, & Rainbird, 2001) believe that it is unrealistic "to think that history is patterned like the nodes and branches of a comparative, phylogenetic, or cladistic tree" (Terrell et al., 1997, p. 184). The appropriate way to represent relationships among human populations, according to this view, is not as a branching tree but as a braided stream, with different channels flowing into one another, then splitting again. The basis of this argument is that humans have always interacted, and thus ideas, innovations, goods, and cultural practices, not to mention genes, have constantly flowed from one community to another. To the extent that language is an exception to this, it is because of the mutual accommodation of individuals' idiolects to one another that is required if speakers are to understand each other. The blending hypothesis predicts that the similarities and differences among cultures can best be represented by a maximally connected network or reticulated graph (Terrell, 2001). It also predicts that there will be a close relationship between cultural patterns and the frequency and intensity of contact among populations, the usual proxy of which is geographic proximity.

It has been asserted that blending has been the dominant cultural evolutionary process in the ethnohistorical period and is likely to have always been more significant than branching in cultural evolution (e.g., Dewar, 1995; Moore, 1994, 2001; Terrell, 1988, 2001; Terrell et al. 1997, 2001). The pervasiveness of human interaction obviously cannot be denied. In the words of Bellwood (1996, p. 882), "humans flourish in interactive groups, and total isolation of any human group has been very rare in prehistory." However, in our view, whether blending is the dominant cultural process is open to question. First, the archaeological record frequently demonstrates the existence of long-lasting cultural traditions with recognisable coherence, despite evidence for the extensive movement of materials and artifacts across boundaries (e.g., Pétrequin, 1993). Second, ethnographic work indicates that in non-commercial settings, cultural transmission is often both vertical and conservative, with children learning skills from their parents with relatively little error (e.g., Childs & Greenfield, 1980; Greenfield, 1984; Greenfield, Maynard, & Childs, 2000 Hewlett & Cavalli-Sforza, 1986; Shennan & Steele, 1999). Third, recent work in psychology suggests that humans may possess evolved cognitive mechanisms that lead them to interact preferentially

with individuals who are similar to themselves (Buston & Emlen, 2001) and to be prejudiced against individuals from unfamiliar ethnic groups (Gil-White, 2001; Schaller, Park, & Faulkner, 2003). Fourth, empirical and theoretical research suggests that, as counterintuitive as it may seem, interaction between people can actually lead to the emergence of cultural barriers and distinctions where none previously existed (e.g., Barth, 1969; Hodder, 1982; McElreath, Boyd, & Richerson, 2003). Lastly, most contributions to the branching/blending debate published to date have focused on cultural evolution in specific regions of the world often over relatively short spans of time rather than dealing with it as a general phenomenon (e.g., Borgerhoff Mulder, 2001; Collard & Shennan, 2000; Guglielmino et al., 1995; Hewlett et al., 2002; Jordan & Shennan, 2003; Kirch & Green, 1987; Shennan & Collard, 2005; Tehrani & Collard, 2002; Welsch et al., 1992). A few papers have addressed the debate's key issues in global terms, but in these works either the evidence discussed is anecdotal (e.g., Moore, 1994, 2001; Terrell, 1988, 2001) or the analyses reported are informal (e.g., Jones, 2003). As such, it is currently unclear from an empirical perspective whether cultural evolution is dominated by branching or blending processes.

In this paper, we report a study that goes some way towards rectifying the latter situation. In the study, we assessed how tree-like patterns in cultural data sets are compared with patterns in biological data sets. Essentially, we fitted the bifurcating tree model that biologists use to represent the relationships of species to a group of data sets pertaining to cultural phenomena such as artifacts and rituals, and to a group of biological data sets that have been used to reconstruct the relationships of species and higher level taxa. We then compared the average fit between the cultural data sets and the model with the average fit between the biological data sets and the model. Given that the biological data sets can be confidently assumed to have been structured by speciation, which is a branching process, our assumption was that, if the blending hypothesis is correct and cultural evolution is dominated by blending processes, the fit between the bifurcating tree model and the cultural data sets. Conversely, if the blending hypothesis is incorrect and cultural evolution is dominated by branching processes, the fit between the bifurcating tree model and the cultural data sets should be no worse than the fit between the bifurcating tree model and the cultural data sets should be no worse than the fit between the bifurcating tree model and the cultural data sets should be no worse than the fit between the bifurcating tree model and the cultural data sets.

2. Materials and methods

Our first step was to obtain biological and cultural data sets suitable for phylogenetic analysis. Acquiring the biological data sets was straightforward, as they are readily available in the literature and many of them can also be downloaded from on-line databases, such as TreeBASE (Sanderson, Donoghue, Piel, & Eriksson, 1994). Accordingly, we were able to assemble a group of 21 biological data sets. An effort was made to include a broad range of taxa and characters. Thus, the biological data sets included DNA data for lizards, lagomorphs, and carnivores, morphological data for fossil hominids, seals, and ungulates, and behavioural data for bees, seabirds, and primates. Currently, cultural data sets suitable for phylogenetic analysis are much less easy to come by than their biological counterparts. We had six data sets

in our possession from previous work conducted on this topic by researchers associated with the AHRB Centre for the Evolutionary Analysis of Cultural Behaviour (Collard & Shennan, 2000; Croes, Kelly, & Collard, 2005; Jordan & Shennan, 2003; Tehrani, 2004; Tehrani & Collard, 2002; Venti, 2004). To these, we were able to add 14 data sets from the literature (Barnett, 1937, 1939; Driver, 1937; Drucker, 1937, 1941, 1950; Gifford, 1940; Gifford & Kroeber, 1937; Jorgenson, 1969; Moylan, Graham, Borgerhoff Mulder, Nunn, & Håkansson,

Table 1 Biological data sets analysed in this study

Data set	Source	Notes
Austalasian teal mtDNA	Kennedy and Spencer (2000)	Downloaded from TreeBASE. Data for ATPase 6, ATPase 8 and 12S genes.
Corbiculate bee behaviour	Noll (2002)	C C
Pelecaniforme bird behaviour	Kennedy, Spencer, and Gray (1996)	
Anoles lizards morphology	Guyer and Savage (1986)	Downloaded from TreeBASE.
Primate behaviour	DiFiore and Rendall (1994)	
Strepsirhine primate morphology	Yoder (1994)	
Fossil hominid morphology	Lieberman, Wood, and Pilbeam (1996)	
New World monkey morphology	Horowitz, Zardoya, and Meyer (1998)	Craniodental data.
Ungulate morphology	O'Leary and Geisler (1999)	Downloaded from TreeBASE. Data
		from Runs 5 and 6.
Phalacrocoracid bird mtDNA	Kennedy, Gray, and Spencer (2000)	Provided by Martyn Kennedy,
		University of Otago. Data for 12S,
		AlPase 6 and 8 genes.
Phoeid seal morphology	Bininda-Edwards and Russell (1996)	Downloaded from IreeBASE.
Hawaiian fruit fly mtDNA	Baker and DeSalle (1997)	Downloaded from IfeeBASE. Data
Hominoid primate	Collard and Wood (2000)	Qualitative data set
cranial morphology	Conard and wood (2000)	Qualitative data set.
Carnivore mtDNA	Wayne et al. (1997)	Downloaded from TreeBASE
Mammal mtDNA with emphasis	Vang and Voder (2003)	Downloaded from the website of
on Malagasy primates	Tung und Todor (2005)	Anne Yoder, Yale University, Data
on Managasy primates		for COII and cytochrome b genes
Carnivore mtDNA with	Yoder et al. (2003)	Downloaded from the website of
emphasis on Malagasy taxa		Anne Yoder, Yale University. Data
		for cytochrome b gene.
Mammal mtDNA	Yoder and Yang (2000)	Downloaded from the website of
		Anne Yoder, Yale University.
Insectivore mtDNA	Stanhope et al. (1998)	Downloaded from TreeBASE.
		Data for 12S-16S genes.
Lagomorph mtDNA	Halanych and Robinson (1999)	Downloaded from TreeBASE.
		Data for 12S gene.
Hominoid primate	Gibbs, Collard, and Wood (2002)	
soft-tissue morphology		
Anolis lizard mtDNA	Jackman, Larson, de Queiroz,	Downloaded from TreeBASE.
	and Losos (1999)	Data for ND2 and tRNA genes.

in press; Steward, 1941; Stewart, 1941; Welsch et al., 1992; O'Brien, Darwent, & Lyman, 2001). This gave us a total of 20 cultural data sets to work with. Details of the biological and cultural data sets are provided in Tables 1 and 2, respectively. Copies of the NEXUS files will be made available on request.

Next, we measured the fit between the bifurcating tree model and each data set. To do so, we employed an analytical approach from evolutionary biology known as "phylogenetic systematics" or, more commonly, "cladistics." First presented coherently in the 1950s (Hennig, 1950), cladistics is now the dominant method of phylogenetic reconstruction used in biology (Kitching, Forey, Humphries, & Williams, 1998; Schuh, 2000). Based on a null model in which new taxa arise from the bifurcation of existing ones, cladistics define phylogenetic relationship in terms of relative recency of common ancestry. Two taxa are deemed to be more closely related to one another than either is to a third taxon if they share a common ancestry is evolutionarily novel or "derived" character states. Two taxa are inferred to share a common ancestor to the exclusion of a third taxon if they exhibit derived character states that are not also exhibited by the third taxon. In its simplest form, cladistic analysis

Table 2

Cultural data sets analysed in this study

Data set	Source	Notes
Gulf of Georgia Salish food	Barnett (1939)	
taboos and prescriptions		
Neolithic pottery	Collard and Shennan (2000)	
Californian Indian basketry	Jordan and Shennan (2003)	
Eastern North American projectile points	O'Brien et al. (2001)	
Coast and inland Salish cultural practices	Jorgensen (1969)	
New Guinea material culture	Welsch et al. (1992)	
Turkmen weaving designs	Tehrani and Collard (2002)	
Northwest Coast tribal religion and ritual	Drucker (1950)	
Early Christian doctrinal beliefs	Venti (2004)	
Iranian tribal weavings	Tehrani (2004)	
Northwest Coast archaeology	Croes et al. (2005)	Stone, bone-antler, and shell artifacts
Pomo structures	Gifford and Kroeber (1937)	
Oregon Coast tribal puberty rites	Barnett (1937)	
Southern Sierra Nevada tribal	Driver (1937)	
death and mourning practices		
Nevada Shoshoni tribal mutilations	Steward (1941)	
Southern California tribal body-	Drucker (1937)	
and dress-related practices		
Yuman-Piman warfare-related practices	Drucker (1941)	
Apache-Pueblo houses	Gifford (1940)	
African cultural practices	Moylan et al. (in press)	Downloaded from the website of Monique Borgerhoff Mulder, University of California-Davis.
Northern Paiute birth rituals	Stewart (1941)	

proceeds via four steps. First, a character state data matrix is generated. This shows the states of the characters exhibited by each taxon. Next, the direction of evolutionary change among the states of each character is established. Several methods have been developed to facilitate this, including communality analysis (Eldredge & Cracaft, 1980), ontogenetic analysis (Nelson, 1978), and stratigraphic sequence analysis (Nelson & Platnick, 1981). Currently the favoured method is outgroup analysis (Arnold, 1981). Outgroup analysis entails examining a close relative of the study group. When a character occurs in two states among the study group, but only one of the states is found in the outgroup, the principle of parsimony is invoked and the state found only in the study group is deemed to be evolutionarily novel with respect to the outgroup state. Having determined the probable direction of change for the character states, the next step in a cladistic analysis is to construct a branching diagram of relationships for each character. As shown in Fig. 1, this is done by joining the two most derived taxa by two intersecting lines, and then successively connecting each of the other taxa according to how derived they are. Each group of taxa defined by a set of intersecting lines corresponds to a clade, and the diagram is referred to as a cladogram or tree. The final step in a cladistic analysis is to compile an ensemble cladogram from the character cladograms. Ideally, the distribution of the character states among the taxa will be such that all the character cladograms imply relationships among the taxa that are congruent with one another. Normally, however, a number of the character cladograms will suggest relationships that are incompatible. This problem is overcome by generating an ensemble cladogram that is consistent with the largest number of characters and therefore requires the smallest number of ad hoc hypotheses of character appearance or "homoplasies" to account for the distribution of character states among the taxa.

We identified the most parsimonious cladogram for each data set with the aid of the popular phylogenetics computer program PAUP* 4 (Swofford, 1998). In all the analyses, the characters were treated as unordered, and the most parsimonious cladogram was detected via the heuristic search routine. We then used PAUP* 4 to evaluate how well the most parsimonious cladogram explains the distribution of similarities and differences within each data set. The goodness-of-fit measure we used was the retention index, or RI, of Farris (1989a; 1989b). Equivalent to the Archie's (1989) homoplasy excess ratio maximum index (Farris, 1989b; 1991; Archie, 1989), the RI is a measure of the number of homoplastic changes that a cladogram requires that are independent of its length (Farris, 1989a; 1989b). The RI of a single character is calculated by subtracting the number of character state changes required by the focal cladogram (s) from the maximum possible amount of change required by a cladogram in which all the taxa are equally closely related (g). This figure is then divided by the result of subtracting the minimum amount of change required by any conceivable cladogram (m) from g. The RI of two or more characters is computed as (G-S)/(G-M), where G, S, and M are the sums of the g, s, and m values for the individual characters. A maximum RI of 1 indicates that the cladogram requires no homoplastic change, and the level of homoplasy increases as the index approaches 0. The RI is a useful goodnessof-fit measure when comparing data sets because, unlike some other measures (e.g., the Consistency Index), it is not affected by number of taxa or number of characters. The RIs for the 21 biological data sets and the 20 cultural data sets are presented in Table 3. Also shown

Table 3

Goodness-of-fit values associated with most parsimonious cladograms derived from 21 biological and 21 cultural data sets

Data set	NT	NC	PI	RI	Dataset	NT	NC	PI	RI
Austalasian teal mtDNA	7	1172	73	0.94	Gulf of Georgia Salish food	11	77	51	0.57
					taboos and prescriptions				
Corbiculate bee behaviour	23	42	41	0.94	Neolithic pottery	59	35	33	0.71
Pelecaniforme bird behaviour	20	37	36	0.84	Californian Indian basketry	40	219	184	0.71
Anoles lizards morphology	24	18	16	0.79	Eastern North American projectile points	17	8	6	0.70
Primate behaviour	38	34	34	0.73	Coast and inland Salish cultural practices	29	78	75	0.63
Strepsirhine primate morphology	29	43	43	0.72	New Guinea material culture	31	47	47	0.51
Fossil hominid morphology	9	48	48	0.71	Turkmen weaving designs	6	90	56	0.44
New World monkey morphology	20	76	65	0.70	Northwest Coast tribal religion and ritual	18	220	137	0.65
Ungulate morphology	40	123	122	0.70	Early Christian doctrinal beliefs	12	18	15	0.61
Phalacrocoracid bird mtDNA	24	1141	234	0.65	Iranian tribal weavings	10	110	92	0.60
Phocid seal morphology	27	196	184	0.60	Northwest Coast archaeology	48	69	69	0.50
Hawaiian fruit fly mtDNA	17	2550	501	0.50	Pomo structures	20	43	31	0.52
Hominoid primate cranial morphology	6	96	57	0.49	Oregon Coast tribal puberty rites	10	109	39	0.55
Carnivore mtDNA	25	2001	615	0.47	Southern Sierra Nevada tribal death and mourning practices	23	181	138	0.48
Mammal mtDNA with emphasis on Malagasy primates	36	1812	932	0.47	Nevada Shoshoni tribal mutilations	19	48	22	0.78
Carnivore mtDNA with emphasis on Malagasy taxa	35	1140	498	0.47	Southern California tribal body- and dress-related practices	18	98	78	0.52
Mammal mtDNA	31	10806	6049	0.44	Yuman-Piman warfare-related practices	8	185	110	0.69
Insectivore mtDNA	43	2086	866	0.44	Apache-Pueblo houses	20	140	120	0.63
Lagomorph mtDNA	12	739	97	0.39	African cultural practices	35	54	54	0.42
Hominoid primate soft-tissue morphology	5	171	154	0.38	Northern Paiute birth rituals	14	128	86	0.43
Anolis lizard mtDNA	55	1456	866	0.35	Northeastern Missouri projectile points	22	13	?	0.66

NT, number of taxa; NC, number of characters; PI number of parsimony informative characters; RI, Retention Index. A maximum RI of 1 indicates that the cladogram requires no homoplastic change, and the level of homoplasy increases as the index approaches 0.

in Table 3 is an RI associated with the most parsimonious cladogram obtained by Darwent and O'Brien (in press) from a Northeastern Missouri projectile point data set.

In the next stage of the study, we compared the RIs of the 21 biological data sets with the 21 cultural RIs with a view to determining whether they are significantly different. This was accomplished with the Mann–Whitney U test function of SPSS 11.

3. Results

The RIs associated with the most parsimonious cladograms derived from the biological and cultural data sets (Table 2) suggest that the fit between the bifurcating tree model and the cultural data sets is little different from the fit between the bifurcating tree model and the biological data sets. Not only are the averages similar, but also the ranges are comparable. The mean, minimum, and maximum biological RIs are 0.61, 0.35, and 0.94, respectively. The corresponding figures for the cultural RIs are 0.59, 0.42, and 0.78. Thus, the descriptive statistics do not support the hypothesis that blending is more important than branching in cultural evolution. On average, the cultural data sets appear to be no more reticulate than the biological data sets.

The result of the Mann–Whitney U test is in line with the descriptive statistics. The biological and cultural RIs are not significantly different according to the test (Mann–Whitney U=215.5, p=.900). Thus, once again, the hypothesis that blending is more important than branching in cultural evolution is not supported.

4. Discussion

To evaluate the assertion that blending has always been a more important cultural evolutionary process than branching is, we fitted the bifurcating tree model that biologists use to represent relationships among species to a set of cultural data sets and to a set of biological data sets that have been used to reconstruct the relationships of species and higher level taxa. We then compared the average fit between the cultural data sets and the model with the average fit between the biological data sets and the model. What we found was that the goodness-of-fit measures derived from the cultural data sets. Given that the latter can be confidently assumed to have been structured by a branching process, namely, speciation, this implies that branching processes were more important than blending processes in structuring the cultural data sets. Thus, our analysis does not support the suggestion that blending processes have always dominated cultural evolution.

The failure of our analysis to support the claim that blending is the dominant cultural evolutionary process is in line with the region-specific quantitative studies that have been published to date (Borgerhoff Mulder, 2001; Collard & Shennan, 2000; Guglielmino et al., 1995; Hewlett et al., 2002; Jordan & Shennan, 2003; Moore & Romney, 1994, 1996; Roberts, Moore, & Romney, 1995; Shennan & Collard, 2005; Tehrani & Collard, 2002; Welsch, 1996; Welsch et al., 1992). Several of these studies have focused on cultural variation among villages on the North Coast of New Guinea, using geographic distance and linguistic affinity as proxies for blending and branching, respectively. Using regression and correspondence analysis of presence/absence data, Welsch et al. (1992; see also Welsch, 1996) found that the material culture similarities and differences among the villages are strongly associated with geographic propinquity and unrelated to the linguistic relations of the villages. In contrast, correspondence and hierarchical log-linear analyses of frequency

data carried out by Moore and colleagues indicated that geography and language have equally strong effects on the variation in material culture among the villages (Moore & Romney, 1994; Roberts et al., 1995). Moore and Romney (1996) obtained the same result in a reanalysis of the presence/absence data of Welsch et al. using correspondence analysis, thereby accounting for one potential explanation for the difference in findings, namely the use of different data sets. Recent work by Shennan and Collard (2005) supports the assessment of Moore and Romney that a combination of both branching and blending was operating in this case.

Three quantitative studies have examined cultural evolution in African societies: Guglielmino et al. (1995), Borgerhoff Mulder (2001), and Hewlett et al. (2002). The first of these explored the roles of branching, blending and local adaptation in the evolution of 47 cultural traits among 277 African societies. Models of the three processes were generated, and then correlation analyses undertaken in which language was used as a proxy for branching, geographic distance was used as a proxy for blending, and vegetation type was used as a proxy for adaptation. These analyses found that most of the traits fit best the branching model. The distributions of only a few traits were explicable in terms of adaptation to local conditions and even fewer traits supported the blending model. The results of Hewlett et al. were less clear-cut than those of Guglielmino et al., but they nevertheless supported the branching hypothesis. Hewlett et al. investigated the processes responsible for the distribution of 109 cultural attributes among 36 African ethnic groups. Using phenetic clustering and regression analysis, they tested three explanatory models: demic diffusion, which is equivalent to branching, cultural diffusion, which is equivalent to blending, and local invention. Hewlett et al. found that 32% of the cultural attributes could not be linked with an explanatory model, and that the distributions of another 27% of the cultural attributes were compatible with two of the models. Of the remaining cultural attributes, 18% were compatible with demic diffusion, 11% were compatible with cultural diffusion, and just 4% were compatible with local invention. The results of Borgerhoff Mulder's (2001; see also Borgerhoff Mulder, George-Cramer, Eshleman, & Ortolani, 2001) analysis of correlations between cultural traits associated with kinship and marriage patterns in 35 East African societies were more equivocal. In this study, analyses of phylogenetically controlled data supported roughly half the number of statistically significant correlations returned by analyses of phylogenetically uncorrected data. These results failed to support the Borgerhoff Mulder's preferred hypothesis, which is that adaptation to local environments plus diffusion between neighbouring populations erases any phylogenetic signature. Were that the case, then the correlations between different traits in the phylogenetically controlled analysis would have returned very similar results to a conventional statistical analysis of the raw data, which was not the case. However, Borgerhoff Mulder's results also do not lend unqualified support to the branching hypothesis either because a high proportion of correlations remained unaffected by phylogenetic correction. In these cases, the trace of descent is obscured either by a relatively fast rate of cultural evolution and adaptation to local conditions, or by the mixing and merging between cultural groups that has been reported in ethnographic and historical sources on East African societies. Thus, two of the three African studies offer strong support for the branching hypothesis, while the third is equivocal regarding the relative importance of branching and blending.

Three other quantitative contributions to the branching/blending debate have been published: Collard and Shennan (2000), Tehrani and Collard (2002) and Jordan and Shennan (2003). The first of these investigated the relative contribution of branching and blending to cultural evolution by applying phylogenetic techniques from biology to assemblages of pottery from Neolithic sites in the Merzbach valley, Germany. The analyses indicated that, while both branching and blending were involved in generating the patterns observed among the Merzbach pottery assemblages, branching was the dominant process. The study of Tehrani and Collard applied biological phylogenetic techniques to a data set comprising decorative characters from textiles produced by Turkmen tribes between the 18th and 20th centuries. The analyses focused on two periods in Turkmen history: the era in which most Turkmen practiced nomadic pastoralism and were organised according to indigenous structures of affiliation and leadership; and the period immediately following their defeat by Tsarist Russia in 1881, which is associated with the sedentarization of nomadic Turkmen and their increasing dependence on the market. The analyses of Tehrani and Collard indicated that branching was the dominant process in the evolution of Turkmen carpet designs both before and after their incorporation into the Russian Empire. The study of Jordan and Shennan (2003) used multivariate and cladistic methods to examine Californian Indian basketry variation in relation to linguistic affinity and geographic proximity. The analyses suggested that the variation is best explained by blending rather than branching, or rather that linguistic affiliation has not provided a strong canalising force on the distribution of basketry attributes, which appears to be mainly determined by geographical proximity and, therefore, presumably, frequency of interaction.

Thus, the suggestion that blending has always been a more important cultural evolutionary process than branching is also not supported by the region-specific quantitative studies that have been published to date. Blending seems to have been the dominant process in the evolution of the Californian data set, but branching was at least as important as blending in generating the New Guinea, Neolithic, and African data sets, and it was clearly the major process in producing the Turkmen data set.

5. Conclusions

The results of the quantitative comparative study described here do not support the claim that blending processes such as trade and exchange have always been more important in cultural evolution than the branching process of population fissioning (e.g., Dewar, 1995; Moore, 1994, 2001; Terrell, 1988, 2001; Terrell et al., 1997, 2001). Collectively the cultural data sets in our sample do not differ from the biological data sets in terms of how tree-like they are. The claim that blending has always been more important in cultural evolution than branching is also not supported by the region-specific quantitative assessments of cultural evolution that have been published to date. Blending processes clearly structured some data sets, but branching processes are equally clearly responsible for structuring other data sets. It

appears, therefore, that branching cannot be discounted as a process in cultural evolution. This, in turn, suggests that, rather than deciding how cultural evolution has proceeded a priori (e.g., Moore, 1994; Terrell, 1988, 2001; Terrell et al., 1997, 2001), researchers need to ascertain which model or combination of models is relevant in a particular case and why (Shennan & Collard, 2005; Tehrani & Collard, 2002).

Acknowledgments

We thank Samantha Banks, Peter Jordan, Martyn Kennedy, Mike O'Brien, and Anne Yoder for assisting us with this project. Useful comments were provided by Stephen Lycett, Martin Daly, Margo Wilson, and two anonymous referees. Lastly, we would like to express our gratitude to the UK's Arts and Humanities Research Board for their ongoing support of our work on cultural evolution.

References

- Ammerman, A. J., & Cavalli-Sforza, L. L. (1984). The neolithic transition and the genetics of populations in Europe. Princeton, NJ: Princeton University Press.
- Archie, J. W. (1989). A randomization test for phylogenetic information in systematic data. *Systematic Zoology*, 38, 219–252.
- Arnold, E. N. (1981). Estimating phylogenies at low taxonomic levels. Zeitschrift f
 ür Zoologische Systematik und Evolutionsforschung, 19, 1–35.
- Baker, R., & DeSalle, R. (1997). Multiple sources of character information and the phylogeny of Hawaiian Drosophilids. Systematic Biology, 46, 654–673.
- Barnett, H. G. (1937). Culture element distributions: VII. Oregon coast. Anthropological Records, 1, 155-204.
- Barnett, H. G. (1939). Culture element distributions: IX. Gulf of Georgia Salish. Anthropological Records, 5, 221–295.
- Barth, F. (1969). Introduction. In F. Barth (Ed.), *Ethnic groups and boundaries: The social organisation of culture difference* (pp. 9–38). Boston, MA: Little Brown.
- Bellwood, P. (1996). Phylogeny vs. reticulation in prehistory. Antiquity, 70, 881-890.
- Bellwood, P. (2001). Early agriculturalist diasporas? Farming, languages, and genes. Annual Review of Anthropology, 30, 181–207.
- Bininda-Emonds, O. R. P., & Russell, A. P. (1996). A morphological perspective on the phylogenetic relationships of the extant phocid seals (Mammalia: Carnivora: Phocidae). *Bonner Zoologische Monographien*, 41, 1–256. Boas, F. (1940). *Race, language, and culture*. Chicago: Chicago University Press.
- Borgerhoff Mulder, M. (2001). Using phylogenetically based comparative methods in anthropology: More
- questions than answers. Evolutionary Anthropology, 10, 99–111.
- Borgerhoff Mulder, M., George-Cramer, M., Eshleman, J., & Ortolani, A. (2001). A study of East African kinship and marriage using a phylogenetically based comparative method. *American Anthropologist*, 103, 1059–1082.
- Boyd, R., Borgerhoff Mulder, M., Durham, W. H., & Richerson, P. J. (1997). Are cultural phylogenies possible? In P. Weingart, S. D. Mitchell, P. J. Richerson, & S. Maasen (Eds.), *Human by nature* (pp. 355–386). Mahwah, NJ: Lawrence Erlbaum.
- Boyd, R., & Richerson, P. J. (1985). Culture and the evolutionary process. Chicago: University of Chicago Press.
- Buston, P. M., & Emlen, S. T. (2001). Cognitive processes underlying human mate choice: The relationship between self-perception and mate preference in Western society. *Proceedings of the National Academy of Sciences*, 100, 8805–8810.

- Cavalli-Sforza, L. L., & Feldman, M. W. (1981). Cultural transmission and evolution: A quantitative approach. Princeton, NJ: Princeton University Press.
- Cavalli-Sforza, L. L., Menozzi, P., & Piazza, A. (1994). The history and geography of human genes. Princeton, NJ: Princeton University Press.
- Cavalli-Sforza, L. L., Piazza, A., Menozzi, P., & Mountain, J. (1988). Reconstruction of human evolution: Bringing together genetic, archaeological and linguistic data. *Proceedings of the National Academy of Sciences of the United States of America*, 85, 6002–6006.
- Childs, C. P., & Greenfield, P. M. (1980). Informal modes of learning and teaching: The case of Zinacanteco weaving. In N. Warren (Ed.) *Studies in Cross-Cultural Psychology* (vol. 2, pp. 269–316). New York: Academic Press.
- Collard, M., & Shennan, S. J. (2000). Ethnogenesis versus phylogenesis in prehistoric culture change: A casestudy using European Neolithic pottery and biological phylogenetic techniques. In C. Renfrew, & K. Boyle (Eds.), Archaeogenetics: DNA and the population prehistory of Europe (pp. 89–97). Cambridge: McDonald Institute for Archaeological Research.
- Collard, M., & Wood, B. A. (2000). How reliable are human phylogenetic hypotheses? Proceedings of the National Academy of Sciences of the United States of America, 97, 5003–5006.
- Croes, D., Kelly, K. M., & Collard, M. (2005). Cultural historical context of Q^wu?g^wes (Puget Sound, USA): A preliminary investigation. *Journal of Wetland Archaeology*, 5, 141–154.
- Darwent, J., & O'Brien, M. J. (in press). Using cladistics to construct lineages of projectile points from Northeastern Missouri. In C. P. Lipo, M. J. O'Brien, M. Collard, & S. J. Shennan (Eds.), *Mapping our* ancestors: Phylogenetic methods in anthropology and prehistory. Hawthorne, NY: Aldine de Gruyter.
- Dewar, R. E. (1995). Of nets and trees: Untangling the reticulate and dendritic in Madagascar's prehistory. World Archaeology, 26, 301–318.
- Diamond, J., & Bellwood, P. (2003). Farmers and their languages: The first expansions. Science, 300, 597-603.
- DiFiore, A., & Rendall, D. (1994). Evolution of social organization: A reappraisal for primates by using phylogenetic methods. *Proceedings of the National Academy of Sciences of the United States of America*, 91, 9941–9945.
- Driver, H. E. (1937). Culture element distributions: VI. Southern Sierra Nevada. *Anthropological Records*, 1, 53–154.
- Drucker, P. (1937). Culture element distributions: V. Southern California. Anthropological Records, 1, 1-52.
- Drucker, P. (1941). Culture element distributions: XVII. Yuman-Piman. Anthropological Records, 6, 91-230.
- Drucker, P. (1950). Culture element distributions: XXVI. Northwest Coast. Anthropological Records, 9, 157-294.
- Durham, W. H. (1991). Co-evolution: Genes, culture, and human diversity. Stanford: Stanford University Press.
- Durham, W. H. (1992). Applications of evolutionary culture theory. *Annual Review of Anthropology*, 21, 331–355.
- Eldredge, N., & Cracraft, J. (1980). Phylogenetic patterns and the evolutionary process: Method and theory in comparative biology. New York: Columbia University Press.
- Farris, J. S. (1989a). The retention index and homoplasy excess. Systematic Zoology, 38, 406-407.
- Farris, J. S. (1989b). The retention index and the rescaled consistency index. Cladistics, 5, 417-419.
- Farris, J. S. (1991). Excess homoplasy ratios. *Cladistics*, 7, 81-91.
- Gibbs, S., Collard, M., & Wood, B. A. (2002). Soft tissue anatomy of the extant hominoids: A review and phylogenetic analysis. *Journal of Anatomy*, 200, 3–49.
- Gifford, E. W. (1940). Culture element distributions: XII. Apache-Pueblo. Anthropological Records, 4, 1-207.
- Gifford, E. W., & Kroeber, A. L. (1937). Culture element distributions: IV. Pomo. University of California Publications in American Archaeology and Ethnology, 37, 117–254.
- Gil-White, F. J. (2001). Are ethnic groups biological "species" to the human brain? *Current Anthropology*, 42, 515–554.
- Goodenough, W. H. (1999). Outline of a framework for a theory of cultural evolution. *Cross-Cultural Research*, 33, 84–107.
- Greenfield, P. M. (1984). A theory of the teacher in the learning activities of everyday life. In B. Rogoff, & J. Lave (Eds.), *Everyday cognition* (pp. 117–138). Cambridge, MA: Harvard University Press.

- Greenfield, P. M., Maynard, A. E., & Childs, C. P. (2000). History, culture, learning, and development. Cross-Cultural Research, 34, 351–374.
- Guglielmino, C. R., Viganotti, C., Hewlett, B., & Cavalli-Sforza, L. L. (1995). Cultural variation in Africa: Role of mechanisms of transmission and adaptation. *Proceedings of the National Academy of Sciences of the United States of America*, 92, 7585–7589.
- Guyer, C., & Savage, J. M. (1986). Cladistic relationships among Anoles (Sauria: Iguanidae). Systematic Zoology, 35, 509–531.
- Halanych, K. M., & Robinson, T. J. (1999). The utility of cytochrome b and 12S rDNA data for phylogeny reconstruction of leporid (Lagomorpha) genera. *Journal of Molecular Evolution*, 48, 369–379.
- Hennig, W. (1950). Grundzüge einer Theorie der Phylogenetischen Systematik. Berlin: Deutscher Zentralverlag.
- Hewlett, B. S., & Cavalli-Sforza, L. L. (1986). Cultural transmission among Aka pygmies. American Anthropologist, 88, 922–934.
- Hewlett, B. S., de Silvestri, A., & Guglielmino, C. R. (2002). Semes and genes in Africa. Current Anthropology, 43, 313–321.
- Hodder, I. (1982). Symbols in action: Ethnoarchaeological studies of material culture. Cambridge: Cambridge University Press.
- Horowitz, I., Zardoya, R., & Meyer, A. (1998). Platyrrhine systematics: A simultaneous analysis of molecular and morphological data. *American Journal of Physical Anthropology*, 106, 261–281.
- Hurles, M. E., Matisoo-Smith, E., Gray, R. D., & Penny, D. (2003). Untangling Oceanic settlement: The edge of the unknowable. *Trends in Ecology and Evolution*, 18, 531–540.
- Jackman, T. R., Larson, A., de Queiroz, K., & Losos, J. B. (1999). Phylogenetic relationships and tempo of early diversification in Anolis lizards. *Systematic Biology*, 48, 254–285.
- Jones, D. (2003). Kinship and deep history: Exploring connections between culture areas, genes and language. *American Anthropologist*, 105, 501–514.
- Jordan, P., & Shennan, S. J. (2003). Cultural transmission, language, and basketry traditions amongst the Californian Indians. *Journal of Anthropological Archaeology*, 22, 42–74.
- Jorgensen, J. G. (1969). Salish language and culture. Bloomington, IN: Indiana University.
- Kennedy, M., Gray, R. D., & Spencer, H. G. (2000). The phylogenetic relationships of the shags and cormorants: Can sequence data resolve a disagreement between behaviour and morphology? *Molecular Phylogenetics and Evolution*, 17, 345–359.
- Kennedy, M., & Spencer, H. G. (2000). Phylogeny, biogeography, and taxonomy of Australasian Teals. Auk, 117, 154–163.
- Kennedy, M., Spencer, H. G., & Gray, R. D. (1996). Hop, step and gape: Do the social displays of the Pelecaniformes reflect phylogeny? *Animal Behaviour*, 51, 273–291.
- Kirch, P. V., & Green, R. C. (1987). History, phylogeny, and evolution in Polynesia. *Current Anthropology*, 28, 431–456.
- Kirch, P. V., & Green, R. C. (2001). Hawaiki, Ancestral Polynesia: In essay in historical anthropology. Cambridge: Cambridge University Press.
- Kitching, I. J., Forey, P. L., Humphries, C. J., & Williams, D. M. (1998). Cladistics: The theory and practice of parsimony analysis. Oxford: Oxford University Press.
- Kroeber, A. L. (1948). Anthropology: Race, language, culture, psychology, prehistory. New York: Brace.
- Lieberman, D. E., Wood, B. A., & Pilbeam, D. R. (1996). Homoplasy and early *Homo*: An analysis of the evolutionary relationships of *H. habilis sensu stricto* and *H. rudolfensis. Journal of Human Evolution*, 30, 97–120.
- Lumsden, C. J., & Wilson, E. O. (1981). *Genes, mind, and culture: The co-evolutionary process*. Cambridge, MA: Harvard University Press.
- McElreath, R., Boyd, R., & Richerson, P. J. (2003). Shared norms and the evolution of ethnic markers. *Current Anthropology*, 44, 122–129.
- Mesoudi, A., Whiten, A., & Laland, K. N. (2004). Is human cultural evolution Darwinian? Evidence reviewed from the perspective of *The Origin of Species*. *Evolution*, 58, 1–11.

- Moore, C. C., & Romney, A. K. (1994). Material culture, geographic propiniquity, and linguistic affiliation on the North Coast of New Guinea: A reanalysis of Welsch, Terrell, and Nadolski (1992). *American Anthropologist*, 96, 370–396.
- Moore, C. C., & Romney, A. K. (1996). Will the "real" data please stand up? Reply to Welsch (1996). Journal of Quantitative Anthropology, 6, 235–261.
- Moore, J. H. (1994). Putting anthropology back together again: The ethnogenetic critique of cladistic theory. *American Anthropologist*, 96, 370–396.
- Moore, J. H. (2001). Ethnogenetic patterns in native North America. In J. E. Terrell (Ed.), *Archaeology, language and history: Essays on culture and ethnicity* (pp. 30–56). Wesport: Bergin and Garvey.
- Morgan, L. H. (1870). Systems of consanguinity and affinity of the human family. Washington, DC: Smithsonian Institution Press.
- Moylan, J. W., Graham, C. M., Borgerhoff Mulder, M., Nunn, C. L., Håkansson, T. (in press). Cultural traits and linguistic trees: Phylogenetic signal in East Africa. In C. P. Lipo, M. J. O'Brien, M. Collard, S. J. Shennan (Eds.) *Mapping our ancestors: Phylogenetic methods in anthropology and prehistory*. Hawthorne, NY: Aldine de Gruyter.
- Nelson, G. (1978). Species and taxa: Systematics and evolution. In D. Otto, & J. A. Endler (Eds.), *Speciation and its consequences* (pp. 60–81). Sunderland, MA: Sinauer Associates.
- Nelson, G., & Platnick, N. (1981). Systematics and biogeography: Cladistics and vicariance. New York: Columbia University Press.
- Noll, F. B. (2002). Behavioral phylogeny of corbiculate apidae (Hymenoptera; Apinae), with special reference to social behavior. *Cladistics*, *18*, 137–153.
- O'Brien, M. J., Darwent, J., & Lyman, R. L. (2001). Cladistics is useful for reconstructing archaeological phylogenies: Paleoindian points from the southeastern United States. *Journal of Archaeological Science*, 28, 1115–1136.
- O'Leary, M. A., & Geisler, J. H. (1999). The position of Cetacea within Mammalia: Phylogenetic analysis of morphological data from extinct and extant taxa. *Systematic Biology*, 48, 455–490.
- Pétrequin, P. (1993). North wind, south wind: Neolithic technological choices in the Jura Mountains, 3700–2400 BC. In P. Lemonnier (Ed.), *Technological choices* (pp. 36–76). London: Routledge.
- Petrie, W. M. F. (1939). The making of Egypt. London: Sheldon.
- Renfrew, C. (1987). Archaeology and language: The puzzle of Indo-European origins. London: Cape.
- Renfrew, C. (1992). Archaeology, genetics and linguistic diversity. Man (New Series), 27, 445-478.
- Rivers, W. H. R. (1914). The history of Melanesian society. Cambridge: Cambridge University Press.
- Roberts, J. M., Moore, C. C., & Romney, A. K. (1995). Predicting similarity in material culture among New Guinea villages from propinquity and language: A log-linear approach. *Current Anthropology*, 36, 769–788.
- Romney, A. K. (1957). The genetic model and Uto-Aztecan time perspective. *Davidson Journal of Anthropology*, 3, 35–41.
- Sanderson, M. J., Donoghue, M. J., Piel, W., & Eriksson, T. (1994). TreeBASE: A prototype database of phylogenetic analyses and an interactive tool for browsing the phylogeny of life. *American Journal of Botany*, 81, 183.
- Schaller, M., Park, J. H., & Faulkner, J. (2003). Prehistoric dangers and contemporary prejudices. *European Review of Social Psychology*, 14, 105–137.
- Schmidt, W. (1939). The culture historical method of ethnology. New York: Fortuny's.
- Schuh, R. T. (2000). Biological systematics: Principles and applications. Ithaca, NY: Cornell University Press.
- Shennan, S. J., & Collard, M. (2005). Investigating processes of cultural evolution on the North Coast of New Guinea with multivariate and cladistic analyses. In R. Mace, S. J. Shennan, & C. J. Holden (Eds.), *The evolution of cultural diversity: A phylogenetic approach* (pp. 133–164). London: University College London Press.
- Shennan, S. J., & Steele, J. (1999). Cultural learning in hominids: A behavioural ecological approach. In H. O. Box, & K. R. Gibson (Eds.), *Mammalian social learning: Comparative and ecological perspectives* (pp. 367–388). Cambridge: Cambridge University Press.

- Smith, E. A. (2001). On the coevolution of cultural, linguistic and biological diversity. In L. Maffi (Ed.), On biocultural diversity: Linking language, knowledge, and the environment (pp. 95–117). Washington, DC: Smithsonian Institution Press.
- Smith, G. E. (1933). The diffusion of culture. London: Watts.
- Stanhope, M. J., Waddell, V. G., Madsen, O., de Jong, W., Hedges, S. B., Cleven, G. C., Kao, D., & Springer, M. S. (1998). Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 9967–9972.
- Steward, J. H. (1941). Culture element distributions: XIII. Nevada Shoshoni. Anthropological Records, 4, 209–259.
- Stewart, O. C. (1941). Culture element distributions: XIV. Northern Paiute. Anthropological Records, 4, 361-446.
- Swofford, D. L. (1998). PAUP* 4. Phylogenetic analysis using parsimony (*and Other Methods). Version 4. Sunderland: Sinauer.
- Tehrani, J. J. (2004). *Processes of cultural diversification in the evolution of Iranian tribal craft traditions*. Unpublished PhD dissertation, University College London.
- Tehrani, J. J., & Collard, M. (2002). Investigating cultural evolution through biological phylogenetic analyses of Turkmen textiles. *Journal of Anthropological Archaeology*, 21, 443–463.
- Terrell, J. E. (1988). History as a family tree, history as a tangled bank. Antiquity, 62, 642-657.
- Terrell, J. E. (2001). Introduction. In J. E. Terrell (Ed.), Archaeology, language, and history: Essays on culture and ethnicity (pp. 1–10). Wesport: Bergin and Garvey.
- Terrell, J. E., Hunt, T. L., & Gosden, C. (1997). The dimensions of social life in the Pacific: Human diversity and the myth of the primitive isolate. *Current Anthropology*, 38, 155–195.
- Terrell, J. E., Kelly, K. M., & Rainbird, P. (2001). Foregone conclusions? In search of "Papuans" and "Austronesians". *Current Anthropology*, 42, 97–124.
- Venti J. F. (2004). Methods for investigating the evolutionary pattern of adaptive radiations in cultural history: A preliminary cultural evolutionary pattern analysis of early Christianity. Unpublished MA thesis, University College London.
- Wayne, R. K., Geffen, E., Girman, D. J., Koepfli, K. P., Lau, L. M., & Marshall, C. R. (1997). Molecular systematics of the Canidae. Systematic Biology, 46, 622–653.
- Welsch, R. L. (1996). Language, culture and data on the north coast of New Guinea. Journal of Quantitative Anthropology, 196, 209–234.
- Welsch, R. L., Terrell, J. E., & Nadolski, J. A. (1992). Language and culture on the North Coast of New Guinea. *American Anthropologist*, 94, 568–600.
- Whaley, L. J. (2001). Manchu-Tungusic culture change among Manchu-Tungusic peoples. In J. E. Terrell (Ed.), Archaeology, language, and history: Essays on culture and ethnicity (pp. 103–124). Wesport, CT: Bergin and Garvey.
- Yang, Z., & Yoder, A. D. (2003). Comparison of likelihood and Bayesian methods for estimating divergence times using multiple gene loci and calibration points, with application to a radiation of cute-looking mouse lemur species. *Systematic Biology*, 52, 705–716.
- Yoder, A. D. (1994). The relative position of the Cheirogaleidae in strepsirhine phylogeny: A comparison of morphological and molecular methods and results. *American Journal of Physical Anthropology*, 94, 25–46.
- Yoder, A. D., Burns, M. M., Zehr, S., Delefosse, T., Veron, G., Goodman, S. M., & Flynn, J. J. (2003). Single origin of Malagasy Carnivora from an African ancestor. *Nature*, 421, 734–737.
- Yoder, A. D., & Yang, Z. (2000). Estimation of primate speciation dates using local molecular clocks. *Molecular Biology and Evolution*, 17, 1081–1090.