View metadata, citation and similar papers at core.ac.uk
brought to you by CORE
provided by UCL Discovery

Chapter 16

Testing functional hypotheses about cross-cultural variation: a maximum-likelihood comparative analysis of Indo-European marriage practices

Laura Fortunato and Ruth Mace, Department of Anthropology, UCL

Introduction

Behavioural ecology is the branch of biology dealing with the study of animal behavioural variation within and across taxa; it addresses questions about the function of behaviour, focusing on its survival value in relation to the environment (Tinbergen’s (1963) ‘why’ questions; Krebs and Davies 1993: 382). Human behavioural ecology investigates variation in human behaviour, including cultural behaviour, within and across societies (Winterhalder and Smith 2000).

Investigation into the function of behaviour involves making hypotheses based on observations, deriving testable predictions from the hypotheses, and testing. Three strategies are available for testing functional hypotheses: examination of variation among individuals within a group, experiments, and examination of variation among groups (Krebs and Davies 1993: 24). Given that human behaviour is generally not amenable to experimental manipulation, the study of human behavioural variation is largely restricted to comparison within and among groups.

In this paper we provide an example of the application of the behavioural ecology approach to the study of variation in cultural practices across groups, focusing on wealth transfers at marriage. In the first part, we review the observations that led to the evolutionary interpretation of these practices, and previous analyses of their distribution; in the second part, we illustrate the use of a phylogenetic comparative method with data on wealth transfers at marriage in Indo-European groups.

The case of transfers of wealth at marriage

Observations and hypothesis

The transfer of resources at marriage is a widespread practice; resources may be in the form of women, services, or property (Westermarck 1926: 156). Property may be transferred from the groom or his kin to the bride's kin (bridewealth) or to the bride (indirect dowry, Goody 1973: 2), or from the bride's kin to the bride (dowry). Alternatively, the families of the spouses may exchange goods in reciprocation. These practices are not distributed evenly across world regions; dowry in particular is restricted to circum-Mediterranean and East Asian societies (Jackson and Romney 1973). What factors led to this uneven distribution?

Here we will investigate the hypothesis that practices of wealth transfer at marriage represent forms of sex-biased parental investment. Parental investment is defined as any investment in an individual offspring that increases his or her chance of surviving and reproducing. Given that parents have access to a limited pool of resources, this concomitantly reduces their ability to invest in other offspring (Trivers 1972: 139). Parental investment theory predicts that parents should allocate resources among their offspring in ways that maximise their own reproductive success. The observed distribution of wealth transfer practices should thus reflect some condition determining sex-biases in parental investment.

Wealth correlates positively with reproductive success in traditional human societies in which property is individually owned (e.g. Irons 1979). In these societies, parents may influence the reproductive success of their offspring directly through the provision of resources to be invested in reproduction; this indirectly affects their own long-term reproductive outcome. Two observations indicate that wealth transfers at marriage may serve this purpose. Parents, and to a lesser extent other kin, are typically involved in their negotiation and provision (e.g. Lambiri-Dimaki 1985: 173), indicating that they have an interest in the outcome of marriage arrangements (cf. also Wiessner, this volume). The fact that the value of the transfer may be affected by the reproductive potential of the prospective spouse (e.g. Borgerhoff Mulder 1995) suggests that this shared interest may well be a reproductive one.

Predictions and tests

Put crudely, the issue at stake is whether parents are on average more likely to increase their number of grandchildren by investing a given amount of wealth in the reproduction of their sons or daughters (Gaulin and Boster 1990). In humans, as in other sexually reproducing species, males invest less in gametes than females, and thus have higher potential reproductive rates; in these species the variance in reproductive success is potentially greater among males than among females (Trivers 1972). It follows that parents investing their wealth in the reproduction of their sons will, on average, increase their number of grandchildren more than parents investing the same amount of wealth in the reproduction of their daughters (Hartung 1976). Hartung (1982) predicted that this pattern would result in male-biases in property allocation where marriage is polygynous. Fitting this prediction, he found a strong positive relationship between degree of polygyny and occurrence of bridewealth in Murdock's (1967) *Ethnographic atlas*. In these codes, degree of polygyny is operationalized as no polygyny (polygyny not permitted or encouraged), limited polygyny (< 20% of married males in polygynous unions), and general polygyny (> 20% of married males in polygynous unions). For the 850 societies coded as practicing bridewealth or as characterised by the absence of significant considerations, bridewealth is present in 37.5% of societies with no polygyny, in 52.8% of societies with limited polygyny, and in 90.8% of societies with general polygyny.

Where polygyny is not allowed, however, the difference in variance in reproductive success between the sexes is greatly reduced, as consequently is the benefit to parents of biasing investment towards the reproduction of their sons. Where the prohibition on polygynous marriage coincides with significant differences in status and resources among males, parents may more profitably use their wealth to gain access to the resources of high status husbands for their daughters. Exclusive access to these resources may translate in greater reproductive success for their daughters and for their daughters' children. Gaulin and Boster (1990) argued that the provision of daughters with wealth at marriage may represent one of a number of strategies employed in this competition. Dowry, for example, is commonly provided in hypergynous marriages (e.g. Dickemann 1979); accordingly, the occurrence of this practice should be most likely in non-polygynous, stratified societies. Fitting this prediction, they found that in the *Ethnographic atlas* dowry is most common in societies characterised by absence of polygyny and presence of stratification. They operationalized these variables as polygyny (limited or general) vs. no polygyny (no polygyny/monogamy or polyandry), and as stratification vs. no stratification. Dowry occurs in less than 1% of the 994 societies that are either polygynous or non-polygynous but not stratified, and in 37.5% of the 72 stratified non-polygynous societies, resulting in its being 50 times more common in the latter.

The models tested by Hartung (1982) and Gaulin and Boster (1990) perform equally well on subsets of the *Ethnographic atlas*, including Murdock and White's (1969) *Standard cross-cultural sample*. These subsets are devised to control for the effect of historical relatedness on the distribution of cultural practices, an issue known in anthropology as 'Galton's problem'. Societies may in fact share cultural traits by virtue of descending from a common ancestor; consequently, they may not be treated as independent data points in statistical analyses of the distribution of cultural practices. An approach commonly used to address this issue is to restrict the analysis to a set of societies sampled widely across geographic regions or linguistic groups. The *Standard cross-cultural sample*, for example, was obtained by grouping the 1267 societies in the *Ethnographic atlas* in 186 geographic provinces, and by subsequently choosing the most accurately described one for each province. This approach reduces the possibility that a society may be counted more than once because it was artificially subdivided. However, it does not solve the problem of historical relatedness, but simply moves it back in time, while causing the loss of information on variation among closely related societies (Mace and Pagel 1994; Murdock and White 1969).

In order to address the issue in a principled way, Mace and Pagel (1994) proposed the application of phylogenetic comparative methods to the study of cross-cultural variation. These methods are used in evolutionary biology to control for the effect of historical relatedness among biological groups (species or higher taxa) on the outcome of comparative analyses. They test for the association of a phenotypic trait with another phenotypic trait or with an environmental variable on a phylogenetic model of the historical relationships among the groups (Felsenstein 1985; Harvey and Pagel 1991). The traits can be assumed to be related if they appear to change together in a number of independent occasions, as judged from the historical relationships among the groups and from the distribution of traits among them; this is taken as evidence that the traits may be functionally linked. Phylogenetic comparative methods assume vertical transmission of traits along the branches of a phylogeny. For the purpose of testing hypotheses about the function of cultural practices, this corresponds to assuming that cultural traits are transmitted from parent to daughter populations. Independent instances of change include the acquisition or loss of a trait, either by original invention or by copying from another culture; the latter corresponds to horizontal transmission across groups (Mace and Pagel 1994).

Below we illustrate the application of the phylogenetic comparative approach to testing hypotheses about the evolution of wealth transfers at marriage and marriage systems in Indo-European (IE) groups. Building on the findings by Hartung (1982) and Gaulin and Boster (1990), we predicted that bridewealth and dowry should evolve in correlated fashion with polygynous and monogamous marriage, and that changes in wealth transfer practices should reflect changes in marriage systems. We investigated the association of these traits using a likelihood-based phylogenetic comparative method on cross-cultural data. The cross-cultural data were mapped onto a phylogenetic tree obtained from linguistic data, which served as a model of the historical relationships among the groups in the sample.

Data and methods

Collating the cross-cultural dataset

We collated the comparative data by matching speech varieties in Dyen et al.’s (1992) IE basic vocabulary database with societies in Gray (1999), in Levinson (1994), and in primary ethnographic sources. We then used data from the linguistic database to generate a phylogenetic tree for the groups in the sample, as described below. We included in the analyses only groups for which we found evidence for both wealth transfer practice and marriage system.

We coded societies as polygynous or monogamous based on the sanctioned form of marriage. In the model under investigation, dowry is used to gain exclusive access to the resources of, rather than exclusive sexual access to, high status husbands; we reasoned that, since monogamous marriage is usually associated with ‘monogamous resource flow’ (Gaulin and Boster 1997: 374), it would not matter whether monogamous marriage did not coincide with monogamous mating.

We coded societies as practicing bridewealth or dowry based on the direction of the parental investment (transfer from groom's vs. transfer from bride's kin). We preferred the pre-industrial pattern for groups that recently ceased the traditional practice of transferring wealth at marriage, and coded groups with evidence of both practices based on the prevalent mode of transfer, e.g. we preferred the form in variable 6 (primary mode of marriage) to the form in variable 7 (alternate mode of marriage) in Gray (1999).

We coded the outgroup Hittite as practicing monogamy and dowry based on the information contained in the Hittite code of laws, a compendium of approximately 200 clauses dating back to at least 1650 BC (Bryce 2002: 34), as reported in Gurney (1975) and Bryce (2002). The lack of reference to multiple spouses in any clause of the code suggests that only monogamous marriages were legally sanctioned. In particular, the rights and obligations specified by the large number of clauses dealing with marriage provisions, including the detailed accounts of the property and inheritance rights of marriage partners and their offspring, only applied to officially recognised monogamous unions (Bryce 2002: 132-133).

Hittite marriage was accompanied by a symbolic gift generally referred to as 'bridewealth' (*kusata*) and by a substantial dowry (*iwaru*) (Bryce 2002: 120; Gurney 1975: 100). *Kusata* marriage was used to formalise unions between slave and free: it was required in order for the free partner to retain free status and for the descendants to acquire it. Accordingly, it was provided by a male slave marrying a free woman and by the father of the bride when a free man married into a slave family (Bryce 2002: 121-124). As such, *kusata* is not bridewealth in the strict sense, nor does it fit with either category of sex-biased parental investment.

Obtaining a model of population history

The IE basic vocabulary database includes the forms of the meanings in the Swadesh 200-word list of items of basic vocabulary for 95 modern IE speech varieties (languages, dialects and creoles), classified into cognate classes; two or more forms of a meaning are cognate if they share a common origin. The Swadesh lists consist of items of cross-culturally universal vocabulary such as pronouns, body parts, and numerals, that are less prone to innovation and borrowing than other meanings. The database is available from http://www.ntu.edu.au/education/langs/ielex/IE-DATA1.

M. Pagel provided the coded linguistic data matrix, including data for Hittite. Hittite belongs to the extinct monophyletic sister group to the IE clade, the Anatolian languages; these two clades together form the Indo-Hittite language family (Rexová, et al. 2003). We used Hittite as the outgroup for rooting the tree.

We generated the phylogenetic tree using a maximum parsimony optimality criterion, as implemented by PAUP* 4.0b4a (Swofford 2002), on the linguistic data for the varieties associated with the 52 groups included in the cross-cultural sample. Meanings were coded as multi-state, with each state representing a cognate class. Character states were unordered, and multiple character states for a variety were treated as uncertainty. We used a heuristic strategy to search for the optimal tree or set of trees, running 1000 replications of tree bisection-reconnection (TBR) with random addition sequence, storing up to 2000 trees in memory per search.

We performed an initial search with all characters having equal weights; based on this search, we then assigned weights to the characters through *a posteriori* successive approximations (Farris 1969). We conducted the consecutive heuristic searches with the new weights performing 1000 replications of TBR with random addition sequence, again storing up to 2000 trees in memory. We used bootstrap analysis of the weighted characters to estimate the support for the individual clades on the tree obtained with this procedure, using heuristic searches with 20 TBR random addition sequence replicates on 500 bootstrap samples.

Testing hypotheses about evolution

We used the likelihood-based method for the comparative analysis of binary traits described in Pagel (1994; 1997), implemented by the programme *Discrete*. *Discrete* is available from http://www.evolution.reading.ac.uk/BayesPhy.html.

The method consists in fitting statistical models of the way the traits may have evolved to the comparative data mapped onto a phylogeny, using maximum likelihood to estimate the likelihood of producing the observed data under each model. It works by reconstructing the evolution of the two traits to make the observed distribution of character states most likely, given a model of the historical relationships among the taxa and a statistical model of the way evolution proceeds (Pagel 1994, 1999).

We initially fitted a model of independent evolution I, under which each trait changes between its two character states independently of the other, and a model of dependent evolution D, under which changes in character state for the two traits are interdependent (Figure 1). By fitting alternative versions of these models to the data, we tested hypotheses on the probable direction of change from the estimated ancestral state, on the relative ordering of changes, and on the most likely route of evolution of the traits, as described in Pagel (1994). The alternative models are obtained by restricting one or more parameters in models I and D to be equal to each other or to arbitrary values. *Discrete* estimates the probability of ancestral states at internal nodes on the phylogeny using the method described in Pagel (1999).

[Figure 1 approximately here]

We used likelihood ratio (LR) tests to assess whether pairs of likelihood values obtained under alternative models differed significantly. Significant differences indicate that the model resulting in the higher value is more likely to have produced the observed data; this suggests that it is a better description of the way the two traits have evolved.

We fitted the parameter κ by maximum likelihood for all models; κ stabilizes the results across runs by smoothing the likelihood surface where fitting likelihood models proves difficult, e.g. for trees with a large range of branch lengths (Pagel 1994). We repeated all analyses a minimum of three times; here we report the highest values for each set; however, results were stable across runs for all analyses.

Results

Tree-building

Unweighted parsimony yielded a set of 252 optimal trees with treelength 3372.00, consistency index CI = 0.9001, retention index RI = 0.8966, and rescaled consistency index RC = 0.8075. After weighting the characters, three searches were necessary for two consecutive ones to converge on the same tree and for the character weights to remain unchanged; the optimal tree had treelength 2711.83, CI = 0.9152, RI = 0.9129, and RC = 0.8361 (Figure 2). Figure 3 shows the 50% majority-rule consensus tree for the bootstrap sample of trees obtained from the weighted dataset.

[Figure 2 approximately here]

[Figure 3 approximately here]

We computed the CIs for the 187 parsimony-informative characters. This statistic measures the level of character fit on the tree; the high values indicate a predominantly branching pattern of evolution for IE basic vocabulary. This suggests that horizontal transmission of items of basic vocabulary is limited in IE languages; consequently, a tree model is an appropriate representation of the historical relationships among them.

The commonly recognised elementary IE clades (Celtic, Romance, Germanic, Albanian, Indic, Iranian) received bootstrap support > 90%, as did the Balto-Slavonic and Indo-Iranian clades (Figure 3); these groups were all monophyletic. Higher-level groups received lower support, reflecting the failure of comparative linguistics to untangle the pattern of relationship among them.

These results are highly consistent with those obtained by Rexová et al. (2003) using unweighted parsimony on a subset of the IE basic vocabulary database including 84 speech varieties, with Hittite as the outgroup; these, in turn, are highly consistent with traditional IE classification, which suggests that our tree represents an adequate model of the relationships among IE groups for use in the comparative analyses.

Comparative analyses

Figure 4 shows the geographic distribution of societies in the sample. The cultural traits are highly clustered, both geographically and on the phylogeny (Figures 2 and 4), emphasising the need to use a phylogenetic comparative approach.

[Figure 4 approximately here]

The log-likelihood of the independent model of evolution I is significantly lower than the log-likelihood of the eight-parameter dependent model D, indicating that wealth transfer practices and marriage systems evolve in correlated fashion (omnibus test, Table 1). The four states in model D are bridewealth with polygyny (state 1: 0, 0), bridewealth with monogamy (state 2: 0, 1), dowry with polygyny (state 3: 1, 0), and dowry with monogamy (state 4: 1, 1) (Figure 5). Estimation of the ancestral state at the root indicates the latter as most likely, with probability 0.86.

[Table 1 approximately here]

[Figure 5 approximately here]

We performed the tests in Table 1 to determine the most likely route of evolution of the two traits from the ancestral state. The eight alternative model tests indicate that the transitions specified by rates q_{12}, q_{24}, q_{31}, q_{43} do not differ significantly from zero, leaving a minimum model with parameters q_{13}, q_{21}, q_{34}, q_{42} (Figure 5). The flow diagram suggests that both bridewealth with polygyny (state 1: 0, 0) and dowry with monogamy (state 4: 1, 1) are relatively stable: of the four transitions in the minimum model differing significantly from zero, the two leading to these states (q_{21} and q_{34} respectively) are specified by rates one order of magnitude larger than the two leaving them (q_{13} and q_{42} respectively). It follows that the transitions leading to bridewealth with monogamy (state 2: 0, 1) and to dowry with polygyny (state 3: 1, 0) are specified by rates (q_{42} and q_{13} respectively) one order of magnitude smaller than the two leaving them (q_{21} and q_{34} respectively), making these states relatively unstable. The values of the transition rate parameters are shown in Figure 5.

Contingent change tests indicate that the occurrence of changes from monogamy to polygyny is contingent on wealth transfer practice, as setting $q_{21} = q_{43}$ significantly reduces the likelihood of the model. In model D, q_{43} does not differ significantly from zero, indicating that changes from monogamy to polygyny in the presence of dowry are highly unlikely.

Temporal order/relative rate tests indicate that changes from bridewealth to dowry and from polygyny to monogamy occur in no specific order, whereas changes from dowry to bridewealth and from monogamy to polygyny occur at different relative rates, as setting $q_{42} = q_{43}$ significantly reduces the likelihood. In model D $q_{42} >> q_{43}$, indicating that changes from dowry to bridewealth are likely to precede changes from monogamy to polygyny.

These results indicate that wealth transfer practices and marriage systems evolve in correlated fashion in IE groups. Further, they suggest that changes from monogamy to polygyny are contingent on wealth transfer practice and never occur in the presence of dowry; accordingly, changes from dowry to bridewealth precede changes from monogamy to polygyny. The most likely pathway of coevolution for these traits can be summarised as follows. First, a transition occurred from the ancestral state of dowry with monogamy to bridewealth with monogamy (specified by q_{42}). Polygyny was then rapidly acquired by groups in which this transition had taken place, with the preservation of bridewealth as wealth transfer practice (transition specified by q_{21}). Only transitions to dowry with polygyny (specified by q_{13}) occurred from this state, which however rapidly reverted to dowry with monogamy (transition specified by q_{34}).

Discussion

The difference between male and female reproductive potential plays a major role in determining animal mating and parenting strategies. Extending this framework to human cultural behaviour, cross-cultural variation in marriage practices may be partly understood in terms of this difference. Transfers of wealth at marriage, for example, may be viewed as tools used by parents to influence the reproductive success of their offspring, while ultimately attempting to maximise their own reproductive outcome. Parents should use bridewealth to have their sons marry polygynously where polygyny is allowed, and dowry to have their daughters' children born into high status families where it is not (Hartung 1997: 344). In line with these predictions, bridewealth is most common where the degree of polygyny is highest (Hartung 1982), and dowry where the prohibition on polygynous marriage coincides with stratification (Gaulin and Boster 1990).

By applying the phylogenetic comparative approach to cross-cultural data, we showed that in IE groups the association of bridewealth with polygyny and of dowry with monogamy is not an artefact of historical relatedness; rather, wealth transfer practices and marriage systems evolve in correlated fashion, suggesting that they may be functionally related. Our model indicates that dowry with monogamy represents the most likely ancestral state; this finding is supported by estimation of the diachronic development of bridewealth and dowry in IE groups (Fortunato et al. 2006). Reconstruction of the most likely pathway of evolution from the ancestral state indicates that bridewealth with polygyny and dowry with monogamy represent relatively stable states in the coevolution of these practices. The other possible combinations of traits – bridewealth with monogamy and dowry with polygyny – are instead relatively unstable. As noted above, a prohibition on polygynous marriage greatly reduces the difference in variance in reproductive success between male and female offspring, and consequently any benefit to parents of investing preferentially in their sons. Conversely, in polygynous societies the benefit to parents of securing daughters with access to the resources of high status husbands is offset by the dilution of those resources among multiple wives.

In the theoretical model for non-human species, the mating system brings into effect the potential difference in within-sex variance in reproductive success between males and females, which in turn determines patterns of parental investment; based on this model, we predicted that changes in marriage systems would drive changes in wealth transfer practices. The results suggest, however, that in IE groups changes in marriage systems reflect changes in wealth transfer practices.

An alternative explanation for this pattern may be derived from models that view human social groups primarily as units of production rather than reproduction. Goody (1976), for example, suggested that in Eurasia the advent of advanced agriculture through irrigation and ploughing led to scarcity of land, caused by the increase in land productivity and exploitation on the one hand, and by the population expansion these allowed on the other. The tendency to keep scarce resources within the productive unit, usually the nuclear family, led to the crystallisation of status differences based on resource control, and to the emphasis of vertical transmission of property to maintain this status differentiation. Direct vertical transmission from parents to children resulted in the provision of daughters as well as of sons, as opposed to ‘homogenous transmission’ to collateral kin where direct heirs of the same sex as the endower were not available. This ‘diverging devolution’ of property took the form of both inheritance and dowry for daughters; dowry in particular served as a way to control their status through marriage to husbands of appropriate standing (p. 20). Goody (1976) tested the theory through path analysis of the *Ethnographic atlas*; in the resulting model, advanced agriculture and stratification are causally linked to diverging devolution, which is in turn causally linked to the occurrence of marriage-related practices such as father’s brother’s daughter marriage, endogamy, prohibition on premarital sex, and monogamy (p. 29). According to Goody (1976), this system of property distribution involved the commitment of property from both spouses to the establishment of some type of conjugal fund, which required matching of the dowry with property from the husband; this restricted the ability of men to enter multiple marriages, leading to a shift from polygynous to monogamous marriage (pp. 51, 109). Testing of this model using the phylogenetic comparative approach will be necessary to determine whether the observed relationships between wealth transfer practices and marriage systems evolved in response to the relative advantage – productive, reproductive or both – offered by certain combinations of traits over others.

Methodological issues

We have illustrated how the framework used to test functional hypotheses about animal behavioural variation can be applied to the study of human cultural behaviour. In particular, we focused on the application of phylogenetic comparative methods to the study of variation in cultural practices. Here we briefly address some methodological issues, while acknowledging the need to replicate our analyses with both better methods and data.

In the comparative analyses, we used a phylogenetic tree to model the historical relationships among the groups in the sample. By definition, a phylogeny represents a hypothesis about the historical relationships among the groups under study, and it is a well known problem of the phylogenetic comparative approach that results may be affected by the phylogeny used (e.g. Martins and Housworth 2002). As recognised by the first advocates of this approach in evolutionary biology, however, not using an explicit model of population history corresponds to implicitly assuming that the groups under investigation are equally related to one another (Felsenstein 1985); this seems a worse approximation of the past than a properly constructed phylogeny, for biological and human groups alike. Further, in recent years phylogenetic inference has moved towards statistical approaches that simultaneously provide an estimate of phylogenetic relationships and quantify the uncertainty in the estimation (Bayesian MCMC inference, reviewed in Holder and Lewis 2003; Huelsenbeck et al. 2001). This has spurred the development of phylogenetic comparative methods that take into account the uncertainty in the estimation of both the phylogenetic relationships and the parameters of interest to the comparative questions (e.g. Huelsenbeck and Rannala 2003; Pagel and Meade 2005, 2006; Pagel et al. 2004). The application of these methods to the comparative analysis of cultural practices (e.g. Fortunato et al. 2006; Pagel and Meade 2005) offers a promising framework for testing functional hypothesis about human behaviour.[1]

Given the limited scope for experimental manipulation in studies of human behaviour, comparative analyses are likely to play an increasingly important role in understanding human cultural variation. We feel it is therefore worth noting a general limitation of the comparative approach that extends to phylogenetic methods. Comparative methods ultimately look for correlation between pairs of traits; correlation is taken as evidence that selection repeatedly converged on the same solution to a problem, suggesting that that solution conveys a relative advantage. However, selection may be acting on a third trait that is causally linked to one or both of the traits under investigation. Possible candidates for the study of human marriage practices include, for example, type of subsistence and degree of societal stratification, which determine patterns of property distribution in Goody's (1976) model. As for any method based on correlational evidence, there is no simple way to address this issue. One possibility to discriminate between alternative hypotheses is to look for independent support across different samples, and to use the results of comparative analyses in conjunction with other approaches. For the purpose of cross-cultural research, these may include studies of variation within groups (e.g. Borgerhoff Mulder 1995), and systematic analyses of the diachronic development of cultural practices (e.g. Fortunato et al. 2006).

Of course, the difficulties of cross-cultural research also extend to the phylogenetic comparative analysis of cultural traits. These difficulties (reviewed in Levinson and Malone 1980: 9-15) mainly stem from the need to extrapolate discrete variables from complex cultural phenomena, a simplification most anthropologists seem unwilling to take responsibility for. This may partly explain why, despite its long history – Edward B. Tylor pioneered the quantitative study of cross-cultural data in (1889) – cross-cultural research has played a minor role in anthropology compared to the role played by comparative analysis in evolutionary biology. With Hartung (1983), we feel anthropologists should "be willing to test less then perfect hypotheses with less then perfect data" (p. 125), and we may add, with less than perfect methods, if anthropology is to be promoted to the rank of science. Methods, data and hypotheses can all be perfected where made explicit.

Acknowledgements

We thank Mark Pagel for providing the coded linguistic data and for *Discrete*, and Andrew Meade for valuable advice on their use. Clare Holden provided helpful comments; Tom Currie provided the map used in Figure 4. The ESRC, Fondazione Aldo Gini, and UCL Graduate School provided financial support.

Footnote to p. 13

Nunn et al. (2006) used computer simulation to assess the ability of the method of phylogenetic independent contrasts (Felsenstein 1985) to correctly infer patterns of evolution under different modes of trait transmission across societies. Results indicate that when traits are not correlated and are transmitted vertically (i.e. inherited from parent to daughter populations), Type I error rates are not significantly different from the expected value for the phylogenetic method, whereas they are highly inflated if phylogenetic relationships are not taken into account; in both cases, Type I error rates increase with increasing probability of horizontal transmission (i.e. copying a trait from another population). When traits are correlated, increasing probability of horizontal transmission causes the statistical power of both tests to increase (i.e. lower Type II error rate) at intermediate levels of correlation, and to decrease (i.e. higher Type II error rate) at high levels of correlation. According to Nunn et al. (2006), and to one Reviewer of this chapter, application of the phylogenetic comparative approach to cross-cultural data is therefore only appropriate when traits are transmitted across societies in a strictly vertical fashion. However, given that *both* methods are sensitive to horizontal transmission, the phylogenetic comparative framework seems preferable to approaches that do not take phylogeny into account, at least until the development of methods that are robust to mode of trait transmission. With regards to our analyses, empirical studies of trait transmission across societies have shown that traits relating to family and kinship, including marriage practices, are transmitted vertically (e.g. Guglielmino et al. 1995). Further, it seems premature to extend Nunn et al.’s (2006) results to any application of the phylogenetic approach to cross-cultural data. The method of phylogenetic independent contrasts uses continuous data, a Brownian model of trait evolution, and works by reconstructing a unique set of ancestral states at the internal nodes of a phylogeny to be used for comparative hypothesis testing; the likelihood-based method uses discrete data, a Markov model of trait evolution, and was developed specifically to avoid treating an inferred set of states as actual observed data (Pagel 1994). These differences may well affect the sensitivity of each method to horizontal transmission (Mace and Pagel 1997: 307).

Figure captions

Figure 1

Models of evolution for two binary traits X and Y taking states 0/1. a) Model of independent evolution I: each of the two traits X and Y is allowed to change independently of the other. α and β represent the estimated rates of change, which are used to obtain the probability of change for each trait. b) Model of dependent evolution D: the probability of change for one trait depends on the state of the other trait. The four states represent the possible combinations of character states for X, Y; diagonal transitions are not permitted, implying that only one trait is allowed to change at any one time. The possible transitions are described by eight transition rate parameters represented as q_{ij}, which are used to estimate the probability of each transition. Subscripts to q denote transitions from state *i* to state *j*, e.g. q_{12} is the rate parameter for transitions from state 1 (0, 0) to state 2 (0, 1), i.e. changes in trait Y from 0 to 1.

Figure 2

RC weighted parsimony tree of IE speech varieties (plus the outgroup Hittite). The tips are labelled with wealth transfer and marriage system practice for the groups associated with the speech varieties. Solid grey: bridewealth with polygyny; outline grey: dowry with polygyny; outline black: bridewealth with monogamy; solid black: dowry with monogamy.

Figure 3

Bootstrap 50% majority-rule consensus tree of IE speech varieties (plus the outgroup Hittite). Compatible groups found in less than 50% of the trees are also included; the actual number of trees (out of a hundred) in which a clade appears is reported at each node.

Figure 4

Geographic distribution of the speech varieties associated with groups in the cross-cultural sample; locations represent the mid-point of the language area, based on data from Gordon (2005). Labels indicate wealth transfer and marriage system practice for the groups associated with the speech varieties. Solid grey: bridewealth with polygyny; outline grey: dowry with polygyny; outline black: bridewealth with monogamy; solid black: dowry with monogamy. 1 Afghan; 2 Albanian G; 3 Albanian T; 4 Armenian Mod; 5 Baluchi; 6 Bengali; 7 Breton List; 8 Bulgarian; 9 Byelorussian; 10 Catalan; 11 Czech; 12 Dutch List; 13 English ST; 14 French; 15 German ST; 16 Greek MD; 17 Gujarati; 18 Icelandic ST; 19 Irish B; 20 Italian; 21 Kashmiri; 22 Khaskura; 23 Lahnda; 24 Lithuanian O; 25 Macedonian; 26 Marathi; 27 Nepali List; 28 Ossetic; 29 Panjabi ST; 30 Persian List; 31 Polish; 32 Portuguese ST; 33 Russian; 34 Sardinian C; 35 Serbocroatian; 36 Singhalese; 37 Slovak; 38 Slovenian; 39 Spanish; 40 Swedish List; 41 Tadzik; 42 Ukrainian; 43 Vlach; 44 Wakhi; 45 Walloon; 46 Waziri; 47 Welsh N.

Figure 5
Flow diagram of the most likely pathway for the coevolution of wealth transfer practices and marriage systems in IE groups. The different letter types for the four states follow the coding scheme used in Figures 2 and 4. Thick arrows represent rate transitions one order of magnitude larger than thin ones; dashed arrows represent rate transitions not significantly different from zero.

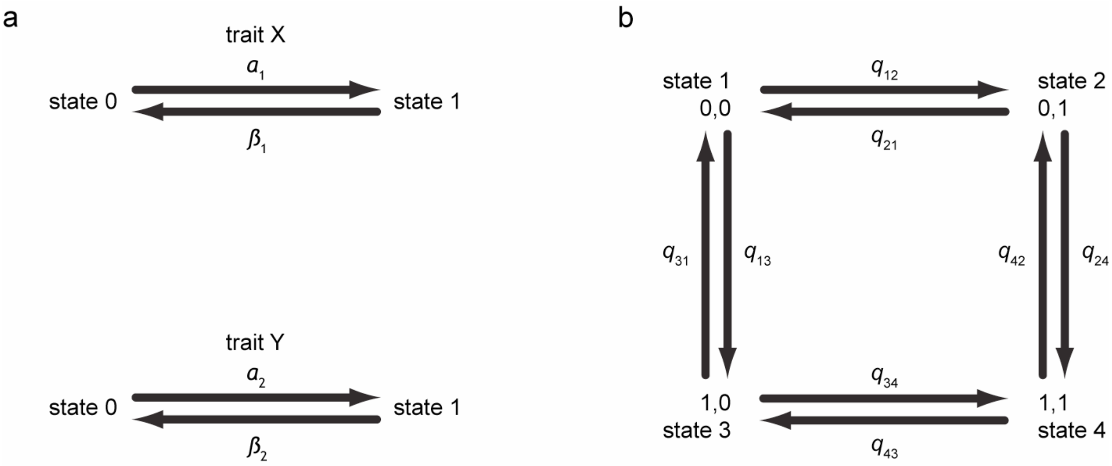
a
trait X
α_1
state 0
state 1
β_1
trait Y
α_2
state 0
state 1
β_2
b
state 1
0,0
q_{12}
state 2
0,1
q_{21}
q_{31}
q_{13}
q_{42}
q_{24}
q_{34}
1,0
state 3
q_{43}
1,1
state 4

Figure 1

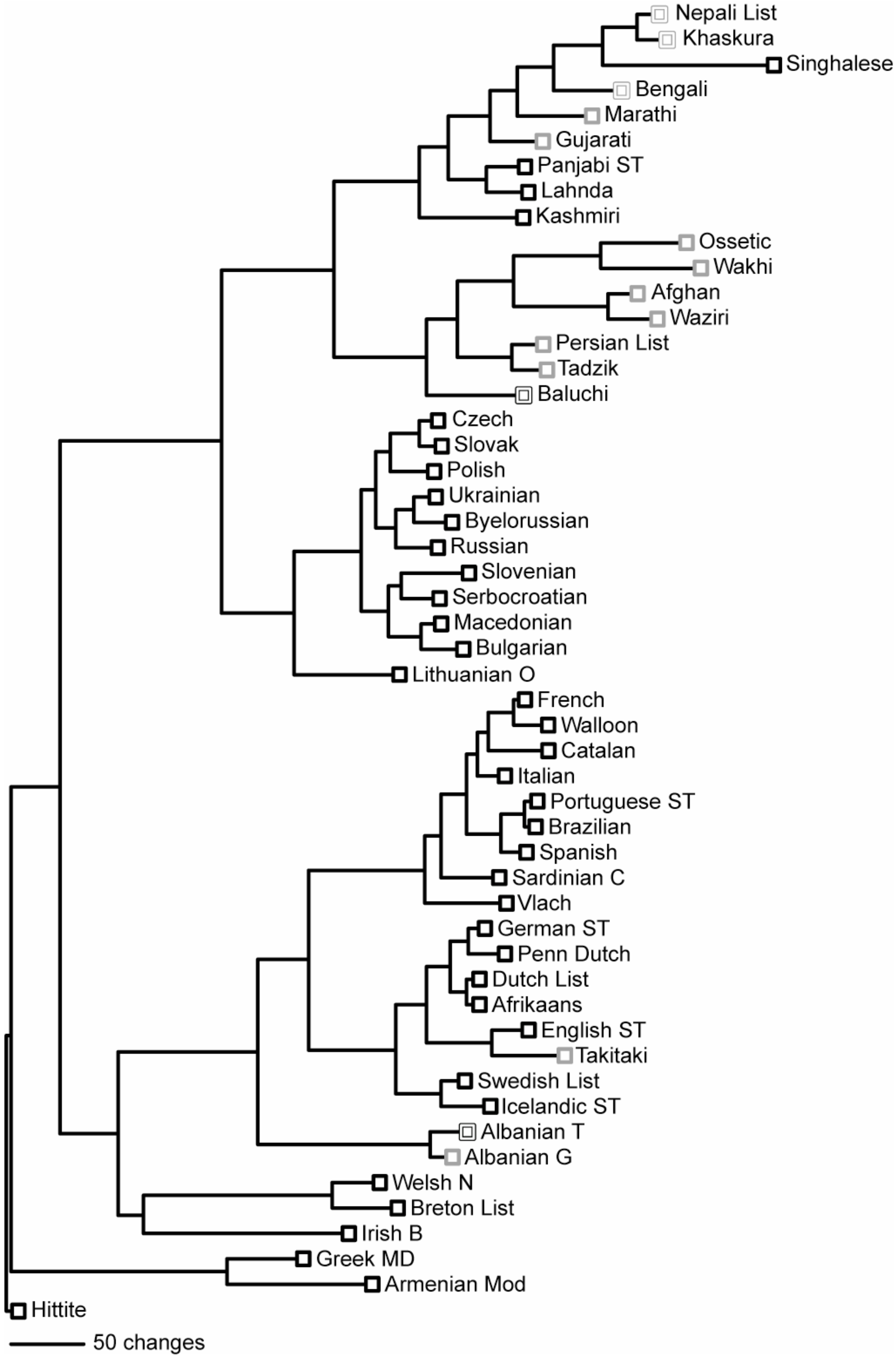
Nepali List
Khaskura
Singhalese
Bengali
Marathi
Gujarati
Panjabi ST
Lahnda
Kashmiri
Ossetic
Wakhi
Afghan
Waziri
Persian List
Tadzik
Baluchi
Czech
Slovak
Polish
Ukrainian
Byelorussian
Russian
Slovenian
Serbocroatian
Macedonian
Bulgarian
Lithuanian O
French
Walloon
Catalan
Italian
Portuguese ST
Brazilian
Spanish
Sardinian C
Vlach
German ST
Penn Dutch
Dutch List
Afrikaans
English ST
Takitaki
Swedish List
Icelandic ST
Albanian T
Albanian G
Welsh N
Breton List
Irish B
Greek MD
Armenian Mod
Hittite
50 changes

Figure 2

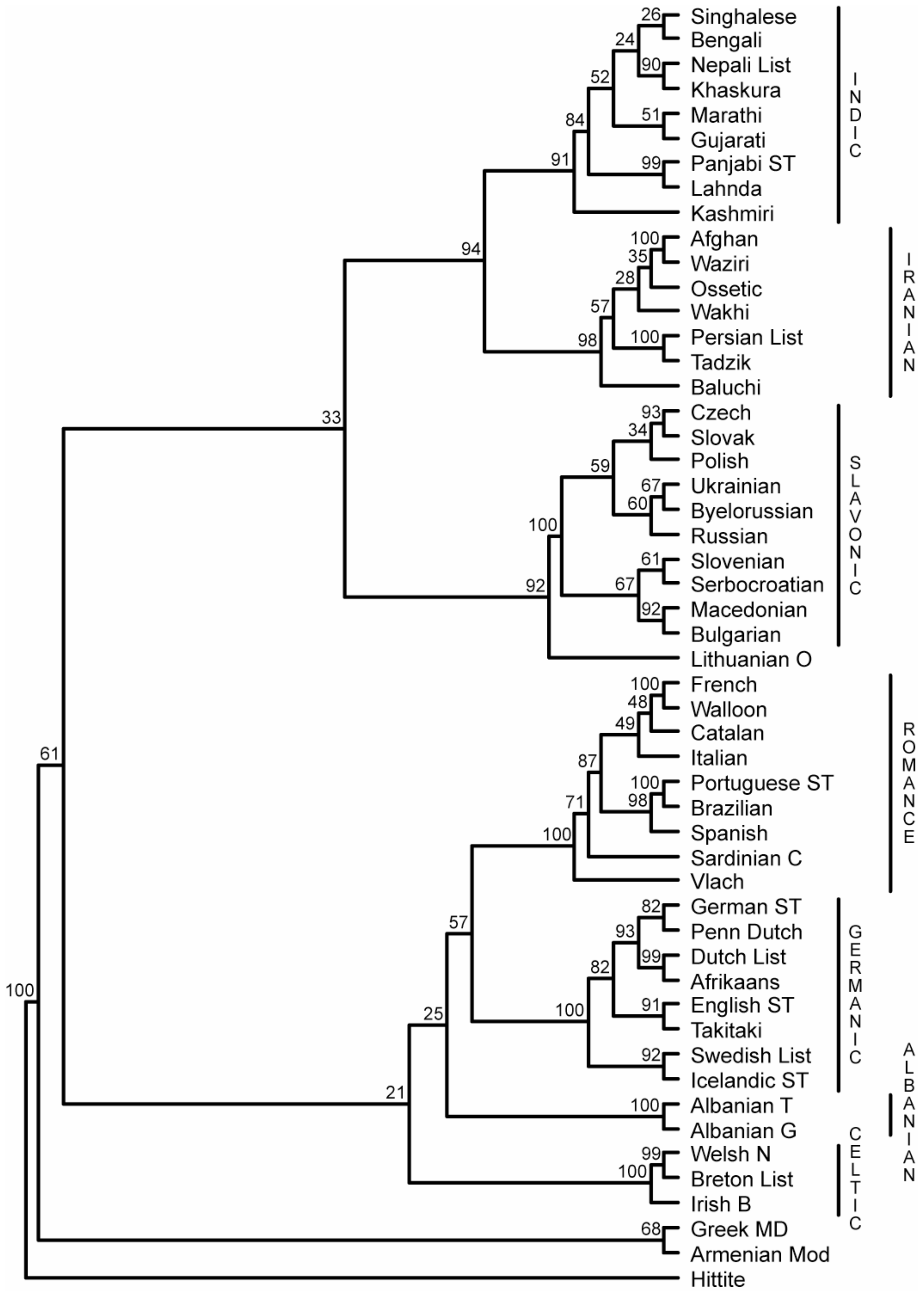
26
Singhalese
24
Bengali
90
Nepali List
52
Khaskura
84
51
Marathi
Gujarati
91
99
Panjabi ST
Lahnda
Kashmiri
INDIC
100
Afghan
94
35
Waziri
28
Ossetic
57
Wakhi
98
100
Persian List
Tadzik
Baluchi
IRANIAN
33
93
Czech
34
Slovak
Polish
59
67
Ukrainian
60
Byelorussian
100
Russian
61
Slovenian
92
67
Serbocroatian
92
Macedonian
Bulgarian
Lithuanian O
SLAVONIC
100
French
48
Walloon
49
Catalan
61
87
Italian
100
Portuguese ST
71
98
Brazilian
100
Spanish
Sardinian C
Vlach
ROMANCE
82
German ST
57
93
Penn Dutch
99
Dutch List
82
Afrikaans
100
25
100
91
English ST
Takitaki
92
Swedish List
Icelandic ST
GERMANIC
21
100
Albanian T
Albanian G
ALBANIAN
99
Welsh N
100
Breton List
Irish B
CELTIC
68
Greek MD
Armenian Mod
Hittite

Figure 3

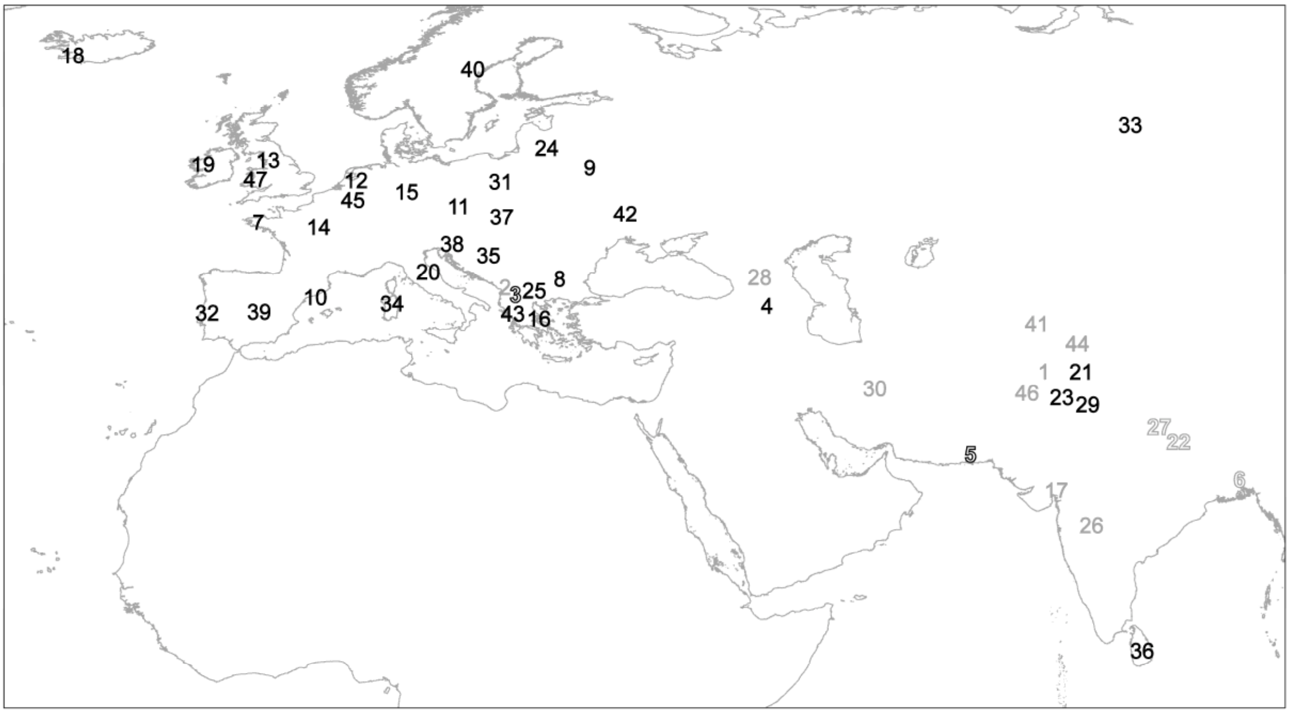
18
40
33
24
19
13
9
47
12
31
45
15
11
42
37
7
14
38
35
20
28
8
2
3
25
10
34
4
32
39
43
16
41
44
1
21
30
46
23
29
27
22
5
6
17
26
36

Figure 4

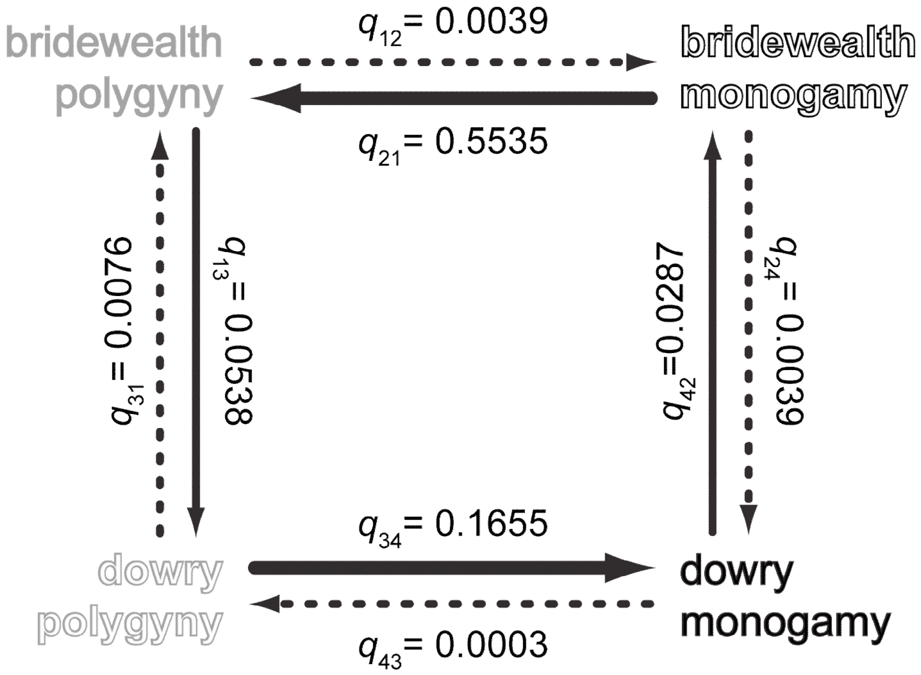
bridewealth polygyny
q_{12}= 0.0039
bridewealth monogamy
q_{21}= 0.5535
q_{31}= 0.0076
q_{13}= 0.0538
q_{42}=0.0287
q_{24}= 0.0039
q_{34}= 0.1655
dowry polygyny
dowry monogamy
q_{43}= 0.0003

Figure 5

Table 1 Comparison of likelihood values for alternative models of evolution of wealth transfer practices and marriage systems in IE groups

Test (d.f.)[a, b]	**Hypothesis**[a]	**Description**[a, c]	**Log-likelihood**[d]	**LR**[d]	**p**
Omnibus (4)	I < D	Correlated evolution	log(I) = -35.95	9.38	0.0009
Alternative model (1)	$q_{12} = 0$	Transition q_{12} excluded	log(D_7) = -26.82	0.50	n.s.
	$q_{13} = 0$	Transition q_{13} excluded	log(D_7) = -28.65	4.17	0.0413
	$q_{21} = 0$	Transition q_{21} excluded	log(D_7) = -30.21	7.28	0.0070
	$q_{24} = 0$	Transition q_{24} excluded	log(D_7) = -26.76	0.39	n.s.
	$q_{31} = 0$	Transition q_{31} excluded	log(D_7) = -26.79	0.44	n.s.
	$q_{34} = 0$	Transition q_{34} excluded	log(D_7) = -28.64	4.15	0.0416
	$q_{42} = 0$	Transition q_{42} excluded	log(D_7) = -28.94	4.75	0.0294
	$q_{43} = 0$	Transition q_{43} excluded	log(D_7) = -26.57	0.00	n.s.
Minimum model (4)	$q_{12} = q_{24} = q_{31} = q_{43} = 0$	Transitions q_{12}, q_{24}, q_{31}, q_{43} excluded	log(D_4) = -26.57	0.00	n.s.
Contingent change (1)	$q_{12} \neq q_{34}$	Change polygyny → monogamy depends on state of wealth transfer	log(D_7) = -26.95	0.77	n.s.
	$q_{21} \neq q_{43}$	Change monogamy → polygyny depends on state of wealth transfer	log(D_7) = -30.89	8.64	0.0033
	$q_{13} \neq q_{24}$	Change bridewealth → dowry depends on state of marriage system	log(D_7) = -26.72	0.30	n.s.
	$q_{31} \neq q_{42}$	Change dowry → bridewealth depends on state of marriage system	log(D_7) = -26.70	0.27	n.s.
Temporal order/ relative rate (1)	$q_{12} \neq q_{13}$	Order of change polygyny → monogamy vs. bridewealth → dowry	log(D_7) = -26.98	0.83	n.s.
	$q_{42} \neq q_{43}$	Order of change dowry → bridewealth vs. monogamy → polygyny	log(D_7) = -28.60	4.07	0.0438

[a] Refer to Pagel (1994) for details.

[b] The degrees of freedom (d.f.) correspond to the difference between the number of parameters of the two models being compared.

[c] The four states in the dependent model are bridewealth with polygyny (state 1: 0, 0), bridewealth with monogamy (state 2: 0, 1), dowry with polygyny (state 3: 1, 0), and dowry with monogamy (state 4: 1, 1).

[d] I and D_n represent the likelihoods of the four-parameter independent and n-parameter dependent models, respectively. The log-likelihoods are compared to the log-likelihood of the eight-parameter dependent model D = - 26.57.

References

Borgerhoff Mulder, M. 1995. Bridewealth and its correlates: quantifying changes over time. *Current Anthropology* 36(3): 573-603.

Bryce, T. 2002. *Life and society in the Hittite world*. Oxford: Oxford University Press.

Dickemann, M. 1979. Female infanticide, reproductive strategies, and social stratification: a preliminary model. In N. Chagnon and W. Irons (eds.), *Evolutionary biology and human social behavior: an anthropological perspective*, pp. 321-367. North Scituate, MA: Duxbury Press.

Dyen, I., J.B. Kruskal and P. Black 1992. An Indoeuropean classification: a lexicostatistical experiment. *Transactions of the American Philosophical Society* 82(5): 1-132.

Farris, J.S. 1969. A successive approximations approach to character weighting. *Systematic Zoology* 18(4): 374-385.

Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125(1): 1-15.

Fortunato, L., C. Holden and R. Mace 2006. From bridewealth to dowry? A Bayesian estimation of ancestral states of marriage transfers in Indo-European groups. *Human Nature* 17(4): 355-376.

Gaulin, S.J.C. and J.S. Boster 1990. Dowry as female competition. *American Anthropologist* 92(4): 994-1005.

Gaulin, S.J.C. and J.S. Boster 1997. When are husbands worth fighting for? In L. Betzig (ed.), *Human nature: a critical reader*, pp. 372-374. New York, NY: Oxford University Press.

Goody, J. 1973. Bridewealth and dowry in Africa and Eurasia. In J. Goody and S.J. Tambiah (ed.), *Bridewealth and dowry*, pp. 1-58. Cambridge: Cambridge University Press.

Goody, J. 1976. *Production and reproduction: a comparative study of the domestic domain*. Cambridge: Cambridge University Press.

Gordon, R.G. (ed.) 2005. *Ethnologue: languages of the world*. 15th ed. Dallas, TX: SIL International.

Gray, J.P. 1999. A corrected *Ethnographic Atlas*. *World Cultures* 10(1): 24-136.

Guglielmino, C.R., C. Viganotti, B.S. Hewlett and L.L. Cavalli-Sforza 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(16): 7585-7589.

Gurney, O.R. 1975. *The Hittites*. London: Allen Lane.

Hartung, J. 1976. On natural selection and the inheritance of wealth. *Current Anthropology* 17(4): 607-622.

Hartung, J. 1982. Polygyny and inheritance of wealth. *Current Anthropology* 23(1): 1-12.

Hartung J. 1983. In defense of Murdock: a reply to Dickemann. *Current Anthropology* 24(1): 125-126.

Hartung, J. 1997. If I had it to do over. In L. Betzig (ed.), *Human nature: a critical reader*, pp. 344-348. New York, NY: Oxford University Press.

Harvey, P.H. and M.D. Pagel 1991. *The comparative method in evolutionary biology*. Oxford: Oxford University Press.

Holder, M. and P.O. Lewis 2003. Phylogeny estimation: traditional and Bayesian approaches. *Nature Reviews Genetics* 4(4): 275-284.

Huelsenbeck, J.P. and B. Rannala 2003. Detecting correlation between characters in comparative analysis with uncertain phylogeny. *Evolution* 57(6): 1237-1247.

Huelsenbeck, J.P., F. Ronquist, R. Nielsen and J.P. Bollback 2001. Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* 294(5550): 2310-2314.

Irons, W. 1979. Cultural and biological success. In N. Chagnon and W. Irons (eds.), *Evolutionary biology and human social behavior: an anthropological perspective*, pp. 257-272. North Scituate, MA: Duxbury Press.

Jackson, G.B. and A.K. Romney 1973. Historical inference from cross-cultural data: the case of dowry. *Ethos* 1(4): 517-520.

Krebs, J.R. and N.B. Davies 1993. *An introduction to behavioural ecology*. Third edition. Oxford: Blackwell Scientific.

Lambiri-Dimaki, J. 1985. Dowry in modern Greece: an institution at the crossroads between persistence and decline. In M.A. Kaplan (ed.), *The marriage bargain: women and dowries in European history*, pp. 165-178. New York, NY: The Institute for Research in History and the Haworth Press, Inc.

Levinson, D. 1994. *Encyclopedia of world cultures*. New York, NY: G.K. Hall & Co.

Levinson, D. and M.J. Malone 1980. *Toward explaining human culture: a critical review of the findings of worldwide cross-cultural research*. New Haven, CT: HRAF Press.

Mace, R. and M. Pagel 1994. The comparative method in anthropology. *Current Anthropology* 35(5): 549-564.

Mace, R. and M. Pagel 1997. Tips, branches and nodes: seeking adaptation through comparative studies. In L. Betzig (ed.), *Human nature: a critical reader*, pp. 297-310. New York, NY: Oxford University Press.

Martins, E.P. and E.A. Housworth 2002. Phylogeny shape and the phylogenetic comparative method. *Systematic Biology* 51(6): 873-880.

Murdock, G.P. 1967. *Ethnographic Atlas*. Pittsburgh, PA: University of Pittsburgh Press.

Murdock, G.P. and D.R. White 1969. Standard Cross-Cultural Sample. *Ethnology* 8(4): 329-369.

Nunn, C.L., M.B. Mulder and S. Langley 2006. Comparative methods for studying cultural trait evolution: a simulation study. *Cross-Cultural Research* 40(2): 177-209.

Pagel, M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society B* 255(1342): 37-45.

Pagel, M. 1997. Inferring evolutionary processes from phylogenies. *Zoologica Scripta* 26(4): 331-348.

Pagel, M. 1999. The maximum likelihood approach to reconstructing ancestral character states on phylogenies. *Systematic Biology* 48(3): 612-622.

Pagel, M. and A. Meade 2005. Bayesian estimation of correlated evolution across cultures: a case study of marriage systems and wealth transfer at marriage. In R. Mace, C. Holden and S. Shennan (eds.), *The evolution of cultural diversity: a phylogenetic approach*, pp. 235-256. London: UCL Press.

Pagel, M. and A. Meade 2006. Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *American Naturalist* 167(6): 808-825.

Pagel, M., A. Meade and D. Barker 2004. Bayesian estimation of ancestral character states on phylogenies. *Systematic Biology* 53(5): 673-684.

Rexová, K., D. Frynta and J. Zrzavý 2003. Cladistic analysis of languages: Indo-European classification based on lexicostatistical data. *Cladistics* 19(2): 120-127.

Swofford, D.L. 2002. *Phylogenetic Analysis Using Parsimony (*and Other Methods)*. 4.0 edition. Sunderland, MA: Sinauer Associates.

Tinbergen, N. 1963. On aims and methods of ethology. *Zeitschrift für Tierpsychologie* 20: 410-433.

Trivers, R.L. 1972. Parental investment and sexual selection. In B. Campbell (ed.), *Sexual selection and the descent of man 1871-1971*, pp. 136-179. London: Heinemann.

Tylor, E.B. 1889. On a method of investigating the development of institutions; applied to laws of marriage and descent. *The Journal of the Anthropological Institute of Great Britain and Ireland* 18: 245-272.

Westermarck, E. 1926. *A short history of marriage*. London: MacMillan and Co., Ltd.

Winterhalder, B. and E.A. Smith 2000. Analyzing adaptive strategies: human behavioral ecology at twenty-five. *Evolutionary Anthropology* 9(2): 51-72.