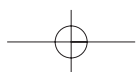
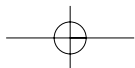
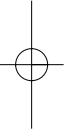
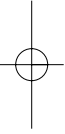


PART II





CHAPTER 10

INTRODUCTION TO PART II ON THE USE OF PHYLOGENETIC COMPARATIVE METHODS TO TEST CO-EVOLUTIONARY HYPOTHESES ACROSS CULTURES

Ruth Mace

In 1994, Mark Pagel and I proposed that phylogenetic comparative methods were appropriate, and indeed essential, for testing co-evolutionary hypotheses in cultural or bio-cultural evolution (Mace and Pagel 1994). It is worth clarifying that we do not mean the comparative method as used by linguists (which means the comparison of words to identify common origins); we use the term 'comparative method' as do evolutionary biologists, who use it to refer to comparison across populations or species to test an adaptive hypothesis.

Comparative methods are one of three main techniques that behavioural and evolutionary ecologists use to test functional hypotheses (Krebs and Davies 1993). The others are experimental manipulations and optimality modelling, generally tested by examining the range of individual differences in behaviour and outcomes in terms of reproductive success, or some correlate thereof. The opportunities for experimental manipulations are limited in human studies. Furthermore, because so many cultural traits are (almost by definition) a property of a whole society rather than just an individual (see Chapter 1 this book), there are few opportunities for examining individual variation. For these reasons, cross-cultural comparison is always going to be an important tool for testing functional hypotheses.

Before introducing the three cross-cultural comparative studies in this section of the book, I will clarify several common misunderstandings of comparative methods that persist in the literature.

'USE OF PHYLOGENIES BRINGS LOSS OF STATISTICAL POWER'

Historically in anthropology, quantitative cross-cultural comparison consisted of seeking simple correlations across cultures of the coincidence of a cultural trait and some ecological or other cultural trait. Such correlations frequently suggest significant relationships; but they have not been popular with most anthropologists, contributing to the already strong suspicion that many cultural anthropologists have of any quantitative analysis. One reason for the suspicion is that many of the supposedly functional associations that have been reported from simple cross-cultural correlations do not seem to be very meaningful.

200 The Evolution of Cultural Diversity

If cultures arise from mother cultures by descent with modification, then cultures cannot be considered independent data points – this is known as Galton’s problem. Whether or not cultural evolution is tree-like was a central topic in Part 1, and from here on I shall assume that, broadly, it is. Figure 10.1 illustrates two of the many possible scenarios for the evolution of nine historically related cultures, in which there is a perfect correspondence between the occurrence of A with B and A’ with B’. A simple chi-squared test might suggest a significant association across cultures, but any p-value would be suspect and at grave risk of a Type I error. This is because neither the five cases of A occurring with B, nor the four cases of A’ occurring with B’ are necessarily independent instances of A changing to A’ facilitating the evolution of B into B’. That could have occurred on four separate occasions, as in Figure 10.1b. Alternatively it might only have occurred once, as in

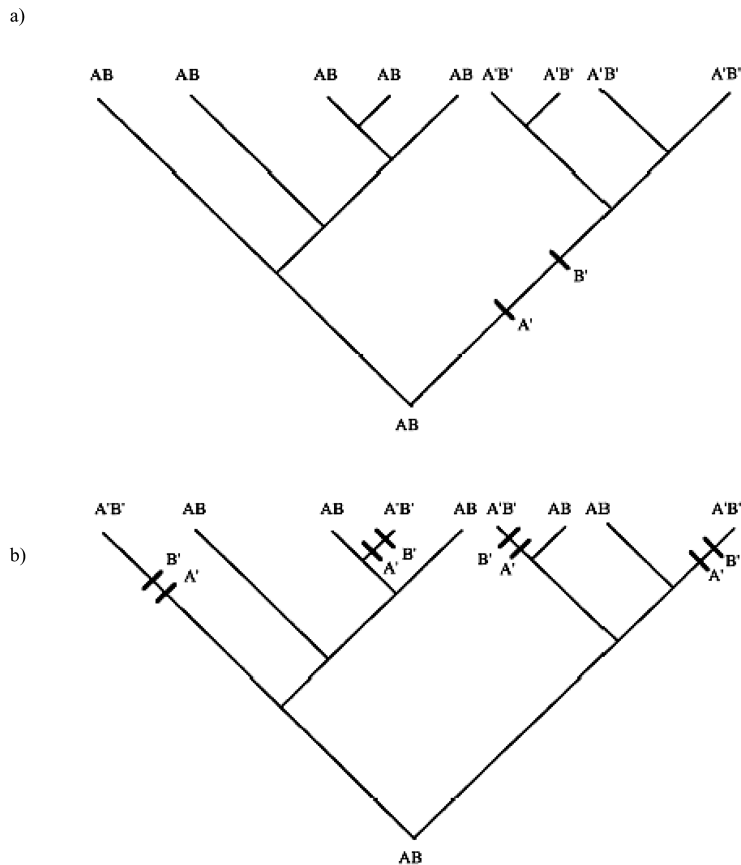


Figure 10.1 Two possible historical reconstructions of the evolution of two traits in nine, hierarchically related cultures (from Mace and Pagel 1994).

Figure 10.1a. Any ahistorical (non-phylogenetic) analysis would not distinguish between these two cases. Whereas one single case of B changing to B' after A turned to A' is not strong evidence of A' and B' co-evolving, this sequence occurring four times independently is. In the latter case it is far less likely that the two traits arose either coincidentally or because of some common third variable. We need to make every attempt to distinguish between these two different historical scenarios in order to test adaptive hypotheses. Phylogenetic comparative methods do this.

Some have argued that by forcing investigators to count only independent events, rather than cultures, phylogenetic approaches make it harder to find significant relationships – that 'statistical power is reduced'. It may be true that simple cross-cultural correlations return a higher frequency of significant relationships, but this is not evidence of greater statistical power. 'Power' is the probability of detecting a true relationship when it exists. The point about simple cross-cultural correlations is that an unacceptable proportion of the significant ones are Type I errors: that is, the null hypothesis is in fact true. So, the complaint about loss of statistical power is erroneous and confuses two very different things.

Fiona Jordan and I (Chapter 11) provide an example of a study where the use of non-phylogenetic statistics would have returned several ostensibly significant correlations that would not be correct. We use a method that uses generalised least squares in a phylogenetically controlled correlation of a continuously varying trait – in this case the sex ratio at birth in human populations. The sex ratio is correlated with various biological and cultural factors. A cross-cultural correlation would have suggested that gene-culture co-evolution could be occurring between marriage system and sex ratio at birth; but a phylogenetic correlation suggests that this is in fact just an artefact of the clumping of both low sex ratios and brideprice (which co-evolves with polygyny) in the African cultures: sex ratio at birth and brideprice are not correlated. Thus, from these data (albeit rather crude, country-level data), there is no evidence of genes and culture co-evolving, unfortunately, as the idea was rather appealing. However, there is evidence that sex ratio in adulthood is correlated with brideprice – males have to pay to get married when the adult sex ratio is high (females are more scarce). This suggests cultural evolution in response to the demographics of the population.

'CONTROLLING FOR PHYLOGENETIC INERTIA'

Using comparative methods that take into account the phylogenetic relationships between cultures is sometimes described as controlling for phylogenetic inertia or phylogenetic constraints. Phylogenetic inertia implies that evolution is weak, slow, or for some reason cannot change a trait, with the result that all of the descendants of a particular species, or culture, inherit a range of traits from their ancestor even if those traits actually no longer serve any adaptive function. However, the fact that members of a clade (related cultures with a common ancestor) all contain the same trait is not evidence of phylogenetic inertia: they may all have the trait for very good adaptive reasons. Consider that most

mammals have five digits at the end of their forelimbs and hindlimbs. This is not because they couldn't have it any other way, but very likely because it is useful: the evidence ironically, lies in the exceptions. Where five digits have been lost or marginalised, such as in the grazing animals, it is because a smaller number is better. The existence of this variation shows that the retention of five digits in the others is not attributable to inertia. Indeed it was probably one of the adaptations that contributed to the success of the mammals.

So, if lack of variation in a trait isn't evidence of inertia, why use comparative methods? The reason has been given above in the discussion of independent events. Lack of variation may indicate that some trait or traits have evolved only once or a small number of times. To be sure that any apparent correlation between them is real, it is necessary to identify independent events of their co-evolution. Phylogenetic comparative methods recognise when apparent correlation is likely to be an artefact of two traits appearing to be correlated but for reasons other than the two being functionally linked.

'NOT ACCOUNTING FOR HORIZONTAL TRANSMISSION'

Sometimes it is argued that phylogenetic comparative methods cannot be applied to cultural evolution, because so much of cultural evolution arises from the horizontal transmission of cultural traits. The first part of the book reports analyses of the extent to which cultural transmission is vertical. These analyses show that in a wide range of cases, despite some horizontal transmission, it has been possible to see a phylogenetic signal in data on cultural traits. This is most especially so in the case of language (eg, Holden 2002; Gray and Atkinson 2003), although phylogenetic signals can also be found in other aspects of culture too. Language trees often show strong and reliable phylogenetic signals, indicating a preponderance of vertical transmission. Equally, language trees can be informative about when the hypothesis of vertical transmission is unlikely to hold.

Assuming that it is reasonable to make a phylogenetic tree, then any question that horizontal transmission of cultural traits invalidates phylogenetic comparative studies evaporates. The tree means that one can ask whether some cultural traits move around the tree horizontally (jumping from one branch to another) or vertically (moving down the tree branches from mother to daughter culture). This would be impossible without a tree.

Changes in cultures can arise from *de novo* innovations, or from borrowing (horizontal transmission). Both are potentially of equal significance in testing an adaptive hypothesis. Why re-invent the plough if you can copy the idea from some neighbouring population? Similarly, if you have no use for the plough, then why would you bother to copy your neighbour? To test the hypothesis that the plough is associated with some other changes in the human societies that adopt it, it is not necessary or indeed sufficient to restrict analyses to instances of the independent invention of a tool used as a plough. If a society from some very different branch of the phylogenetic tree in which the plough originally arose,

adopted the plough and then they acquired some other trait that is commonly seen in the other plough-using cultures, then this provides some of the very strongest evidence in favour of co-adaptation (some functional link between the plough and that other trait). Horizontal transmission is not ignored, nor does it invalidate the phylogenetic comparative method; it provides the method with much of its power to understand cultural co-evolution.

If it were true that most cultural traits were simply infectious, spreading like viruses without any benefit to the individuals or cultures that adopted them, then phylogenetic comparative methods could be suspect in some circumstances. If very few traits behave in this infectious way, then the chances that both of the traits under consideration in a co-evolutionary hypothesis were spreading in that way would be very small – so the chance of spurious correlations between two traits would be low. However, if this kind of ‘cultural infection’ is common, then taking the adoption of two traits as being of statistical relevance to a functional hypothesis could be suspect, because both could move together simply due to geographic proximity even though they were not functionally related.

But what reasons are there to believe that maladaptive cultural traits are so infectious? Richerson and Boyd (2004) have pointed out that the Amish of North America, who wish to preserve a way of life that in many ways is reminiscent of the 19th century, have isolated themselves culturally, to prevent the infiltration of their culture by modern American customs and technology; for example, they are not allowed to watch television. However, the need to do this has probably arisen because the use of modern technology would make their lives easier and is thus appealing to those exposed to it. Other Americans exposed repeatedly to Amish culture do not seem in a great hurry to make their daily lives more arduous by forgoing their motor cars, not to mention buttons and zips. It has been argued that some memes do act more like viruses, in that they parasitise our cognitive structures to reproduce themselves in hosts to whom they give no benefit. Some forms of religious belief might fall into this category. But the evidence that most cultural change is of this type is simply not there.

WHAT TYPE OF COMPARATIVE METHOD TO USE

There are a number of different statistical comparative methods that have been developed to test co-evolutionary hypotheses. Any attempt to take into account the hierarchical relationships between cultures is better than ignoring this problem entirely, but some methods are more powerful than others. Often the nature of the method used is constrained by the nature of the data available.

Sometimes we may have historical information from archaeological or other sources that can tell us about extinct cultures and help inform our understanding of cultural change over time. But such information is usually very limited. Then methods have to infer the likely historical pattern of cultural changes statistically, from the distribution of cultural traits observed in extant cultures (or whatever data is at the tips of the tree), and the tree. All comparative methods use some

form of optimising criteria to do this. Most early methods used parsimony, that is, a method which seeks the smallest number of evolutionary changes that could have given rise to the distribution of traits observed on the tree. Parsimony is useful, but of course evolution in general and cultural evolution in particular may not always be parsimonious. Reversals, when a trait switches and then switches back again, possibly even more than once along a branch of the tree, might be common. Many recent studies in evolutionary biology are now using comparative methods based on maximum likelihood (Pagel 1999a, 1999b). In these methods, the full range of possible evolutionary pathways are explored, and weighted according to how likely they are to have occurred, given their current distribution and the tree. These methods are powerful, and have only been possible to implement since powerful computers became widely available. The methods used in the chapters in Part II of the book all use maximum likelihood to test evolutionary hypotheses. These are not the only usable methods by any means, but we have chosen them for a number of reasons which make them especially useful for testing hypothesis in cultural evolution.

Table 10.1 summarises some of the differences between parsimony and maximum likelihood for testing evolutionary hypotheses. In comparative methods using likelihood, evolutionary models are much more explicit and precise so that it is possible to calculate whether some models of evolution are more likely than others to have given rise to the patterns of diversity that we observe in our data. Explicit estimates of the rates and patterns of evolutionary change can be generated. It is possible to test the direction of evolutionary change, as well as simply whether or not two traits are correlated. Ancestral states can be described as probabilities rather than just as one or other condition. Whilst the certainty of a single 'answer' may be appealing, it is usually spurious. Most

Table 10.1 Differences between comparative methods based on parsimony and based on maximum likelihood.

Parsimony approaches	Likelihood approaches
Intuitive	Not so much
Computationally quick	More intensive
Treats ancestral states as known : may underestimate the amount of change. Single value assigned to each character at internal nodes	Incorporates uncertainty : good when trait evolution is rapid. Probability distribution of character states at internal nodes
Branch length information may not be incorporated into model	Branch length information used to calculate rates of character transition
All types of change treated as equally likely	Transition-rate parameters estimate all kinds of change
Difficult to detect order of change. Simply seeks correlations	Model of evolutionary change is explicit. Can detect order of change

ancestral states are uncertain, and the ability to estimate and take into account that uncertainty is one of the most important advantages of the methods that use likelihood.

Clare J Holden and I (Chapter 12) use a method developed by Mark Pagel (1994) to analyse the co-evolution of discrete characters, in this case matrilineal or patrilineal descent, and the presence or absence of cattle-herding. The likelihood of a model in which the two traits evolve independently of each other is compared with the likelihood of a model in which the state of one trait influences the rate of change in the other trait; in other words, the two traits are co-evolving. We find that the dependent model, in which one trait influences the rate of evolution in the other, is significantly more likely than the model in which the two traits evolve independently. The adoption of cattle means that the culture concerned is more likely to become patrilineal.

In both Chapters 11 and 12, we use trees that are inferred using parsimony methods, either from language data (Chapter 12) or from genetic data (Chapter 11); and we consider the trees to be correct for the purposes of our analyses. But the comparative methods used to test for the co-evolution of cultural or bio-cultural traits on the tree use likelihood to evaluate the different evolutionary models. However, Mark Pagel and Andrew Meade (Chapter 13) describe a new development of the comparative method which not only incorporates the uncertainty in the evolution of the cultural traits being examined, but also considers the uncertainty in the tree itself, using MCMC and Bayesian statistics. In this case they examine the co-evolution of dowry and monogamy in a sample of Indo-Europeans. Over 500 possible Indo-European language trees, all weighted according to their likelihood, are used in the comparative analysis, so the results cannot be considered a product of just one tree that could be incorrect. The example given takes a simple dataset, so the results themselves need to be considered as preliminary, but they show a significant correlation between dowry and monogamy, as predicted by evolutionary theory. But the important point here is that many of the problems associated with the inevitable uncertainty over historical relationships between cultures can be overcome by taking that uncertainty into account in the analysis. The analysis in this last chapter represents the cutting edge of the field.

All the methods used in this part of the book are readily available (see references in the relevant chapters) and do not require users to have particular computational or mathematical expertise to apply them. Ultimately, all these comparative methods will be evaluated by their ability to tell us new things about our evolution.

