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Part 1
Comparative methods

Editor's introduction

Our ability to analyse variation within and between taxonomic groups has been enhanced by the development of techniques for the statistical manipulation of comparative data, but we have yet to reach a consensus on which techniques are appropriate for specific analyses. Thus, several possible approaches are presented. A comprehensive overview of the pros and cons, as well as how to carry out different comparative techniques can be found in Harvey and Pagel (1991).

It should be noted that there are two separate issues involved in phylogenetic analyses. The first of these is fundamentally *statistical*. Although it has long been recognised that the use of 'species' data in comparative analyses on closely related taxa may violate statistical assumptions of independence of data points (e.g. Crook, 1965), this was elaborated in relation to phylogenetic similarity in allometry by Felsenstein (1985). Stated simply, closely related taxa may share traits derived through that genealogical relationship rather than as a result of selection, and species as such are not independent within lineages. This issue had been at least partially explored in earlier socioecological and life history research on primates through data reduction techniques – the use of mean values for different taxonomic levels – the 'higher node' approach (e.g. genera: Clutton-Brock and Harvey, 1977; subfamily: Harvey, Martin and Clutton-Brock, 1987).

But there is a second, more interesting, question raised by comparative analyses, that of the *evolutionary* similarity within and between related taxa (Purvis and Harvey, 1995), and it is in this context that the value of phylogenetically controlled comparisons is most apparent. One of the most common and accessible techniques, Comparative Analysis by Independent Contrasts (CAIC), is presented by Purvis and Webster in Chapter 3. The value of CAIC lies in its simplicity and in the detailed primate phylogeny derived by Purvis. Some problems with the method are also considered.

The fundamental question, however, remains whether the comparative study seeks to determine if evolutionary change in traits has occurred, or

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whether it seeks to identify variation between species or groups of species in an attempt to determine causality in this observed variation. Often, a comparison of the results obtained from several different analytical techniques may allow for more robust interpretations. This procedure is used in a number of the chapters in subsequent parts of the book. Another technique for exploring evolutionary variation is that of nested analysis of variance. Originally devised to determine which taxonomic level explained the observed variance in a trait, and thus to limit comparisons to that 'independent' level, it has a further utility in partitioning variance between these taxonomic levels and thus provoking evolutionary explanations. Methods such as correcting for degrees of freedom in nested ANOVAs also address the problem of statistical dependence (see Smith, 1994). Interestingly, there may be times when different taxonomic levels explain variation for distinct variables, suggesting that it would be difficult, if not impossible, to 'control' for phylogeny by selecting a single independent higher taxonomic node for analysis. For example, among primates, variance in adult body weight is greatest at the level of the subfamily, whereas that of density is greatest at the population level (Vella, 1995).

If two species share traits, is this the result of evolutionary convergence or simply due to sharing ancestral traits between closely related descendants? If we are exploring evolution within and between lineages, then obviously the lineages themselves are part of the data we are examining. It becomes critical to know both the phylogenetic relationships and to tease apart the ancestor–descendant traits, as noted by Purvis and Webster. The potential to determine separate evolutionary events by cladistic analysis is outlined by Robson-Brown (Chapter 2). Such techniques are far more accessible with current programs, but users need to be aware of the debates about homology and analogy explored by Robson-Brown.

Other techniques, which rely on 'species' data but allow for an assessment of the effects of phylogeny on the observed patterns, are potentially available; for example the use of maximum likelihood estimators for coevolution in discrete traits (e.g. Pagel, 1994; Mace and Holden, Chapter 15), or multidimensional scaling of traits which can produce visible clusters among close phylogenetic relatives (e.g. Bean, Chapter 13). MacLarnon, Chivers and Martin (1986) produced evidence for phylogenetic similarity in gut areas among primates using multidimensional scaling, with a consistent cluster of colobines in analytical space, despite observed differences in diets from fruits, through seeds to mature leaf (Davies and Oates, 1996). The power of such analyses lies in their ability to explore patterns explicitly due to shared descent. Other possible means for incorporating phylogeny that do not rely on phylogenetic subtraction, and thus the assumption that the mean of nodes reconstructs a single ancestral state (e.g. Pagel and Harvey, 1988; Stearns, 1992), could lie in non-linear modelling, in nested analysis of covariance, or in principle components data reduction techniques. Consensus on the 'most' appropriate technique is still to be found.

The point of providing several different techniques and perspectives in this book is to focus researchers on making explicit the hypothesis being tested. Is it an evolutionary explanation, a mechanical or physiological one, or a functional relationship? These issues are presented by MacLarnon in a general overview of methodology (Chapter 1). When and why should species be expected to vary? How do rates of evolution within lineages vary? What are the effects on traits? Are predictive trends the aims of the analysis or are we seeking mechanisms in evolution? The technique used, or combinations of methods, needs to be tailored to suit the questions. Even after 30 years of debate, no single method can yet be considered sufficient or even the most appropriate, and it is the question not the methodology that should drive the exploration.

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1 The comparative method: principles and illustrations from primate socioecology

ANN MACLARNON

Introduction

There are two major means of investigation across a wide range of sciences, both natural and social. These are the experimental method and the comparative method. In the so-called hard sciences – physics and chemistry – and also the 'harder' end of biology, investigation is more commonly by experimental manipulation. Other biological questions, notably those concerning evolutionary history and adaptation, are more or less inaccessible to experimentation, as are other aspects of the natural world, such as astronomical phemonena. Exploration of these areas and the development of explanations are undertaken largely by the comparative method, whereby common patterns and principles of variability are sought out, providing the basis for possible interpretation in terms of causes and effects. Similarly, in the social sciences, comparisons can be made across space and time of different societies, divisions or aspects of societies, with the aim of uncovering the origins and explanations of present features and past changes.

The comparative method has its origins in the realisation of the Enlightenment that the natural world can be understood and explained in terms of common principles and predictable variation. It involves testing the generality of suggested explanations for characteristics or phenomena, in contrast to *ad hoc*, one-off explanations that may merely reflect coincidence rather than causal connection. Predictions can be made from proposed general principles, and tested on further species, societies, stars or galaxies, and if borne out, they provide increased support for the validity of a principle.

The fundamentals of the comparative method were first expounded in the mid-nineteenth century by John Stuart Mill in his book *A System of Logic* (1872, 1967) in the chapter 'Of four methods of experimental inquiry'. These four methods essentially describe the basic principles of logical deduction used in scientific inquiry today, including the comparative method. Despite the fact that Stuart Mill's examples mostly come from the physical rather than the living world, the applications of the methods as outlined, their difficulties and limitations, are entirely pertinent to the comparative method in biology, including socioecology. The four methods are as follows:

1. Method of Agreement. 'If two or more instances of the phenomenon under investigation have only one circumstance in common, the circumstance in which alone all the instances agree is the cause (or effect) of the given phenomenon.' (1967, p. 255).
2. Method of Disagreement. 'If an instance in which the phenomenon under investigation occurs, and an instance in which it does not occur, have every circumstance in common save one, that one occurring only in the former; the circumstance in which alone the two instances differ is the effect, or the cause, or an indispensable part of the cause, of the phenomenon.' (1967, p. 256).

   These two methods can be combined in the Joint Method of Agreement and Difference:

   'If two or more instances in which the phenomenon occurs have only one circumstance in common, while two or more instances in which it does not occur have nothing in common save the absence of that circumstance, the circumstance in which alone the two sets of instances differ is the effect, or the cause, or an indispensable part of the cause, of the phenomenon.' (1967, p. 259).
3. Method of Residues. 'Subduct from any phenomenon such part as is known by previous inductions to be the effect of certain antecedents, and the residue of the phenomenon is the effect of the remaining antecedents.' (1967, p. 260).

   (Note: By 'antecedent' Stuart Mill is referring to conditions rather than ancestors.)
4. Method of Concomitant Variation. 'Whatever phenomenon varies in any manner whenever another phenomenon varies in some particular manner, is either a cause or an effect of that phenomenon, or is connected with it through some fact of causation.' (1967, p. 263).

The main principles of scientific inquiry are established in the first two Methods, while the third and fourth can be seen as special cases of the Method of Difference. The Method of Difference describes a basic principle of good experimental design whereby all factors bar one are the same for all samples, and thus any difference in findings between the samples is related to the one differing factor (see also Chapter 3). As Stuart Mill discusses, this is a better form of experimental design than the Method of Agreement, because it is easier to ensure that virtually all circumstances are identical, as the Method of Difference requires, than to be certain that one, and only one circumstance of relevance is the same, for the Method of Agreement. However, the strict conditions required by the Method of Difference can rarely be found in the natural world, where observations of similarities and differences between natural phenomena are the only available sources of data and where experimental manipulation is not possible. The requirements of the pure Method of Difference are highly unlikely to be met if the experimental design cannot be controlled. As Stuart Mill puts it, ‘In the spontaneous operations of nature there is generally such complication and such obscurity . . . and [these operations are] therefore so seldom exactly alike in any two cases, that a spontaneous experiment, of the kind required by the Method of Difference, is commonly not to be found’ (1967, p.257). Hence, when using the comparative method rather than experimental inquiry, the Method of Agreement is generally more appropriate.

For the Method of Agreement, the circumstances in common must be the only ones that could possibly have a cause-and-effect relationship with the phenomenon of interest. In practice, it is difficult to be certain that this requirement is met, even when the experimental design can be controlled. Hence, if the experimental design is controllable, the Method of Difference is preferable. However, the Method of Agreement can still be useful even when the absolute exclusion of other possible relevant common circumstances is not possible. At the very least, even if phenomenon *a* is only found when circumstance *A* is in place, then circumstance *A* may be a *condition* for the existence of *a*, though they are not necessarily related as cause and effect. This is where the Joint Method of Agreement and Difference enables closer approximation to the determination of a cause-and-effect relationship, and in fact many of the applications of the comparative method in evolutionary biology essentially use the Joint Method of Agreement and Difference. By comparing different circumstances under which a phenomenon occurs and does not occur, it can be deduced which of the different circumstances are at least *conditions* for the presence or absence of a phenomenon, even if a causal link cannot be established with certainty. It is always possible that another, unidentified, third factor actually *causes* both the variation in circumstances and the presence or absence of the phenomenon. Put into modern terms, ‘correlation does not mean causation’. However, establishing a conditional link is a useful step that other information or comparisons may help to make firmer.

The Method of Residues can be seen as the Method of Difference under special circumstances, in which a phenomenon is caused by several factors. If a case in which all but one of these factors is present is compared with another case in which all the factors occur, the difference in the size of the phenomenon between the first and second instances is related to the differing factor. As with the Method of Difference, the difficulty in using this method for deduction from observations of the natural world comes in making the assumption that all circumstances are similar save one. Nevertheless, the Method of Residues as described by Stuart Mill forms an interesting parallel with the method of phylogenetic contrasts recently developed for comparative biology (see Chapter 3). This method utilises subtraction (or calculation of residues) between the sizes of a phenomenon or feature in pairs of closely related taxa, which share many factors because of common ancestry. It investigates whether such subtracted differences are associated with differences between the paired taxa in some other feature of biological or adaptive concern.

Stuart Mill's Method of Concomitant Variation is applicable in cases in which phenomena are always present to a greater or lesser extent, and hence it is not possible to compare the effects of their presence and absence. In such cases, comparison can be made between the size of two phenomena in different contexts, and rules can be deduced about the relationship between changes in one phenomenon and changes in the other, which may reflect a cause-and-effect relationship. This method therefore applies to phenomena or variables that are continuous as opposed to categorical variables. Like the Method of Residues, the Method of Concomitant Variation is really a special case of the Method of Difference, and it is widely used in comparative biology, including applications of phylogenetic contrasts to continuous variables.

Throughout his explanation of the four methods, Stuart Mill emphasises the difficulty of determining which of two related phenomena is the cause, and which the effect. In an extended example investigating the cause of dew formation, the problem is resolved by recognising the primacy of basic physical properties such as the heat conduction of different materials, and these are therefore identified as the causal factors. In comparative biology, reference to basic biological laws and knowledge is similarly useful.

The use of the comparative method in evolutionary biology essentially follows the methods outlined by Stuart Mill and encounters the difficulties he describes. The resulting logical deductions resemble those possible from experimental results, but with the handicap that research design played no part in determining the combination of phenomena and circumstances, variables and subjects in each 'natural experiment'. There are therefore inevitable gaps in a simple line of deduction, and the comparative method involves making best use of whatever 'natural experiments' are available, for example the species (populations, higher level taxa, etc.) that exist. Good biological knowledge of the factors and features that vary between sample species, and of fundamental biological laws and processes is essential. Detailed methodological issues are also important where they affect results. The chapters of this book provide rich and varied examples of the use of the comparative method in socioecology.

The first step: investigation of patterning

The first step in comparative analyses is to describe the patterns of distribution of the characteristics of interest across a chosen sample, in order to establish whether the conditions for one of the four methods exist. This involves investigating whether particular variants of one categorical variable are associated with particular variants of another, or whether continuous variables are correlated across the sample. Essentially, this is a similar process whether the variables concerned are categorical or continuous, and many features can be described either way. For example, dietary variation can be categorised according to the predominant food, as insectivory, frugivory etc., or measured according to the proportion of a particular food type in the diet, such as percentage fruit (e.g see Chapter 13). Where there is a choice of either a categorical or continuous measure, factors such as the nature and quality of available data, and the question under investigation are important. For example, duration of lactation is a measure used in both Lee and van Schaik *et al.*'s chapters (Chapters 5 and 8). Lee's study focuses on variation in the length of the lactation period itself and the degree of correlation with other continuous life history variables. However, for van Schaik *et al.*, the feature of interest is categorical: whether the lactation period is longer or shorter than the gestation period. If it is shorter, post-partum oestrus, enabling reconception immediately following a birth, would be a viable evolutionary option, given that energetically the mother must wean one infant before having to feed a second. It should be borne in mind, however, that where it is possible to choose between categorical and continuous versions of a variable, this could affect the results, particularly levels of significance.

In comparing different species, variation in overall body size is commonly an important factor. The question of interest may be how a variable, say brain size, correlates with body size, or attention may be focused on residual variation from scaling relationships, such as relative brain size. Both types of investigation are utilised in this volume (e.g. Chapters 4 and 5). Allometric methods of analysis are commonly necessary in cross-species comparisons as many features do not scale to body size, or to each other, in a linear fashion. Rather, they are related through power functions. Thus, simple ratios, for example of neonate weight to maternal weight, should only be used with great care. The intention may be to ‘remove size’ from the comparison of species, but such ratios will not be ‘size free’ unless the variables concerned scale linearly with one another – that is, with the same exponent in relation to body size. For example, Charnov’s recent life history theory (see Chapters 4 and 6) predicts that several life history characteristics will scale to body size with the same exponent (0.25). Hence, ratios of these variables are expected to be constant across species. However, instances of size-free ratios are rare in comparative biology.

The analyses presented by van Schaik *et al.* (Chapter 8) illustrate the centrality of investigating patterning to the comparative method. Data were collected for primate species for a wide range of features such as the incidence of infanticide, infant care styles, whether lactation is longer or shorter than gestation, mating patterns during pregnancy, the presence or absence of post-partum oestrus, the development of sex skin, and whether females produce calls related to mating. These data were examined to determine whether the pattern of distribution across species of variants of one feature is associated with that of another – the basic requirement if variables are causally or functionally related. For example, the species in which the mother alone carries the infant do not have post-partum oestrus, whereas most of those which park their infants, or in which carrying is shared with other individuals, do. In Ross and Jones’ study (see Chapter 4), patterning is similarly fundamental, but here the variables are largely quantitative, such as maternal weight, age at first reproduction, mortality rates and interbirth intervals. The first step was to investigate the pattern of correlation between the variables. For example, across primates, taking variation in body weight into account, levels of mortality among infants and juveniles are correlated with birth rates, and species with higher pre-reproductive mortality reproduce faster. However, adult mortality rates are not correlated negatively with age of first reproduction for females, as was predicted; species with higher adult mortality do not start reproducing earlier (at least not in the small sample available).

The question of homology

A fundamental requirement of the comparative method is that the features compared across a sample should be homologous. Robson-Brown (Chapter 2) provides an overview of attempts to define homology and their