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Comparing Life Histories Using Phylogenies

Paul H. Harvey and Anne E. Keymer

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Comparing life histories using phylogenies

PAUL H. HARVEY AND ANNE E. KEYMER

Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.

SUMMARY

The comparative method as recently developed can be used to identify statistically independent instances of life-history evolution. When life-history traits show evidence for correlated evolutionary change with each other or with ecological differences, it is often possible to single out the trade-offs and selective forces responsible for the evolution of life-history diversity. Suites of life-history characters often evolve in concert, and recent optimality models incorporating few variables show promise for interpreting that evolution in terms of few selective forces. Because hosts provide well-defined environments for their parasites, when host–parasite phylogenies are congruent it is possible to test ideas about the evolution of particular life-history and size-related traits.

1. INTRODUCTION

Life histories have evolved to differ among species. In this paper we ask how those differences should be examined if we are to make sense of why they evolved. The answer to our question involves two steps. First, we shall describe how comparisons across species are used in evolutionary biology. Second, we shall use the life-history theory described by previous contributors as a basis for deciding which comparisons are likely to prove the most useful for distinguishing among conflicting ideas. Throughout, we shall illustrate our points with examples based on life-history variation drawn from various animal groups.

2. THE COMPARATIVE METHOD IN EVOLUTIONARY BIOLOGY

Like astronomy or geology, evolutionary biology is largely a science about history. Evolutionary biologists must, therefore, use methods that are appropriate for retracing history. The role of experimentation is limited for several reasons, not least of which are the timescales involved. Similarly, observations of evolution in action are both scanty and likely to be of very limited relevance to major questions about the diversity of life on earth. The comparative method, however, provides a means for testing many ideas about why evolution has taken particular routes. It also provides a natural way of cataloguing diverse data sets.

The important processes that make the comparative method work are parallel and convergent evolution: when similar evolutionary responses occur to similar selective pressures, then evolutionary biologists are able to identify independently evolved correlations between characters and environments. Indeed, whole clusters of characters are likely to show correlated evolutionary change, so a successful comparative analysis can have considerable explanatory power. For example, Turner (1975) pointed out that the association of certain butterfly caterpillars with toxic food plants was, as expected, linked with an ability to sequester toxins (and consequent avoidance by predators), the evolution of aposematic or warning coloration, small home range sizes and ranges of courtship, communal roosting, delayed sexual maturity, and increased longevity. From a simple change in diet, associated responses in morphology, behaviour, and life history seem to follow in this one taxonomic group.

As mentioned above, the logic of the comparative method rests on the processes of parallel and convergent evolution. It is, therefore, important to recognize that similarity among extant species may be inherited from common ancestors, rather than having evolved by parallel or convergent evolution. (There are many reasons why closely related species are likely to remain similar: speciation into similar niches and phylogenetic time lags are two. These and others are discussed by Harvey & Pagel (1991).) Accordingly, species values do not provide independent data for comparative analyses, and the best comparative tests must utilize available material on phylogenetic relatedness among the species in a sample. Take the phylogenetic tree in figure 1 in which the higher nodes denote generic status, the next lower nodes family status, and the bottom node shows that all species belong to the same order. Species within genera are very similar to each other on characters X and Y. However, species within the same family but belonging to different genera are more similar to each other than species from different families. This means that neither family nor generic averages provide suitable data points for comparative analyses. How, then, should such analyses be performed?

Two types of procedure are available, which we call

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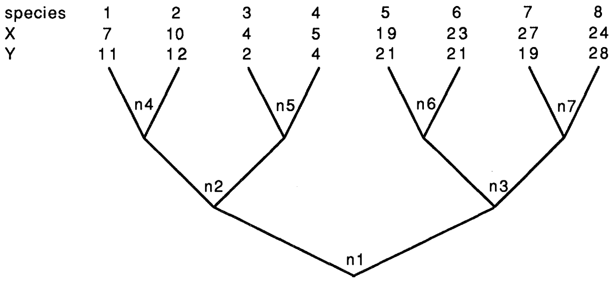

Figure 1. A hypothetical phylogenetic tree showing the relation between eight extant species. Pairs of species emanating from each of the four higher nodes in the figure (n4, n5, n6, n7) are from the same genus, and pairs of genera arising from the intermediate level nodes (n2, n3) are from the same family. Characters X and Y differ among the species, but species with more recent common ancestors have more similar values for both X and Y.

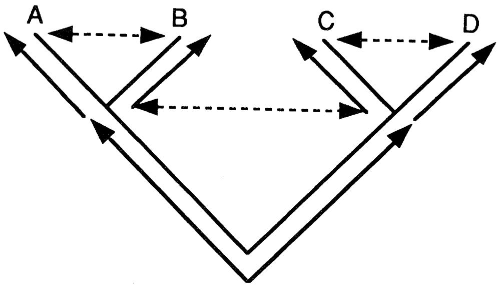

Figure 2. A hypothetical phylogenetic tree showing the relation between four species. The six full-arrowed lines denote directional comparisons that are possible between ancestors and descendants. The three dotted-arrowed lines denote non-directional comparisons. If the phylogenetic tree is known but character states are available for only extant species, there would be only three degrees of freedom in the data (the number of species minus one) and non-directional analyses are appropriate. If ancestral character states for the nodal species are also known there will be six degrees of freedom in the data (the number of species plus the number of nodes minus one), thus allowing directional analyses to be used.

'directional' and 'non-directional' analyses. For the phylogenetic tree shown in figure 2, the full arrows denote directional analyses which involve comparisons between seven different ancestral and descendant taxa. If ancestral phenotypes are known, such directional analyses are satisfactory – the number of nodes plus extant species is seven, allowing six comparisons to account for all the degrees of freedom in the data. Unfortunately, ancestral phenotypes are usually not known and with data for only four extant species being available, three independent non-directional comparisons are possible. Felsenstein (1985) points out that, under a Brownian motion model of evolutionary change, the three non-directional comparisons labelled by dotted lines are statistically independent. The dotted line between the two nodes is a comparison between generic values, calculated as the averages of constituent species values. The non-directional comparisons have a ready evolutionary interpretation: they denote differences that have evolved between daughter taxa emanating from a common ancestor.

Grafen (1989) and Pagel & Harvey (1989) have described methods for applying Felsenstein's non-directional comparative technique to real data. Their methods are designed to overcome a number of problems, including how to deal with multiple nodes (many genera consist of three or more species which presumably mask two or more dichotomies) and how to determine branch lengths from real data. Here we sweep aside such details and summarize the procedures for a primitive non-directional comparative test in figure 3. As is evident from the figure, ultimately a series of contrasts for one variable, perhaps a life-history variable, is compared with a series of contrasts for another variable, perhaps a measure of lifestyle or ecology. Usually, larger contrasts will be associated with lower nodes – differences between families in an order are likely to be larger than those between species within a genus. Evidence for correlated evolution is provided by contrasts for one character not changing independently of those for another character. It is always important to examine scatterplots of contrasts to check for instances of nonlinear correlated evolution (see Harvey & Pagel 1991).

(*a*) *An example of a non-directional comparative analysis*

We present here a summary of a typical non-directional comparative test of a theory about life-history differences. It has often been suggested that species with high metabolic rates for their body sizes live faster and shorter lives: that is, they have higher fecundity (measured in terms of number of young produced per unit time) and shorter lifespans (see, for example, Calder & King 1974; Fenchel 1974; Millar 1977; Blueweiss *et al.* 1978; Sacher 1978; McNab 1980, 1986; Western & Ssemakula 1982; Swihart 1984). Avian phylogenetic relations are now reasonably well known, owing in large part to the work of Sibley and his colleagues using DNA–DNA hybridization methods (see Sibley *et al.* 1988). Furthermore, avian basal metabolic rates and life histories are also widely described in the literature. Now that the data are available, it is possible to test whether the metabolic rate theory holds.

Trevelyan *et al.* (1990) used a non-directional independent comparisons method to determine whether there was evidence for correlated evolution between metabolic rate and life histories across a sample of 325 bird species when body size was held constant. Eleven life-history variables were used in the analysis: hatchling mass, egg mass, clutch size, incubation time, age at fledging, age at independence, age at first breeding, lifespan, number of broods per year, interval between eggs, and clutch mass. Three sets of contrasts were calculated: one for the life-history variable of interest, one for body mass, and one for metabolic rate. There was clear evidence for correlated

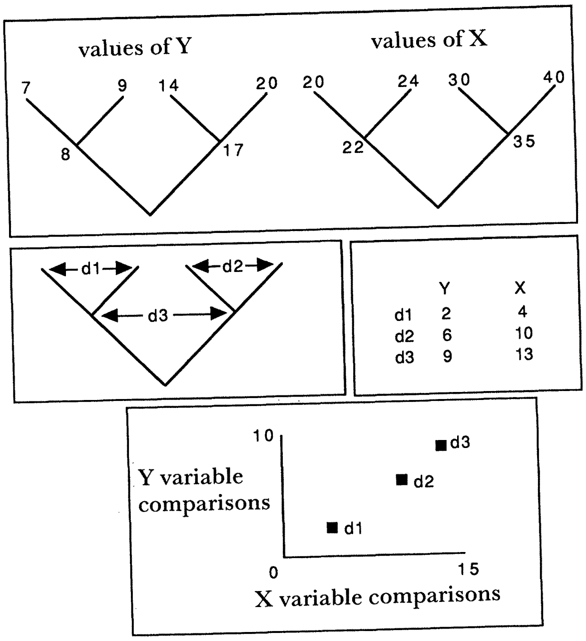

Figure 3. A non-directional contrast analysis. Under a Brownian motion model of evolution, d1, d2 and d3 provide independent comparisons (Felsenstein 1985). In the example, positive correlated evolutionary change between the X and Y variables is evident: large positive change in X is associated with large positive change in Y, while a small positive change in X is associated with a small positive change in Y. Each of the three comparisons in X is conditioned to be positive.

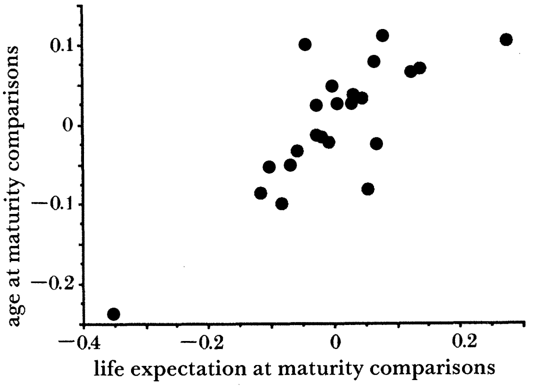

Figure 4. Independent comparisons calculated from Millar & Zammuto's (1983) data. Age at maturity and life expectation comparisons are both corrected for body mass in the figure, being given as the residuals from the regressions of each set of comparisons on body mass comparisons. The correlation is highly significant ($r = 0.80$, $n = 23$, $p < 0.001$). The bottom left point is a comparison between *Ochotona princeps* and *Sylvilagus floridanus*, and when this outlier is removed the correlation remains highly significant ($r = 0.66$, $n = 22$, $p < 0.001$). After Harvey & Pagel (1991).

evolution between all three variables, but partial correlation analysis on the contrasts showed that life-history variation was not usually significantly correlated with variation in metabolic rate when body mass was held constant: of eleven life-history variables tested, only one partial correlation was significant at the 5% level. However, life-history variation was significantly correlated with variation in body mass when variation in metabolic rate was held constant: nine of the eleven partial correlations were significant at the 5% and three at the 1% level. It seems, then, that metabolic rate differences might not play such a central role in avian life-history variation as had been thought. Similar analyses on mammal life histories, metabolic rates and body masses lead to similar conclusions (Harvey *et al.* 1991).

3. ASKING THE RIGHT QUESTIONS

(*a*) *Identifying trade-offs*

The key to understanding life-history variation is provided by identifying correctly the trade-offs that prevent organisms from being what Law (1979) has called 'Darwinian Demons'. If trade-offs were not involved, each species would start producing copious offspring at birth and continue doing that through to eternity. In practice, there are trade-offs between components of fecundity, between components of mortality, and between fecundity and mortality. Different environments select for different optimal life-histories, and Southwood (1977, 1988) has prescribed an agenda that seeks natural ways of classifying habitats according to certain templets that are the key determinants influencing changes in optimal life-histories.

If they are to start with basic questions, comparative studies might be used to identify those trade-offs that are important in life-history evolution. It has often been pointed out (see Partridge & Harvey 1985, 1988) that comparative data can fail to identify trade-offs that exist, or even suggest positive associations between the component variables of a real trade-off. For example, imagine that there is a trade-off between clutch size and survival in a temperate passerine bird species such that if an individual female lays a larger clutch she is less likely to survive to breed again. Even when such trade-offs exist within species, comparative tests can show positive correlations: the fittest birds in a population may lay large clutches and have a higher chance of overwinter survival. However, this does not mean that cross-taxonomic comparative evidence for trade-offs is not with pursuing.

Recently, Blackburn (1991) has reported the first comparative study to use a non-directional comparative analysis for identifying a trade-off in life-history evolution. Blackburn's analysis is of particular interest because it tests for one of the classic trade-offs in life-history studies, that between egg size and clutch size in birds. Lack (1967) suggested that individual female birds could allocate their finite resources to producing few larger eggs, or more smaller eggs. Given that many large eggs will produce a greater number of more viable offspring, Lack was hypothesizing a trade-off between egg size and clutch size. Lack's idea was likely to be particularly appropriate to precocial taxa in which the mother feeds the offspring little if at all, so nutrient limitation during egg production would limit fecundity. Accordingly, Lack performed a comparative test of his idea using the waterfowl (Anatidae), and found the predicted negative relation between clutch size and egg size.

Rohwer (1988) questioned Lack's conclusions, partly on methodological grounds but also in the light of more reliable data that had recently become available. Larger females are likely to have more resources to invest in their offspring, and so Rohwer controlled statistically for body size in his analysis. He found that the variance in clutch size accounted for only 13% of the variance in egg mass when female body size was controlled for.

Blackburn pointed out that while Rohwer's data were better than Lack's, his method of analysis remained primitive and may have led to the wrong conclusions. Residuals from a major axis line were used by Rohwer to control for the effects of body mass, which is an incorrect procedure because those deviations (unlike deviations from a Model I regression line) were correlated with body mass. Furthermore, taxonomic association was not properly controlled for in Rohwer's study, which meant that some speciose taxa (e.g. 42 of the 151 species belong to the genus *Anas*) could influence the results. Blackburn calculated contrasts using Rohwer's data in a non-directional phylogenetic comparative analysis of the sort described above. When partial correlation analysis was done on the contrasts, clutch size accounted for 29% of the variance in egg mass after controlling for female body size. Read & Harvey (1989) found similar evidence for a trade-off between litter size and neonatal mass in mammals, independent of maternal body mass. Partridge & Sibly (this symposium) mention the importance of controlling for differences in other life-history characters and for differences in habitat when seeking to identify trade-offs. When Blackburn (1990) performed such tests, the negative correlation between contrasts for egg mass and clutch size was strengthened. However, even though such comparative studies leave little room for doubt about the presence of particular trade-offs, we agree with Partridge & Sibly that they do not allow the construction of accurate trade-off curves.

The central role of trade-offs in life-history theory means that comparative patterns must often be interpreted in terms of appropriate trade-offs, and the interpretations subject to test. An example is provided by work on age at maturity among female mammals. It has often been argued that age at maturity is allometrically related to body mass, that is it relates to body size according to a power function, so that a double-logarithmic plot reveals a linear relation between age at maturity and adult body mass. Such allometric relations require explanation. For example, larger animals take longer to grow to adult size and so will mature at a later age. However, for their body size, some mammals mature at a later age than others. Why should this be? Harvey & Zammuto (1985) pointed out that mammals with low mortality rates for their body mass were the ones with late ages at maturity. Harvey & Zammuto's analysis, and a subsequent modification by Sutherland *et al.* (1986) which plotted age at maturity against life expectation at maturity, were based on a cross genus comparison. Such analyses, as we pointed out in the discussion above relating to figure 1, are not fully appropriate. However, when the analysis is repeated using a non-directional contrasts analysis, the pattern is still evident (see figure 4).

It is a matter of demographic necessity that birth rates must ultimately match death rates if populations are to persist at demographic equilibrium, with the consequence that some components of fecundity will match some components of mortality (Sutherland *et al.* 1986). However, this will not explain why some species apparently delay reproduction beyond an age when they are fully grown. In particular, these ages at maturity, while varying a little with state of nutrition, do not change sufficiently in well fed zoo populations to account for the relation in figure 4. Instead, it has been argued, we might invoke a trade-off to explain such results (Ashmole 1963; Charlesworth 1980): if there is a cost to reproduction but the efficiency of reproduction increases with age, then species with low rates of mortality will have been selected to delay the onset of reproduction (Harvey *et al.* 1989*b*). For example, consider a species of mammal that will die after producing young (such semelparous species are known). If they can produce two offspring as two-year olds or ten offspring as three-year olds, they will delay reproducing until they are three so long as adult mortality is sufficiently low. If the chance of surviving from age two to three is just 1%, the mammal will have been selected to breed as a two-year old. Here the trade-off is between delaying reproduction to a time when reproductive efficiency is high and dying while waiting.

The explanation we have just given for the relation in figure 4 involved an increase in reproductive efficiency with age: producing offspring should cost older (but not senescent) animals less, or older mothers should produce more offspring for the same cost. Is there evidence for this? Indeed, there is circumstantial evidence – in various species, older mothers produce larger offspring, larger litters, young with higher rates of survival, and have shorter interbirth intervals (Promislow & Harvey 1990). However, some or all of these patterns may result from experience of older parents, and experiments will be necessary to distinguish age from experience. It is possible that such experiments have been reported in the agricultural literature.

(*b*) *Comprehensive models*

Simple relations, such as that between age at maturity and rate of mortality, may be explained in terms of simple trade-offs, but the comparative method in life history is providing evidence for suites of correlated life-history characters. For example, Read & Harvey (1989) found that several measures of increased fecundity covaried across orders of mammals: short gestation lengths, early ages at weaning, and short periods as independent juveniles before maturation were highly correlated with each other independent of adult body mass. Similar patterns have been found in birds (Bennett & Harvey 1988; Saether 1988). It is possible to produce *ad hoc* but testable theories to explain many or all of these different correlations (for examples, see Harvey *et al.* 1989*b*). Perhaps more exciting, however, is the prospect of producing integrated optimality models of life-history evolution that incorporate known functional relations between growth rates, body mass, mortality rates, and various life-history parameters. Such models inevitably incorporate both constraints and trade-offs. Charnov (1991) has recently made a start in this direction in a model of mammalian life-history evolution which predicts many of the interspecific relations that we actually find in nature. We consider Charnov's example in a little detail, attempting a purely verbal exposition because we are less concerned with the precise numerical values and functional relations involved than we are with his overall approach.

Charnov takes as his starting point the assumption that mammals grow according to a fixed growth law, which dictates that the amount of weight put on per unit time increases with time and, therefore, with weight. In other words, bigger mammals grow faster. Charnov assumes that mammals cease growing when they mature, and the energy that could have been channelled into growth is diverted into offspring production. This means that larger mammals have more energy to put into offspring production per unit time. However, larger-bodied mammals produce larger offspring, with the net result that their fecundity is lower. Now, mammals are selected to maximize their lifetime reproductive success, which depends on fecundity, adult mortality, and juvenile mortality. Charnov views adult mortality as extrinsic to the system, with natural selection acting on the age at maturity to maximize lifetime reproductive success. Increasing the age of maturity increases size and, thereby, reduces fecundity. It also prolongs the period of immaturity and decreases the probability of a juvenile surviving to reproduce. Charnov considers that mortality rates plateau well before maturity so that adult mortality rates are not influenced by changes in the age at maturity. In contrast, altering adult mortality rate changes the optimal age at maturity (set as the age that maximizes lifetime reproductive success), thereby dictating adult body mass. For a population in demographic equilibrium, of course, the average number of daughters produced during a female's lifetime is one. Charnov considers that average juvenile mortality adjusts so that this equality holds.

Some interesting factors emerge from Charnov's formulation. First, for animals with similar growth curves and for which adult body mass determines body mass at weaning, fecundity (number of offspring produced by a female per unit time) is considered to ary simply with the efficiency with which females can ransfer units of potential growth into units of offspring. econd, adult mortality rate is extrinsic to the system nd is not influenced by adult body mass. In fact the verse is true, with adult mortality rate influencing dult body mass through its effect on the optimal age maturity. Third, as we can describe age at maturity terms of adult body mass (because of the universal growth law), any variable that can be defined in terms of adult body mass can equally well be defined in terms of age at maturity. For example, the growth relation can be used to eliminate adult body size from equations describing fecundity, adult mortality rate, and average immature mortality producing dimensionless numbers (the topic of Charnov's paper in this symposium). Fourth, since age at maturity, adult mortality rate, fecundity and average immature mortality can each be expressed in terms of adult body mass, we can examine the relation between those variables when adult mass is held constant.

The relations between the four variables (age at maturity, pre-adult mortality, adult mortality, fecundity) are defined precisely so long as the various assumptions of Charnov's model hold. Let us review some of those assumptions: there is a fixed growth law, juvenile mass is defined precisely by adult mass, and the efficiency of transfer from units of parental growth into units of young is fixed. Each of these assumptions gives rise to a constant in Charnov's equations. If those constants are changed in value, so are age at maturity, adult body mass, fecundity, and average immature mortality. What is important for the purposes of this article is that the assumptions will not quite hold, so that the constants differ a little among species. If they differ among species in an uncorrelated fashion (e.g. changes in the growth law are not accompanied by predictable changes in the efficiency of transfer of energy from adult growth to production of young) then Charnov predicts the various size-independent correlations between life-history variables and between mortality and fecundity found by Harvey & Zammuto (1985), Sutherland *et al.* (1986), Read & Harvey (1989), and Promislow & Harvey (1990).

Let us return to our example of the positive relation between early age at maturity and high adult mortality. Can we see why in Charnov's model this relation should hold independently of differences in body mass? The way that we have described the model, fecundity is higher for smaller mammals because the extra energy for reproduction that is available to larger mammals is more than offset by the increased size of the weaned offspring that they produce. However, when Charnov applies optimality theory to find the age at maturity, he assumes that mass at weaning is fixed. Within that portion of his model, therefore, larger animals can produce more offspring per unit time if they mature later (i.e. at a greater mass). In short, reproductive efficiency increases with age at maturity in Charnov's model. The trade-off, then, is between increasing reproductive output by delaying reproduction, and dying while waiting. A useful component of Charnov's formulation, therefore, is that by specifying relations precisely it allows us to identify relevant trade-offs. Interestingly, the trade-off implicit in Charnov's model is not the same as that suggested earlier in this paper. The previous model assumed increased reproductive efficiency with age per se, and a cost to reproduction in terms of continued adult survival. Charnov makes neither assumption, but he does assume increased efficiency of reproduction with an increased age at maturity and, for his

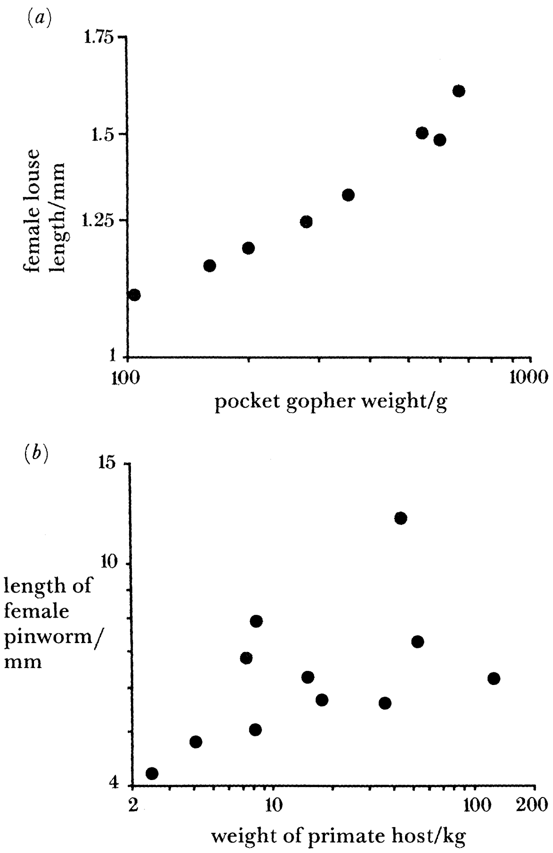

Figure 5. Size relations across species between (*a*) pocket gophers and their associated chewing lice, and (*b*) between primates and their pinworms.

optimization, that all phenotypes wean offspring of the same mass.

(*c*) *From correlated evolution to coevolution*

So far in this article we have focussed on the use of comparative methods to show correlated evolution between life-history traits. As we have mentioned, and as Southwood and others have emphasized, different habitats probably favour the evolution of different lifestyles. We saw one example with Turner's butterflies where association with toxic plants favours the evolution of a long lifespan and delayed maturity. One case where convergent evolution of life-history traits has been identified is in primates. Ross (1987) found that primate species living in tropical rain forests lived much slower lives for their body sizes than those in secondary forests, riverine forests or savannah. Harvey *et al.* (1989*a*) pointed out that the same trend was found in five of six different families in the sample and, therefore, had evolved on separate occasions. Alternative explanations invoking r/K selection (Ross 1987) and differential mortality (Harvey *et al.* 1989*a*) have been suggested for the pattern. Such examples of the correlated evolution of life-history traits with differences in environments are, however, not common as has been discussed elsewhere (see, for example, Partridge & Harvey 1988; Harvey *et al.* 1989*b*).

In addition to studying correlated evolution, the new comparative techniques discussed in this paper open up the unexplored possibility of studying coevolution between life-history traits, where 'the study of coevolution is the analysis of reciprocal genetic changes that might be expected to occur in two or more ecologically interacting species and the analysis of whether the expected changes are actually realized' (Futuyma & Slatkin 1983, pp. 2–3). Our aim is to understand the reasons for the evolution of life-history differences. That means defining the selective forces responsible for those differences. It is usually impractical to define fine-grained components of environmental diversity that might be responsible for the evolution of life-history differences among closely related species. Some host–parasite relations might provide an exception. Closely related hosts can have markedly different life histories, which should impose life-history differences on their parasites. The host constitutes a predictable and homeostatically controlled environment for a parasite, and those aspects of the host environment most likely to affect parasite life history (such as resource availability and temporal stability) are well characterized by the life history of the host. In turn, parasites invariably influence their host's fitness. Accordingly, when parasite phylogeny is congruent with host phylogeny it should be possible to use the methods of independent comparisons to examine coevolution, although cause and effect can only by hypothesized in the absence of information about ancestral character states.

To provide simple illustrations of the potential use of such methods, we sought examples of host-specific parasites that had speciated with their hosts, so that we had congruent host–parasite evolutionary trees. Of course, no taxa fit these criteria completely: most parasites have more than one host species, and among the specialists there is usually clear evidence for switching among host lineages. Even for the most appropriate taxa, the data on parasite life histories are extremely limited. We choose two examples: chewing lice and roundworms. Specifically, we concentrate on lice of the mallophagan family Trichodectidae which infect pocket gophers in the rodent family Geomyida (Hafner & Nadler 1988), and pinworms of the genu *Enterobius* found in primates (Brooks & Glen 1982) Life-history data for the mammals were extracted fro sources given by Read & Harvey (1989) and supple mented by information on pocket gopher life-histori supplied to us by Dr Mark Hafner. Life history data f the parasites were taken from a variety of publish sources (Cameron 1929; Sandosham 1950; Skrjabin *al.* 1960; Yen 1973; Quentin *et al.* 1979; Price Hellenthal 1980, 1981; Timm & Price 1980; Hugot Tourte-Schaefer 1985; Hugot 1987; Hellenthal Price 1989*a*, *b*).

Simple cross-species analyses reveal clear relati (figure 5): large parasites are associated with la hosts in both parasite–host groups. But how do control for possible phylogenetic effects in both para *and* host? In these examples, the phylogenies are m or-less congruent (figure 6: the examples are illustrative purposes only – we have ignored evidence for host-switching in the lice, while

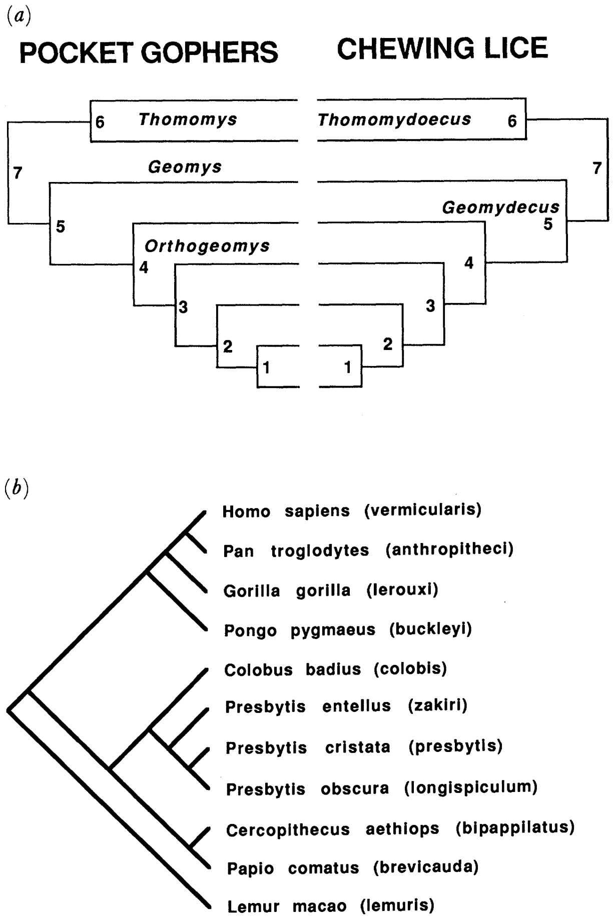

Figure 6. Congruent phylogenetic trees of (*a*) pocket gophers and their chewing lice, and of (*b*) primates and their *Enterobius* pinworms. Uncertainties of tree structure have, for the purposes of illustration, been decided in favour of congruence in each case. References for tree reconstruction are given in the text.

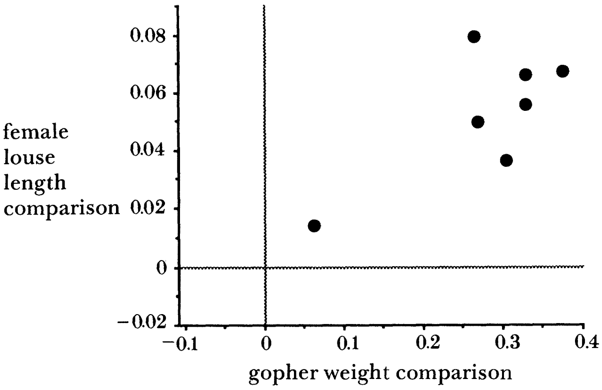

Figure 7. Independent evolutionary non-directional comparisons of chewing louse length on gopher host adult body weight. In each case, increased host weight is associated with increased louse length (all points are in the upper right-hand quadrant).

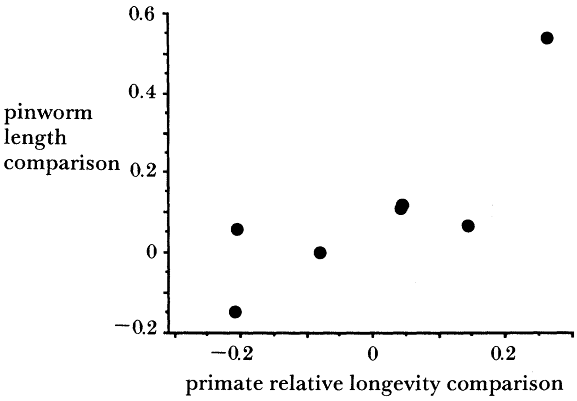

Figure 8. Independent evolutionary comparisons between pinworm length and primate longevity corrected for body size ($r = 0.81$, $n = 7$, $p < 0.05$).

Enterobius our parasite phylogeny is derived in part from the host one), so independent comparisons were made in exactly the manner already described (see figure 3). Life-history data were not readily available for pocket gophers or their associated lice but, in an independent comparisons test, we can see that the evolution of increased body size in the host is invariably associated with increased size of parasites (figure 7). This is, perhaps, a surprising finding because we should not have expected host size per se to set a constraint on the size of its lice. However, it is generally the case that larger female invertebrates are more fecund (see, for example, Sibly & Calow 1986). Perhaps the large size of the lice is really a consequence of the longer lives of their hosts – lice living on larger hosts have longer to grow before the host perishes. The trade-off, then, would be between increased fecundity with larger size and increased mortality while waiting to attain that size. The primate–pinworm association allows us one test of that idea.

Larger primate species act as hosts to larger pinworms, but primate lifespan is also correlated with pinworm size. We used an independent comparisons test to ask if the evolution of long primate lifespans when controlled for increases in primate body size was associated with increased pinworm size. Indeed it was (figure 8). The procedure for the test was to calculate three sets of non-directional comparisons: one for primate mass, one for primate lifespan, and one for pinworm size. We then regressed the comparisons for primate lifespan on those for primate mass, and plotted the residuals from that regression against the appropriate comparisons for pinworm size. Our results, therefore, support the idea that pinworm sizes evolve in response to the longevity of their hosts.

In our examples, we have assumed the simplest scenario; congruence between parasite and host phylogenies, with co-speciation and no host switching. Future analyses along these lines will probably deal with cases where parasites use more than a single host, and where parasite switching between host lineages occurs. We foresee no great technical problems in developing the appropriate statistical models, whereas the analyses could be profitable indeed because they can be used to tackle questions about coevolution between parasites and their hosts (we assumed here that host life-history determined parasite life-history), about host-specificity, and about speciation itself.

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