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Phylogenetic Analysis and Comparative Data: A Test and Review of Evidence

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abstract: The question is often raised whether it is statistically necessary to control for phylogenetic associations in comparative studies. To investigate this question, we explore the use of a measure of phylogenetic correlation, λ, introduced by Pagel (1999), that normally varies between 0 (phylogenetic independence) and 1 (species' traits covary in direct proportion to their shared evolutionary history). Simulations show λ to be a statistically powerful index for measuring whether data exhibit phylogenetic dependence or not and whether it has low rates of Type I error. Moreover, λ is robust to incomplete phylogenetic information, which demonstrates that even partial information on phylogeny will improve the accuracy of phylogenetic analyses. To assess whether traits generally show phylogenetic associations, we present a quantitative review of 26 published phylogenetic comparative data sets. The data sets include 103 traits and were chosen from the ecological literature in which debate about the need for phylogenetic correction has been most acute. Eighty-eight percent of data sets contained at least one character that displayed significant phylogenetic dependence, and 60% of characters overall (pooled across studies) showed significant evidence of phylogenetic association. In 16% of tests, phylogenetic correlation could be neither supported nor rejected. However, most of these equivocal results were found in small phylogenies and probably reflect a lack of power. We suggest that the parameter λ be routinely estimated when analyzing comparative data, since it can also be used simultaneously to adjust the phylogenetic correction in a manner that is optimal for the data set, and we present an example of how this may be done.

Keywords: generalized least squares, maximum likelihood, phylogenetic correction, phylogenetically independent contrasts.

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Phylogenetic comparative methods are widely used to control for the lack of statistical independence among species (Felsenstein 1985; Grafen 1989; Pagel and Harvey 1989). Nevertheless, there has been repeated questioning of their validity or utility (e.g., Westoby et al. 1995*a*, 1995*b*; Ricklefs and Starck 1996; Björklund 1997) along with calls for diagnosis of when such tests should be applied (e.g., Björklund 1994; Fitter 1995; Losos 1999). Other authors have suggested that the results of both phylogenetic and nonphylogenetic analyses should routinely be presented (Price 1997; Blackburn and Gaston 1998; Garland et al. 1999; Schluter 2000).

Objections to the use of comparative methods fall into two classes. One class of objections concerns interpretation: it is argued that even if a significant component of character variation within natural groupings of species (e.g., species that co-occur in the same ecological community) may be associated with phylogeny, this is irrelevant because the across-species pattern of character variation reflects the fact that closely related species will tend to occupy similar niches. Across-species patterns of trait variation are argued to reflect the immediate ecological factors operating on species rather than evolutionary ones (Westoby et al. 1995*a*, 1995*b*). Such patterns are, however, descriptive and cannot be used to infer either the number of times the pattern has arisen independently or underlying mechanisms (Harvey et al. 1995*a*, 1995*b*; Harvey 1996). Moreover, analysis of data within a phylogenetic framework can reveal patterns of association of ecological characters that would be masked by simple across-species comparisons (Harvey 1996).

The second class of objection concerns the model of evolution. Most commonly employed comparative methods assume either implicitly or explicitly a model of character evolution (or, more generally, a model for character association) typically based on a constant-variance process (sometimes called "Brownian motion"; Felsenstein 1985; Harvey and Pagel 1991). If the model is incorrect, a phylogenetic analysis may produce results that are no more valid than those from a nonphylogenetic analysis or may even be incorrect (Price 1997; Losos 1999; Harvey and

Rambaut 2000). Phylogenetic and nonphylogenetic analyses commonly estimate the same parameter, and in studies of correlated evolution, correlations estimated using the two forms of analysis would be expected on average to correspond closely (e.g., Pagel 1993). However, it is important to note that even if this is the case, Type I error rates of tests of correlated evolution will be higher for nonphylogenetic methods when data exhibit phylogenetic dependence resulting from the simplest neutral model of neutral character evolution (Martins and Garland 1991; Diaz-Uriarte and Garland 1996; Harvey and Rambaut 1998).

These debates highlight the need for a simple technique that allows diagnosis of whether or not data require a phylogenetic analysis (e.g., Losos 1999) or, more specifically, to determine the degree to which trait variation is related to phylogeny and to adjust the analysis appropriately. Cheverud et al. (1985), Gittleman and Kot (1990), Lynch (1991), Björklund (1997), Diniz-Filho et al. (1998), and Abouheif (1999) all propose diagnostic tests for phylogenetic independence, but their tests are not based on models of trait evolution. This restricts their applicability and means that they cannot be used to test among competing evolutionary models.

Other authors have suggested measures based on the constant-variance random walk or Brownian motion model of trait evolution. One approach uses likelihood ratio tests to determine whether phylogenetically based analyses describe the trait data better than a nonphylogenetic "across species" analysis (e.g., Christman et al. 1997; Pagel 1999; Butler et al. 2000). Pagel (1999) suggested a general way in which a test for phylogenetic dependence can be performed in a generalized linear model. The test assumes a constant-variance random effects model of trait evolution and adjusts the analysis for levels of phylogenetic dependence between the extremes of complete phylogenetic independence and the phylogenetic dependence expected under a constant-variance model. A similar approach (Lynch 1991) uses a mixed-effects model to split the variance of the trait data into two components, one being a Brownian component resulting from phylogenetic associations and the other being a non-species-specific component that is independent of phylogeny. The ratio of these two components of variance is used as an index of phylogenetic dependence in the data.

In this article, we use a quantitative measure of phylogenetic dependence introduced by Pagel (1999) to assess in a range of real and simulated data sets the issue of whether there is evidence of a significant phylogenetic component to character variation. In addition to providing an index of phylogenetic association, this index may also be used to adjust the phylogeny to match the degree of phylogenetic correlation in hypothesis tests, and we illustrate how this may be done.

Methodology

Modeling Trait Evolution and Phylogenetic Dependence

Let t be the time since ancestor 0; then, for trait y in species i,

$$y_i = \alpha + \sum_{j=1}^{T_i} \varepsilon_{i,j} t_{i,j}, \tag{1}$$

where α is the state at time 0 (i.e., the state of the trait in ancestor 0), ε is a normally distributed random noise term with mean 0 and variance σ^2, and the summation is across the T branches linking the root to species i; $t_{i,j}$ is the length of branch j in species i. This is a constant variance random walk or Brownian model. After t units of time, the expected value of y is normally distributed with mean α and variance $\sigma^2 t$. More generally, if n species are undergoing independent Brownian motion, then $\boldsymbol{y}$, the $1 \times n$ vector of character states, will have a multinormal probability density given by

$$p(\boldsymbol{y}) = \frac{1}{(2\pi\sigma^2 t)^{n/2}} \exp\left[-\frac{(\boldsymbol{y} - \alpha\boldsymbol{X})^T(\boldsymbol{y} - \alpha\boldsymbol{X})}{2\sigma^2 t}\right], \tag{2}$$

where $\boldsymbol{X}$ is a vector, termed the "design matrix," of which all of the entries are set to 1; $\boldsymbol{X}$ can include a range of terms, such as regressor variables or multilevel factors, in order to accommodate a range of statistical designs.

Equation (2) predicts the distribution of character states only if the evolution of each species is independent. More realistically, species will be expected to exhibit similarity owing to common ancestry, and under a Brownian model this similarity scales in direct proportion to shared evolutionary path lengths. If species i and j share a common ancestor at time t_a, the covariance between their character states is expected to be

$$\mathrm{cov}(y_i, y_j) = \sigma^2 t_a. \tag{3}$$

For all $n \times n$ pairs of species, the variance and covariance of character states can be predicted by calculating shared path lengths (see fig. 1 for an example of this). This generates an $n \times n$ element variance-covariance matrix, $\sigma^2\mathbf{V}$.

Given $\mathbf{V}$, equation (2) is readily modified to incorporate phylogenetically correlated evolution (e.g., Felsenstein 1973):

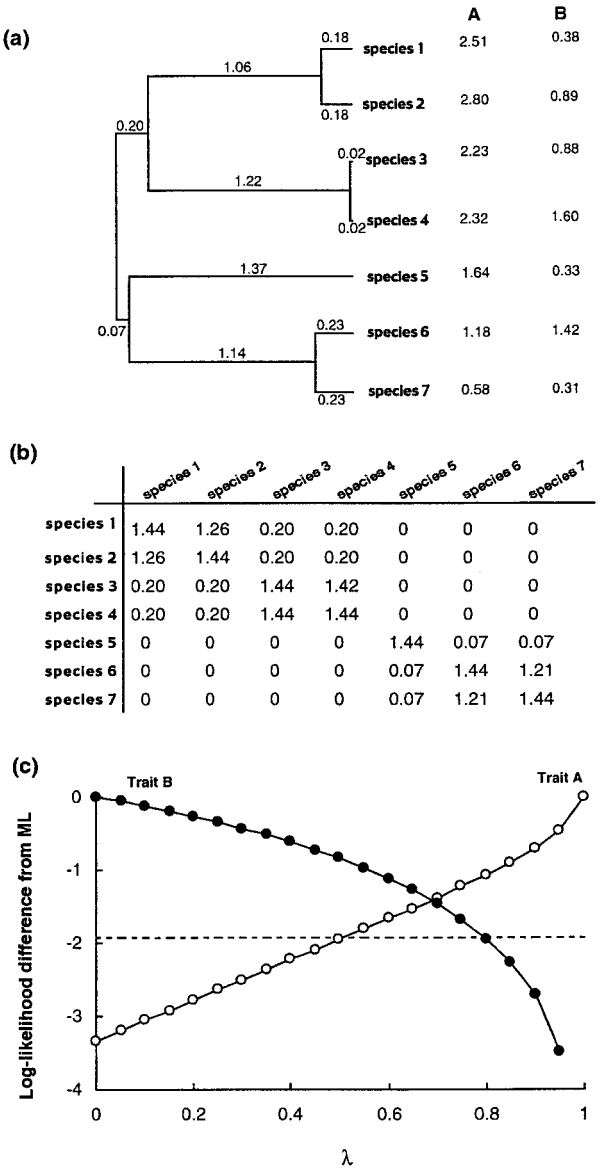

Figure 1: Example of how λ is estimated given a phylogeny and trait data. *a*, A phylogeny of seven species, together with data on two traits, *A* and *B*. The aim is to determine whether the data exhibit significant phylogenetic dependence. The data are fictitious; trait *A* was evolved on the phylogeny according to a Brownian process and, hence, should exhibit significant phylogenetic dependence, while the values of trait *B* were assigned at random and should exhibit no significant phylogenetic dependence. The numbers above the branches of the phylogeny are branch lengths. *b*, The variance-covariance matrix implied by the phylogeny in *a*. The variance elements (*main diagonal*) are measured as the distance from root to tip, that is, the total time of evolution of each species. The covariance elements (*off diagonal*) are given by the total shared path length for each species. For example, species 1 and species 2 share path lengths 0.20 and 1.06 from the root. In the variance-covariance matrix, the covariance entry for these species is therefore 1.26. In comparison, species 1 and species 5 share no path lengths after the root of the phylogeny; therefore, the traits of these species have zero expected covariance, and the variance-covariance matrix entry is 0. *c*, λ is used to transform the variance-covariance matrix in *b* and the likelihood of the data estimated across a range of values of λ. At each value of λ, the matrix in *b* is transformed by multiplying its off-diagonal elements by λ. Then, this transformed matrix is used to generate maximum likelihood estimates of the parameters of equation (4) and, hence, an overall likelihood for the data set at each value of λ. As shown, the maximum likelihood value of λ for trait *A* is 1, whereas that for trait *B* is 0. The dashed line shows the critical value of the log-likelihood ratio test. Thus, the value of λ for trait *A* is significantly different from 0, and that of trait *B* is significantly different from 1.

$$p(\boldsymbol{y}) = \frac{1}{(2\pi\sigma^2)^{n/2}} |\mathbf{V}|^{-1/2} \times \exp\left[-\frac{1}{2\sigma^2}(\boldsymbol{y} - \boldsymbol{X}\alpha)^T \mathbf{V}^{-1}(\boldsymbol{y} - \boldsymbol{X}\alpha)\right]. \quad (4)$$

The difference between equations (2) and (4) is the inclusion of the matrix **V** in equation (4). However, equation (2) could be written in the form of equation (4) but with **V** set as a diagonal matrix in which all elements are equal to t and all off-diagonal elements are set to 0. This difference between the form of **V** in the case of phylogenetically dependent and independent evolution suggests a simple test of whether data show phylogenetic dependence or not (Pagel 1997, 1999). Pagel (1999) defined λ (normally $0 \leq \lambda \leq 1$) as a multiplier of the off-diagonal elements of **V**. Thus, a value of $\lambda = 0$ indicates evolution of traits that is independent of phylogeny, while a value of $\lambda = 1$ indicates that traits are evolving according to Brownian motion on the given phylogeny. Intermediate values of λ indicate that traits have evolved according to a process in which the effect of phylogeny is weaker than in the Brownian model.

This index, λ, is similar to the index H^2 derived from Lynch's (1991) model. Lynch assumes a mixed model in which the variance in traits is decomposed into a component that is phylogenetically conserved and evolves according to a Brownian process acting as a fixed effect and a phylogenetically independent species-specific component that acts as a random effect. The total variance in traits is an additive combination of these two components. The statistic H^2 is defined as the ratio of the phylogenetic component to the total variance and is thus constrained to vary between 0 and 1.

For traits evolving along the branches of a phylogeny entirely by Brownian motion, the expected values of both λ and H^2 are equal to 1.0. Conversely, both measures are expected to be equal to 0 for traits that have no phylogenetic component. However, the two measures are not identical since λ is not interpretable as the percentage of

variance attributable to phylogenetic effects. This difference between the two parameters arises because one optimizes its estimates on the basis of partitioning the data into the phylogenetic and nonphylogenetic components, whereas the other optimizes its estimates on the total or unpartitioned variance in the trait. Thus, λ is defined as the transformation of the phylogeny that makes the unpartitioned trait data best fit the Brownian motion model. This means that λ can also adopt values >1.0. A value of $\lambda > 1.0$ can arise if, for instance, traits are more similar than that predicted by Brownian motion, given the phylogeny. As an example, the value of H^2 is 1.0 for Lynch's (1991) data on body size, but $\lambda = 1.24$. In practice, however, the range of values >1.0 that λ can adopt is restricted since the off-diagonal elements in **V** cannot be larger than the diagonal elements.

Estimation

We used a maximum likelihood approach to estimate λ for a given set of trait data and a phylogeny (implemented in a program Continuous available from M. Pagel [m.pagel@reading.ac.uk]; these methods are also readily adapted in commonly available numerical programming packages, e.g., see Christman et al. 1997; Butler et al. 2000). If $\mathbf{V}(\lambda)$ is **V** modified by multiplying its off-diagonal elements by λ, then for a given value of λ, the maximum likelihood estimates of α is

$$\hat{\alpha} = (\boldsymbol{X}^T\mathbf{V}(\lambda)^{-1}\boldsymbol{X})^{-1}(\boldsymbol{X}^T\mathbf{V}(\lambda)^{-1}\boldsymbol{y}),$$

and the unbiased (restricted maximum likelihood) estimate of σ^2 is

$$\sigma^2 = \frac{1}{(n-1)}(\boldsymbol{y} - \hat{\alpha}\boldsymbol{X})^T\mathbf{V}(\lambda)^{-1}(\boldsymbol{y} - \hat{\alpha}\boldsymbol{X}).$$

There is not a corresponding simple expression for λ, and the maximum likelihood value of λ is found numerically using a direct search procedure. Here we use an optimization algorithm (Brent's method; Brent 1973), selecting the value of λ that maximizes the likelihood of equation (4). This is a one-dimensional search through parameter space, since at any given value of λ, the above equations can be used to solve for the maximum likelihood values of the mean and variance.

The estimate of λ can be tested in order to determine whether data exhibit significant phylogenetic dependence or not. If $L(\hat{\lambda})$ is the log likelihood at the maximum likelihood value of λ, and $L(\lambda')$ is the log likelihood of the data at an alternative value λ′, then the quantity

$$\chi^2 = -2[L(\hat{\lambda}) - L(\lambda')]$$

will be asymptotically χ^2 distributed with one degree of freedom under the null hypothesis that $\hat{\lambda} = \lambda'$. This log-likelihood ratio test may be used to test whether estimated values of λ differ significantly from 0 and 1 or adopted some intermediate value. For example, the implicit value of λ′ in comparative studies that employ phylogenies is 1.0, whereas in simple across-species studies, λ′ is implicitly 0. Figure 1 illustrates how λ is estimated.

Simulations

We conducted computer simulations to assess the power and Type I error rates of λ. We simulated trees containing between 10 and 100 species according to a branching process model in which the per lineage probability of speciation was constant (Yule process). Trait values were simulated according to one of two algorithms. In the first case, traits evolved according to the random effects Brownian model, as described above. In the second, trait values were drawn at random from a normal distribution, for instance, as if traits evolve instantaneously in response to selection. In the first model, traits should show strong phylogenetic dependence ($\lambda = 1$), whereas in the second model there should be no phylogenetic association of traits ($\lambda = 0$).

In the context of fitting a constant variance process, Grafen (1989) suggested that a power transformation could be applied to the variance-covariance matrix implied by the phylogeny and model of evolution in order to scale tree heights and generate the variance-covariance matrix that best describes the data. We explored the performance of such a transformation applied to the matrix **V** (ρ), noting that Grafen (1989) pointed out that such an index was likely to be biased. Note that the index suggested by Grafen (1989) is slightly different in implementation in that here we apply ρ to the shared path lengths, whereas Grafen (1989) applied ρ to the independent time of evolution. The net effect of ρ is different for diagonal and off-diagonal elements of the matrix **V**, since off-diagonal elements are smaller than elements on the diagonal. Large values of ρ increase the diagonal elements relative to off-diagonal ones and indicate little phylogenetic dependence, whereas values of ρ close to 1.0 indicate that traits are evolving according to the Brownian model (eq. [4]). We compared the performance of λ and ρ in order to determine which index performed better in adjusting data for phylogenetic dependence.

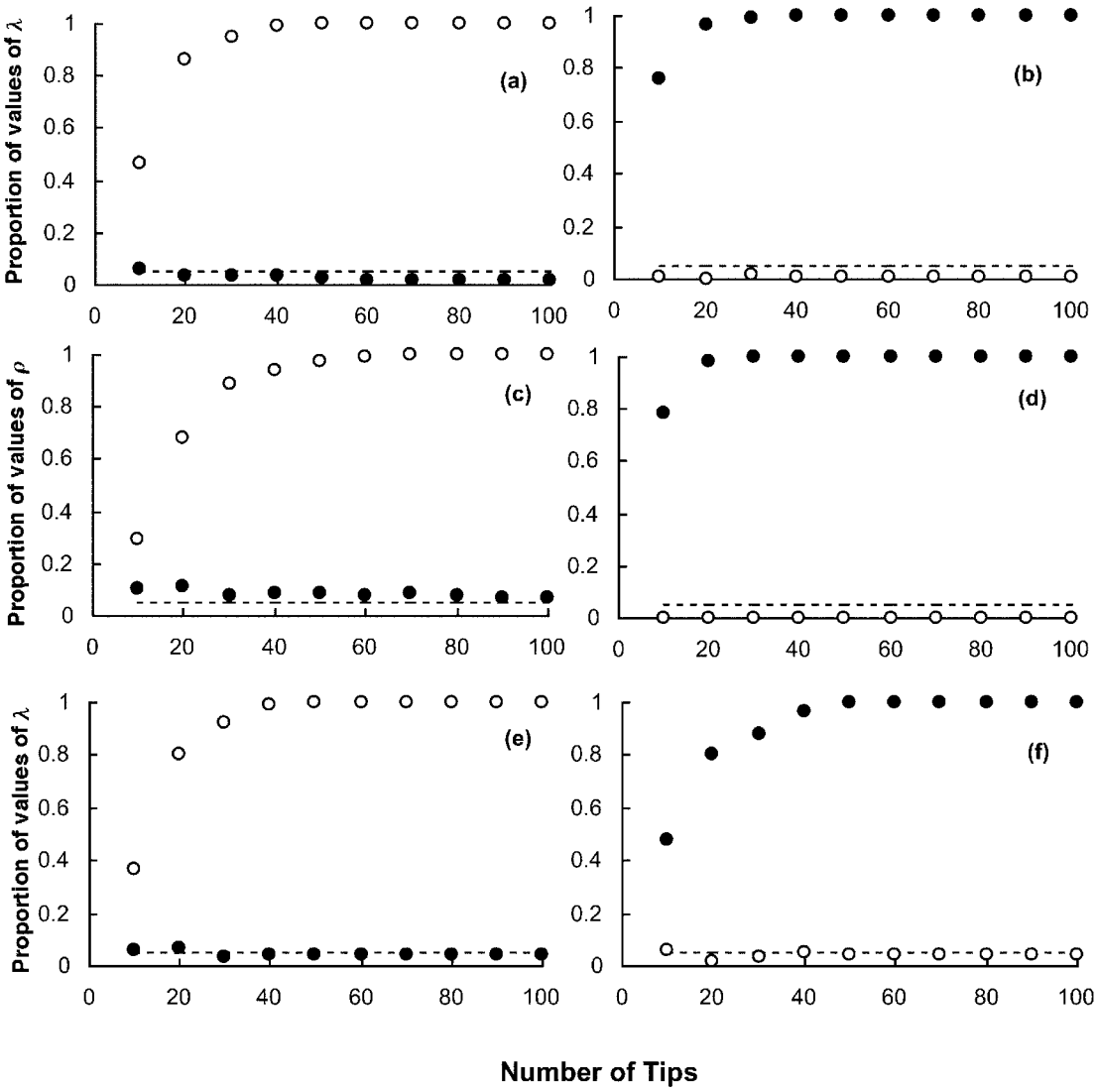

Figure 2: Testing for phylogenetic dependence in simulated data. As outlined in the main text, trees were simulated according to a Yule process, and data was simulated on trees according to one of two processes: phylogenetically correlated Brownian motion (*a*, *c*, *e*) or values were simply assigned to tips at random, thus generating phylogenetically uncorrelated data (*b*, *d*, *e*). The phylogenetic dependence of data was estimated in three ways: using λ, the measure of phylogenetic dependence introduced here (*a*, *b*); using ρ, an existing measure of phylogenetic association (*c*, *d*); and using λ but ignoring branch length information, mimicking a situation in which phylogenetic knowledge is incomplete. Log-likelihood ratio tests were used to perform tests on the parameters. In the case of λ, we tested whether maximum likelihood values were significantly different from 0 (*open circles*) or 1 (*filled circles*). In the case of ρ, we tested whether maximum likelihood values were significantly >1 (*open circles*) or different from 1 (*filled circles*).

Analysis of Published Data

Far more studies have analyzed cross-species data using phylogenetic comparative methods than it would be practical to review. We therefore surveyed data from studies reported in the ecological literature because the degree to which ecological data requires phylogenetic analyses has been the subject of much debate, and because the main objections to the use of comparative techniques have come from authors writing in the ecological literature. Ecological

studies also frequently include a range of traits, including behavioral traits, morphological characters, and variables such as mortality rates and species' ranges, traits that often appear in the comparative literature but may not be regarded as phenotypes in the conventional sense. We excluded studies that reported solely morphological characters since the phylogenetic dependence of such traits is well established (Gould 1977; Clutton-Brock and Harvey 1984). The phylogenies that have been employed in ecological comparative analyses often comprise either "natural" groups (e.g., species occurring within a community or a group of species with the same lifestyle) or simply an assortment of species for which data could be obtained. Hence, the data sets analyzed do not just comprise conventional well-defined taxonomic groups within which we would necessarily expect phylogenetic dependence to be very strong.

We obtained 26 data sets, yielding phylogenetically referenced data on 106 ecological characters for which we were able to estimate λ. We make no claim that these data are representative; rather, they serve to illustrate the range of phylogenetic dependence in comparative data across a variety of kinds of characters. data sets were not chosen or excluded on the basis of the value of λ they returned.

Results

Simulation Results

Figure 2*a* reports the proportion of trees for which λ was estimated to be significantly different from 0 when data were simulated using a Brownian motion process. For trees larger than 20 tips, the power of λ to detect phylogenetic dependence in data is always >90% and nearly 100% for trees with more than 40 tips (fig. 2*a*).

Figure 2*b* reports comparable results for the case of data simulated without phylogenetic dependence. For trees of only 10 tips, λ correctly identifies that the data are not phylogenetically structured in 75% or more of the cases, with this figure rapidly rising to 100% for larger trees. False inference of phylogenetic dependence is rare (fig. 2*b*).

Figure 2*c* and 2*d* shows the corresponding behavior of ρ. The main difference between λ and ρ is that ρ shows higher Type I error rates (>5%) when data are phylogenetically correlated (fig. 2*c*). Thus, phylogenetic dependence is rejected too often. In addition, ρ is biased (Grafen 1989). For example, for the trees in figure 2*c*, the mean value of ρ declines from 2.5 for trees of 10 tips to 1.7 for trees of 100 tips, even though the true value is 1. This means that the values of α and σ^2 (found at the maximum likelihood value of ρ) will also be incorrect (too small). This contrasts with λ, which is unbiased (fig. 2*a*, 2*b*) and yields unbiased estimates of α, the trait value at the root, and σ^2, the Brownian process variance.

The ability of ρ to detect phylogenetically uncorrelated data is acceptable (fig. 2*d*), but the problem of ρ biasing the estimates of α and σ^2 also arises in this context. In the limit, ρ is able to transform the matrix **V** to a diagonal form (representing independence among species) only when it becomes large ($\rho \to \infty$). Given these results, therefore, we employ λ rather than ρ as a measure of phylogenetic dependence.

We repeated the simulations used to generate figure 2*a* and 2*b* but set all branch lengths equal to 1. This simulates the frequently occurring situation of a phylogeny being available but without explicit branch lengths. As shown in figure 2*e* and 2*f*, the power of λ to distinguish phylogenetically dependent and nondependent data is still very high, with generally acceptable Type I error rates for tests of both phylogenetic dependence (fig. 2*e*) and independence (fig. 2*f*). An important general conclusion from figure 2*e* is that even partial phylogenetic information provides a better model of the variance in the data than completely ignoring phylogeny and assuming independence.

Frequency and Intensity of Phylogenetic Correlation

We report in table 1 the maximum likelihood values of λ, along with tests of the hypotheses that $\lambda = 0$ and $\lambda = 1$ for the 26 empirical data sets. In 23 out of 26 phylogenies (88%), at least one character showed significant evidence of phylogenetic correlation (i.e., $\lambda > 0$). Across all phylogenies, the differences between mean estimates of λ were only marginally statistically significant (Kruskall-Wallis test, $H = 30.86$, $n = 19$, $P = .03$; only studies with three or more observations included). We found that λ was statistically >0 for 60% of the characters. In 24% of tests, λ was not significantly different from 0 but was significantly different from 1, consistent with traits evolving independently of the phylogeny. In 16% of cases, λ was not significantly different from either 0 or 1.

Values of the log-likelihood ratio for tests of the hypothesis that $\lambda = 1$ were significantly smaller than for tests of the hypothesis that $\lambda = 0$ (Wilcoxon matched pairs test, $Z = 3.46$, $n = 103$, $P < .001$). This indicates that the maximum likelihood value of λ typically lies closer to 1 than to 0.

Issues of Power

The 16% of cases with equivocal results probably arise from a lack of statistical power, since they are predominantly from studies with small phylogenies. Figure 3 shows

Table 1: Analysis of phylogenetic dependence of "ecological" data derived from the literature

Taxon and character[a]	λ	ln lik	ln lik (λ = 0)	ln lik (λ = 1)	Reference
Invertebrate taxa:					
Termites (87):					
Latitude	1.000	−379.02	**−388.49*****	−379.02[b]	Porter and Hawkins 2001
Annual evapotranspiration	1.000	−85.37	**−100.95*****	−85.37[b]	Porter and Hawkins 2001
Body size	1.000	−161.18	**−214.44*****	−161.18[b]	Porter and Hawkins 2001
Parasite genera (80):					
Host specificity	.705	−101.90	**−108.61*****	−102.88[b]	Poulin 1998
Study effort	.099	−100.96	−101.67[b]	**−109.07*****	Poulin 1998
Prevalence	.533	−132.81	−134.53[b]	**−134.76***	Poulin 1998
Intensity of infection	.000	−94.25	−94.25[b]	**−99.50****	Poulin 1998
Amphipods (76):					
Body size	.799	−75.61	**−87.08*****	**−77.96***	Poulin and Hamilton 1995
Clutch size	.000	−36.80	−36.80[b]	**−42.07****	Poulin and Hamilton 1995
Latitude	.000	−278.63	−278.63[b]	**−290.76*****	Poulin and Hamilton 1995
Depth	.806	−134.02	**−139.06****	**−136.05***	Poulin and Hamilton 1995
Monogean parasites (74):					
Number of hosts per species	.059	−117.60	−117.74[b]	**−127.91*****	Sasal et al. 1999
Body length	1.000	−70.64	**−113.03*****	−70.64[b]	Sasal et al. 1999
Prevalence	.885	−12.40	**−18.95*****	−12.88[b]	Sasal et al. 1999
Lepidoptera (52):					
Fecundity	.818	−58.68	**−61.02***	−59.22[b]	Garcia-Barros 2000
Egg size	.950	24.25	**8.21*****	23.88[b]	Garcia-Barros 2000
Adult size	1.000	−183.96	**−196.70*****	−183.96[b]	Garcia-Barros 2000
Lepidoptera (38):					
Incidence	.302	−136.70	−137.60[b]	**−140.90****	Dennis et al. 2000
Range	.644	−173.80	−174.70[b]	−175.40[b]	Dennis et al. 2000
Niche axis 1	.000	−69.87	−69.87[b]	**−72.43***	Dennis et al. 2000
Niche axis 2	.950	−61.40	**−64.62***	−61.53[b]	Dennis et al. 2000
Drosophila (22):					
Development time	1.000	−41.44	**−45.53****	−41.44[b]	Sevenster and van Alphen 1993
Diet specialization	.950	−43.21	**−45.46***	−43.24[b]	Sevenster and van Alphen 1993
Tiger beetles (13):					
Sympatry	1.000	−18.34	−18.80[b]	−18.34[b]	Barraclough et al. 1999
Body length	.000	−13.44	−13.44[b]	**−17.03****	Barraclough et al. 1999
Mandible length	.000	−15.56	−15.56[b]	−17.43[b]	Barraclough et al. 1999
Vertebrate taxa:					
Australian marsupials (165):					
Weight	.769	−1,246.39	**−1,286.95*****	**−1,262.38*****	Johnson 1998
Range	.527	−224.24	**−229.69*****	**−232.77*****	Johnson 1998
Density	.833	−149.07	**−154.74*****	−150.08[b]	Johnson 1998
Fish (73):					
Body mass	.510	−359.97	**−363.48****	**−364.02***	Poulin 1995
Diet	.970	−69.06	**−85.37*****	−69.37[b]	Poulin 1995
Latitude 1	.567	−260.94	**−265.94****	**−264.46****	Poulin 1995
Parasite density 1	.000	−153.81	−153.81[b]	**−159.20****	Poulin 1995
Number of parasite species 1	.537	−189.89	**−196.24*****	**−194.50****	Poulin 1995
Latitude 2	.000	−147.93	−147.93[b]	**−155.43*****	Poulin 1995
Parasite density 2	1.000	−94.39	**−101.35*****	−94.39[b]	Poulin 1995
Number of parasite species 2	.125	−71.84	−71.85[b]	**−78.16*****	Poulin 1995
Mammals (73):					
Body length	1.000	−140.08	**−174.71*****	−140.09[b]	Ashton et al. 2000
Response to temperature	.260	−52.58	−54.17[b]	**−56.63*****	Ashton et al. 2000

Table 1 (*Continued*)

Taxon and character[a]	λ	ln lik	ln lik (λ = 0)	ln lik (λ = 1)	Reference
Response to latitude	.212	−20.09	−20.76[b]	**−27.49*****	Ashton et al. 2000
Rodents (63):					
Body mass ADMR	.982	−69.60	**−82.64*****	−69.76[b]	Degen et al. 1998
ADMR	.965	−36.15	**−47.56*****	−36.67[b]	Degen et al. 1998
Body mass BMR	.972	−58.12	**−67.34*****	−58.44[b]	Degen et al. 1998
BMR	.973	−42.82	**−53.15*****	−42.93[b]	Degen et al. 1998
ADMR	.901	20.40	**16.96****	18.59[b]	Degen et al. 1998
Mammals (60):					
Body mass	1.000	−132.34	**−161.31*****	−132.34[b]	Poulin 1995
Diet	1.000	−83.06	**−95.21*****	−83.06[b]	Poulin 1995
Latitude	.667	−226.65	**−230.68****	**−228.57***	Poulin 1995
Parasite density	.000	−258.25	−258.25[b]	**−261.77****	Poulin 1995
Number of parasite species	.491	−186.97	**−189.31***	**−190.15***	Poulin 1995
Passeriforms (55):					
Body mass	1.000	−45.58	**−82.62*****	−45.58[b]	Polo and Carrascal 1999
Habitat complexity	.848	−71.03	**−75.33****	−71.08[b]	Polo and Carrascal 1999
Foraging	1.000	−64.55	**−79.68*****	−64.55[b]	Polo and Carrascal 1999
Birds (54):					
Body mass	.963	−77.45	**−97.41*****	−77.57[b]	Poulin 1995
Diet	.645	−62.48	**−70.96*****	**−69.41*****	Poulin 1995
Latitude	.720	−193.44	**−197.95****	**−197.23****	Poulin 1995
Parasite density	.419	−65.40	−66.15[b]	**−70.31****	Poulin 1995
Number of parasite species	.405	−182.27	**−184.99***	**−191.56*****	Poulin 1995
Suckers (47):					
Range size	.660	−105.30	**−109.80****	**−108.20***	Pyron 1999
Body size	.848	−22.43	**−33.70*****	**−24.69***	Pyron 1999
Habitat breadth	.958	−101.10	**−107.50*****	−101.22[b]	Pyron 1999
Abundance	1.000	−44.14	**−55.27*****	−44.14[b]	Pyron 1999
Neotropical birds (47):					
Body mass	1.000	−39.03	**−49.07*****	−39.03[b]	Jullien and Clobert 2000
Survival	.000	2.56	2.56[b]	**−3.16*****	Jullien and Clobert 2000
Mammals (43):					
Body size	.992	−64.69	**−80.65*****	−64.76[b]	Garland et al. 1999
Home range size	.000	−91.25	−91.25[b]	−91.25[b]	Garland et al. 1999
Birds (36):					
BM P/ME	1.000	−57.03	**−63.98*****	−57.03[b]	Konarzewski 1995
BM K_{max}	1.000	−58.15	**−67.21*****	−58.15[b]	Konarzewski 1995
BM P_{max}	1.000	−60.55	**−66.90*****	−60.55[b]	Konarzewski 1995
P P/ME	.937	−54.46	**−58.94*****	−54.60[b]	Konarzewski 1995
P K_{max}	.999	−55.17	**−60.58*****	−55.17[b]	Konarzewski 1995
P P_{max}	1.000	−54.89	**−60.27****	−54.89[b]	Konarzewski 1995
ME P/ME	.930	−55.43	**−60.37****	−55.61[b]	Konarzewski 1995
ME K_{max}	1.000	−52.17	**−60.86*****	−52.17[b]	Konarzewski 1995
ME P_{max}	1.000	−52.91	**−59.59*****	−52.91[b]	Konarzewski 1995
Latitude	.724	−47.99	−48.73[b]	−49.47[b]	Konarzewski 1995
Lacertids (32):					
Habitat use	.711	−55.03	**−59.45****	−55.18[b]	Vanhooydonck and Van Damme 1999
Mammals (26):					
Host sampling effort	.000	−32.46	−32.46[b]	**−39.21*****	Morand and Harvey 2000
Parasite species richness	.435	−24.40	−26.29[b]	**−28.04****	Morand and Harvey 2000
Host density	1.000	−53.28	**−61.80*****	−53.28[b]	Morand and Harvey 2000
Body mass	1.000	−57.36	**−64.22*****	−57.36[b]	Morand and Harvey 2000
BMR	1.000	−47.45	**−54.17*****	−47.45[b]	Morand and Harvey 2000

Table 1 (*Continued*)

Taxon and character[a]	λ	ln lik	ln lik (λ = 0)	ln lik (λ = 1)	Reference
Longevity	1.000	−20.92	**−27.25*****	−20.92[b]	Morand and Harvey 2000
Anolis lizards (23):					
Jaw length	1.000	−57.77	**−68.71*****	−57.77[b]	Losos 1990
Fished fish (22):					
Population trend	.082	62.40	62.40[b]	**58.85****	Jennings et al. 1999
L_{inf}	.000	−23.77	−23.77[b]	**−26.96***	Jennings et al. 1999
K	.000	13.40	13.40[b]	**10.95***	Jennings et al. 1999
T_m	.562	−49.11	−50.58[b]	−50.41[b]	Jennings et al. 1999
L_m	.378	−105.66	−106.04[b]	−107.04[b]	Jennings et al. 1999
Sunfish (21):					
Range size	.000	−30.47	−30.47[b]	−31.12[b]	Pyron 1999
Body size	.781	−17.92	**−22.22****	−18.59[b]	Pyron 1999
Habitat breadth	.249	−43.60	−43.79[b]	−44.76[b]	Pyron 1999
Abundance	.604	−22.97	−23.87[b]	−23.67[b]	Pyron 1999
Ducks (10):					
Male recovery	.000	−19.74	−19.74[b]	−20.62[b]	Promislow et al. 1994
Female recovery	1.000	−18.14	−19.64[b]	−18.14[b]	Promislow et al. 1994
Male mortality	.541	11.54	10.82[b]	10.71[b]	Promislow et al. 1994
Female mortality	.000	10.09	10.09[b]	8.51[b]	Promislow et al. 1994
Mole rats (15):					
Group size	1.000	−77.46	**−87.68*****	−77.46[b]	Faulkes et al. 1997
Body mass	.901	−12.50	−14.38[b]	−12.69[b]	Faulkes et al. 1997
Gestation	.000	−39.68	−39.68[b]	**−42.36***	Faulkes et al. 1997
Geophyte density	.914	−20.75	−21.92[b]	−20.88[b]	Faulkes et al. 1997
Digestible energy	.000	−12.32	−12.32[b]	**−15.97****	Faulkes et al. 1997
Rainfall	.000	−12.20	−12.20[b]	**−16.66****	Faulkes et al. 1997

Note: We estimated λ, the degree of phylogenetic dependence of the data, defined as the maximum likelihood estimate of the multiplier of the off-diagonal elements of the variance-covariance matrix implied by the phylogeny (see fig. 1). The table records the reference, the number of tips (extant species in the phylogeny), and a brief description of the ecological character recorded. The maximum likelihood estimate of λ is given together with its associated log likelihood. Also shown are the log-likelihood values for the model, with λ set to either 0 or 1. Values significantly different from the test value (determined from a log-likelihood ratio test) are indicated in bold, together with the significance level. Abbreviations: lik = likelihood; ADMR = average daily metabolic rate; BMR = basal metabolic rate; BM = body mass; P = rate of production of new tissue; ME = daily metabolizable energy; latitude = breeding latitude. Parameters of von Bertallanfy growth equation: L_{inf} = maximum length; K = growth rate; T_m = age at maturity; L_m = length at maturity.

[a] Number in parentheses indicates number of tips.

[b] Not significant.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

the value of the log-likelihood ratio statistic for tests of $\lambda = 0$ and $\lambda = 1$ plotted against the number of taxa. The relationship is statistically significant in both cases, indicating that the power of both tests to reject the hypotheses increases as the size of the tree increases. Eleven out of the 16 equivocal cases were recorded for phylogenies with fewer than 30 taxa. In both figure 3*a* and 3*b*, the line of the regression of the likelihood ratio for the test of $\lambda = 0$ lies above the line for the regression of $\lambda = 1$, and this difference is statistically significant (see fig. 3 legend). However, by employing the maximum likelihood value of λ in such cases rather than opting for either a phylogenetic ($\lambda = 1$) or a nonphylogenetic ($\lambda = 0$) approach, the issue of power is obviated.

Application

The advantage of using λ to detect phylogenetic correlation is that it may also be used to correct data for phylogenetic effects in studies of correlation among traits. In the case of several traits, equation (4) becomes

$$p(\boldsymbol{y}) = \frac{1}{(2\pi)^{kn/2}} |\boldsymbol{\Sigma} \otimes \mathbf{V}|^{-1/2} \times \exp\left[-\frac{1}{2}(\boldsymbol{y} - \mathbf{X}\boldsymbol{a})^T(\boldsymbol{\Sigma} \otimes \mathbf{V})^{-1}(\boldsymbol{y} - \mathbf{X}\boldsymbol{a})\right], \quad (5)$$

where $\boldsymbol{y}$ is a vector of length kn, $\boldsymbol{a}$ is a vector of length k,

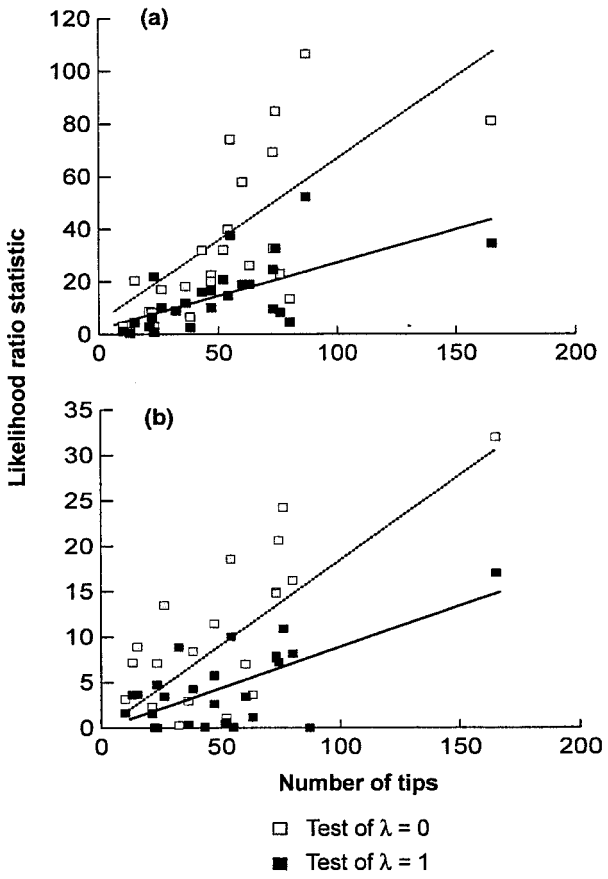

Figure 3: Effect of tree size on detection of phylogenetic dependence. The graphs show the log-likelihood ratio estimated for tests of $\lambda = 0$ (*filled symbols*) and tests of $\lambda = 1$ (*open symbols*) plotted against the number of terminal nodes on the phylogeny. *a*, Plotted as the average log-likelihood ratio statistic across all characters per study. Tests of $\lambda = 1$: $y = 2.67\ (\pm 1.50;\ P = .34) + 0.25x\ (\pm 0.06;\ P = .001)$. Test of $\lambda = 0$: $y = 0.64\ (\pm 1.11;\ P = .93) + 0.623x\ (\pm 0.0185;\ P < .001)$. *b*, Plotted as the maximum log-likelihood ratio observed in each study. Tests of $\lambda = 1$: $y = 0.19\ (\pm 7.26;\ P = .74) + 0.08x\ (\pm 0.02;\ P < .001)$. Test of $\lambda = 0$: $y = -0.05\ (\pm 0.173;\ P = .98) + 0.173x\ (\pm 0.0374;\ P < .001)$. In both cases, there was no significant difference between the slopes of the lines, but ANCOVA indicated that the intercepts were significantly different (average log-likelihood ratio: $F = 17.22$, df $= 1, 39$, $P < .001$; maximum log-likelihood ratio: $F = 17.39$, df $= 1, 39$, $P < .002$). The line for the regression of the test of $\lambda = 0$ on the number of tips is thus significantly higher than that for the regression of the test of $\lambda = 1$ on the number of tips in both *a* and *b*.

Σ is the $k \times k$ variance-covariance matrix of the traits, and the design matrix $\mathbf{X}$ is a $kn \times k$ matrix in which each entry in column i contains a 1 for trait i and a 0 otherwise. As above, equation (5) may be used to generate a likelihood function that solves to yield an estimate of the mean for each trait i:

$$\hat{\alpha}_i = (\boldsymbol{X}^T\mathbf{V}(\lambda)^{-1}\boldsymbol{X})^{-1}(\boldsymbol{X}^T\mathbf{V}(\lambda)^{-1}\boldsymbol{y}_i),$$

in which $\boldsymbol{X}$ is a vector of length n, all of whose entries are set to 1, and $\boldsymbol{y}_i$ is a vector listing the values of trait i. The elements of the variance-covariance matrix Σ are estimated by

$$\Sigma_{i,j} = \frac{1}{(n-k)}(\boldsymbol{y}_i - \mathbf{X}\hat{\alpha}_i)^T\mathbf{V}(\lambda)^{-1}(\boldsymbol{y}_j - \mathbf{X}\hat{\alpha}_j),$$

where the divisor $n - k$ yields an unbiased (restricted) maximum likelihood estimate of the variance. The elements of Σ, the trait variance-covariance matrix, may be used to estimate the correlation between traits. Under this approach, only one value of λ is estimated for the whole data set. By estimating Σ simultaneously with λ, the model finds the covariance between pairs of traits that is optimal under a common random effects Brownian process. The interpretation of λ is the same as before. If $\lambda = 0$, then trait evolution and coevolution are independent of phylogeny, whereas if $\lambda = 1$, then trait evolution follows Brownian motion. By comparison, Lynch (1991) separately estimates H^2 for each trait, generating an estimate of each trait's lineage-specific effect. These effects are then correlated. Under the random effects model, however, no such lineage effects exist.

To illustrate the use of λ in this context, we analyzed data presented by Poulin (1995; table 1). Poulin (1995) analyzed the ecological correlates of parasite species richness (i.e., the number of parasite species recorded) in a range of mammal, fish, and bird genera. We chose this data set because it presented several correlations for which significance tests gave conflicting results depending on whether data were analyzed across species (equivalent to assuming that $\lambda = 0$) or in a phylogenetic framework using independent contrasts (equivalent to assuming that $\lambda = 1$). We estimated the same correlations having set $\lambda = 0$ (e.g., simple nonphylogenetic analysis), with λ set to 1, and with λ set to its maximum likelihood value.

The results of the analysis are presented in table 2. Of the 16 correlations examined, only four suggested no phylogenetic association of the traits. This fraction is in line with our overall data set. Of the 12 correlations that required a phylogenetic analysis, seven yielded a maximum likelihood value of λ not significantly different from 1. The other five correlations yielded a value of λ significantly different from both 0 and 1; that is, these analyses require an intermediate phylogenetic adjustment. In total, seven correlations were statistically significant according to across-species analysis. However, three of these are nonsignificant when calculated using the maximum likelihood value of λ, which was not significantly different from 1 in any of these cases.

In summary, analysis of the values of λ indicates that varying levels of phylogenetic correction are required,

Table 2: Using the index of phylogenetic correlation, λ, to correct data for phylogenetic dependence

Trait	*n*	Correlation across species	λ = 1	λ = ML	ML λ
Mammals:					
Body size	77	.430***	.055[a]	**.055**[a]	1.000***, [a]
Diet	77	−.024[a]	.004[a]	.004[a]	1.000***, [a]
Latitude	77	.194[a]	−.027[a]	−.027[a]	1.000***, [a]
Density	25	.715***	.656***	.758***	.421[a]
Fish (intestinal parasites):					
Body size	72	.635***	.414***	.420**	.991***, [a]
Diet	72	.422***	.204[a]	**.232**[a]	.910***, [a]
Latitude	72	.209[a]	.135[a]	.161[a]	.547***, ***
Density	29	.755***	.700***	.762***	.227[a]
Fish (external parasites):					
Body size	40	.145[a]	.016[a]	.082[a]	.800***, [a]
Diet	40	.063[a]	−.095[a]	.028[a]	.724***, [a]
Latitude	40	−.215[a]	−.237[a]	−.219[a]	.000[a]
Density	18	.276[a]	.033[a]	.285[a]	.000[a]
Birds:					
Body size	54	.356**	.119[a]	**.235**[a]	.696**, **
Diet	54	.012[a]	−.027[a]	.005[a]	.620**, **
Latitude	54	−.191[a]	−.195[a]	−.183[a]	.643**, **
Density	27	.717***	.505**	.619***	.164*

Note: Data are taken from Poulin (1995) and relate to the correlation between parasite species richness and four ecological variables: body size, diet, latitude, and parasite density. The table shows the correlations estimated across species for three groups of species (mammals, fish, and birds) as well as the correlation estimated with λ set to 1 and λ set at its maximum likelihood (ML) value. The maximum likelihood value of λ is shown together with significance tests of λ = 0 and λ = 1 (the results of these tests are denoted by superscripts separated by a comma; e.g., three asterisks followed by superscript "a" denotes that the ML value of λ is not significantly different from 0 but significantly different from 1). Entries in bold are correlations where statistical significance differed between phylogenetic and nonphylogenetic analyses.

[a] Not significant.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

some of which are intermediate between the simple cross-species and contrast analyses. Because the maximum likelihood value is significantly different from 0 in each of the cases for which the nonphylogenetic and phylogenetic analyses gave conflicting results, the phylogenetic analysis is statistically better supported. This considerably simplifies the interpretation of the results. Without the use of an index of phylogenetic dependence such as λ, the reasons for the differences between the results of the phylogenetically controlled and uncontrolled analyses would be unclear. In this data set, we have shown that both phylogenetic and intermediate forms of analysis may be necessary, and in general the results from table 1 indicate that such situations may not be uncommon.

Discussion

We have shown how a parameter λ (Pagel 1999) may be used to characterize the degree of phylogenetic correlation of comparative data. We have applied this parameter to a number of problems that commonly arise in comparative analyses. Specifically, we have used λ to test data for evidence of phylogenetic dependence; to test whether a phylogenetic analysis should be preferred over a nonphylogenetic approach; and to adjust data according to the level of phylogenetic dependence, when λ takes a value indicating that the level of phylogenetic dependence is intermediate between the conventional null model of Brownian motion (λ = 1) and that of no phylogenetic dependence (λ = 0).

Measuring Phylogenetic Dependence

Testing data for phylogenetic dependence has been criticized by Martins (1996). Martins argued that finding evidence for phylogenetic dependence of traits (equivalent to finding $\lambda > 0$) may be used to justify the need for phy-

logenetic analysis. However, she suggested that failing to find evidence for phylogenetic dependence (i.e., finding $\lambda = 0$) cannot be used to justify the use of a nonphylogenetic approach. This is because the test may lack the power to reject the hypothesis of no phylogenetic dependence.

In addition to estimating λ, several other likelihood methods may be used to provide evidence of whether trait variation is associated with phylogeny. Lynch's (1991) method, discussed above, in common with the phylogenetic autocorrelation methods of Cheverud et al. (1985) and Gittleman and Kot (1990), all attempt to assess phylogenetic effects by partitioning the data into phylogenetic and nonphylogenetic components (see Christman et al. 1997 for a more detailed outline of the differences between these methods). As outlined above, λ represents a transformation of the tree matrix rather than a partition of the trait variance. All of these methods work by adjusting data using a continuously varying parameter. Analysis of data at the maximum likelihood value of this parameter allows data to be transformed optimally irrespective of the power of the test. Thus, these methods do not have the drawback that Martins (1996) pointed out. In contrast, other approaches test simply for the presence or absence of phylogenetic dependence (e.g., Abouheif 1999; Ackerly and Donoghue 1999) and may therefore be misleading when phylogenetic dependence is rejected (Martins 1996).

Phylogenetic versus Nonphylogenetic Analysis

In the context of examining correlated trait evolution, it has been recommended that the results of both phylogenetically based and nonphylogenetic analyses should generally be presented in comparative studies (Price 1997; Blackburn and Gaston 1998; Garland et al. 1999; Schluter 2000). However, the two models, representing the extremes of $\lambda = 0$ and $\lambda = 1$, make very different assumptions about how traits are associated, and for any single data set it is impossible that both are correct. More practically, analysis of all possible pairwise correlations between characters in table 1 indicates that the statistical significance (i.e., significant $P < .05$) of correlations using phylogenetic analysis (i.e., λ is set at its maximum likelihood value) was different from that of the corresponding nonphylogenetic test in 16% of cases. This is considerably higher that the nominal Type I error rate, and this is a powerful indication that such a test should be used to distinguish between the two forms of analysis; that is, λ should be estimated and the analysis performed with λ at its maximum likelihood values (this and all other analyses reported in the article can be performed in the Continuous software program).

By applying phylogenetic analysis within the framework of generalized least squares, it is possible to clarify a further objection to the application of phylogenetic analysis to many types of ecological character. Björklund (1997) argued that it may be incorrect to apply a phylogenetic analysis (which assumes a model of evolution) to data on ecological traits that may not meaningfully be said to have evolved or, equivalently, to infer ancestral states for these. As an example, he argued that it may be questionable to apply phylogenetic analysis to data on mortality rates (data taken from Promislow et al. 1994). Other examples would include the data "study effort" (number of studies per taxon) cited by Poulin (1998), since in this case ancestral species were clearly not studied and, hence, ancestral state reconstruction is meaningless. Many other ecological characters would fall into this category.

This objection misunderstands the reason for phylogenetic correction of data. Data are corrected for phylogenetic dependence in comparative studies in order to control for a lack of statistical independence. Similarity arising by descent is a direct way that data points among species may be associated with phylogeny, and frequently we wish to equate the model for statistical association with the model for trait evolution. Other causes of phylogenetic association may be more indirect. For instance, closely related species may live in similar habitats and occupy similar niches yielding similar mortality rates. However, regardless of how the phylogenetic associations arise, they cause the species' data points to be correlated—knowing the value for species x allows one to predict the value for species y better than chance if x and y are related phylogenetically. To control for this, the generalized least squares approach that we employ here (see also Pagel 1997, 1999) gives less weight to species that on average are highly related to other species in the data set. The parameter α in equation (1) can be regarded as an estimate of the ancestral state for traits that have evolved, but equally it is simply the weighted mean for the whole group, and this latter interpretation encompasses traits that have not evolved.

A serious limitation with applying comparative methods is that even as the number of gene sequences increases exponentially, the best working phylogenies for many organisms are taxonomies, and this is likely to remain the case for many groups (Kelly and Woodward 1996). Under such circumstances, an important role for tests of phylogenetic dependence is in deciding whether such coarse or uncertain phylogenetic information improves the description of the data (on the assumption that the data being analyzed in a comparative study are independent of the traits used to compile the taxonomy). Taxonomic information is unlikely to yield information on branch lengths, and, worse still, groups that are classified as monophyletic may have evolutionarily separate origins. Under

such circumstances, the fit between the taxonomic tree and data may be poor, and values of λ would be expected to be low, since the Brownian model would predict that species are more similar than would be observed. In contrast, if the value of λ is close to 1, then this would tend to indicate that there is a good fit between the data and the taxonomic tree and that this tree improves the description of the data, even if the taxonomy is an imperfect representation of the actual phylogeny. The prevalence of maximum likelihood values of λ close to 1 in table 1, in which many phylogenies are based on very coarse information, indicates that such phylogenetic information generally improves the description of data.

Phylogenetic Dependence and Alternative Evolutionary Models

If the wrong model of evolution is applied to comparative data, then the results of phylogenetic analyses may be no more informative than simple cross-species analyses or even misleading (Björklund 1997; Price 1997; Losos 1999; Harvey and Rambaut 2000). In the extreme, the cases of $\lambda = 0$ and $\lambda = 1$ are opposing models for character evolution. In the most general terms, a value of $\lambda < 1$ represents some degree of "loss of history" during the course of trait evolution.

One reason, unconnected with the mode of character evolution, why some values of λ are intermediate between 0 are unity is that λ may be sensitive to the amount of measurement error in the data. For example, the value for each species may be measured with an error, with these errors being unbiased and unconnected with phylogeny. This situation is closest to the one envisaged in Lynch's (1991) model, in which such measurement error could be equivalent to the nonphylogenetic random effect in his model. Since many values of λ in table 1 are equal to 1, it may be that, in practice, measurement error has a minor effect on trait variation relative to the effect of phylogeny. Because of this, and because a range of other models can yield intermediate values of λ, this index should not be generally interpreted as the proportion of trait variance attributed to phylogeny or as the proportion of meaningful (as opposed to error) variation in the data.

In the simplest non-Brownian model, traits may evolve instantaneously in response to selection, in which case traits would show no phylogenetic dependence ($\lambda = 0$). Intermediate levels of phylogenetic dependence ($0 < \lambda < 1$) could result from the mode of evolution represented by models such as the Ornstein-Uhlenbeck model (e.g., Hansen 1997; Martins and Hansen 1997), in which the influence of phylogeny decays through time because species trait values tend to be pulled back toward an evolutionary optimum irrespective of the starting point, and this can affect the results of comparative methods (Martins et al. 2002).

A wide range of models other than Brownian motion will yield phylogenetic dependence ($\lambda = 1$). Niche-filling models (e.g., Price 1997; Harvey and Rambaut 2000) assume that traits change only at speciation in response to selection to exploit new niches and will also yield λ values of 1. Additional tests are required to distinguish these forms of models from the Brownian model, although the data in table 1 are shown by such tests to be essentially Brownian (R. P. Freckleton, unpublished data). In this context, it is important to point out that λ measures phylogenetic dependence conditional on a Brownian model of trait evolution. It does not detect non-Brownian models of evolution.

The information presented in table 1 is not substantial enough to determine whether particular kinds of traits tend to show differing levels of phylogenetic dependence or not; however, this would be an important potential application of λ. Thus, given a range of traits measured on a single phylogeny, or many phylogenies with associated trait data, using λ as well as other transformations of the phylogeny matrix, it may prove possible to generalize about the level and extent to which different kinds of data exhibit phylogenetic dependence, as well as the form of this dependence. This work is ongoing.

Our review indicates that strong phylogenetic dependence exists within a wide range of phylogenies and data. In principle, it should be possible to use the techniques described here, in conjunction with further transformations of branch lengths, to explore the ways that different kinds of characters have evolved (Pagel 1997, 1999). Such analyses require accurate branch length information and are likely to be most revealing when applied to taxonomically and ecologically well-defined groups.

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