Traditional comparative studies examine evolutionary associations of traits by comparing different species, regardless of their phylogenetic relationships. A problem with such an approach is that trait values for each species are not statistically independent. This is because species partially share evolutionary histories (Felsenstein, 1983). Another problem is that "equilibrium" patterns seen among extant (or tip) species may not be reflective of preceding evolutionary "transformation" (Lauder, 1981). To help circumvent these difficulties, two of us (Huey and Bennett, 1987) developed a method to analyze the correlated evolution of continuous traits within an explicitly phylogenetic context. This method was developed specifically to examine "coadaptation" of physiological and behavioral traits related to the thermal biology of a group of Australian scincid lizards. Subsequently, Matthews and Garland (1991) have used computer simulation to compare the statistical properties of the Huey/Bennett approach, and some improvements thereof, with those of traditional nonphylogenetic analyses, and of the independent contrasts method of Felsenstein (1985). In addition, new information on the relationships and divergence times of the Australian lizards in our original study has become available. We have therefore reanalyzed our data according to this new information.

Most of the previously significant correlations between traits have been altered, with implications not only for our own study but also for the design and interpretation of comparative studies in general. Our reanalysis is timely, because interest in phylogenetically based methods for analyzing comparative data has expanded rapidly since 1987 (e.g., Felsenstein, 1988; Bell, 1989; Donoghue, 1989; Grafen, 1989; Lauder, 1990, 1991; Harvey and Pagel, 1991; Lynch, 1991). We apply three new analytical techniques: (1) simple correlation analysis of species values, using empirical tests of correlation coefficients (e.g., Zar, 1984); (2) maximum evolution analyses that estimate values at nodes. Coadaptation was again suggested by significant regressions involving inferred changes (most recent nodes to generic tips, N = 6) in CTF, Tc, and in CTFMax vs. Tc. Because both tests indicated significant positive correlations between thermal preference and measures of thermoregulation, we concluded that thermoregulatory behavior and physiology were at least partially coadapted. This conclusion appeared robust because species partially share evolutionary histories (Felsenstein, 1985). A critical test for the hypothesis that evolutionary changes in preferred body temperatures (Tc) (determined in a laboratory thermal gradient) should be positively associated ("coadapted") with evolutionary changes in functional thermal limits and the thermal sensitivity of sprint running speed. To address the latter, we estimated the optimal temperature for sprinting (Tf) (the body temperature at which animals can run fastest) for 12 species of Australian skinks. These values were compared to previously published determinations for lower (CTMin) and upper (CTMax) critical temperatures for the species (Bennett and John-Alder, 1986). We applied two different analytical methods. First, following suggestions by Clutton-Brock and Harvey (1984), we tested for correlations using generic averages of traits (N = 6), because a nested ANOVA on the phylogeny of the six genera and applying a "minimum evolution" algorithm to estimate ancestral values at nodes. Coadaptation was again suggested by significant regressions involving inferred changes (most recent nodes to generic tips, N = 6) in Tf, Tc, and in CTFMax vs. Tc.

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Fig. 1. Hypothesized phylogenetic relationships and estimated divergence times for 12 species of Australian scincid lizards (based on Baverstock and Donnellan, 1990; Greer, 1990, pers. comm.; Hutchinson et al., 1991; S. C. Donnellan, pers. comm.). For purposes of phylogenetic analyses of thermal data, species trichotomies within Ctenotus and Sphenomorphus were resolved by assuming that species closer in To (conceptually, the independent variable) were also closer phylogenetically. This assumption has a loose parsimony justification (Pagel, manuscript: cf Felsenstein, 1983). Absolute timing of the divergence of the Egernia-Leiolopisma group from the Sphenomorphus group (60 million years) and the diversification within the Sphenomorphus group (10 million years) is based on immunological distance and a molecular clock assumption (Baverstock and Donnellan, 1990; S. C. Donnellan, pers. comm.). Timing of the split between Egernia and Leiolopisma groups is assumed, based on the fact that morphological analyses (Greer, 1990, pers. comm.) indicate Egernia and Leiolopisma as sister taxa, whereas immunological data do not resolve the Egernia-Leiolopisma-Sphenomorphus trichotomy. Species within a genus (Sphenomorphus, Hemiergis, Leiolopisma) were arbitrarily assumed to have diverged one million years ago, except for the three Ctenotus, which are in different species groups (Greer, 1990) and so were assumed to have split at two million year intervals. Timing of other splits is arbitrary.

whether inferred changes in traits are correlated along branches (Martins and Garland, 1991), and (3) independent contrasts methods (Felsenstein, 1985, 1988; Grafen, 1989). These three approaches generally yield the conclusion that the original analyses—though intended to be conservative—were not conservative enough, such that evidence for coadaptation of some traits is weaker than previously thought.

Materials and Methods

Simple Correlation Analysis

Thermal data and hypothesized phylogenetic relationships of the 12 species studied by Huey and Bennett (1987) are given in Table 1 and Figure 1, respectively. (Huey and Bennett (1987) also used a generic mean value for Mabuya for T,, CTMax, and CTMin. As no data are available for To, we have excluded this genus in the present reanalysis.) Pearson product-moment correlations for species (not generic) values of the four thermal variables are presented in Table 2 (first row in each comparison). These correlations constitute a traditional, nonphylogenetic approach, termed "TIPS" by Martins and Garland (1991). The correlations make no assumption as to whether the mode of evolution is punctuational or gradual (see below), but they do assume (inappropriately) that the species values are statistically independent. Conventional significance tests with N - 2 = 10 df indicate that correlations greater than +0.497 (1-tailed) are significant at a < 0.05 (see Zar's, 1984, Table B.16). (One-tailed tests are appropriate for the stated hypothesis of positive coadaptation of thermal variables.) Judged in this way, three of six intercorrelations are significant [T,, with T (r = 0.585) and CTMax (r = 0.885), and To with CTMax (r = 0.619), suggesting coadaptation between behavior and thermal sensitivity. Huey and Bennett (1987), working with generic averages, found similar patterns of significance. The foregoing significance tests make no attempt to correct for phylogenetic nonindependence and therefore tend to overestimate the significance of correlations (Felsenstein, 1985; Grafen, 1989; Martins and Garland, 1991). Valid significance tests are possible, however, by reference to an empirical null distribution of correlation coefficients created via computer simulation. Using programs available from Martins and Garland (1991), we created such a null distribution (below). These simulations require specification of both branch lengths and model of evolutionary change (e.g., gradual or punctuational; Martins and Garland, 1991: cf Friday, 1987) appropriate for the characters being analyzed. The former, based on immunological distance, have recently become available for Australian skinks (see Fig. 1). However, whether evolution in this
TABLE I. Thermal data

<table>
<thead>
<tr>
<th>Species</th>
<th>CTMin</th>
<th>CTMax</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ctenotus serub</em></td>
<td>35.1</td>
<td>36.5</td>
</tr>
<tr>
<td><em>Ctenotus lamellatus</em></td>
<td>35.7</td>
<td>36.5</td>
</tr>
<tr>
<td><em>Ctenotus peronii</em></td>
<td>33.0</td>
<td>33.8</td>
</tr>
<tr>
<td><em>Sphenomorphus kosciuskoi</em></td>
<td>29.8</td>
<td>33.6</td>
</tr>
<tr>
<td><em>Sphenomorphus symplus</em></td>
<td>33.0</td>
<td>32.8</td>
</tr>
<tr>
<td><em>Sphenomorphus quisig</em></td>
<td>29.5</td>
<td>29.0</td>
</tr>
<tr>
<td><em>Eremiascincus fasciolatus</em></td>
<td>34.0</td>
<td>39.0</td>
</tr>
<tr>
<td><em>Hemargus peroni</em></td>
<td>35.1</td>
<td>39.8</td>
</tr>
<tr>
<td><em>Hemargus decresiensis</em></td>
<td>31.6</td>
<td>38.4</td>
</tr>
<tr>
<td><em>Leiolopisma entrecasteauxii</em> B</td>
<td>34.5</td>
<td>45.2</td>
</tr>
<tr>
<td><em>Leiolopisma entrecasteauxii A</em></td>
<td>33.4</td>
<td>42.8</td>
</tr>
<tr>
<td><em>Fogaria whitii</em></td>
<td>34.1</td>
<td>35.3</td>
</tr>
</tbody>
</table>

GROUP was tailed or punctuational (or a combination of both) is unknown. As a result we analyze both extreme cases. First we assume that evolutionary change was gradual (Brownian motion) and that the branch lengths of Figure 1 are correct. Actually, only the proportion of these divergence times need be assumed, that is, all could be of a constant factor without invalidating the analysis. Second, we assume that all evolutionary change was punctuational, occurring only at speciation events, equally in both daughter species, and that all speciation events are represented in Figure 1 (Martins and Garland, 1991). Not all speciation events are depicted: many other extant species are in these genera, and the number of extinct species is unknown. Nevertheless, an analysis assuming punctuational change is at least as useful for heuristic purposes. Moreover, our original analysis (Huey and Bennett, 1987) used a type of minimum evolution analysis that assumed punctuational change (see below). Our use of a punctuational model for analytical completeness should not be taken to imply that we think such a model is realistic; we do not.

We applied Felsenstein's method for the cases of both gradual (FLIG) and punctuational (FLIP) change. If either of these evolutionary models is valid, then resulting correlations can correctly be judged against conventional critical values (+0.497).

Finally, we applied Grafen's (1989) "standard regression," a modification and generalization of Felsenstein's approach. As noted above, the estimates of (relative) branch lengths must accurately indicate expected variance of change in order to apply Felsenstein's (1985) method for hypothesis testing validly. Rather than using these branch lengths directly, Grafen's (1989) programs for the "standard regression" use maximum likelihood techniques to estimate simultaneously correlations (or expressions) and "rho," a parameter that indicates, in essence, the power to which all branch lengths should be raised, as dictated by the data. Thus, a rho of unity would not change relative branch lengths. One degree of freedom is lost in estimating rho.

The only significant correlation found with the minimum evolution methods involving raw species values, Table 2, first rows). For a model of punctuational change, only +0.497 (1-tailed) can be considered statistically significant at a \( p < 0.05 \). Again, only +0.519 (FLIG and FLIP) correctly assigns significance to the correlations between \( Tp \) and \( CTMax \).

**Minimum Evolution Methods**

The significance tests for this method using conventional critical values are valid. As a check on our simulation procedures, significance tests for independent contrasts methods are based on comparisons with conventional critical values (from Zar, 1984). Critical values for 1-tailed tests are as follows: +0.828 (gradual), +0.643 (punctuational: MEIG, +0.789; FLIG, +0.519; FLIG and FLIP, +0.497).

**RESULTS**

**Testing Simple Correlations**

By applying the simulation procedure described above to the phylogeny in Figure 1, we computed appropriate significance levels for "TIPS" correlations (i.e., those involving raw species values, Table 2, first rows). For a model of gradual evolution, the distribution of simple Pearson product-moment correlation coefficients is centered about -0.991 to 0.987. Only correlations greater than +0.828 (1-tailed) can be considered statistically significant at \( p < 0.05 \). Tp is positively correlated with both \( Tp \) and \( CTMax \), but only the latter is significant (Table 2). For a model of punctuational change, only correlations greater than +0.643 (1-tailed) can be considered statistically significant at \( p < 0.05 \). Again, only the correlation between \( Tp \) and \( CTMax \) is significant, although between \( Tp \) and \( CTMax \) just fails short.

Note that the use of conventional statistical tests (\( > +0.497 \), 1-tailed) is significant at \( p < 0.05 \) incorrectly assigns significance to the correlations between \( Tp \) and \( Tp \) and between \( Tp \) and \( CTMax \).

Minimal evolution methods involve \( Tp \) and \( CTMax \), assuming phylogenetic independency (MEIP), third row of Table 2). Although the gradual model (MEIG) actually involves a larger number of comparisons for \( Tp \) and \( CTMax \) than did the punctuational model (MEIP), Felsenstein's method for hypothesis testing validly, \( Tp \) and \( CTMax \) both by themselves are statistically significant at \( p < 0.05 \). This result is probably attributable to the former method having slightly lower power (i.e., ability to detect significant correlations; see Table 3 in Martins and Garland's [1991]). Correlations involving raw species values, Table 2). For a model of punctuational change, only +0.497 (1-tailed) can be considered statistically significant at \( p < 0.05 \). Again, only the correlation between \( Tp \) and \( CTMax \) is significant, although between \( Tp \) and \( CTMax \) just fails short. Thus, the length of branches in Figure 1 seem to standardize the independent contrasts adequately, and conclusions derived from comparisons with conventional critical values are valid. As a check on our simulation procedures, we also computed critical values for Felsenstein's method from its empirical null distributions. These empirical critical values (1-tailed) were +0.303 (gradual model) and +0.519 (punctuational model), versus +0.497 (Zar, 1984).

Grafen's (1989) modification of Felsenstein's (1983) method, applied to the present data and phylogeny, indicates that none of the correlations is statistically significant (A. Grafen, pers. comm.; results not shown). This discrepancy exists because the F statistics for significant
mulation testing are very sensitive to rho, and the data suggest that rho is not equal to zero. Also, because rho must be estimated, resulting in a loss of 1 df, Grafen's standard regression should have somewhat lower power than Felsenstein's (1985) original method, unless rho equals 1.0, which the data suggest is not the case.

The first problem in the original analysis—overestimation of degrees of freedom—is a common one in comparative studies (Felsenstein, 1985; Grafen, 1989). This is ironic, because we intentionally used generic means for the two separate purposes (cf. Grafen, 1989 p. 141). Discrepancies occur because different phylogenetically independent contrasts methods exhibit higher power and yield better estimates of the variance in a particular trait is found among sister genera (see Huey and Bennett, 1987, p. 1103). Third, evolutionary correlation methods based only on inferred changes from most recent nodes to tips are considerably less accurate than those based on inferred changes occurring along all branches (Martins and Garland, 1991). Thus, even though valid significance tests can be obtained by reference to simulated null distributions (assuming the phylogeny and branch lengths are known without error), the TIPS method has little to recommend it. Methods do exist for use with only partial phylogenetic information (Fig. 1) suggests that these 12 Australian skinks belong to essentially three groups, each separated 50-60 million years ago. Indeed, 9 of 9, or 100%, of the correlations between thermal preferences (Tp) and had high critical thermal maxima, which is ironic, because we intentionally used generic means for the two separate purposes (cf. Grafen, 1989). Discrepancies occur because different phylogenetically independent contrasts methods exhibit higher power and yield better estimates of the variance in a particular trait is found among sister genera (see Huey and Bennett, 1987, p. 1103). Third, evolutionary correlation methods based only on inferred changes from most recent nodes to tips are considerably less accurate than those based on inferred changes occurring along all branches (Martins and Garland, 1991). 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available at the time of our original study; thus, the was not apparent [compare our Fig. 1 to Fig. 2 of Huey and Bennett (1987)].

relative nonindependence of some species and genera

cases” (Felsenstein, 1988 p. 465).

comparative study, but it does seem likely that power
topologies. Information on branch lengths was not
depend on the form of the phylogeny in relation to species
to detect significant evolutionary correlation will de-
sampled. This relationship points again to the need for
change in phylogenetic studies (e.g., Maddison et al.,
and others have noted before, “comparative biologists
change. Each point represents changes occurring along
one of the 22 branch segments of Figure 1. Dashed line
at 45° angle represents perfect coadaptation. Correla-
tions are for MElG method (see Table 2). The labels
change in thermal variables, based on minimum evolution re-
constructions of nodal values and assuming gradual
change. Each point represents changes occurring along
branches leading to

species within the Sphenomorphus group, rather than
any Leiolopisma or Eremias (see Fig. 1), which are ef-
ficaciously “outgroups” to the former. However, “out-
groups” are important for establishing directions of
change in phylogenetic studies (e.g., Maddison et al.,
Huey and Bennett, 1987), which would argue for a broader phylogenetic scope. This consideration
suggests more even sampling of the three generic
groups, rather than concentrating on one (of 12 spe-
cies sampled belonged to the Sphenomorphus group).
On the other hand, as we (Huey and Bennett, 1986)
and others have noted before, “comparative biologists
tend to suspect comparisons of distantly related spe-
cies, rather than concentrating on one (9 of 12 spe-
cies sampled belonged to the Sphenomorphus group).

We thank D. Bauwens, A. M. Castilla, and C. R. Petersen for comments on an earlier version of the manuscript and A. Grafen for analyzing the data with his standard regression approach and for helpful
discussions. Supported by National Science Foundation
grants BSR-9005003 to T.G., BSR-8718063 to R.B.H.,
and PCM-8102331 and DCB-8812028 to A.F.B.

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