Zen and the Art of Phylogenetically Independent Contrasts

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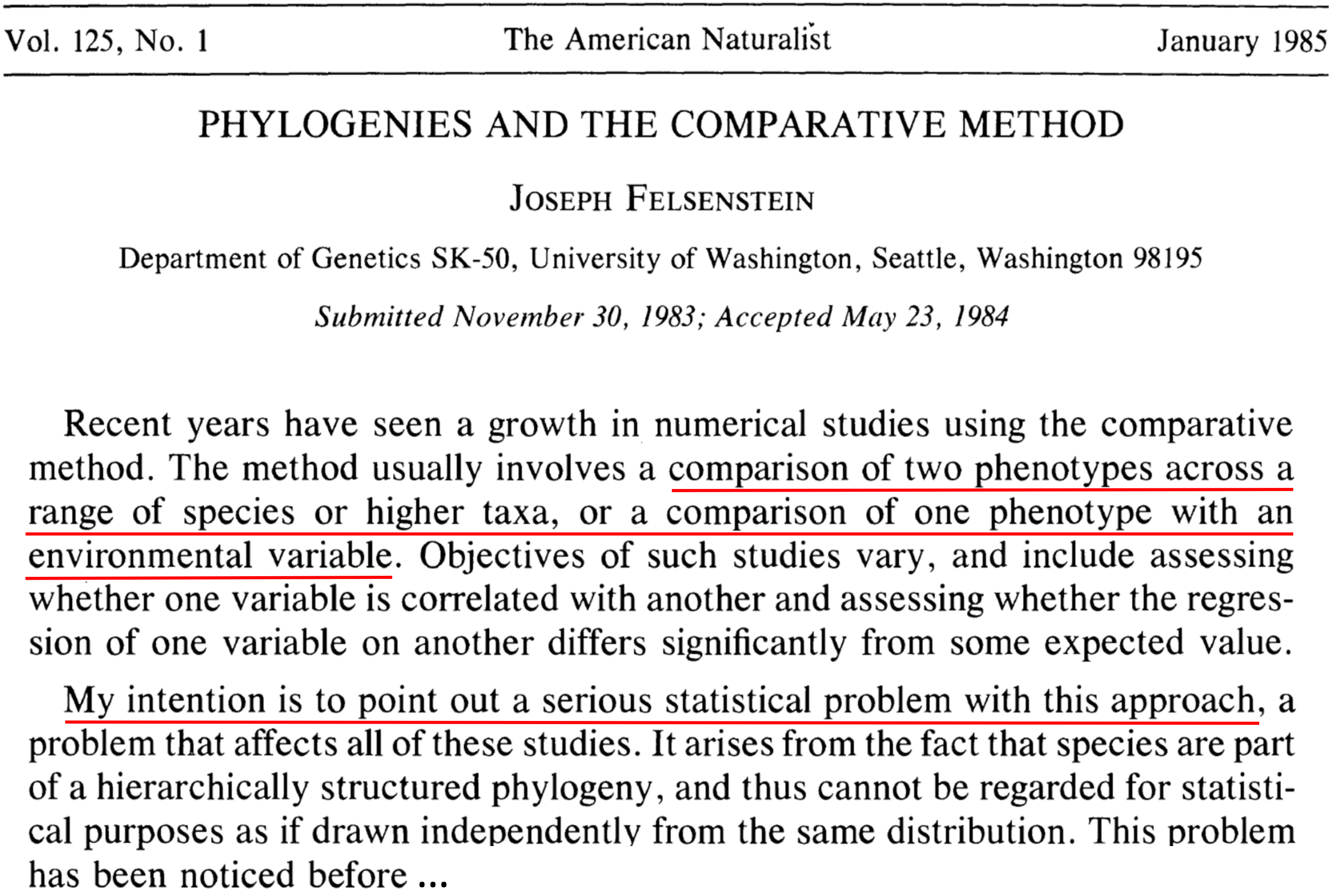
"The shot heard round the world"



Vol. 125, No. 1 The American Naturalist January 1985

PHYLOGENIES AND THE COMPARATIVE METHOD

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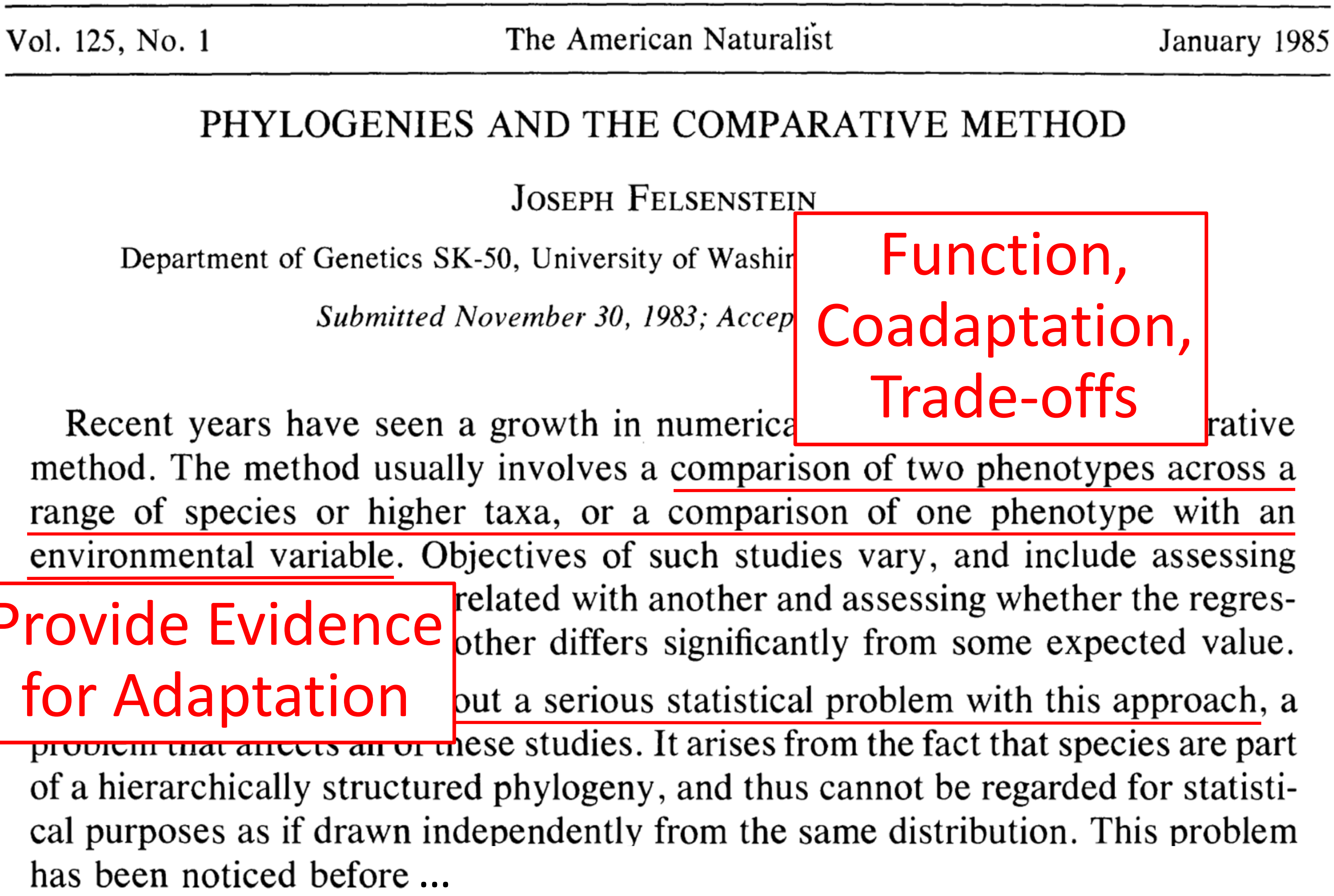
Submitted November 30, 1983; Accepted May 23, 1984

Recent years have seen a growth in numerical studies using the comparative method. The method usually involves a comparison of two phenotypes across a range of species or higher taxa, or a comparison of one phenotype with an environmental variable. Objectives of such studies vary, and include assessing whether one variable is correlated with another and assessing whether the regression of one variable on another differs significantly from some expected value.

My intention is to point out a serious statistical problem with this approach, a problem that affects all of these studies. It arises from the fact that species are part of a hierarchically structured phylogeny, and thus cannot be regarded for statistical purposes as if drawn independently from the same distribution. This problem has been noticed before ...

Ralph Waldo Emerson. 1837. Concord Hymn.

"The shot heard round the world"



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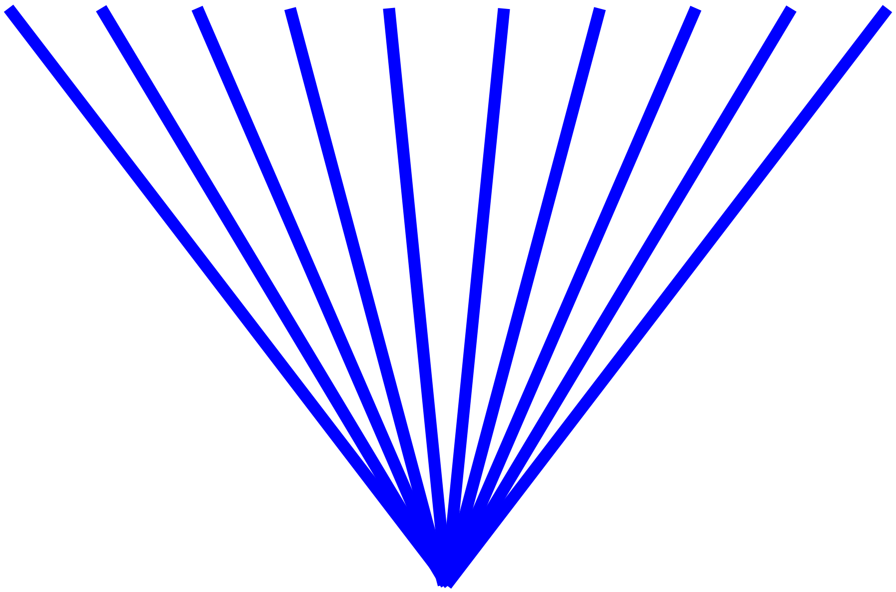
out a serious statistical problem with this approach, a problem that affects all of these studies. It arises from the fact that species are part of a hierarchically structured phylogeny, and thus cannot be regarded for statistical purposes as if drawn independently from the same distribution. This problem has been noticed before ...

Function, Coadaptation, Trade-offs

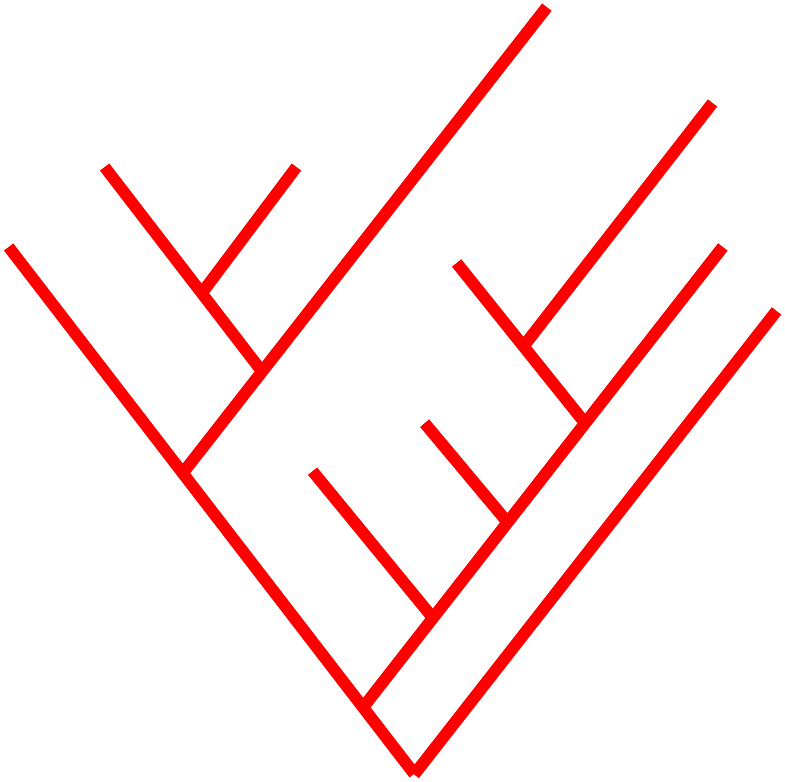
Provide Evidence for Adaptation

Ralph Waldo Emerson. 1837. Concord Hymn.

What Conventional Statistical Methods Assume

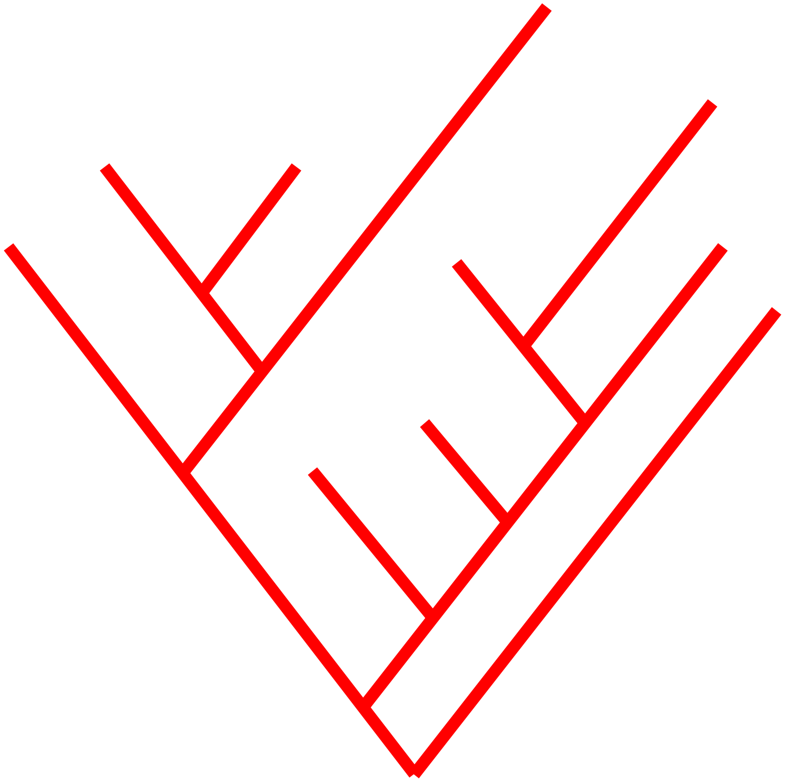


What Evolution Provides



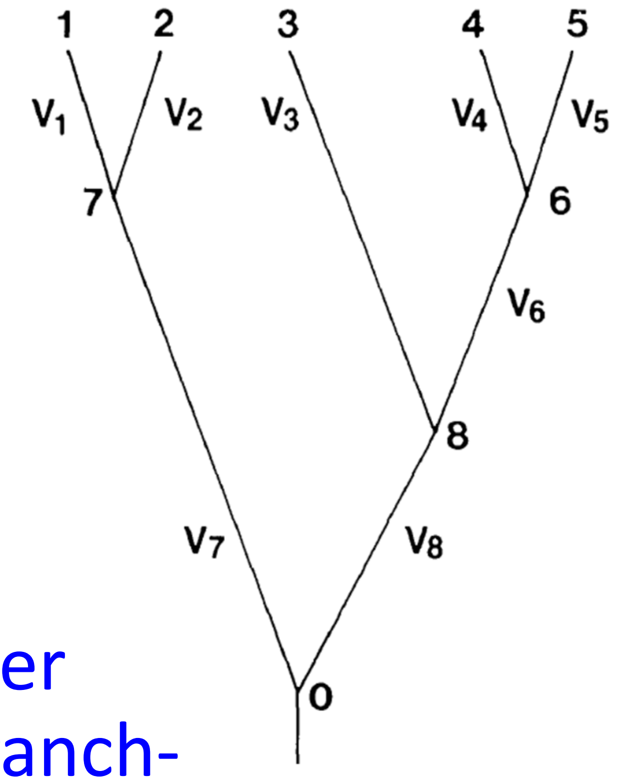
What Evolution Provides

So, tip data and/or residuals from a statistical model probably will ***not*** be **Independent and Identically Distributed**.

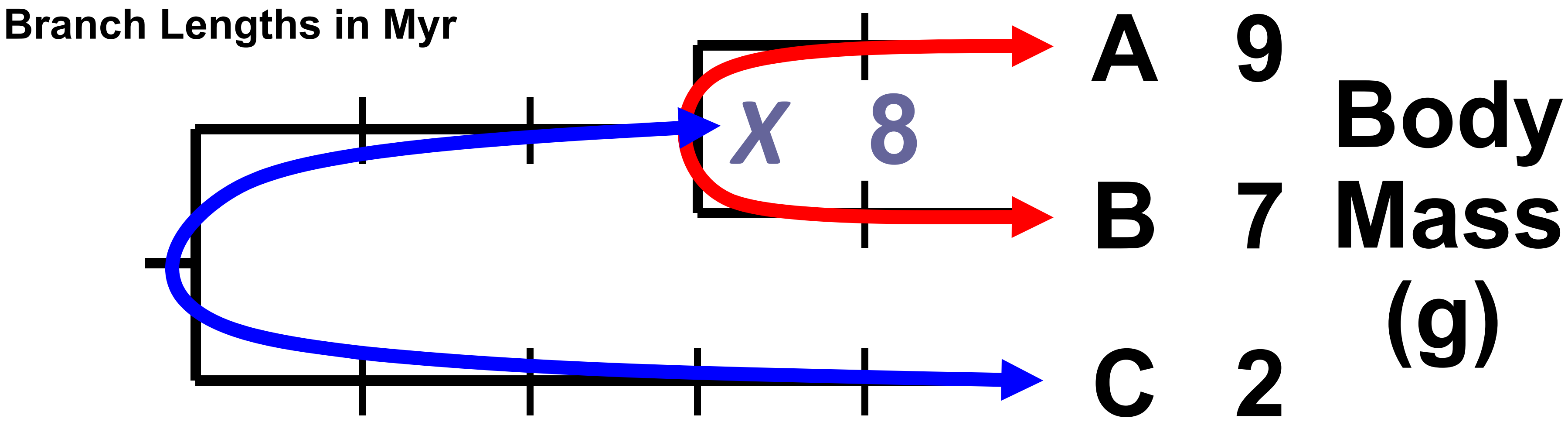


A possible solution: **transform the tip data** to meet the usual I.I.D. assumption

1) Assume tip data are measured without error
2) Assume topology is correct
3) Assume branch lengths available in units proportional to expected variance of trait evolution
4) Assume Brownian-motion like trait evolution, although some other models can be approximated by branch-length transformations, e.g., OU, ACDC



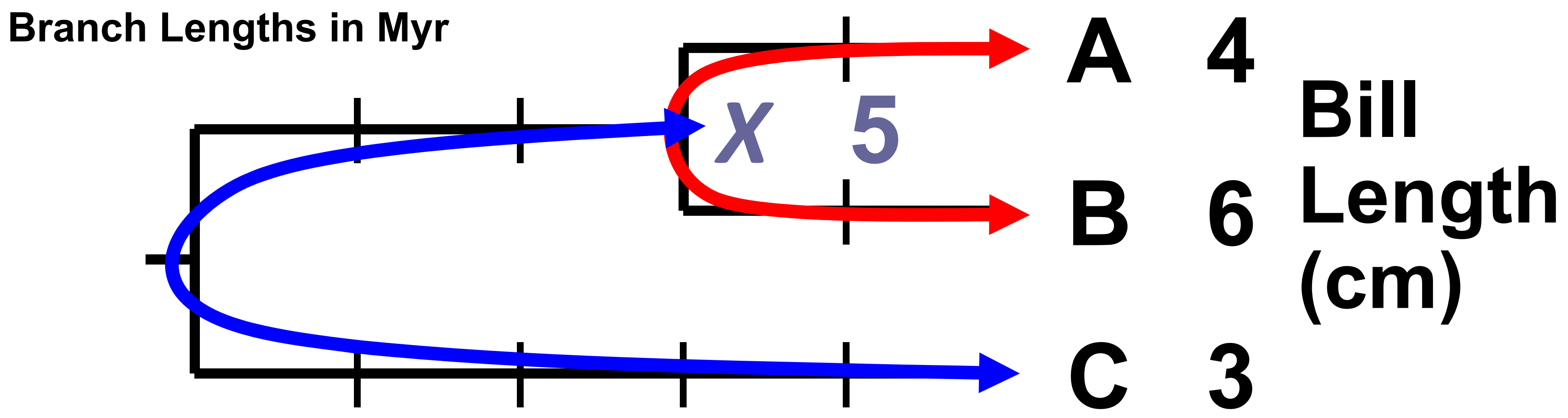
Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist 125:1-15.



Identify and Compute Independent Contrasts

Compute square roots of sums of (corrected) branch lengths = S.D.

Contrast	Value	S.D.	Standardized Contrast
A-B	2	2	1
X-C	6	3	2



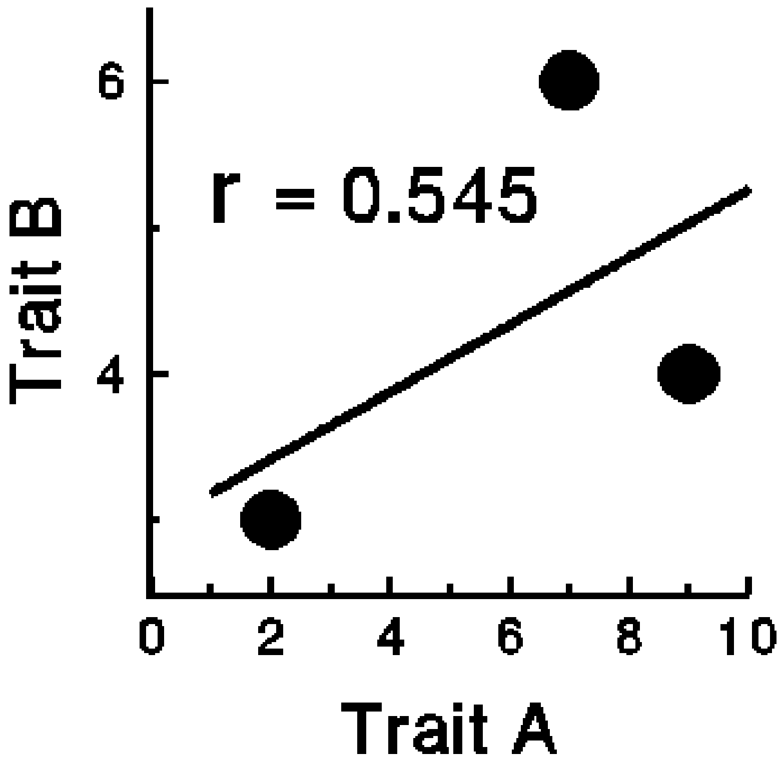
Identify and Compute Independent Contrasts

Compute square roots of sums of (corrected) branch lengths = S.D.

Contrast	Value	S.D.	Standardized Contrast
A-B	-2	2	-1
X-C	2	3	0.667

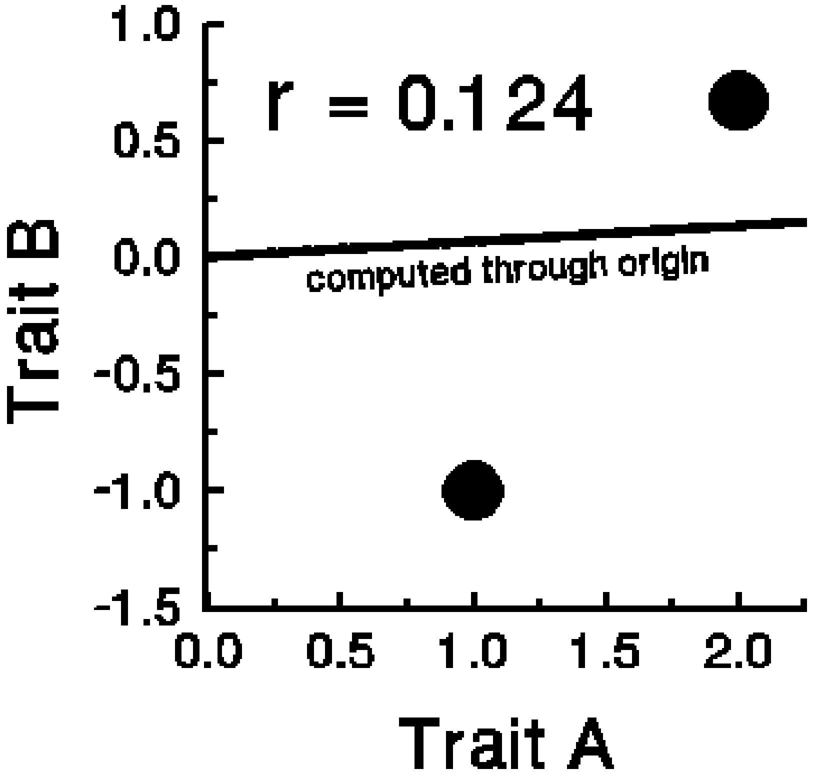
It can make a big difference!

Conventional
Statistical Analysis



d.f. = 1

Phylogenetically
Independent Contrasts



d.f. = 1

Joe's Top 5 Papers by Citations

	Total	Per Yr.
1. CONFIDENCE-LIMITS ON PHYLOGENIES - AN APPROACH USING THE BOOTSTRAP By: FELSENSTEIN, J EVOLUTION Volume: 39 Issue: 4 Pages: 783-791 1985	25,764	781
2. EVOLUTIONARY TREES FROM DNA-SEQUENCES - A MAXIMUM-LIKELIHOOD APPROACH By: FELSENSTEIN, J JOURNAL OF MOLECULAR EVOLUTION Volume: 17 Issue: 6 Pages: 368-376 1981	7,038	190
3. PHYLOGENIES AND THE COMPARATIVE METHOD By: FELSENSTEIN, J AMERICAN NATURALIST Volume: 125 Issue: 1 Pages: 1-15 1985	5,317	161
4. CASES IN WHICH PARSIMONY OR COMPATIBILITY METHODS WILL BE POSITIVELY MISLEADING By: FELSENSTEIN, J SYSTEMATIC ZOOLOGY Volume: 27 Issue: 4 Pages: 401-410 1978	1,943	49
5. PHYLOGENIES FROM MOLECULAR SEQUENCES - INFERENCE AND RELIABILITY By: FELSENSTEIN, J ANNUAL REVIEW OF GENETICS Volume: 22 Pages: 521-565 1988	1,740	58

7 June 2017

Ted's Top 5 Papers by Citations

	Total	Per Yr.
1. PROCEDURES FOR THE ANALYSIS OF COMPARATIVE DATA USING PHYLOGENETICALLY INDEPENDENT CONTRASTS By: GARLAND, T; HARVEY, PH; IVES, AR SYSTEMATIC BIOLOGY Volume: 41 Issue: 1 Pages: 18-32 1992	**1,642**	**63**
2. TESTING FOR PHYLOGENETIC SIGNAL IN COMPARATIVE DATA: BEHAVIORAL TRAITS ARE MORE LABILE By: Blomberg, SP; Garland, T; Ives, AR EVOLUTION Volume: 57 Issue: 4 Pages: 717-745 2003	**1,474**	**98**
3. PHYLOGENETIC ANALYSIS OF COVARIANCE BY COMPUTER-SIMULATION By: GARLAND, T; DICKERMAN, AW; JANIS, CM; et al. SYSTEMATIC BIOLOGY Volume: 42 Issue: 3 Pages: 265-292 1993	**804**	**32**
4. USING THE PAST TO PREDICT THE PRESENT: CONFIDENCE INTERVALS FOR REGRESSION EQUATIONS IN PHYLOGENETIC COMPARATIVE METHODS By: Garland, T; Ives, AR AMERICAN NATURALIST Volume: 155 Issue: 3 Pages: 346-364 2000	**517**	**29**
5. PHYLOGENETIC ANALYSES OF THE CORRELATED EVOLUTION OF CONTINUOUS CHARACTERS - A SIMULATION STUDY By: MARTINS, EP; GARLAND, T EVOLUTION Volume: 45 Issue: 3 Pages: 534-557 1991	**488**	**18**

7 June 2017

Joe's #3 Paper by Citations

3. **PHYLOGENIES AND THE COMPARATIVE METHOD** **5,317** **161**
By: FELSENSTEIN, J
AMERICAN NATURALIST Volume: 125 Issue: 1 Pages: 1-15 1985

“The real purpose of the scientific method is to make sure nature hasn’t misled you into thinking you know something you actually don’t know.”

independent contrasts

“When analytic thought, ~~the knife~~, is applied to experience, something is always killed in the process.” = ultra-adaptationism

— Robert M. Pirsig, 1974, *Zen and the Art of Motorcycle Maintenance: An Inquiry Into Values*

Three Common Misconceptions about Phylogenetically Independent Contrasts

Degrees of Freedom are lower:

Wrong! N contrasts = N tips -1, but you regain a d.f. because all computations are through the origin

Statistical power is lower:

Wrong! Power is same for nonphylogenetic data analyzed with conventional methods and phylogenetically simulated data analyzed with contrasts

They are estimating different things:

Yes and no, somewhat complicated.

Martins E.P. and T. Garland, Jr. 1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. Evolution 45:534–557.
Pagel M.D. 1993. Seeking the evolutionary regression coefficient: an analysis of what comparative methods measure. Journal of Theoretical Biology 164:191–205.
Purvis, A., and T. Garland, Jr. 1993. Polytomies in comparative analyses of continuous characters. Syst. Biol. 42:569-575.
Garland, Jr., T., and S. C. Adolph. 1994. Why not to do two-species comparative studies: limitations on inferring adaptation. Physiological Zoology 67:797-828.

First Use of Independent Contrasts 1987

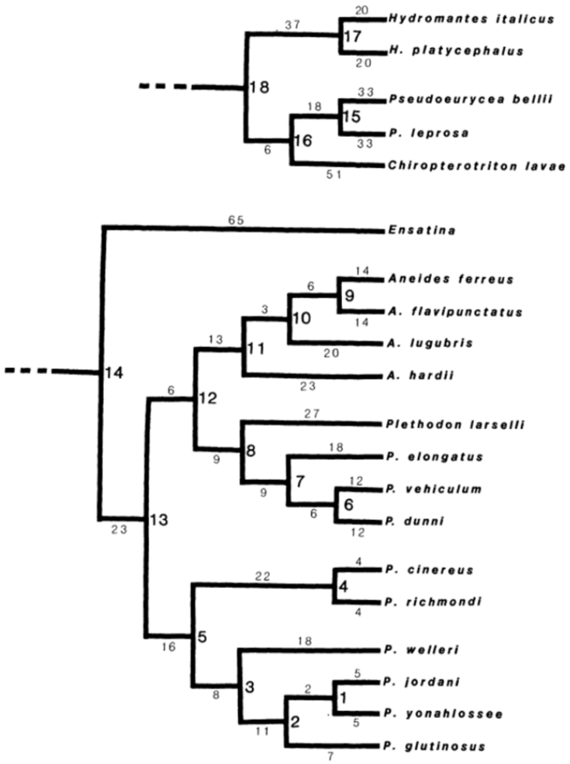


FIG. 3. Phylogenetic tree used to compute independent contrasts for genome size, growth rate, and differentiation rate in plethodontid salamanders (Table 4). Only taxa for which estimates of divergence times are available are included. Numbers (1–18) assigned to the contrasts (from Table 4) represent the nodes of the phylogenetic tree. Estimates of the duration of lineages are given in units of years × 10^7 along branches. These estimates are derived from comparative biochemical data (Wake et al., 1978; Highton and Larson, 1979; Maxson et al., 1979; Larson et al., 1981; Maxson and Wake, 1981), using the calibration of Maxson and Maxson (1979).

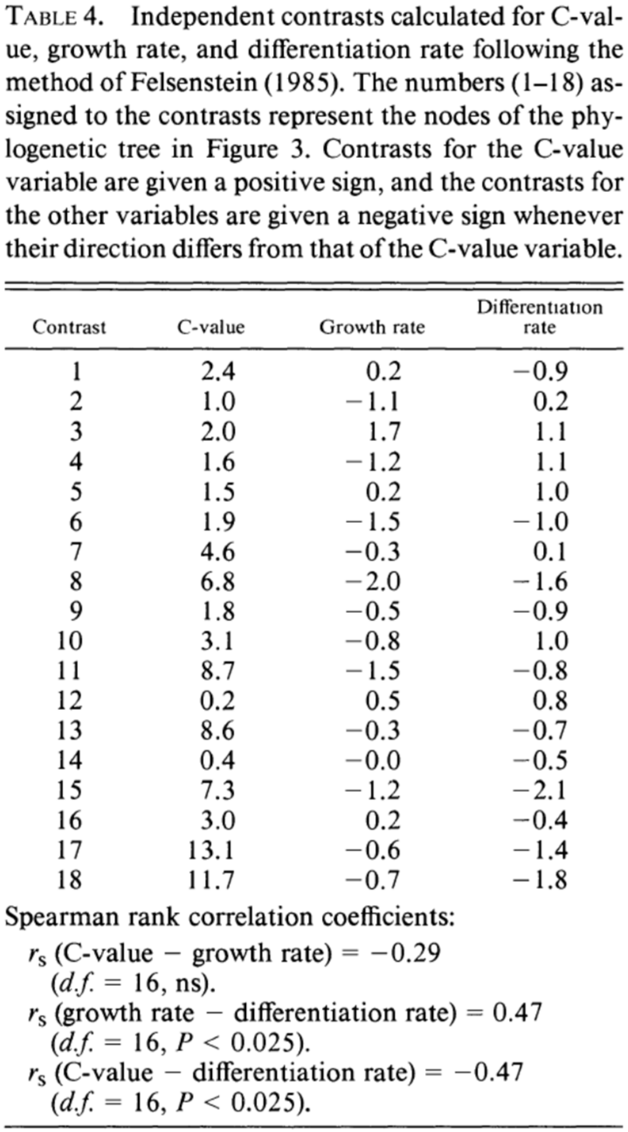


TABLE 4. Independent contrasts calculated for C-value, growth rate, and differentiation rate following the method of Felsenstein (1985). The numbers (1–18) assigned to the contrasts represent the nodes of the phylogenetic tree in Figure 3. Contrasts for the C-value variable are given a positive sign, and the contrasts for the other variables are given a negative sign whenever their direction differs from that of the C-value variable.

Contrast	C-value	Growth rate	Differentiation rate
1	2.4	0.2	−0.9
2	1.0	−1.1	0.2
3	2.0	1.7	1.1
4	1.6	−1.2	1.1
5	1.5	0.2	1.0
6	1.9	−1.5	−1.0
7	4.6	−0.3	0.1
8	6.8	−2.0	−1.6
9	1.8	−0.5	−0.9
10	3.1	−0.8	1.0
11	8.7	−1.5	−0.8
12	0.2	0.5	0.8
13	8.6	−0.3	−0.7
14	0.4	−0.0	−0.5
15	7.3	−1.2	−2.1
16	3.0	0.2	−0.4
17	13.1	−0.6	−1.4
18	11.7	−0.7	−1.8

Spearman rank correlation coefficients:

r_S (C-value − growth rate) = −0.29 ($d.f. = 16$, ns).

r_S (growth rate − differentiation rate) = 0.47 ($d.f. = 16$, $P < 0.025$).

r_S (C-value − differentiation rate) = −0.47 ($d.f. = 16$, $P < 0.025$).

Sessions, S. K., and A. Larson. 1987. Developmental correlates of genome size in plethodontid salamanders and their implications for genome evolution. Evolution 41:1239-1251.

Simulations to Show it Works

Simulations under Brownian motion along this tree

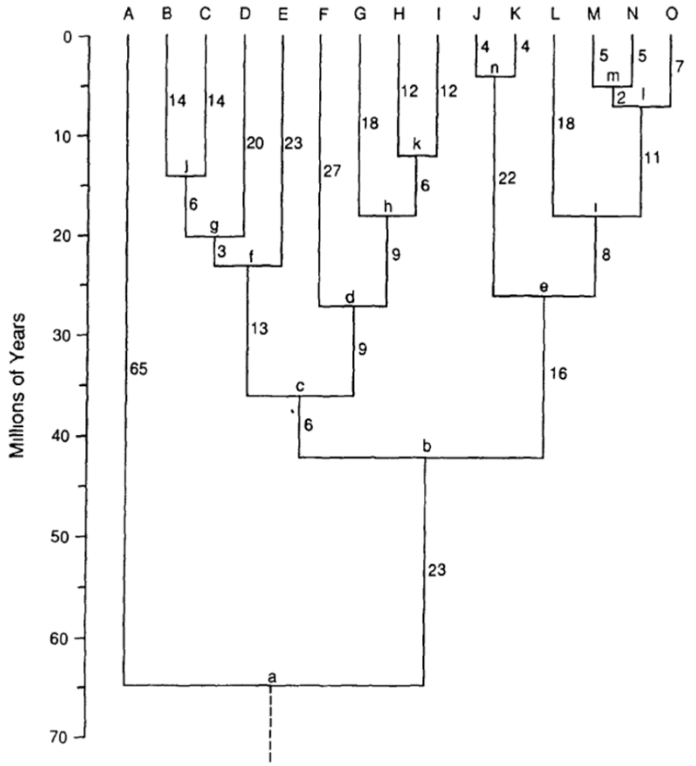
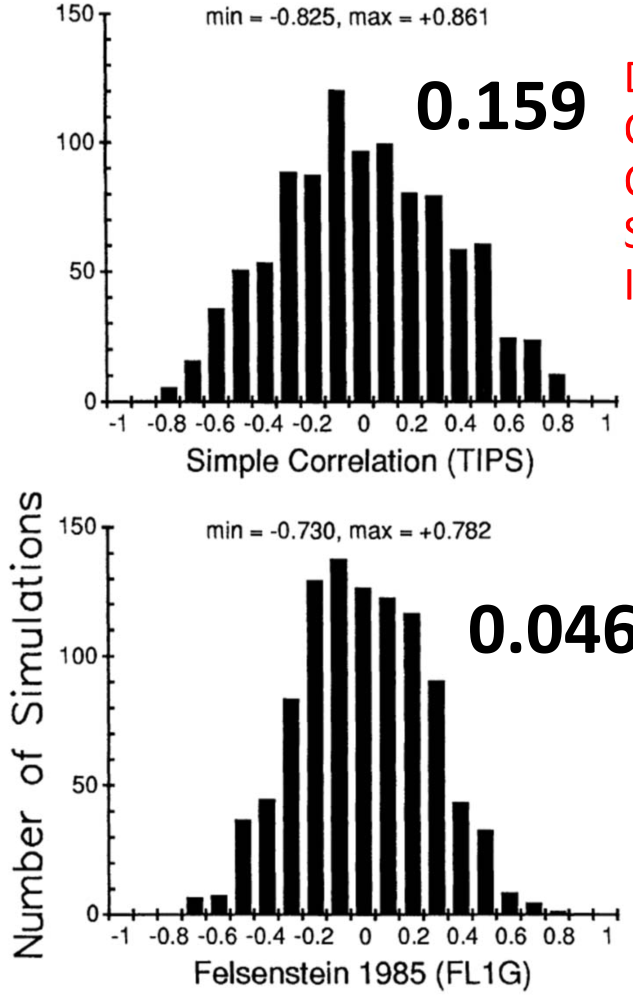


FIG. 2. Phylogeny for 15 species of plethodontid salamanders, from Sessions and Larson's (1987) Figure 3. Vertical axis represents time since divergence; horizontal axis is arbitrary.

Type I error rate with 1,000 simulations, 2-tailed test, and $\alpha = 0.05$



0.159

Distribution of Correlation Coefficients is too Spread Out when Ignoring Phylogeny

0.046

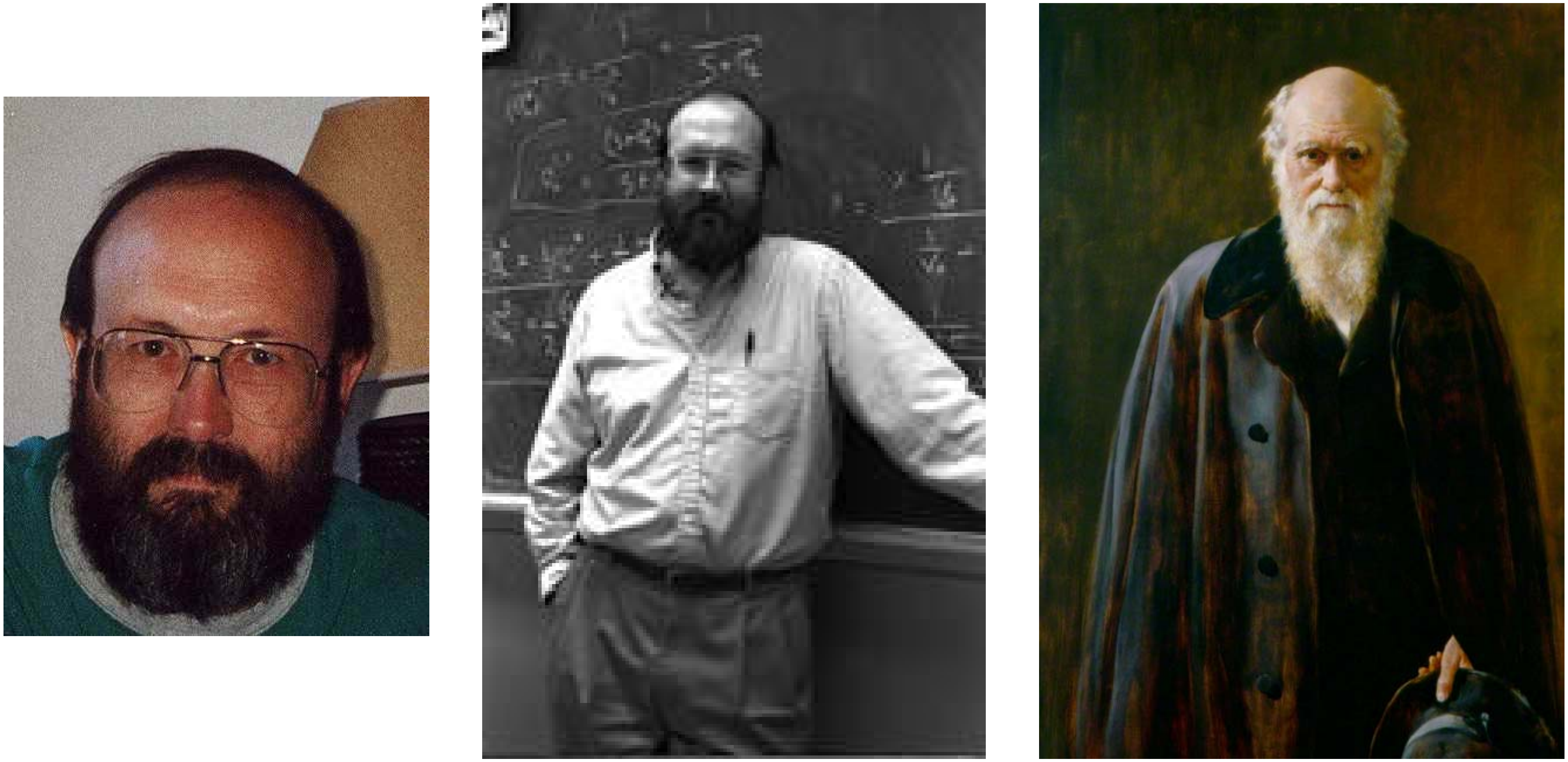
Independent Contrasts Fixes This

Martins, E. P., and T. Garland, Jr. 1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. Evolution 45:534–557.

Phylogenetically Independent Contrasts as an All-purpose Tool

- ✓ Correlation, Regression
- ✓ ANOVA, ANCOVA
- ✓ Principal Components
- ✓ Outlier Tests
- ✓ Rates of Evolution
- ✓ Ancestor Reconstruction
- ✓ Phylogenetic Signal
- ✓ Measurement Error Models

What did Joe know, and when did he know it?

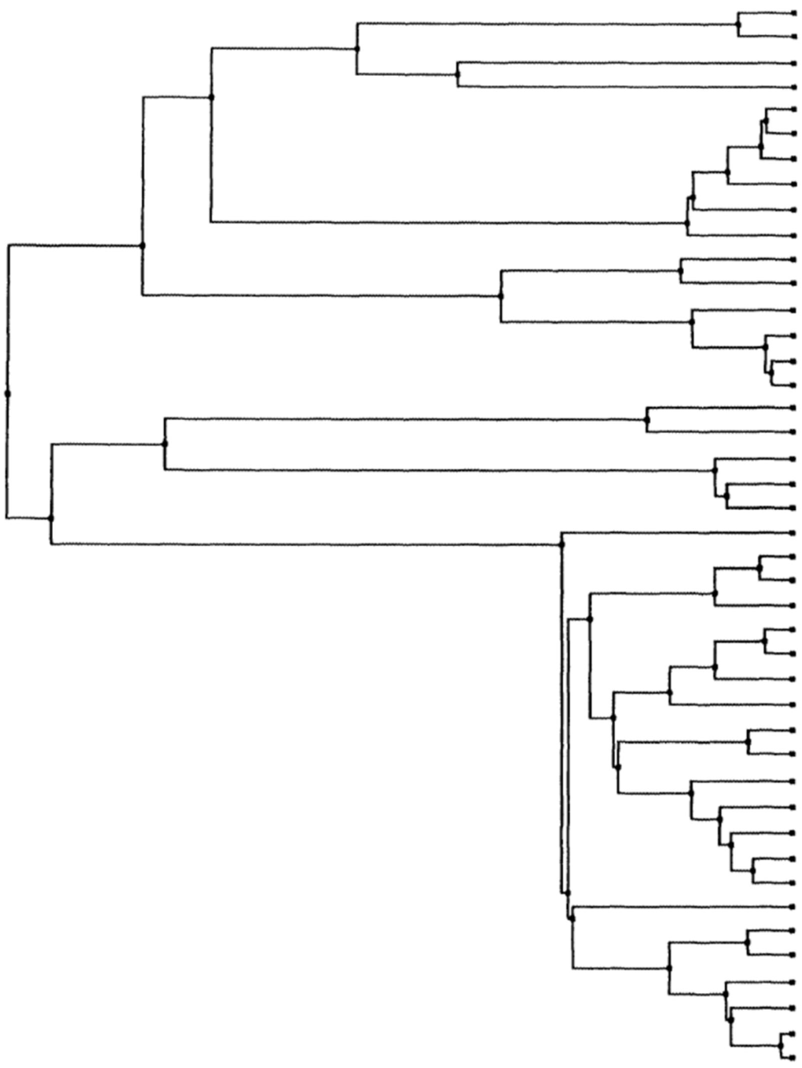


With apologies to Howard H. Baker, Jr., 1973

Practical Aspects

Ideally, you would have "real" branch lengths, such as estimated divergence times from fossils and molecular clocks.

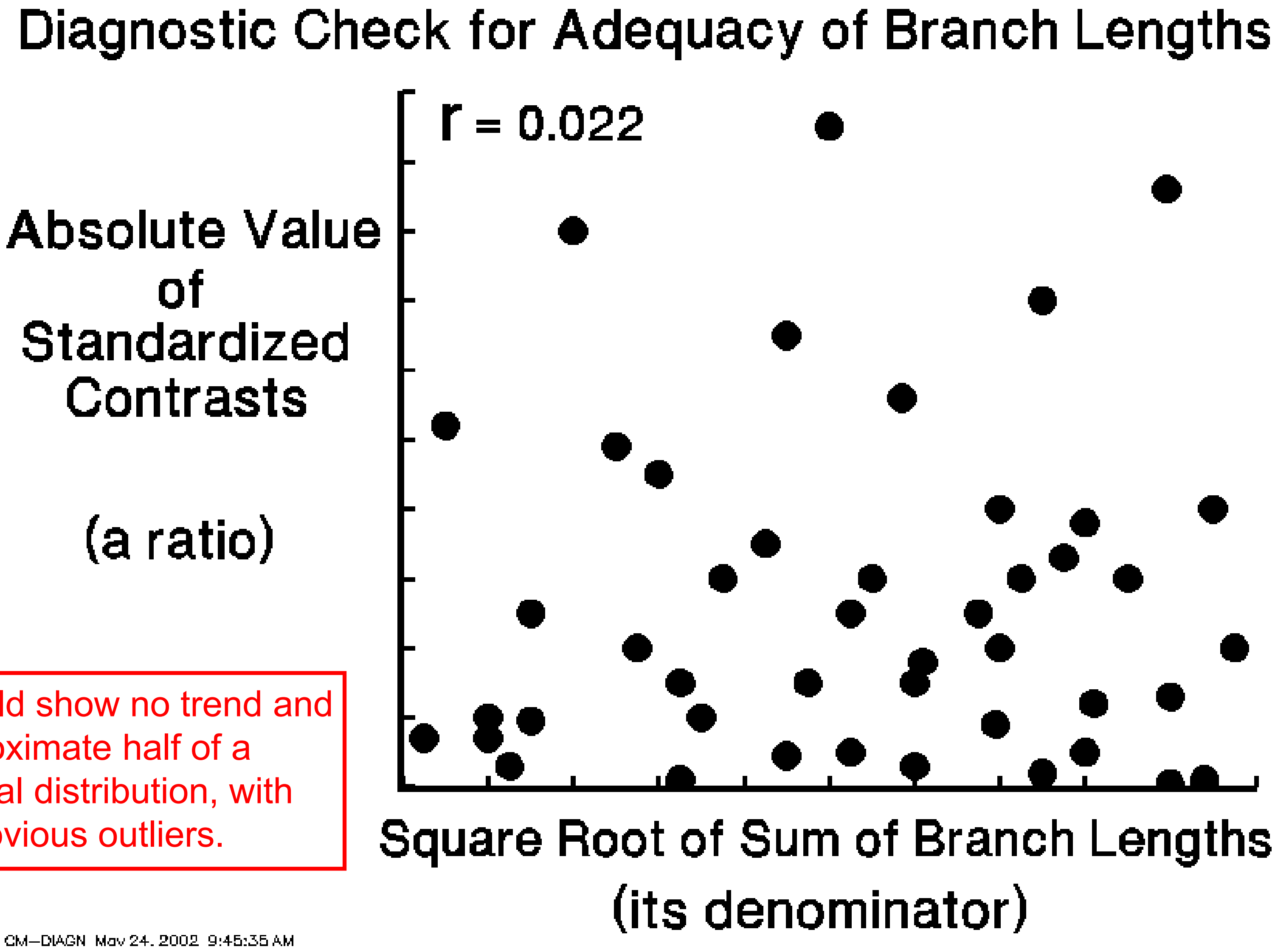
Ideally, you would know that the traits under study had evolved by a process similar to unbounded Brownian motion.



	Body mass (kg)	Home range (km^2)
Ursus horribilis	251.3	82.8
Ursus americanus	93.4	56.8
Mephitis mephitis	2.5	0.09
Meles meles	11.6	0.87
Canis lupus	35.3	394.0
Canis latrans	13.3	45
Lycaon pictus	20	160
Canis aureus	8.8	9.1
Urocyon cinereoargenteus	3.7	1.1
Vulpes fulva	4.8	4.3
Hyaena hyaena	26.8	152.8
Crocutta crocutta	52	25
Acinonyx jubatus	58.8	62.1
Panthera pardus	52.4	23.2
Panthera tigris	161	69.6
Panthera leo	155.8	236
Diceros bicornis	1,200	15.6
Ceratotherium simum	2,000	6.65
Equus hemionus	200	35
Equus caballus	350	22.5
Equus burchelli	235	165
Giraffa camelopardalis	1,075	84.6
Syncerus caffer	620	138
Bison bison	865	133
Taurotragus oryx	511	87.5
Gazella granti	62.5	20
Gazella thomsonii	20.5	5.3
Antilope cervicapra	37.5	6.5
Madoqua kirki	5.0	0.04
Oreamnos americanus	113.5	22.75
Ovis canadensis nelsoni	85	14.33
Hippotragus equinus	226.5	80
Aepyceros melampus	53.25	3.8
Connochaetes taurinus	216	75
Damaliscus lunatus	130	2.2
Alcelaphus buselaphus	136	5.0
Antilocapra americana	50	9.65
Cervus canadensis	300	12.93
Dama dama	55	0.43
Alces alces	384	16.09
Rangifer tarandus	100	30
Odocoileus virginianus	57	1.96
Odocoileus hemionus	74	2.85

Garland, Jr., T., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology 41:18–32.

Practical Aspects: Diagnostics

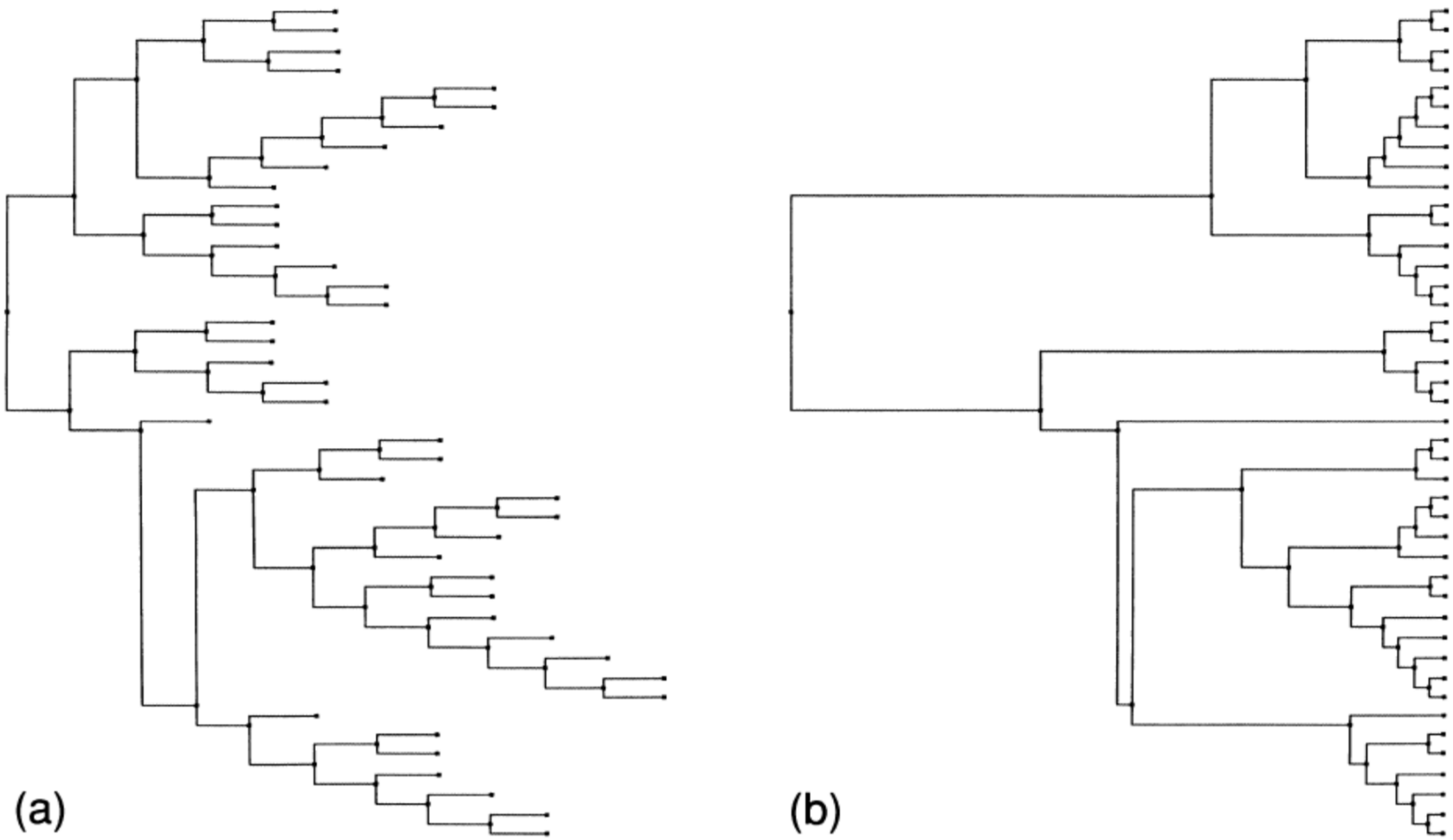


Should show no trend and approximate half of a normal distribution, with no obvious outliers.

Garland, Jr., T., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology 41:18–32.

Practical Aspects: Remedial Measures

When diagnostics fail, OK to try transformed and/or arbitrary branch lengths.
Simulations show this helps in terms of Type I error rates

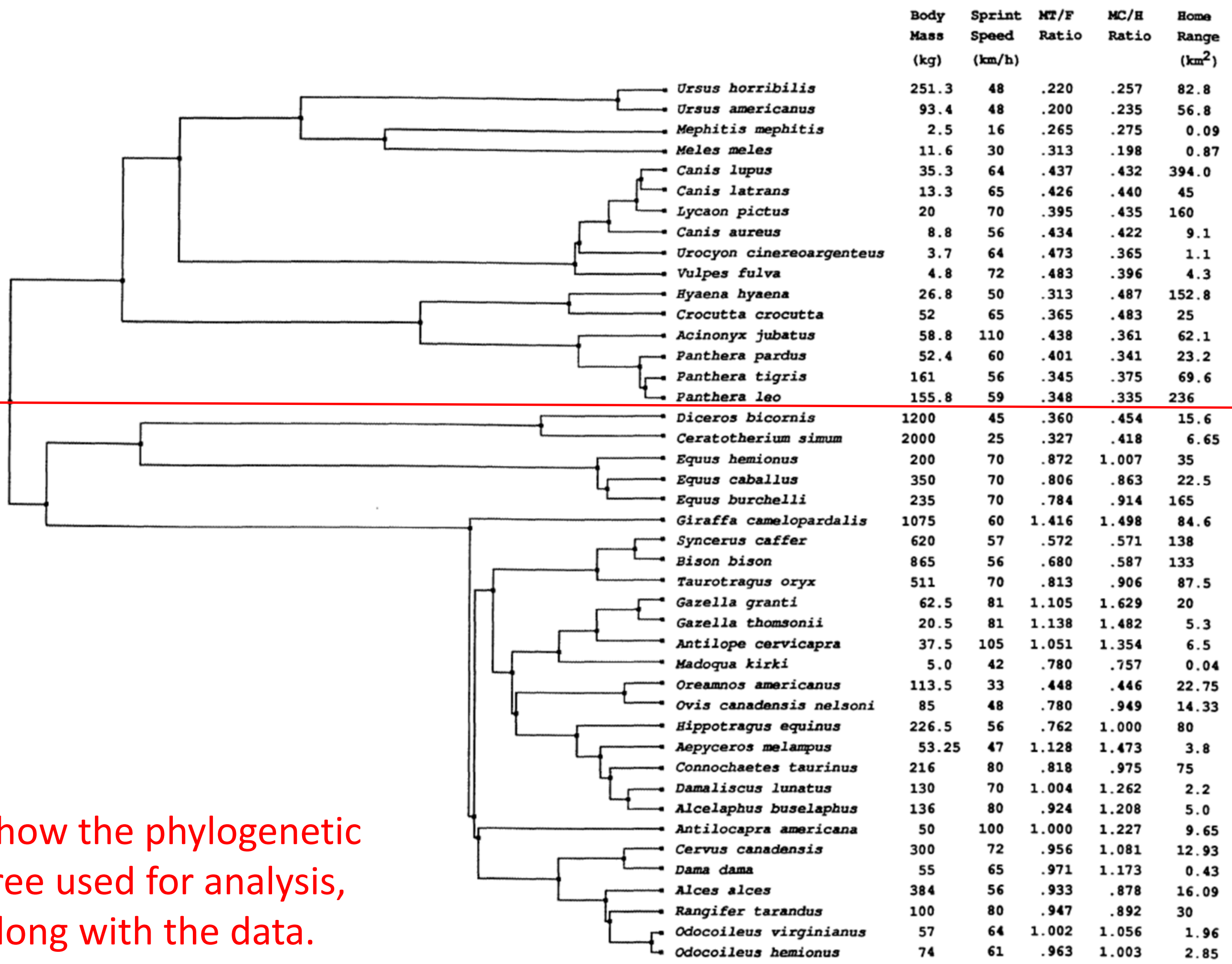


$\log_{10}$ transform

Arbitrary

Garland, Jr., T., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology 41:18-32.
Diaz-Uriarte R. and T. Garland. 1996. Testing hypotheses of correlated evolution using phylogenetically independent contrasts: sensitivity to deviations from Brownian motion. Systematic Biology 45:27–47.

Rate Tests for Phenotypic Evolution



	Body Mass (kg)	Sprint Speed (km/h)	MT/F Ratio	MC/H Ratio	Home Range (km^2)
Ursus horribilis	251.3	48	.220	.257	82.8
Ursus americanus	93.4	48	.200	.235	56.8
Mephitis mephitis	2.5	16	.265	.275	0.09
Meles meles	11.6	30	.313	.198	0.87
Canis lupus	35.3	64	.437	.432	394.0
Canis latrans	13.3	65	.426	.440	45
Lycaon pictus	20	70	.395	.435	160
Canis aureus	8.8	56	.434	.422	9.1
Urocyon cinereoargenteus	3.7	64	.473	.365	1.1
Vulpes fulva	4.8	72	.483	.396	4.3
Hyaena hyaena	26.8	50	.313	.487	152.8
Crocutta crocutta	52	65	.365	.483	25
Acinonyx jubatus	58.8	110	.438	.361	62.1
Panthera pardus	52.4	60	.401	.341	23.2
Panthera tigris	161	56	.345	.375	69.6
Panthera leo	155.8	59	.348	.335	236
Diceros bicornis	1200	45	.360	.454	15.6
Ceratotherium simum	2000	25	.327	.418	6.65
Equus hemionus	200	70	.872	1.007	35
Equus caballus	350	70	.806	.863	22.5
Equus burchelli	235	70	.784	.914	165
Giraffa camelopardalis	1075	60	1.416	1.498	84.6
Syncerus caffer	620	57	.572	.571	138
Bison bison	865	56	.680	.587	133
Taurotragus oryx	511	70	.813	.906	87.5
Gazella granti	62.5	81	1.105	1.629	20
Gazella thomsonii	20.5	81	1.138	1.482	5.3
Antilope cervicapra	37.5	105	1.051	1.354	6.5
Madoqua kirki	5.0	42	.780	.757	0.04
Oreamnos americanus	113.5	33	.448	.446	22.75
Ovis canadensis nelsoni	85	48	.780	.949	14.33
Hippotragus equinus	226.5	56	.762	1.000	80
Aepyceros melampus	53.25	47	1.128	1.473	3.8
Connochaetes taurinus	216	80	.818	.975	75
Damaliscus lunatus	130	70	1.004	1.262	2.2
Alcelaphus buselaphus	136	80	.924	1.208	5.0
Antilocapra americana	50	100	1.000	1.227	9.65
Cervus canadensis	300	72	.956	1.081	12.93
Dama dama	55	65	.971	1.173	0.43
Alces alces	384	56	.933	.878	16.09
Rangifer tarandus	100	80	.947	.892	30
Odocoileus virginianus	57	64	1.002	1.056	1.96
Odocoileus hemionus	74	61	.963	1.003	2.85

Predators,
Carnivora

Prey,
ungulates

Show the phylogenetic tree used for analysis, along with the data.

Garland, Jr., T. 1992. Rate tests for phenotypic evolution using phylogenetically independent contrasts. The American Naturalist 140:509–519.

Rate Tests for Phenotypic Evolution

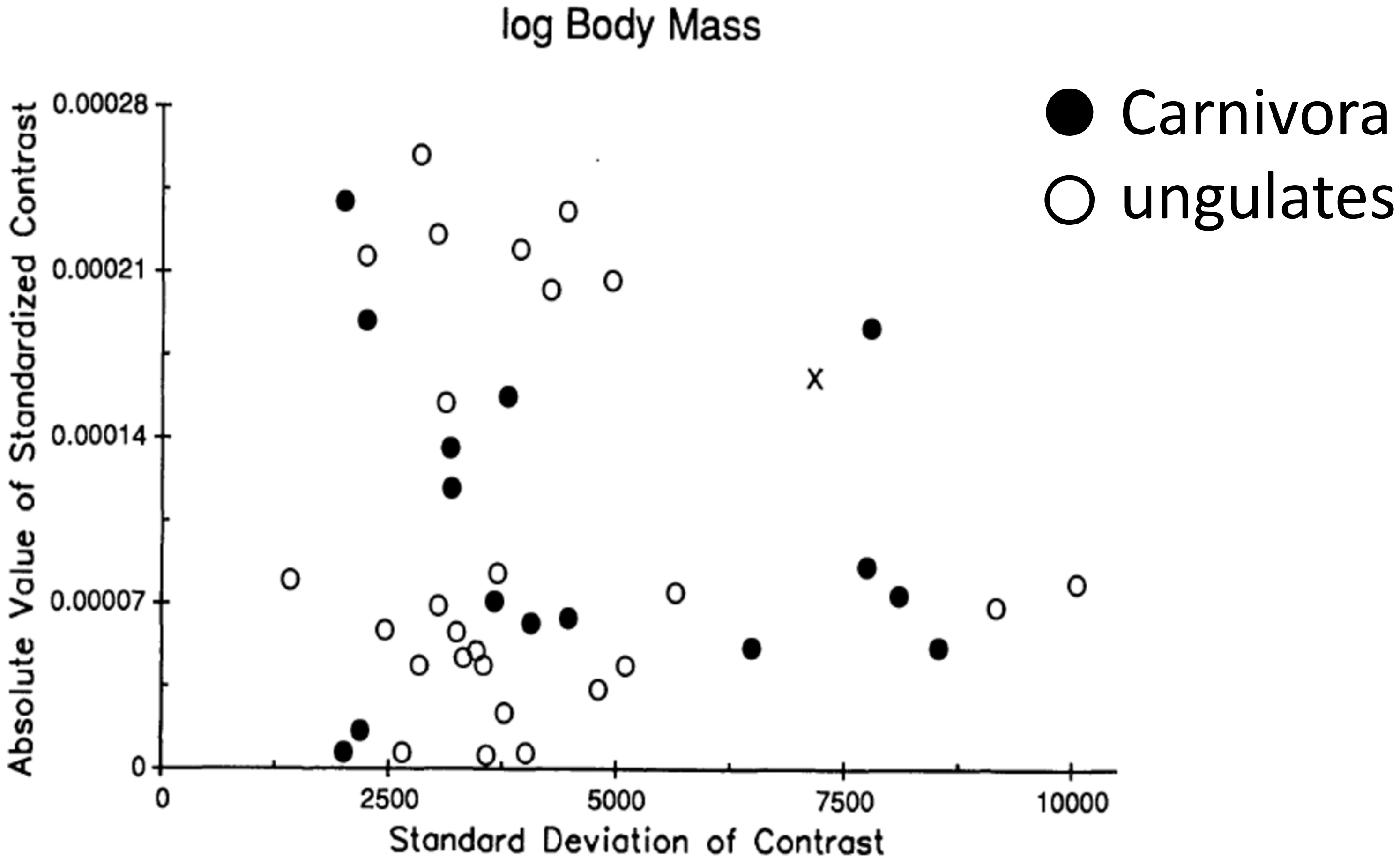
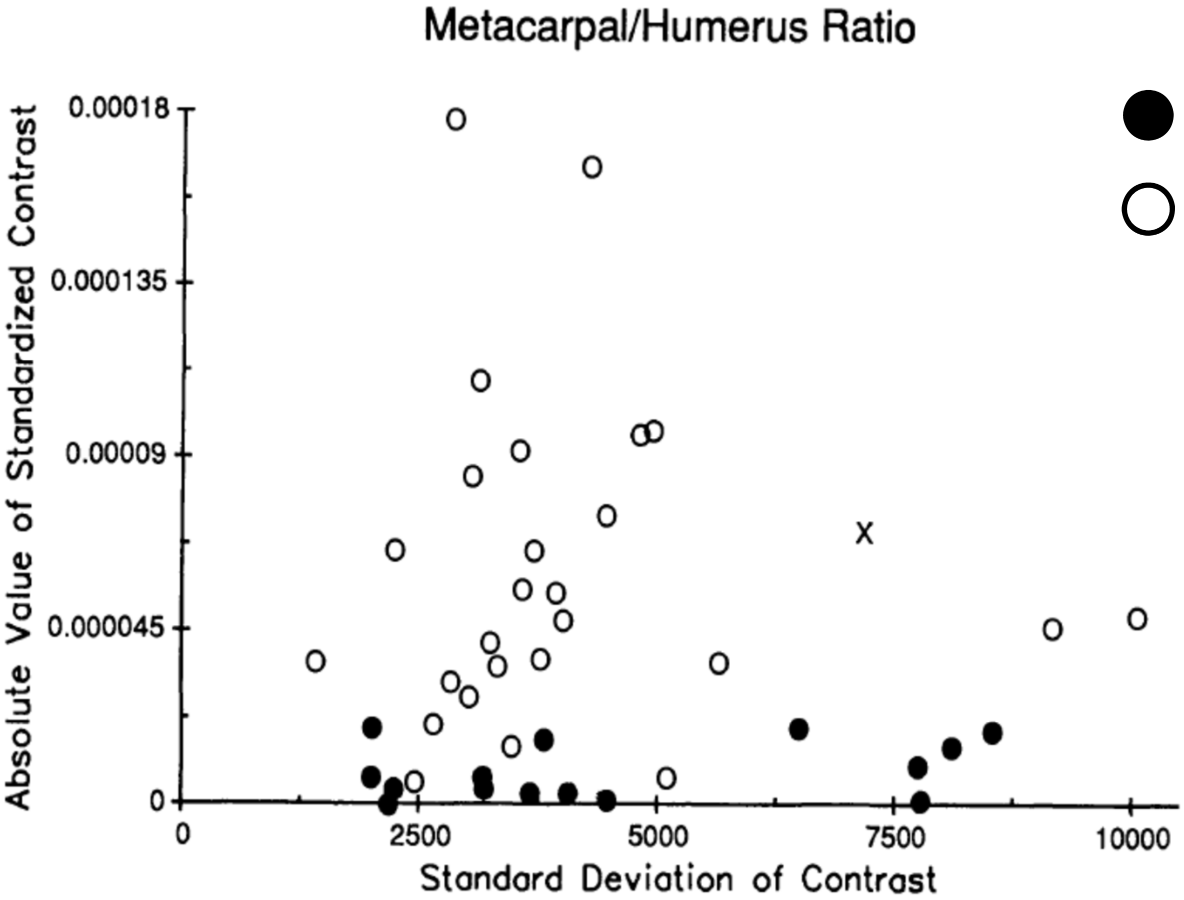


FIG. 3.—Comparison of evolutionary rates for $\log_{10}$ body mass of 16 species of Carnivora and 27 species of ungulates. Symbols are as in fig. 2.

Garland, Jr., T. 1992. Rate tests for phenotypic evolution using phylogenetically independent contrasts. The American Naturalist 140:509–519.

Rate Tests for Phenotypic Evolution



● Carnivora

○ ungulates

FIG. 2.—Comparison of evolutionary rates in metacarpal-humerus ratio (as indicated by standardized phylogenetically independent contrasts) within clades of 16 species of Carnivora (*closed circles*) and 27 species of ungulates (*open circles;* phylogeny from fig. 1); *X* represents

Garland, Jr., T. 1992. Rate tests for phenotypic evolution using phylogenetically independent contrasts. The American Naturalist 140:509–519.

Comparisons of Clade Means

Conventional

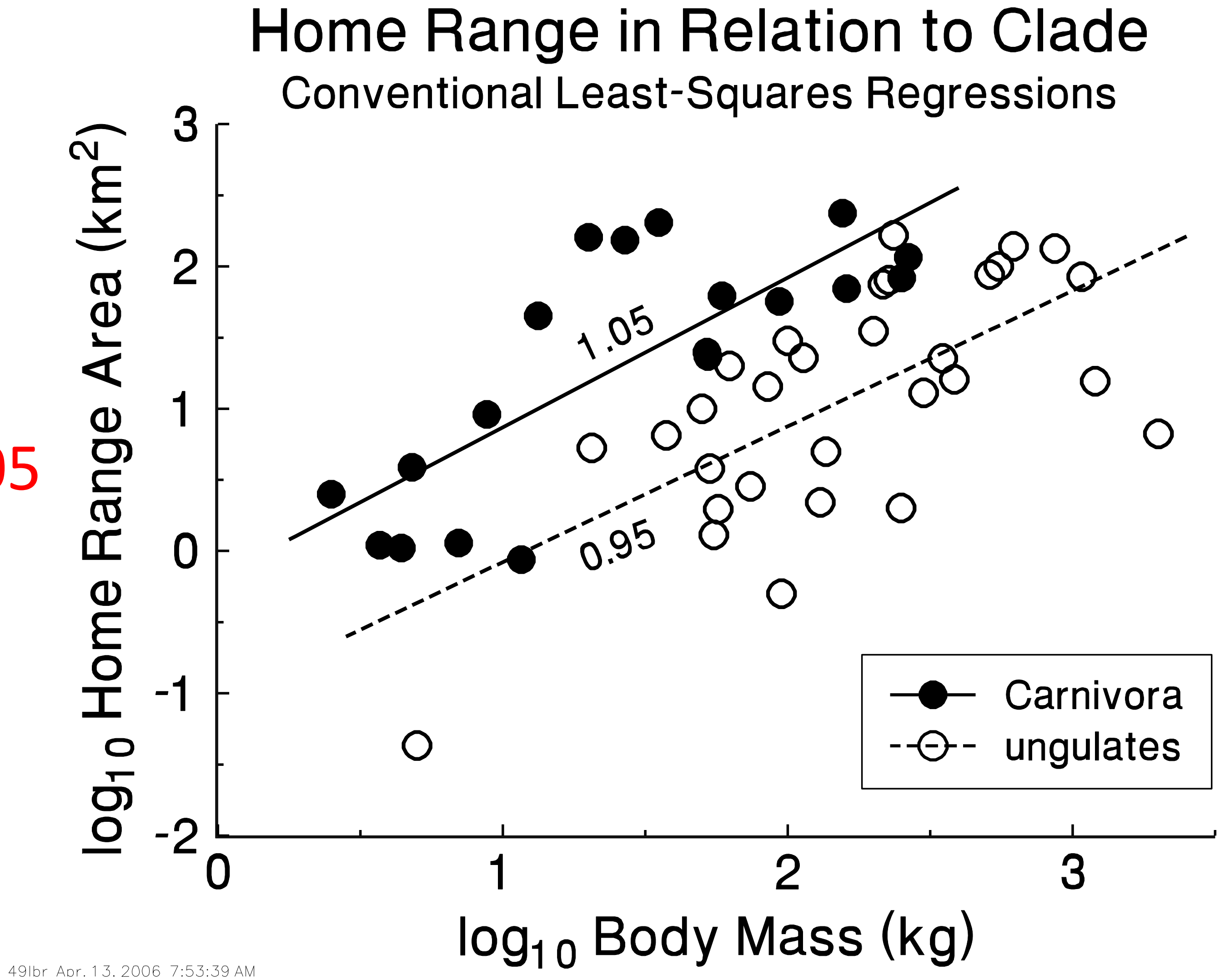
ANCOVA

$F_{1,46} = 23.97$

Critical value =

4.05 for $\alpha = 0.05$

$P < 0.001$

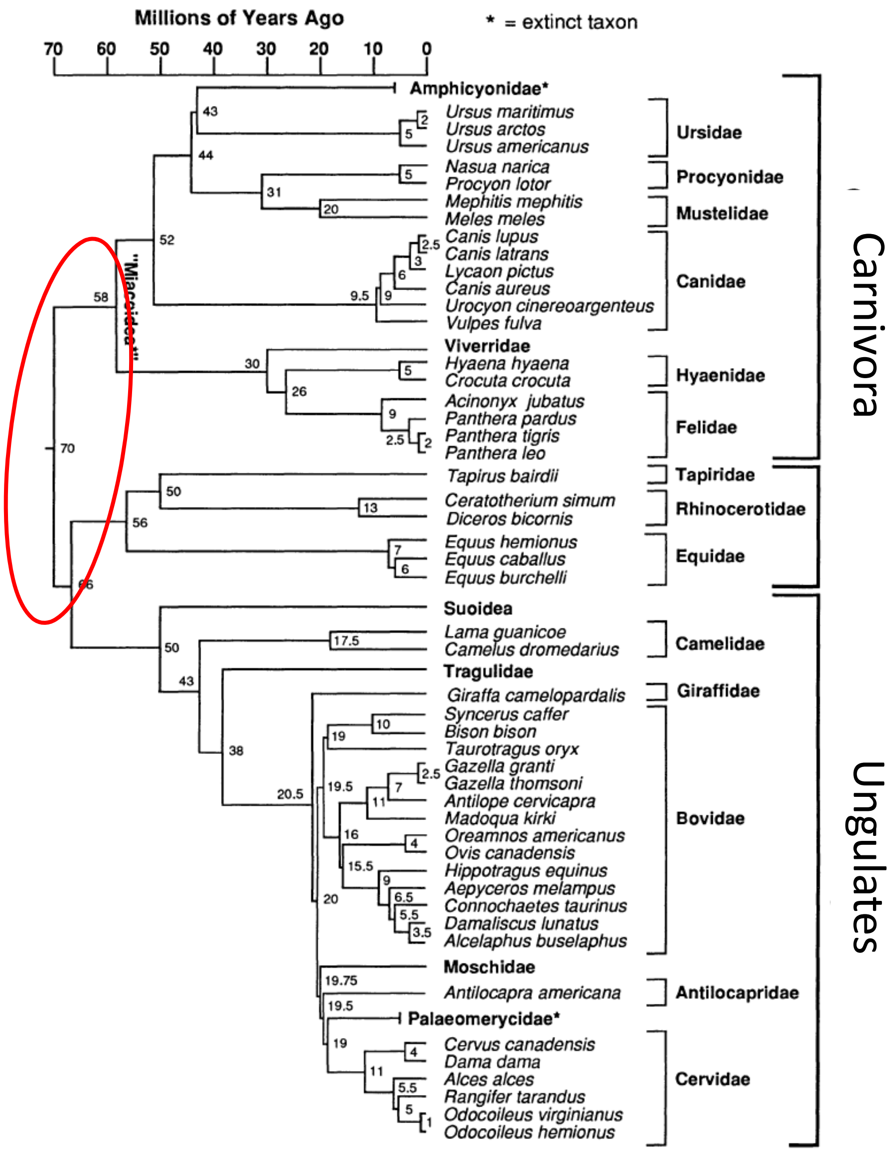


Home Range in Relation to Clade

Conventional Least-Squares Regressions

Garland, Jr., T., A. W. Dickerman, C. M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. Systematic Biology 42:265–292.

Comparisons of Clade Means



Test of whether basal contrast deviates from the within-clade pattern allows test of whether clades differ in mean value.

Garland, Jr., T., A. W. Dickerman, C. M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. Systematic Biology 42:265–292.

Comparisons of Clade Means

The basal contrast does not fall outside the 95% prediction interval for a new observation, either 1-tailed or 2-tailed.

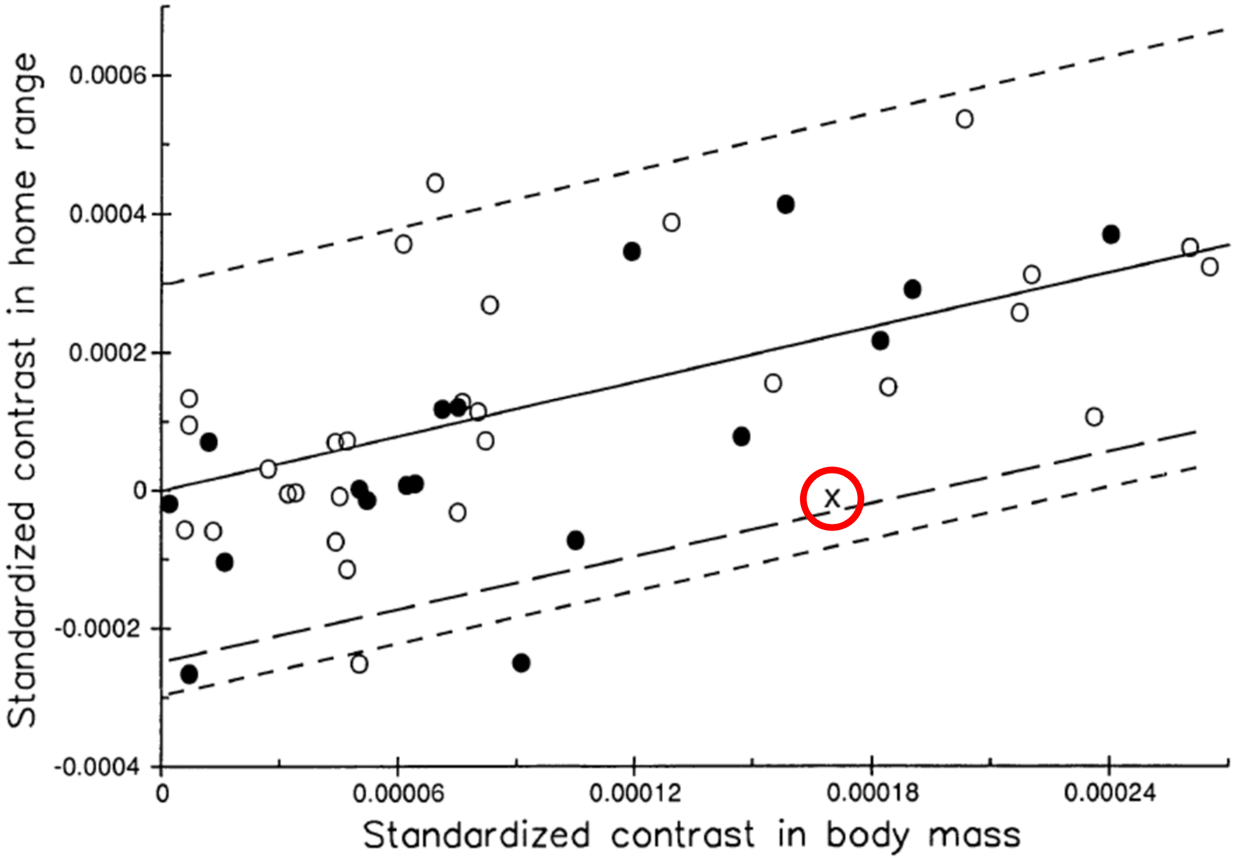


FIGURE 5. Bivariate scatterplot of 48 standardized independent contrasts in $\log_{10}$ home-range area and $\log_{10}$ body mass (redrawn from Garland et al., 1992: fig. 5a). Contrasts within Carnivora (●) and the ungulates (○) are shown, along with the basal contrast (X). In this figure, body mass contrasts have been "positivized" (Garland et al., 1992), and the signs of home-range contrasts changed accordingly. Solid line is least-squares linear regression through the origin for the 47 nonbasal contrasts (slope = 1.3171, $r^2 = 0.544$, $F = 54.90$, $P < 0.0001$). Short dashed lines are the two-tailed 95% prediction interval; long-dashed line is the one-tailed 95% prediction interval (although not immediately obvious from this graph, these prediction intervals become wider farther away from the origin) (formulas from Neter et al., 1989:167–170). The basal contrast falls within these intervals, which indicates no significant difference in home-range area between Carnivora and ungulates.

Does a single species deviate from an allometric expectation?

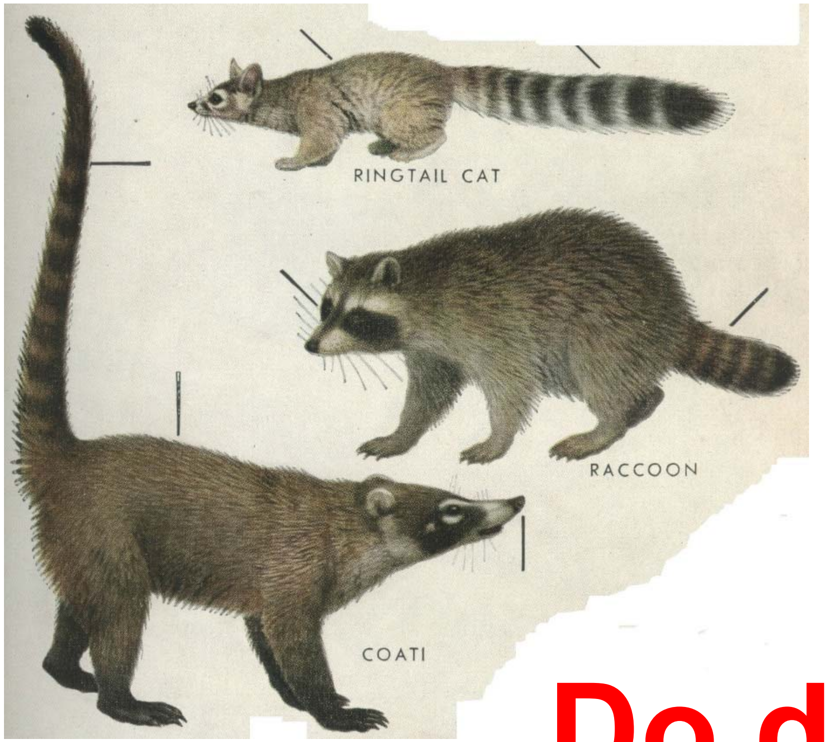
Important general point:

you *can* perform statistical tests that concern unique evolutionary events!!!

Garland, T., Jr., and S. C. Adolph. 1994. Why not to do two-species comparative studies: limitations on inferring adaptation. Physiological Zoology 67:797-828.

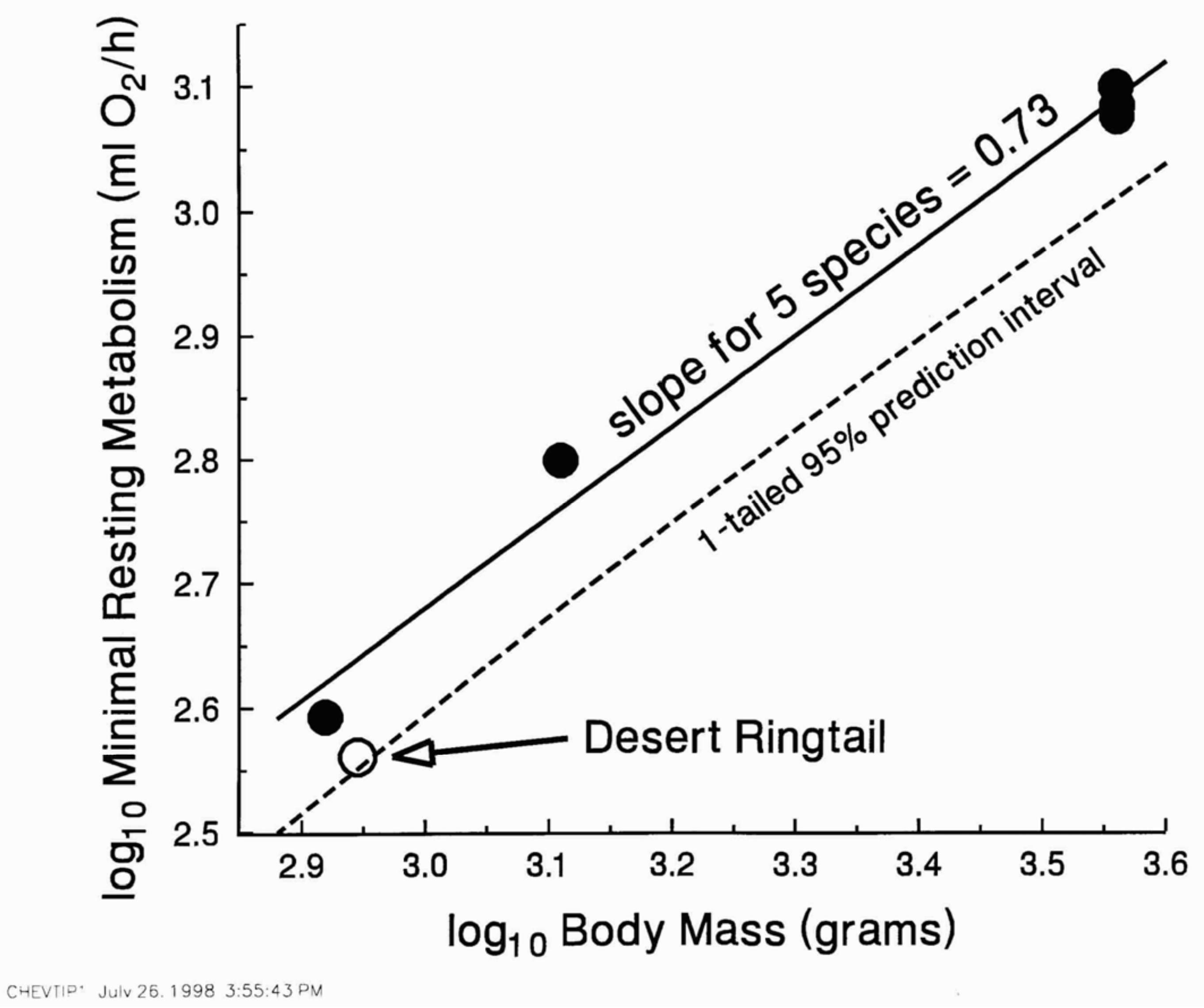
Garland, T., Jr., and A. R. Ives. 2000. Using the past to predict the present: Confidence intervals for regression equations in phylogenetic comparative methods. American Naturalist 155:346-364.

Family Procyonidae



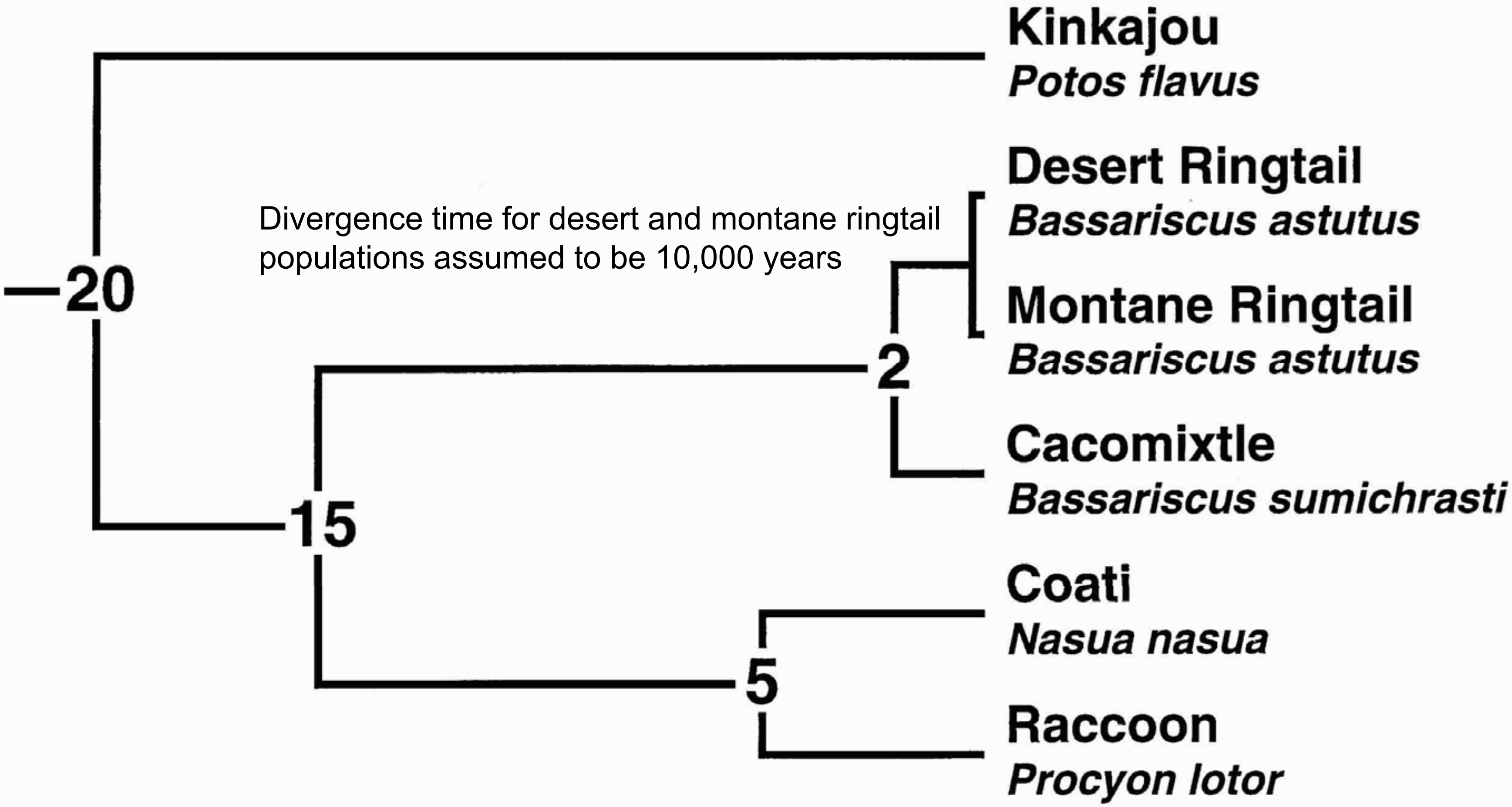
Do desert ringtails have reduced basal metabolic rates?

Does a single species deviate from an allometric expectation? (*a priori*)



This is from Fig. 4 in Garland and Adolph (1994).

Phylogeny of Procyonidae
studied by Chevalier (1991)
Divergence Times in Millions of Years



Divergence time for desert and montane ringtail populations assumed to be 10,000 years

Does a single species deviate from an allometric expectation? (*a priori*)

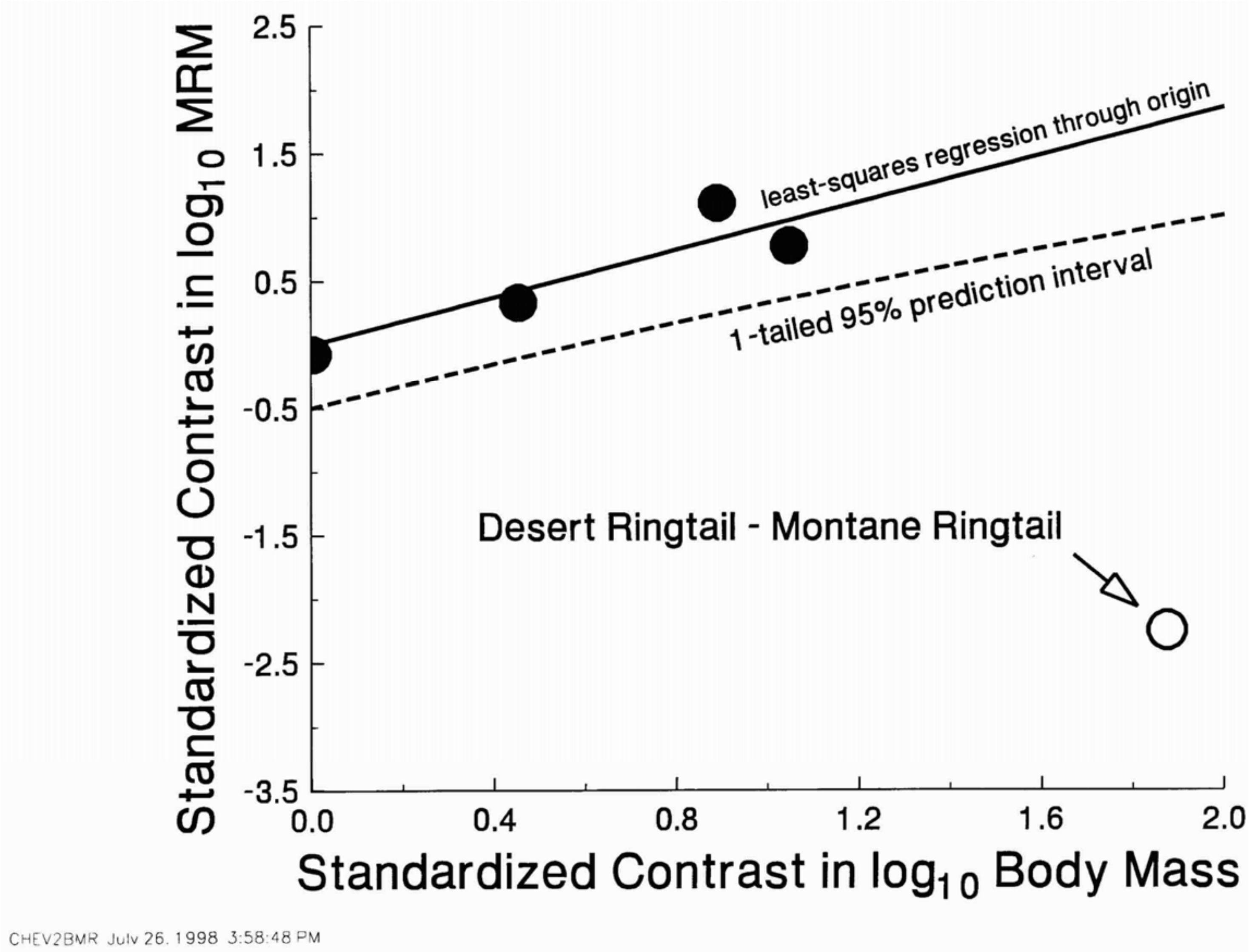
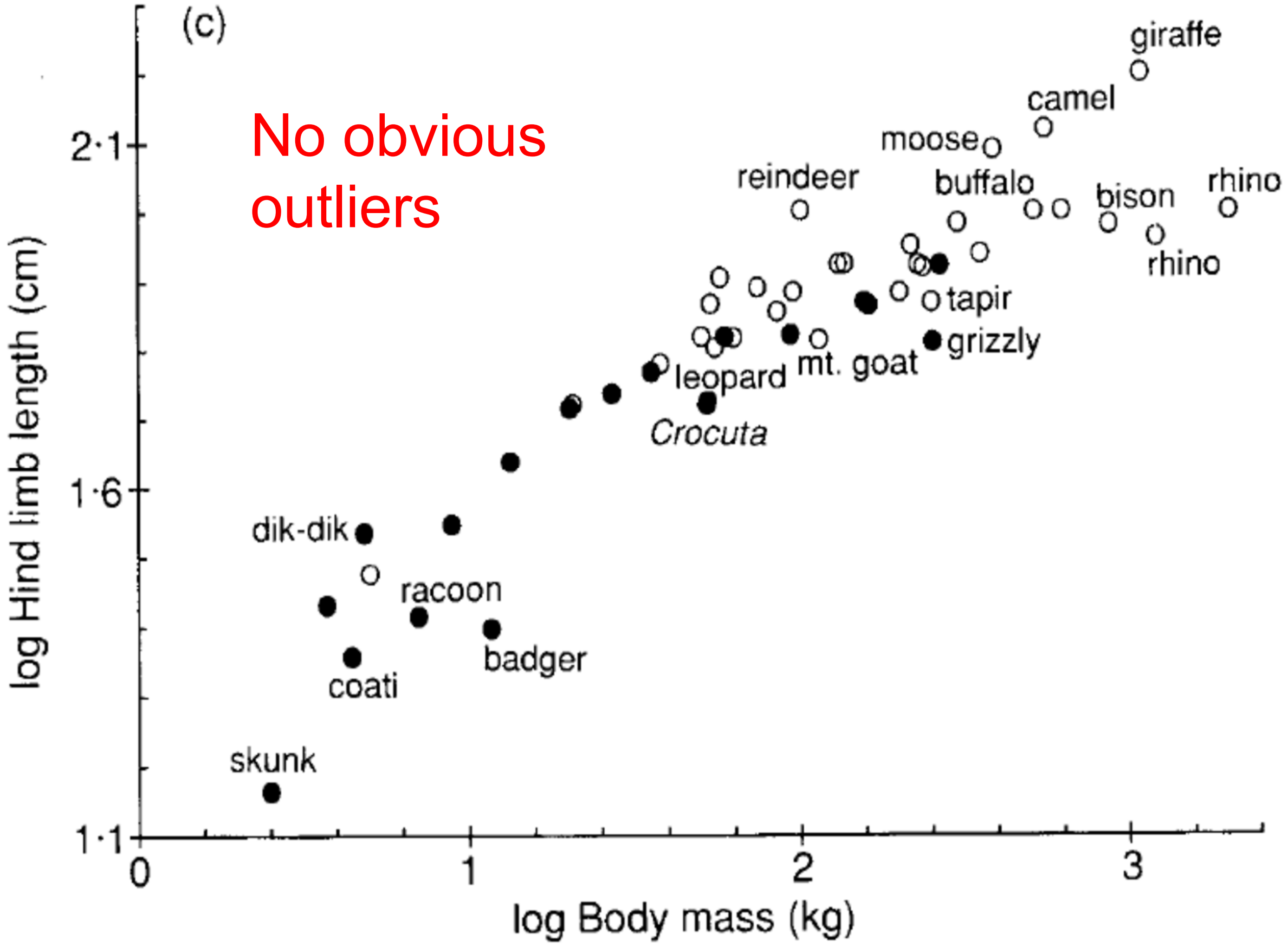


Fig. 4 in G & A 1994

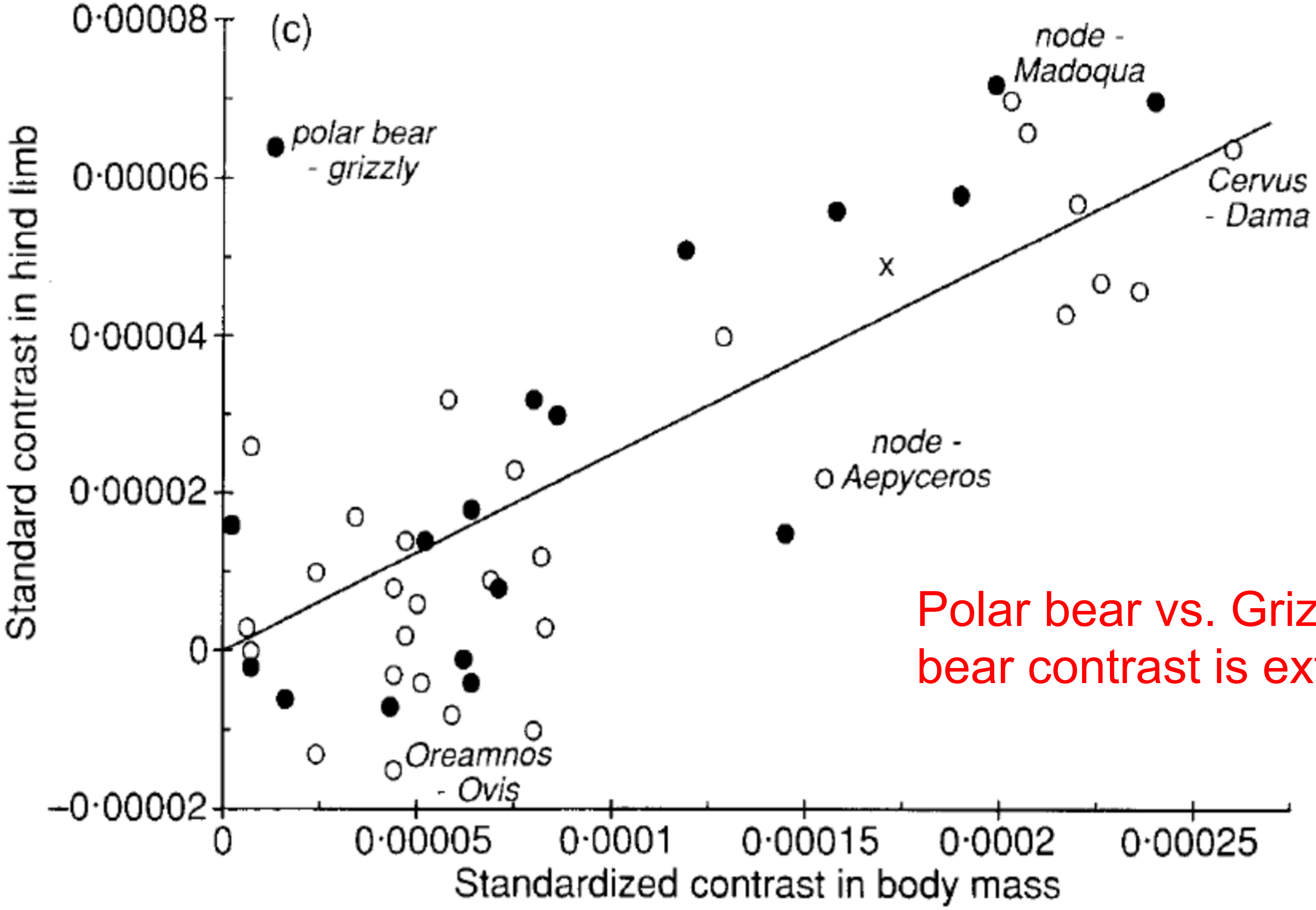
This same example is reanalyzed by GLS methods in Garland and Ives (2000), with same results.

Does a single species deviate from an allometric expectation? (*a posteriori*)



Garland, Jr., T., and C. M. Janis. 1993. Does metatarsal/femur ratio predict maximal running speed in cursorial mammals? Journal of Zoology 229:133–151.

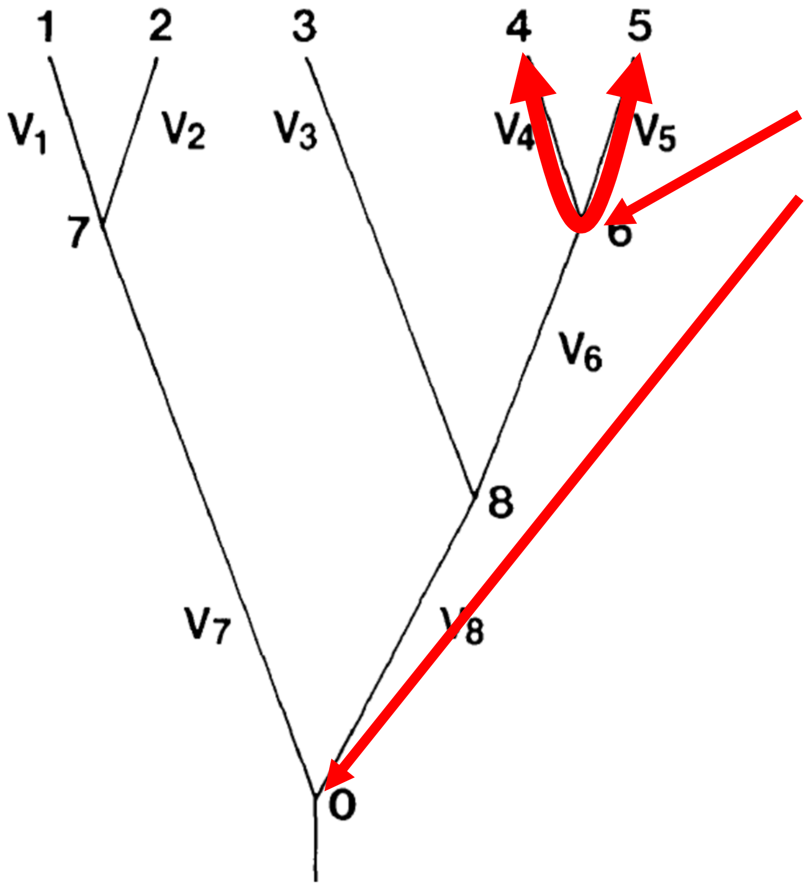
Does a single species deviate from an allometric expectation? (*a posteriori*)



Polar bear vs. Grizzly bear contrast is extreme

Garland, Jr., T., and C. M. Janis. 1993. Does metatarsal/femur ratio predict maximal running speed in cursorial mammals? Journal of Zoology 229:133–151.

Estimation of ancestral states and CIs



Values computed for internal nodes are "local parsimony," except at the root, where it is global parsimony and maximum likelihood.

Estimate for **root node** is also estimate of mean for tips, weighted by phylogenetic relationships.

Contrasts algebra allows **standard error and CI** to be computed, as well as **regression intercept and SE in original data space**.

Can **reroot** tree to get values for any internal node.

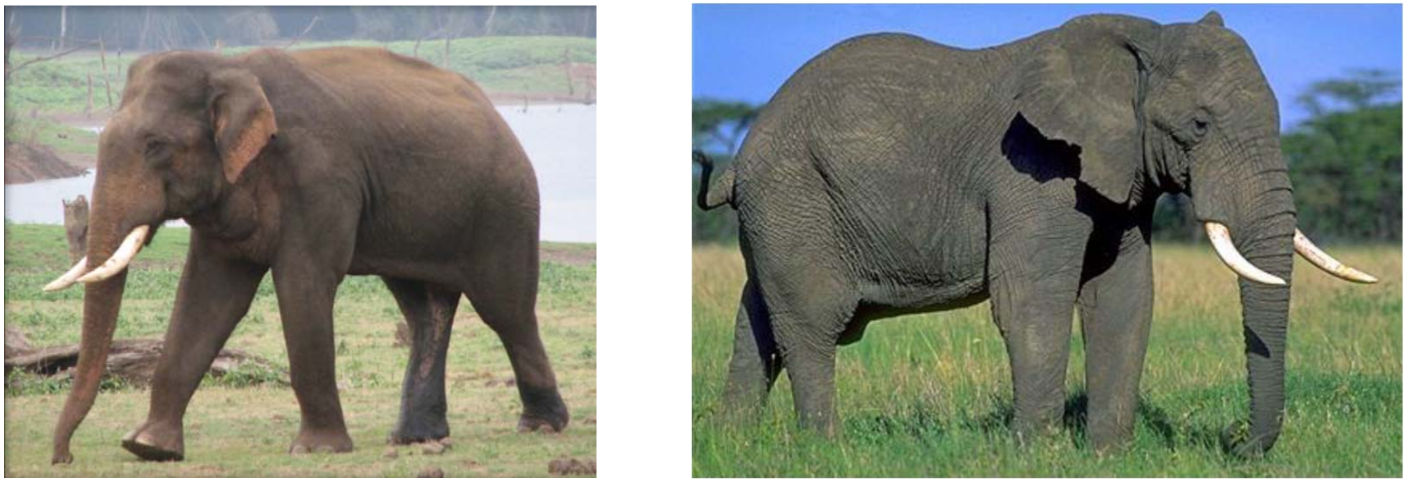
Garland, Jr., T., A. W. Dickerman, C. M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. Systematic Biology 42:265-292.

Garland, T., P. E. Midford, and A. R. Ives. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. American Zoologist 39:374-388.

Bonine, K. E. 2005. Muscle fiber-type variation in lizards (Squamata) and phylogenetic reconstruction of hypothesized ancestral states. Journal of Experimental Biology 208:4529-4547.

Testing for "Phylogenetic Signal" = tendency for related species to resemble each other

For example, elephants look like elephants.



Blomberg, S. P., and T. Garland, Jr. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. J. Evol. Biology 15:899-910.

Blomberg, S. P., T. Garland, Jr., and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–745.

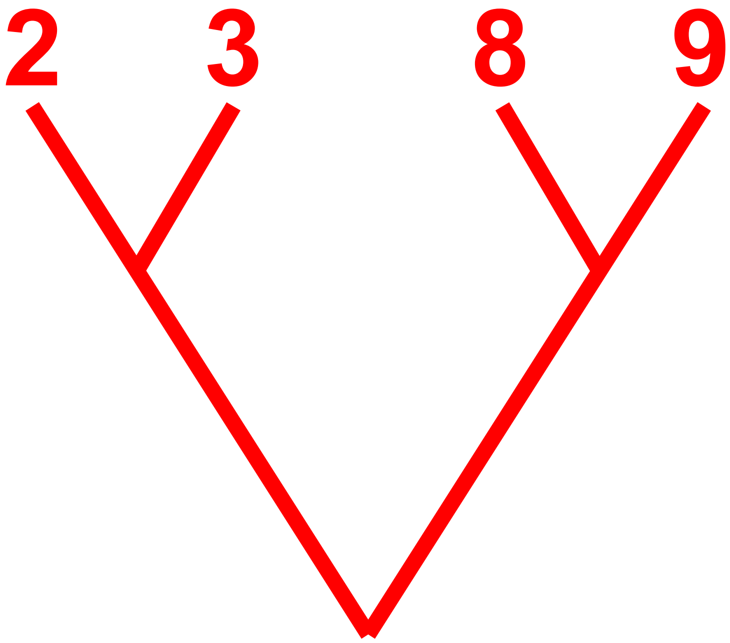
"Phylogenetic Signal"

is ***not*** the same as
phylogenetic inertia
or constraint.

These terms imply more than is easily estimated from comparative data alone, e.g., resistance to change.

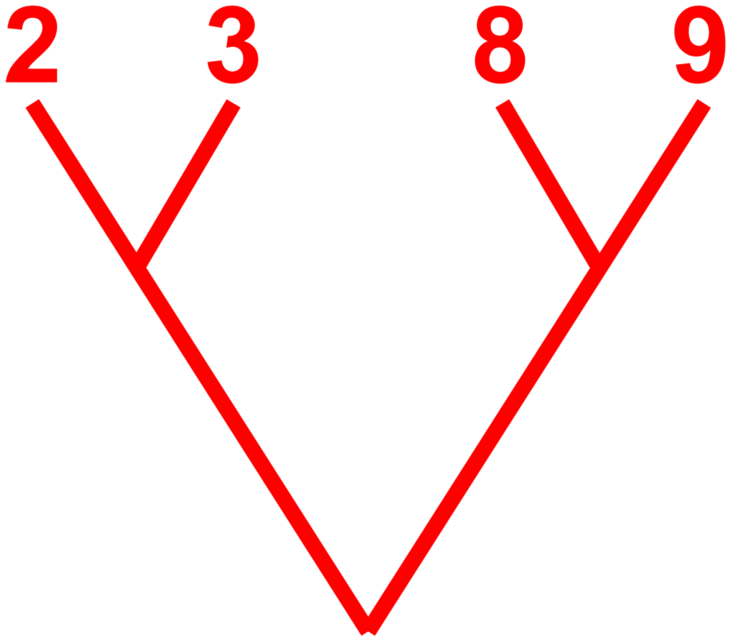
A Test for Phylogenetic Signal via Independent Contrasts

A Tree and Tip Data for 4 Species



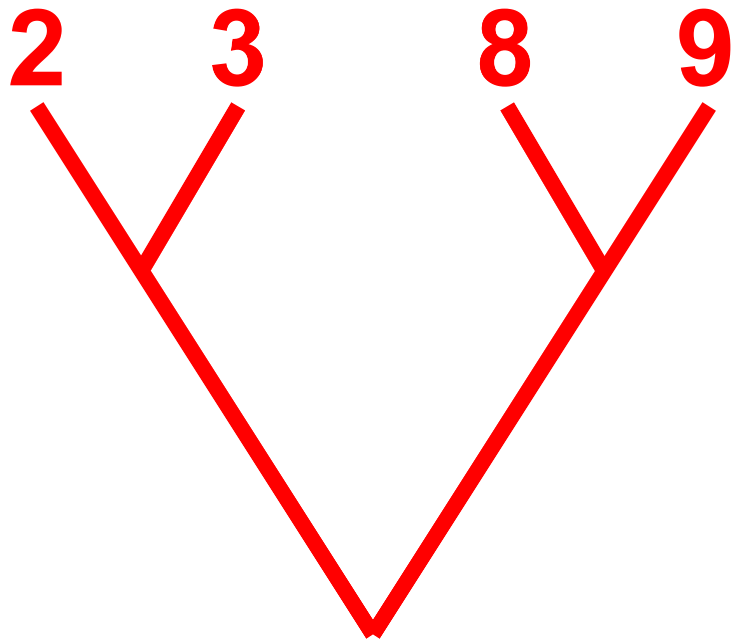
Hypothetical Example

Phylogenetic Signal is Apparent



Relatives Resemble Each Other

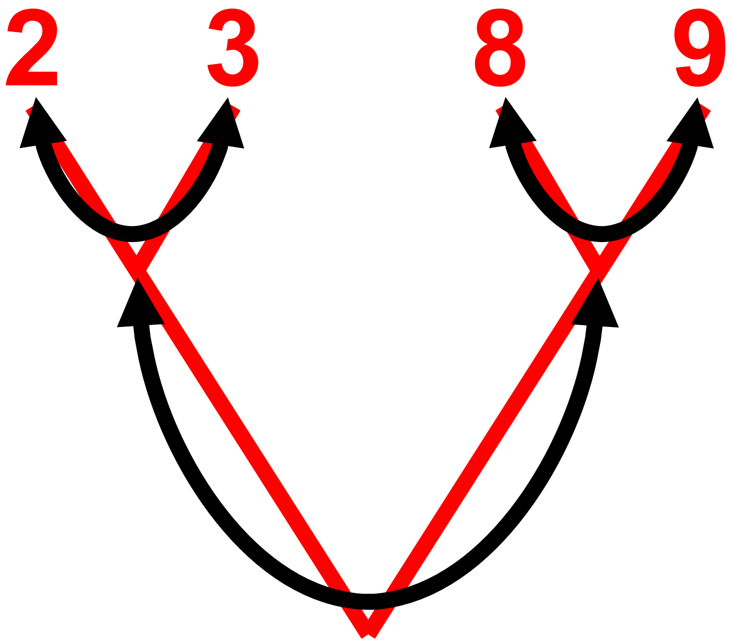
Phylogenetic Signal is Apparent



Statistical significance can be tested using phylogenetically independent contrasts & randomization.

Simulations indicate power ~0.8 with >20 species.

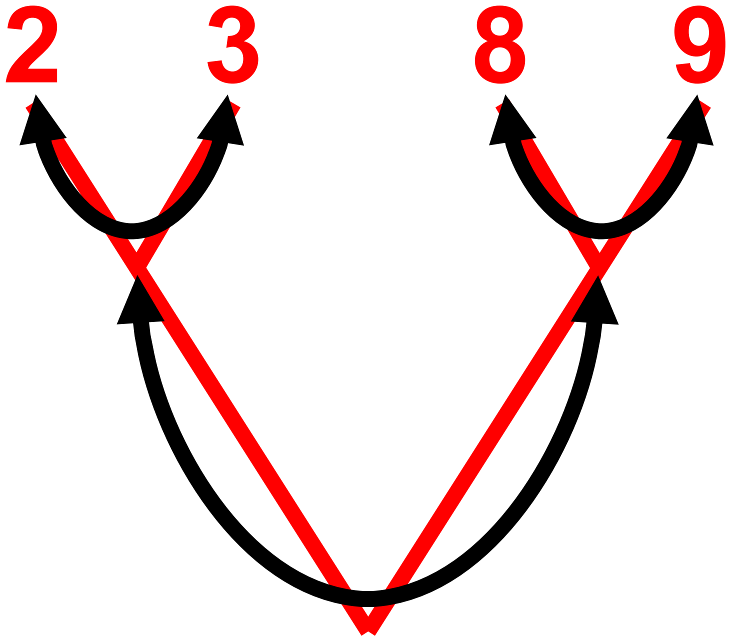
Phylogenetic Signal is Apparent



Compute Contrasts,

including standardizing

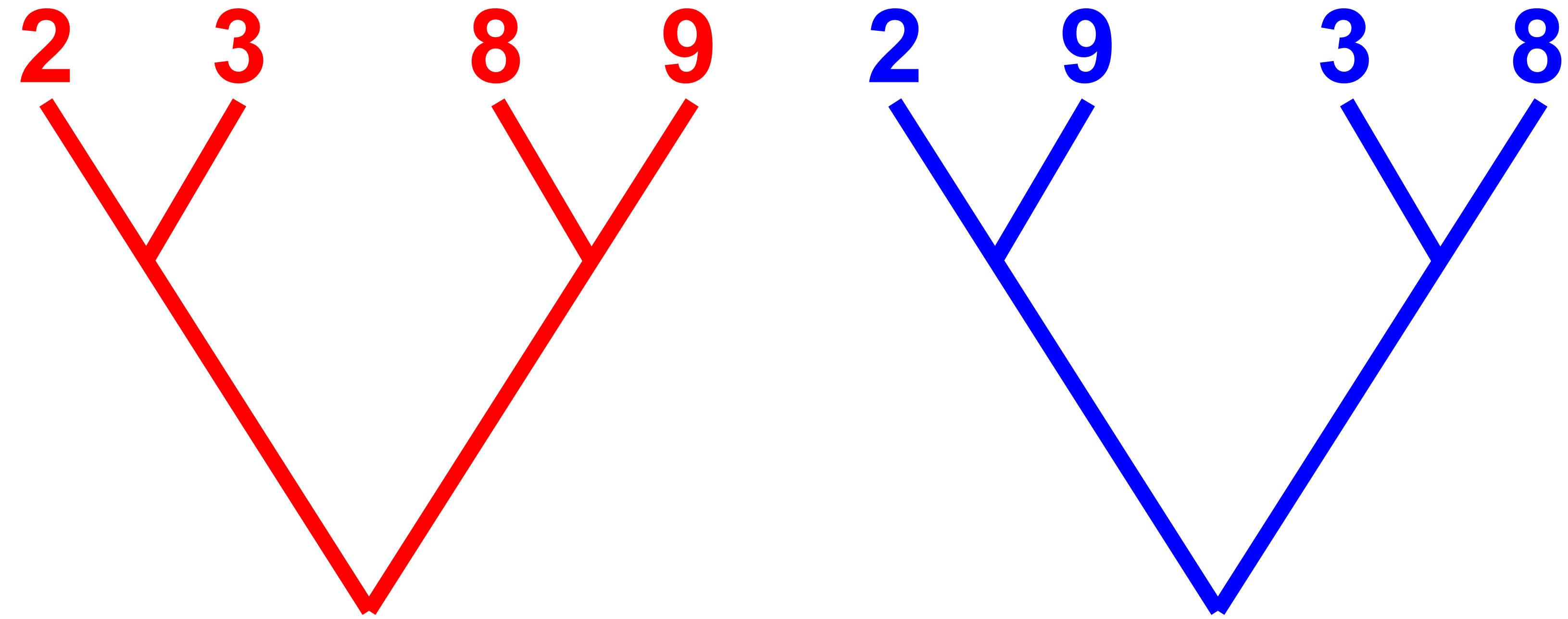
Phylogenetic Signal is Apparent



Low Variance of Contrasts

Phylogenetic Signal is Apparent

No Apparent Phylogenetic Signal

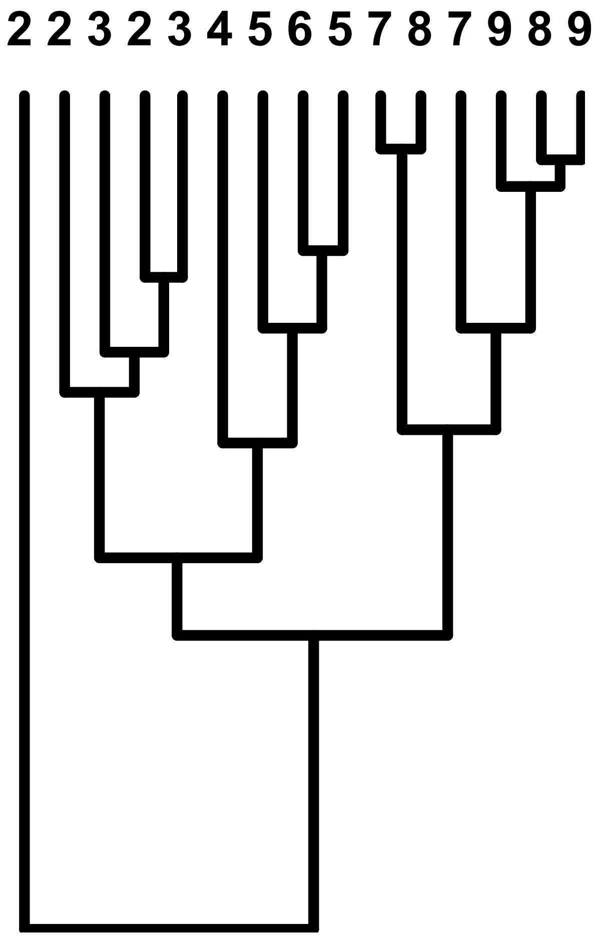


Low Variance of Contrasts
4.10

High Variance of Contrasts
18.50

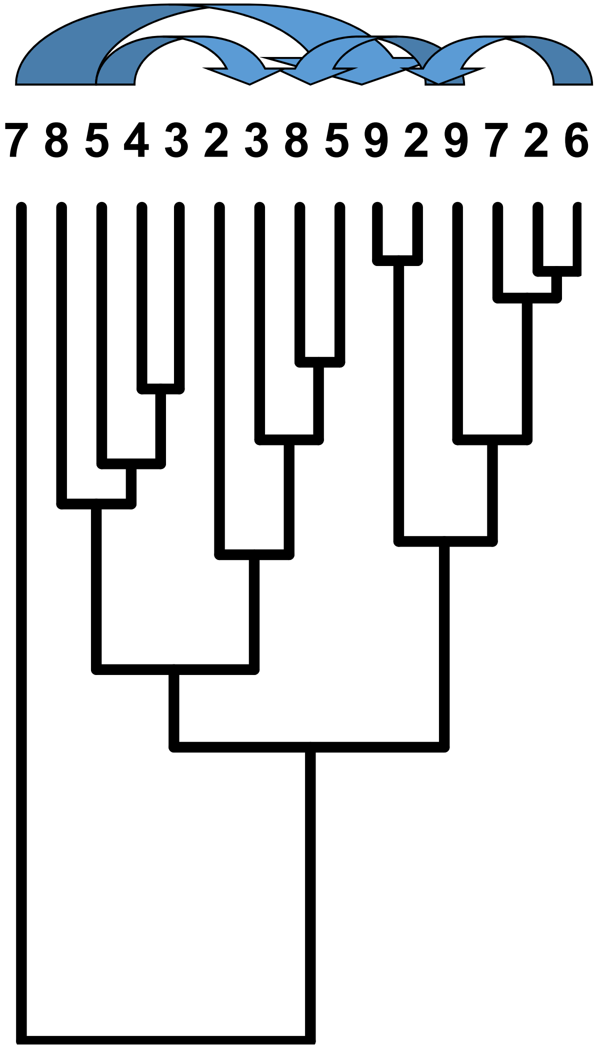
Test Significance via Randomization

Hypothetical tip data for 15 species



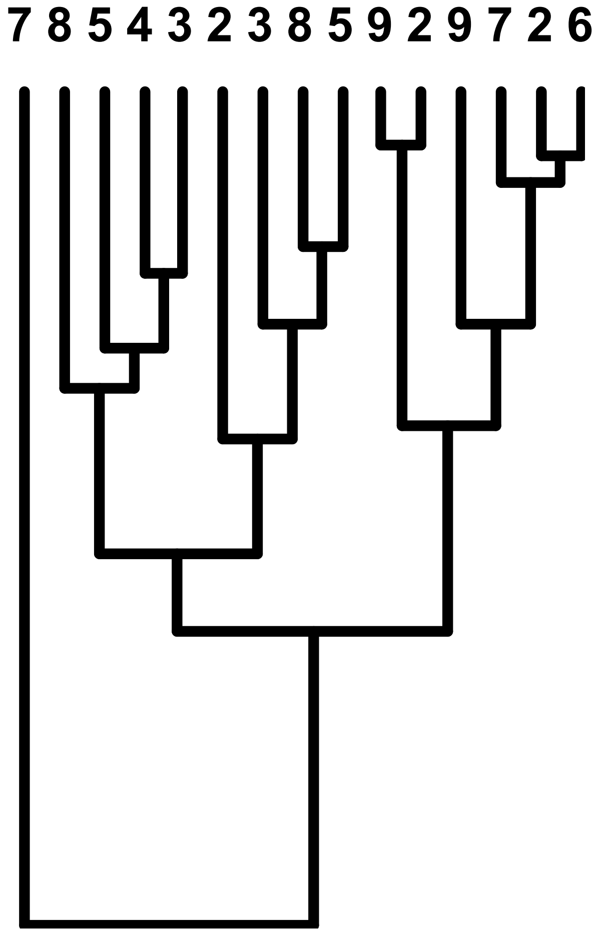
1. Calculate variance of contrasts for data in original position

Shuffling the tip data randomly *destroys* any phylogenetic signal that may have existed …

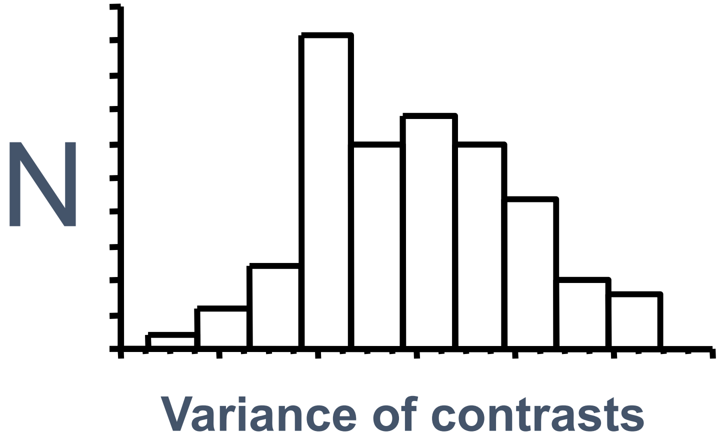


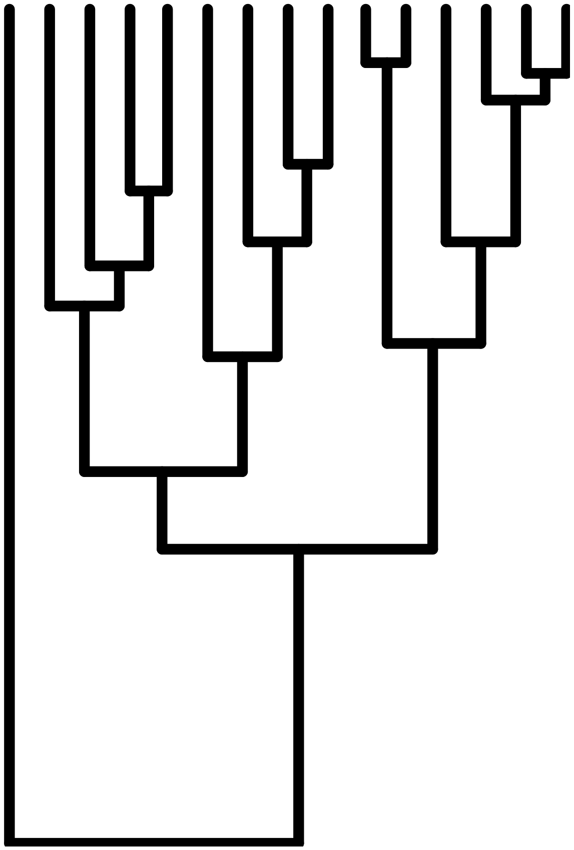
1. Calculate variance of contrasts for data in original position
2. Randomize data

$$\frac{\text{Sum of (contrasts}^2)}{N_{\text{contrasts}} - 1}$$

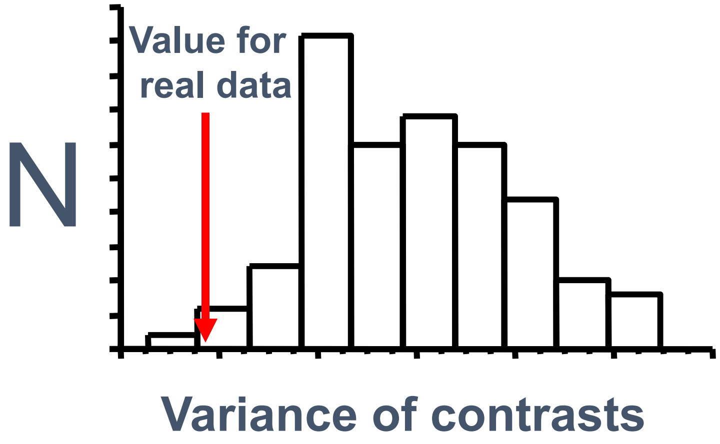


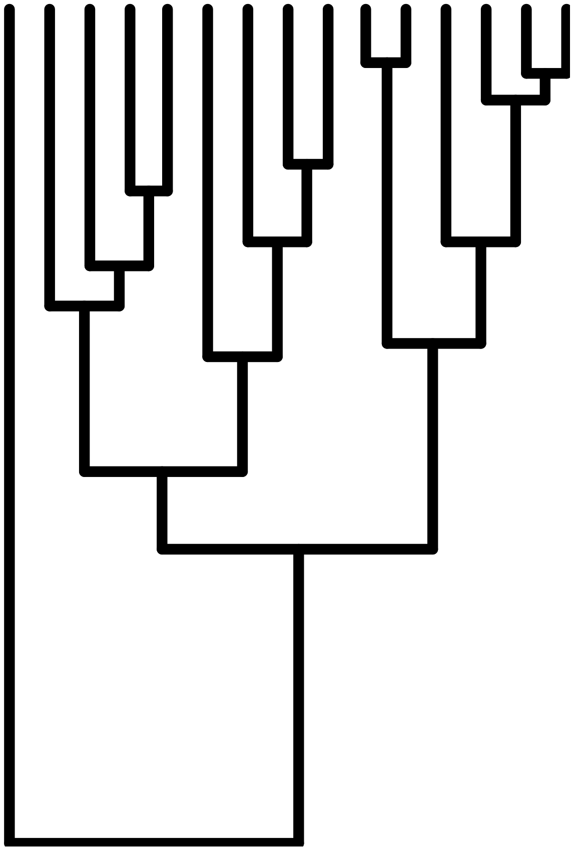
1. Calculate variance of contrasts for data in original position
2. Randomize data
3. **Calculate variance**



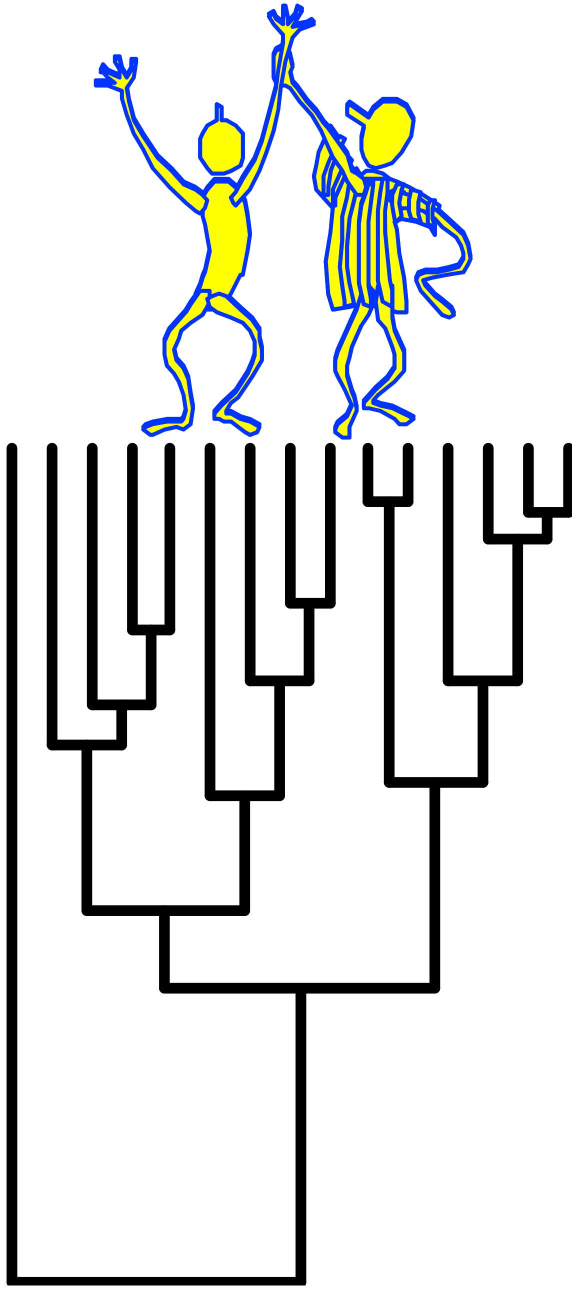


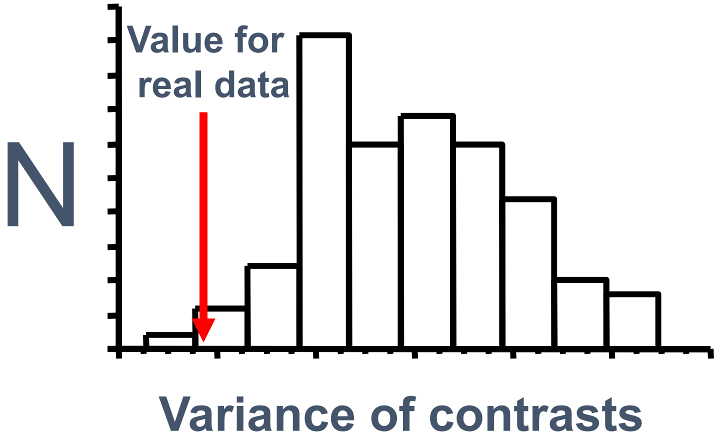
1. Calculate variance of contrasts for data in original position
2. Randomize data
3. Calculate variance
4. **Repeat many times and construct distribution**



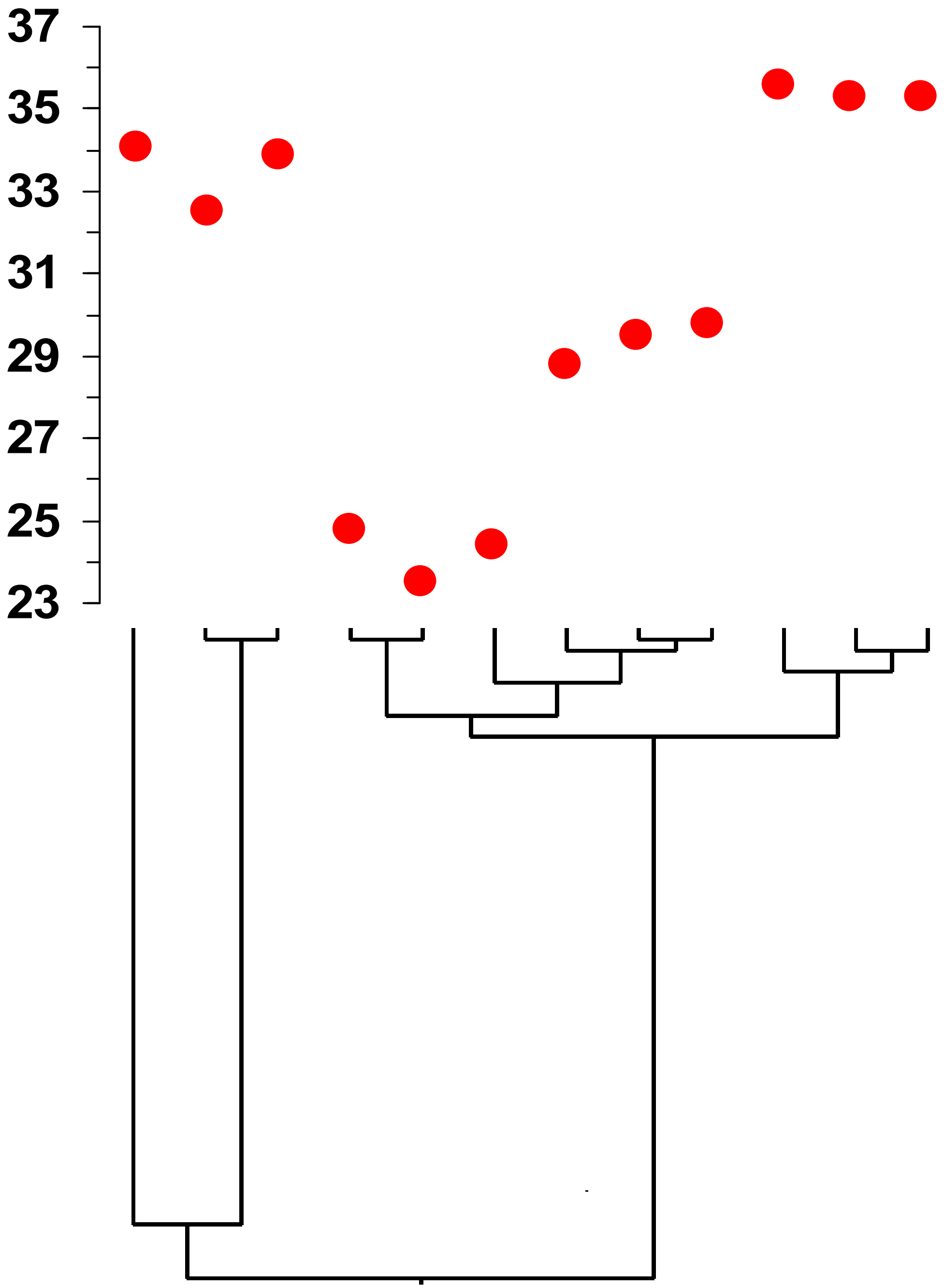


1. Calculate variance of contrasts for data in original position
2. Randomize data
3. Calculate variance
4. Repeat many times and construct distribution
5. **Calculate P as # < real**





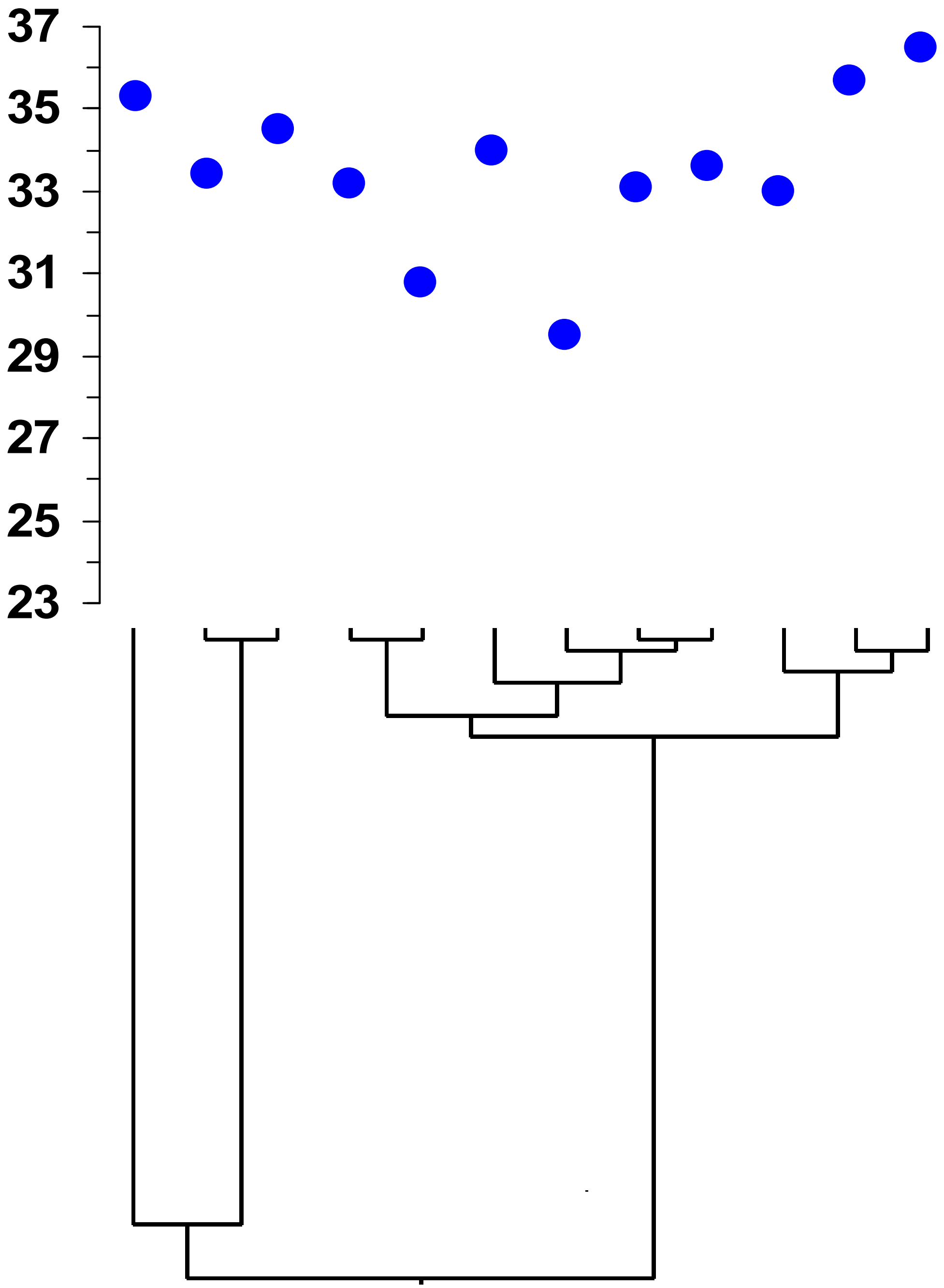
1. Calculate variance of contrasts for data in original position
2. Randomize data (~1000 x)
3. For each, calculate variance of contrasts
4. Construct distribution
5. Calculate P as # < real
6. **Accept or Reject H_0**



Preferred Body Temperatures (°C) of 12 species of Australian skinks:

# P < 0.001

Data from Huey & Bennett, 1987; phylogenetic information updated in Garland et al., 1991



Optimal Body Temperatures for Sprinting (°C) of 12 species of Australian skinks:

P = 0.167

Data from Huey & Bennett, 1987; phylogenetic information updated in Garland et al., 1991

Measurement Error Models

1. **"Measurement-error" includes:**

   sampling variation; pure measurement error; low repeatability caused by hourly, daily, seasonal fluctuations; sex differences; age variation; real individual variation

2. **Most of this is reasonably well encapsulated by Standard Errors for population means.**

3. **These Standard Errors can be used to weight contrasts by lengthening terminal branches.**

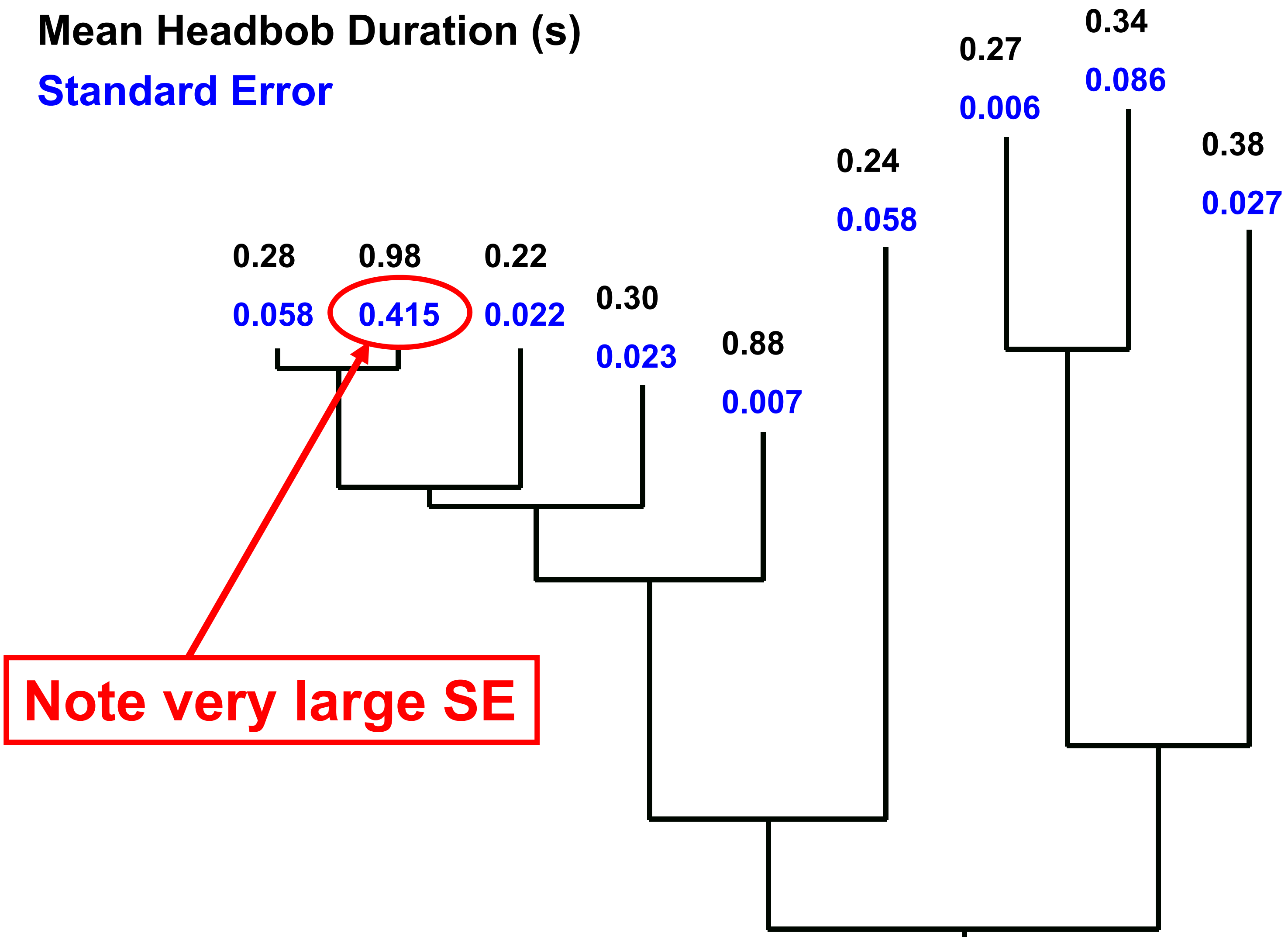
   This is routine in "weighted regression" in ordinary statistical analyses.

Ives, A. R., P. E. Midford, and T. Garland. 2007. Within-species variation and measurement error in phylogenetic comparative methods. Systematic Biology 56:252-270.

Felsenstein, J. 2008. Comparative methods with sampling error and within-species variation: contrasts revisited and revised. The American Naturalist 171:713-725.

Molecular Phylogeny for 9 Species of Iguanas

(Martins & Lamont 1997)



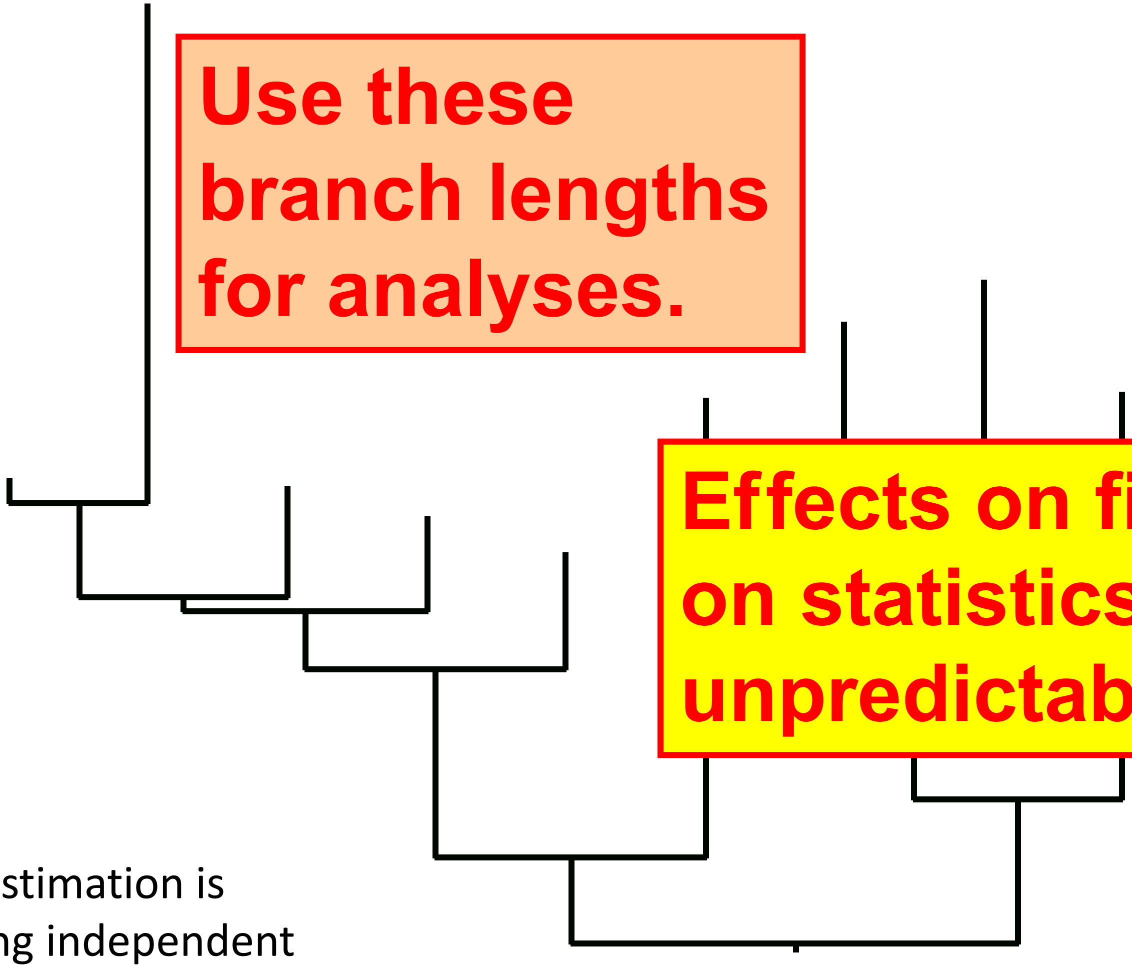
Mean Headbob Duration (s)

Standard Error

Note very large SE

Branch Lengths Adjusted for Standard Errors:

Tips with Large SE are Down-weighted (devalued) Relative to Others



Use these branch lengths for analyses.

Effects on final on statistics are unpredictable.

Univariate EGLS estimation is implemented using independent contrasts in the MS DOS program PD_SE.EXE (available from TG)

Phylogenetically Independent Contrasts as an All-purpose Tool

- ✓ Correlation, Regression
- ✓ ANOVA, ANCOVA
- ✓ Principal Components
- ✓ Outlier Tests
- ✓ Rates of Evolution
- ✓ Ancestor Reconstruction
- ✓ Phylogenetic Signal
- ✓ Measurement Error Models

After graphing your original data, this is often the best place to start your phylogenetic analysis.