Studying Adaptation Using Morphometrics

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"how it works" vs. "how it came to be"

AMER. ZOOL., 24:443–450 (1984)

Science as a Way of Knowing—Evolution: The Biology of Whole Organisms[1]

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SYNOPSIS. Examples of current research of importance to the conceptual
tional bases of evolutionary biology in the areas of morphology, developmen
ecology, population biology, natural history, and systematics are discussed
approach to problems that utilizes ideas and techniques from several are
characterizes much current research, and it is providing new conceptual fra
new, testable hypotheses. Some of the possible problems with methods of pr
we often teach in these areas of biology are considered.

The conceptual and informational bases of evolutionary biology continue to be strengthened through current research. Investigations of the biology of organisms, their relationships, and their interactions with the environment add to our understanding of pattern and process of evolu-

a course, but to use then
concept of evolution as
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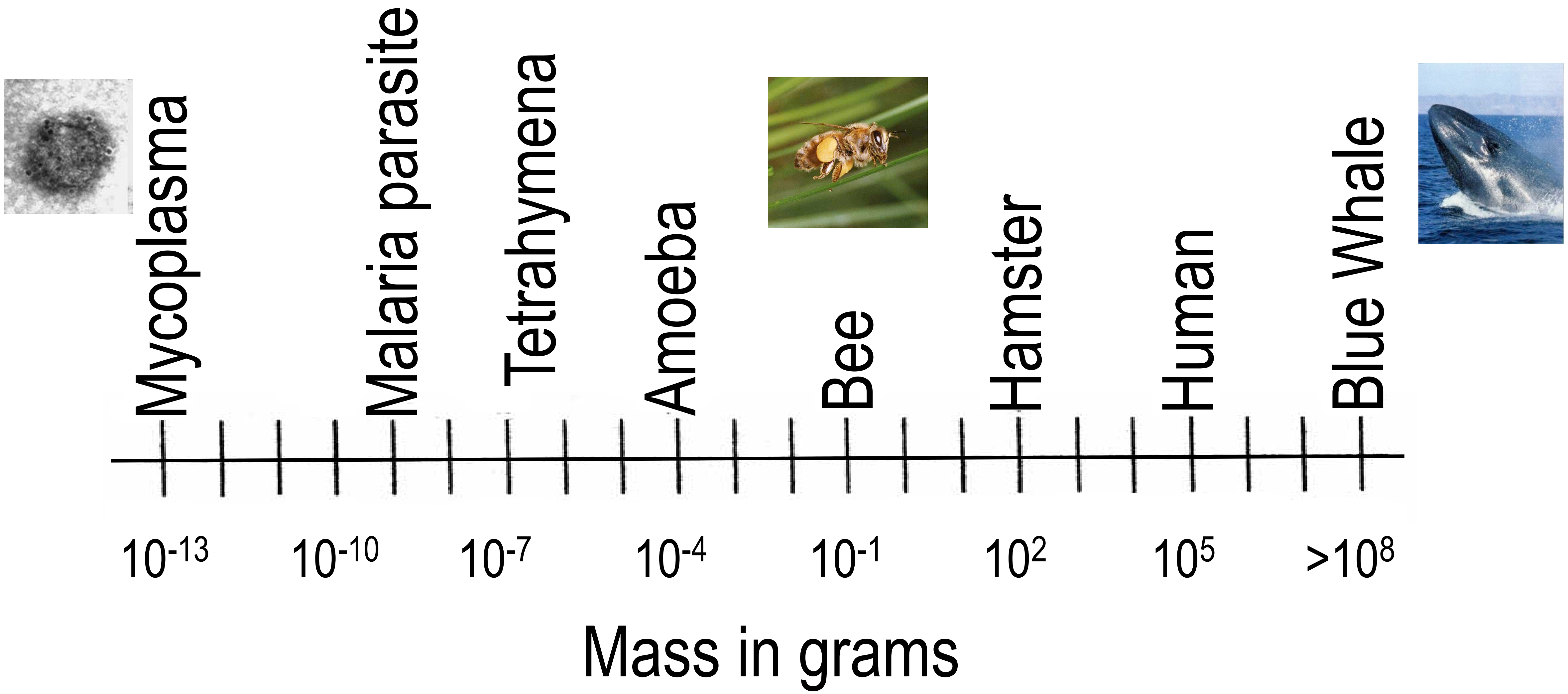
has come to work" halv
important that they be
focused on whole orga

In addition to developmental and phylogenetic constraints on possible sizes and shapes, there are mechanical limits as well. The properties of the materials of which organisms are composed confer these limits, and design constraints are thus inherent. Trees are effectively towers that are open networks of cantilevered beams (stems and branches) that support many solar collectors (leaves) (Wilson and Archer, 1979). The problem is that trees grow, in contrast to engineers' towers. Beams get longer and thicker and produce new beams by branching. Beams (branches) are subject to bending and torsional stresses from the loads of self-weight, wind, etc. As the tree grows these forces increase, so the beams are stiffened to resist the forces against them. Different species have different leaf distributions and designs, and branching patterns, hence design is flexible enough to meet specific mechanical requirements. Strain stimuli affect rate of cell production, gravitational stimuli affect microfibril angle and internal strain; these are feedback systems. Wood rays in a tree limb are located so that they can sense strain in branches. McMahon (1975) demonstrates that these elastic criteria impose limits on biological proportions, and therefore metabolic rates in both plants and animals. Trees too tall

The Scale of Life



The difference between the smallest and the largest organism is 10^{21} !

General Sherman, Biggest Tree in the World

Giant Sequoyah
275 ft tall
25 ft diameter

General Sherman compared to Bonsai

Sequoyah Bonsai
9 in tall
.75 in diameter

http://www.airlinesafety.com/editorials/AboutTheEditor.htm

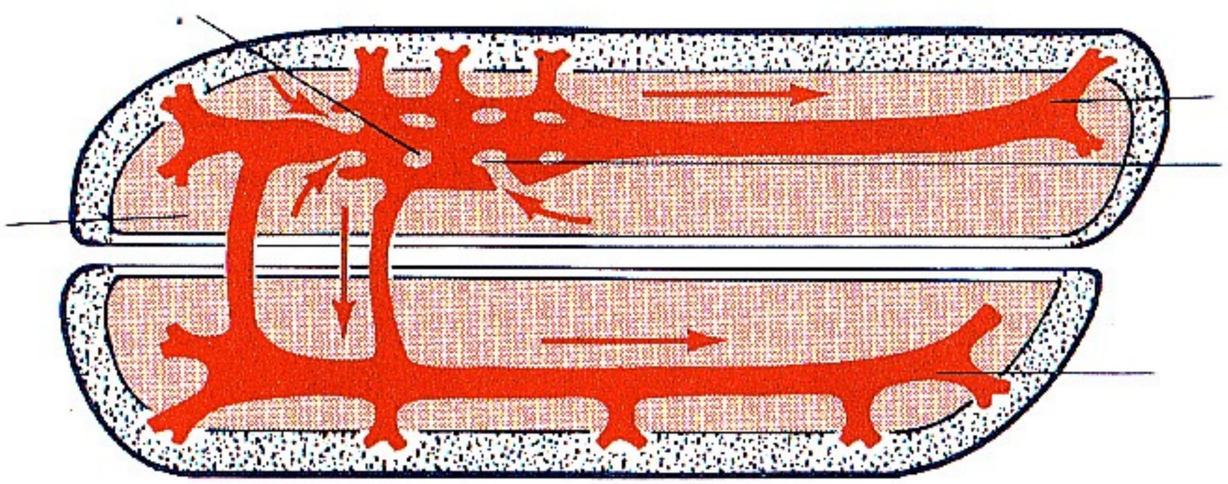
diameter at ground 11.1m (36.5 ft)
1.4m above ground 7.7m (25.1)
18m above ground 5.3m (17.5ft)

Novel Systems

To get large organisms evolve novel transport systems

Circulation

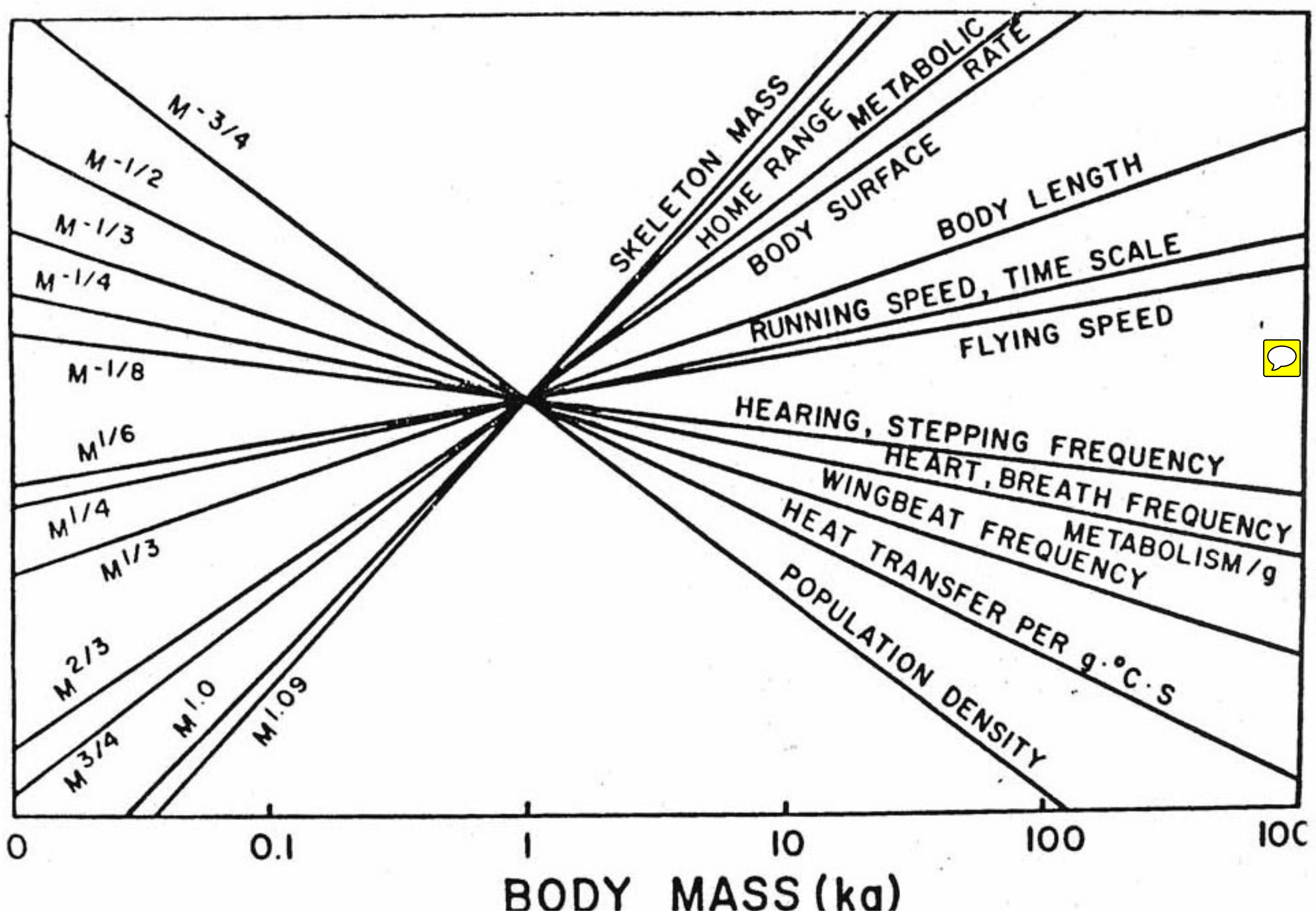
Diffusion Inadequate at Larger Sizes



Size is Functionally Important

Scaling - size dependence of physiological properties

Nearly all structural and functional variables scale!

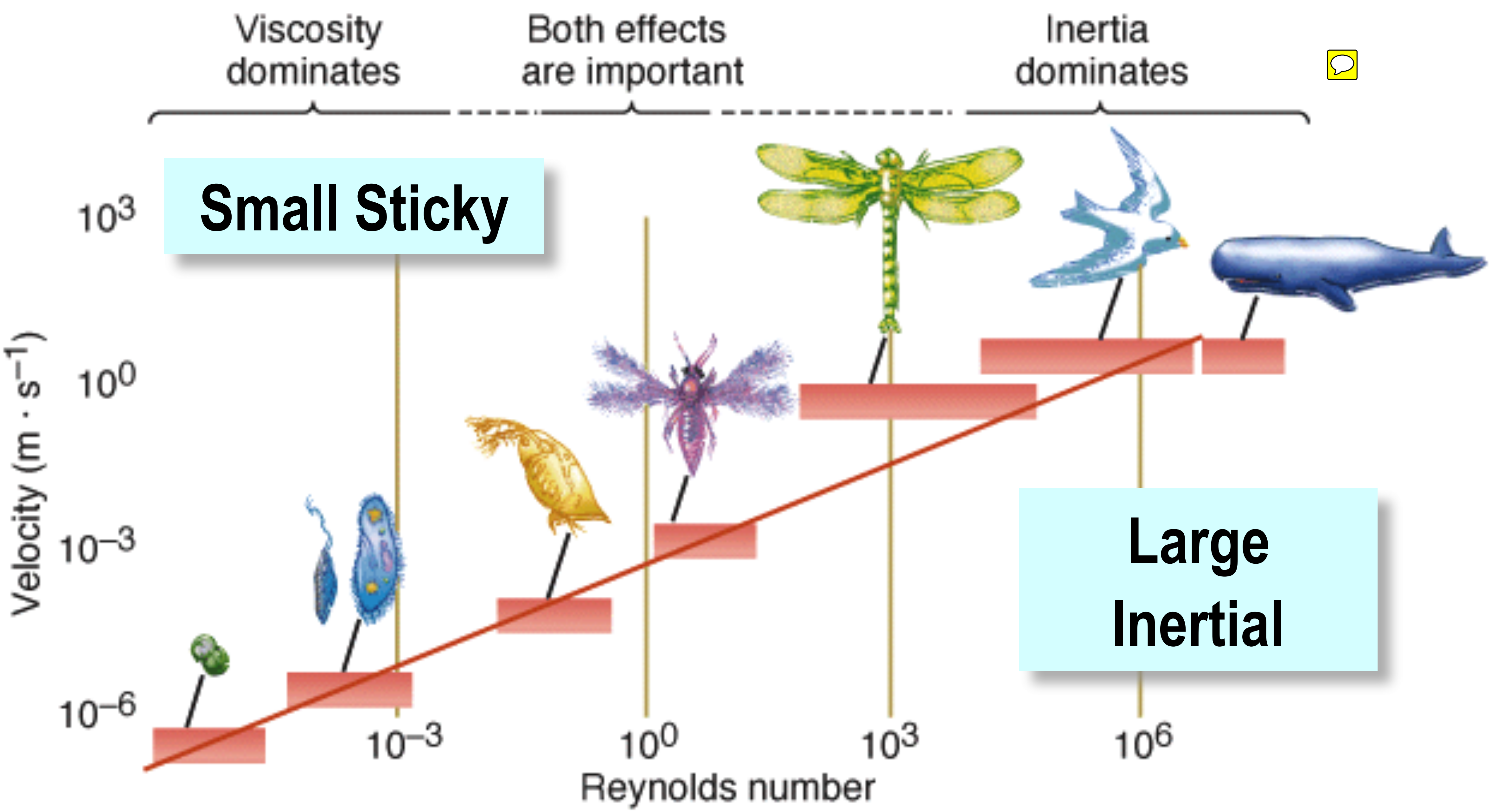


(on log-log plot)

Most relationships do not have a slope of 1.0!

Novel Worlds: Body Size and Media

Reynolds Number = density * length * velocity / viscosity



Ratio of inertial forces to viscosity forces or: Re tells us *how important is viscosity*?
The transition from laminar to turbulent flow occurs at an Re of 2000 (Re is a dimensionless number)

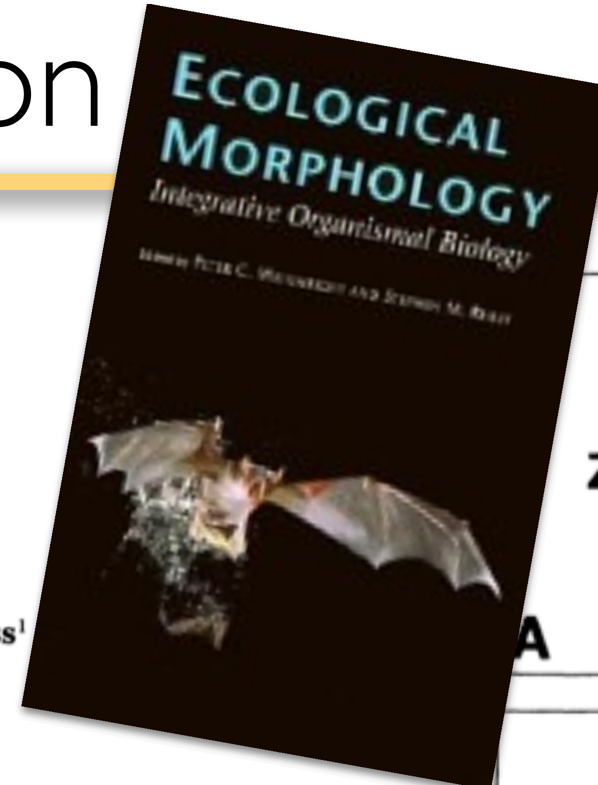
Allometry

Non-Geometric Scaling is called *Allometric Scaling* (Greek allios, different).

Geometric Similarity or Isometry

Regal horned lizards

Morphology and Adaptation



AMER. ZOOL., 23:347–361 (1983)

Morphology, Performance and Fitness[1]

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SYNOPSIS. Selection can be measured in natural populations by the changes it causes in the means, variances and covariances of phenotypic characters. Furthermore the force of selection can be measured in conventional statistical terms that also play a key role in theoretical equations for evolutionary change. The problem of measuring selection on morphological traits is simplified by breaking the task into two parts: measurement of the effects of morphological variation on performance and measurement of the effects of performance on fitness. The first part can be pursued in the laboratory but the second part is best accomplished in the field. The approach is illustrated with a hypothetical analysis of selection acting on the complex trophic morphology of snakes.

INTRODUCTION

My thesis in this paper is that it is possible to measure adaptive significance directly. In particular it is possible to characterize statistically the relationship between fitness and morphology in natural populations. One can argue that this statistical approach constitutes the highest grade of evidence for selection and adaptation. I will stress this direct approach to selection because of the unique insights it can offer and because it has often been neglected.

here rests on recent advances in multivariate selection theory, which deals with the effects of selection acting simultaneously on multiple characters (Lande, 1979, 1980, 1982). These theoretical results, together with recent success in field measurement of fitness, indicate that selection can be measured in nature in the same terms that are used in equations for the evolutionary transformation of populations (Lande and Arnold, 1983). Multivariate selection theory is briefly reviewed

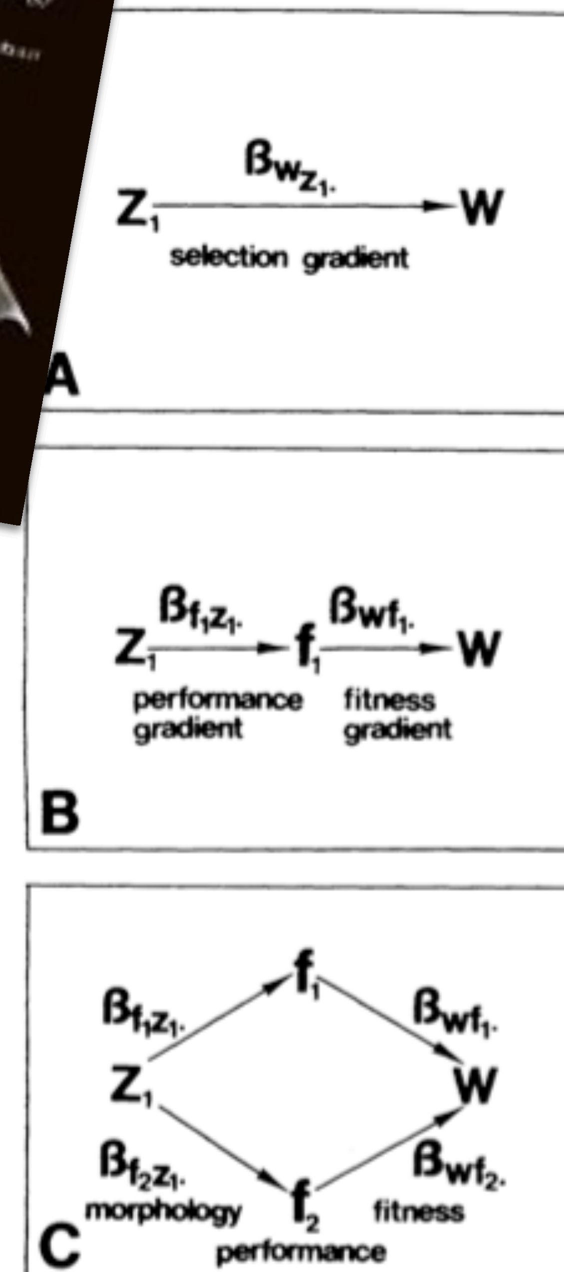

FIG. 4. A diagrammatic partitioning of the selection gradient. The selection gradient for a character (Fig. 4A) can be partitioned into two parts if the character affects a single performance variable, f_1: the performance gradient, $\beta_{f_1z_1\cdot}$ and the fitness gradient $\beta_{wf_1\cdot}$ (Fig. 4B). If the character affects two performance variables, f_1 and f_2, the selection gradient can be partitioned into the paths $\beta_{f_1z_1\cdot}\beta_{wf_1\cdot}$ and $\beta_{f_2z_1\cdot}\beta_{wf_2\cdot}$ (Fig. 4C).

See also
Lande and Arnold 1983
Phillips and Arnold 1989

“Shape” or “Size-Adjusted” Morphology Informs Adaption

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Propulsive impulse as a covarying performance measure in the comparison of the kinematics of swimming and jumping in frogs

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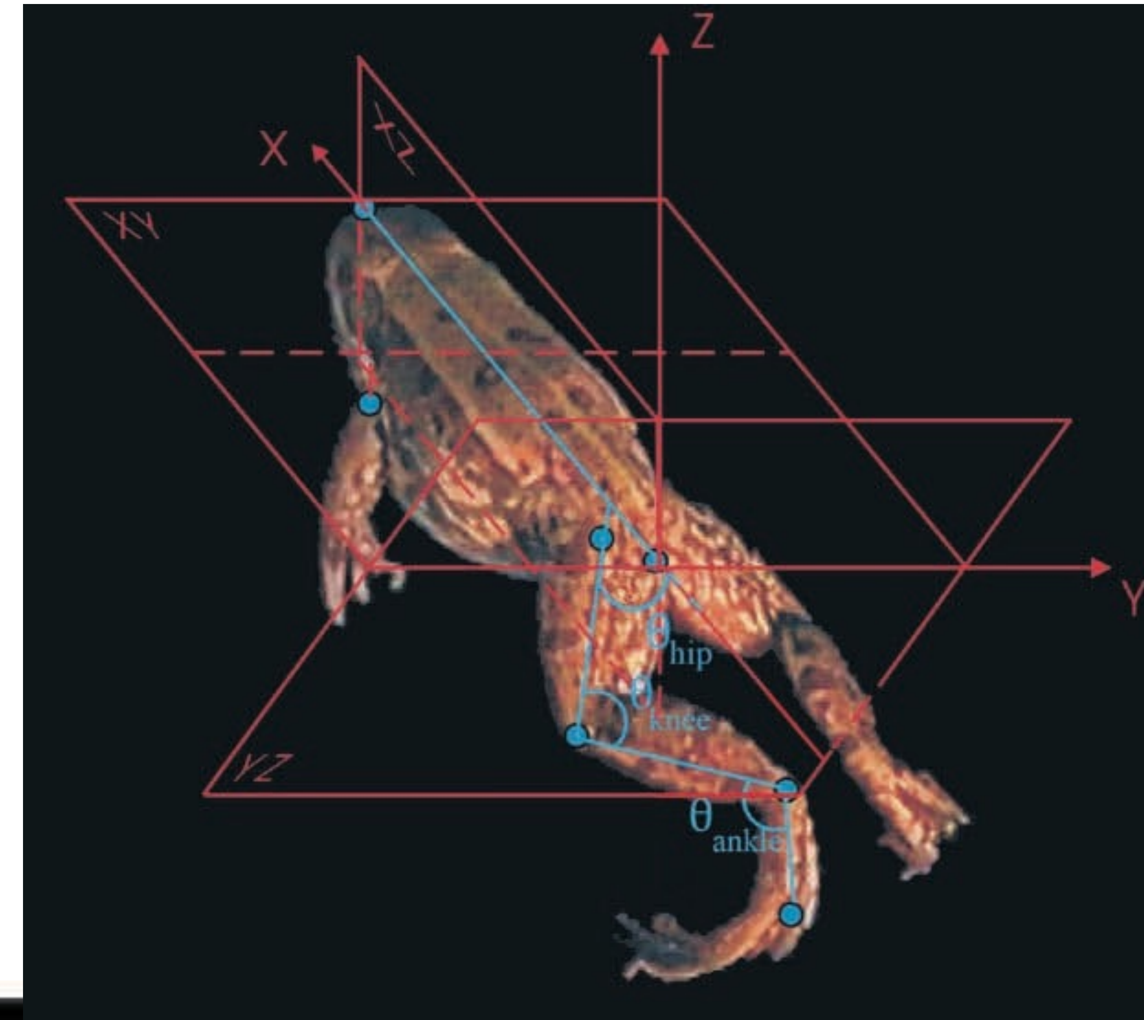

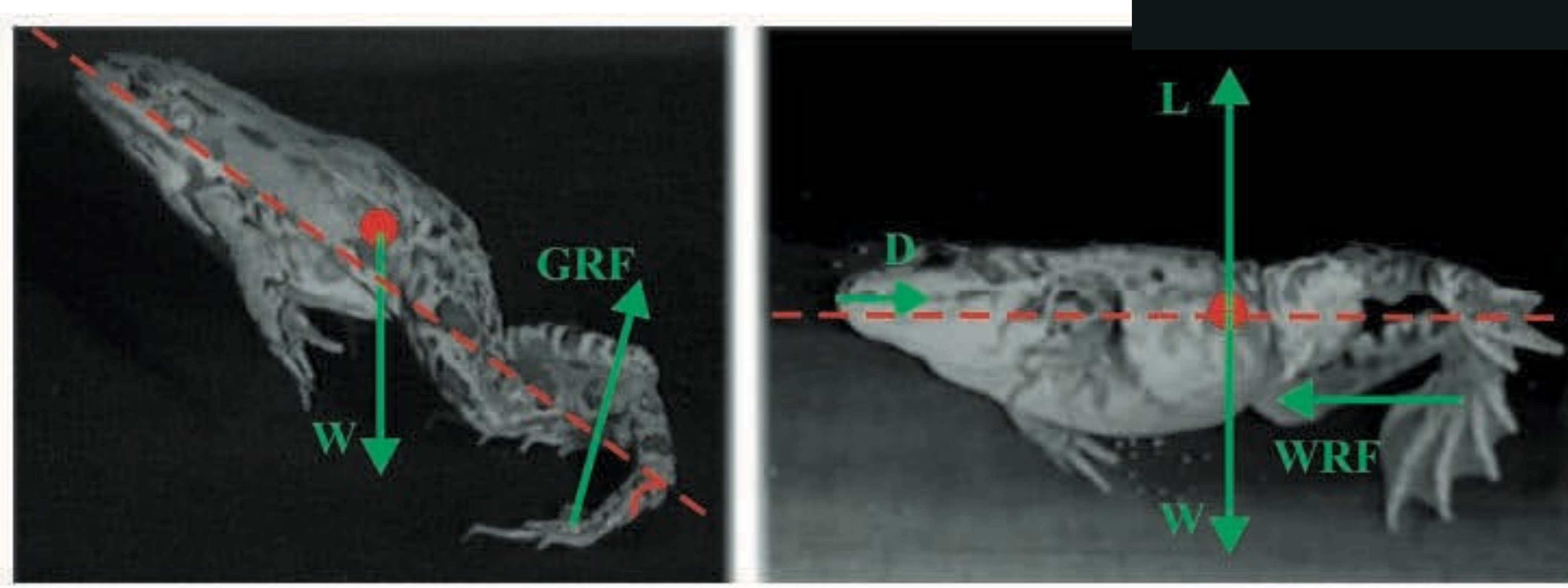

How to Account for Size?

What is Size? — Mass? — Body Length?

What is it that you're trying to normalize?

Is the problem locomotion? metabolism? support?

Mass metabolism, body support

Body Length locomotion, "shape differences"

Geometric Mean
Mosimann (1970)

May want to analyze relative BL,
neither mass nor BL may be satisfactory

SIZE = BodyL * HindLimbL * ForeLimbL * Mass^$^{.33}$ etc.

log(SIZE) = log(BodyL) + log(HindLimbL) + log(ForeLimbL) + 0.33log(Mass)

SABodyL = log(BodyL/SIZE) = log(BodyL) - log(SIZE)

How to Account for Size?

At what level of hierarchy?

Most interspecific studies use species means

Is SIZE a property of the individual?

How? Remove PC1 (interspecific)

Regression with Size (interspecific)

Divide by Size (individual)

Consequences?

Account for phylogeny first or size first?

SIZE-CORRECTION AND PRINCIPAL COMPONENTS FOR INTERSPECIFIC COMPARATIVE STUDIES

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Phylogenetic methods for the analysis of species data are widely used in evolutionary studies. However, preliminary data transformations and data reduction procedures (such as a size-correction and principal components analysis, PCA) are often performed without first correcting for nonindependence among the observations for species. In the present short comment and attached R and MATLAB code, I provide an overview of statistically correct procedures for phylogenetic size-correction and PCA. I also show that ignoring phylogeny in preliminary transformations can result in significantly elevated variance and type I error in our statistical estimators, even if subsequent analysis of the transformed data is performed using phylogenetic methods. This means that ignoring phylogeny during preliminary data transformations can possibly lead to spurious results in phylogenetic statistical analyses of species data.

KEY WORDS: Data transformation, evolutionary regression, least squares, linear regression, PCA, phylogenetic comparative methods, principal components analysis.

Evolution 2009


91513

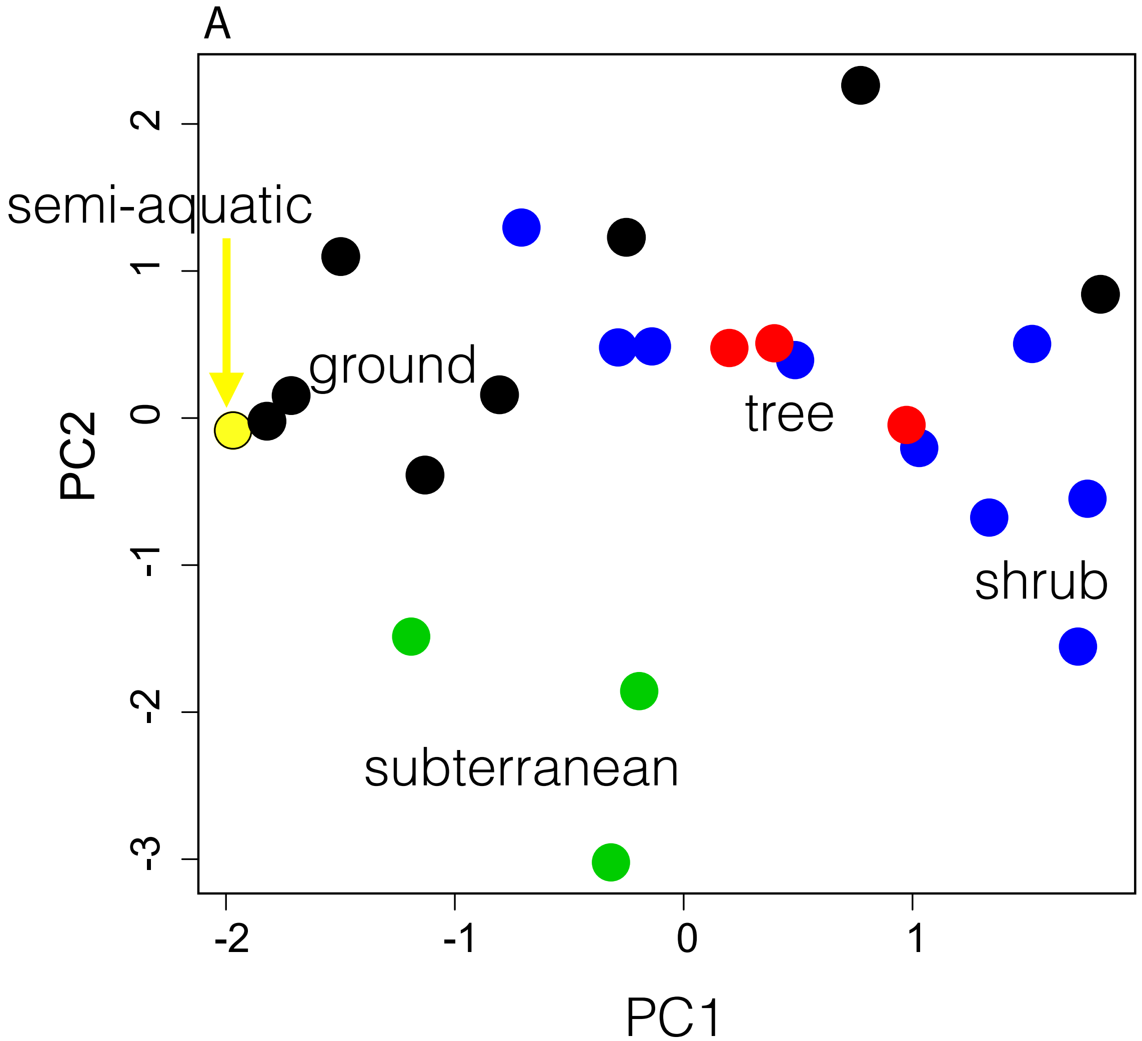
Do Athletic Abilities Covary?

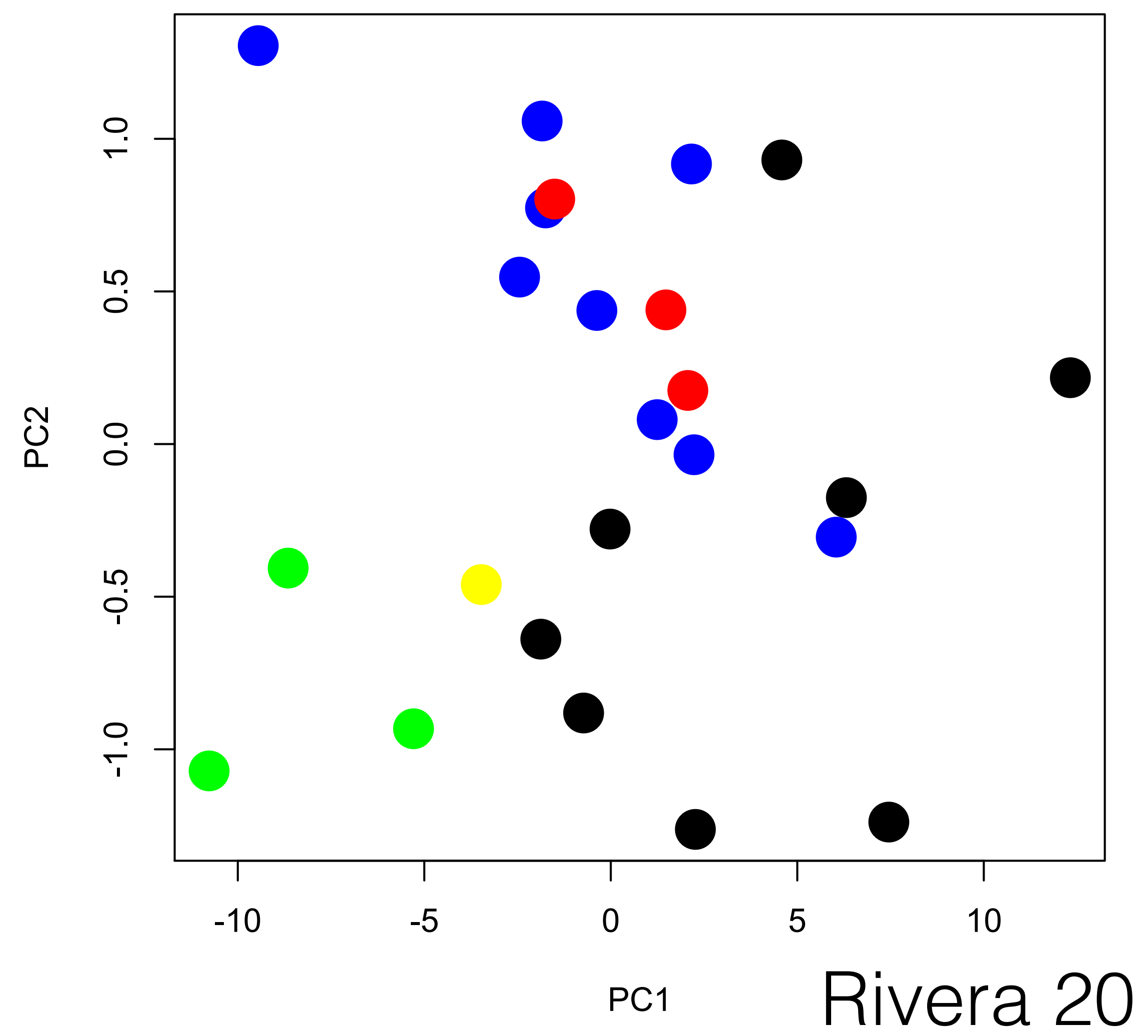
Size-Adjusted PCA

	PC1	PC2
clinging	0.71	0.38
swimming	-0.71	0.37
jumping	0.00	0.85

SA Phylogenetic PCA

	PC1	PC2
clinging	0.28	0.96
swimming	0.27	-0.48
jumping	0.99	-0.01

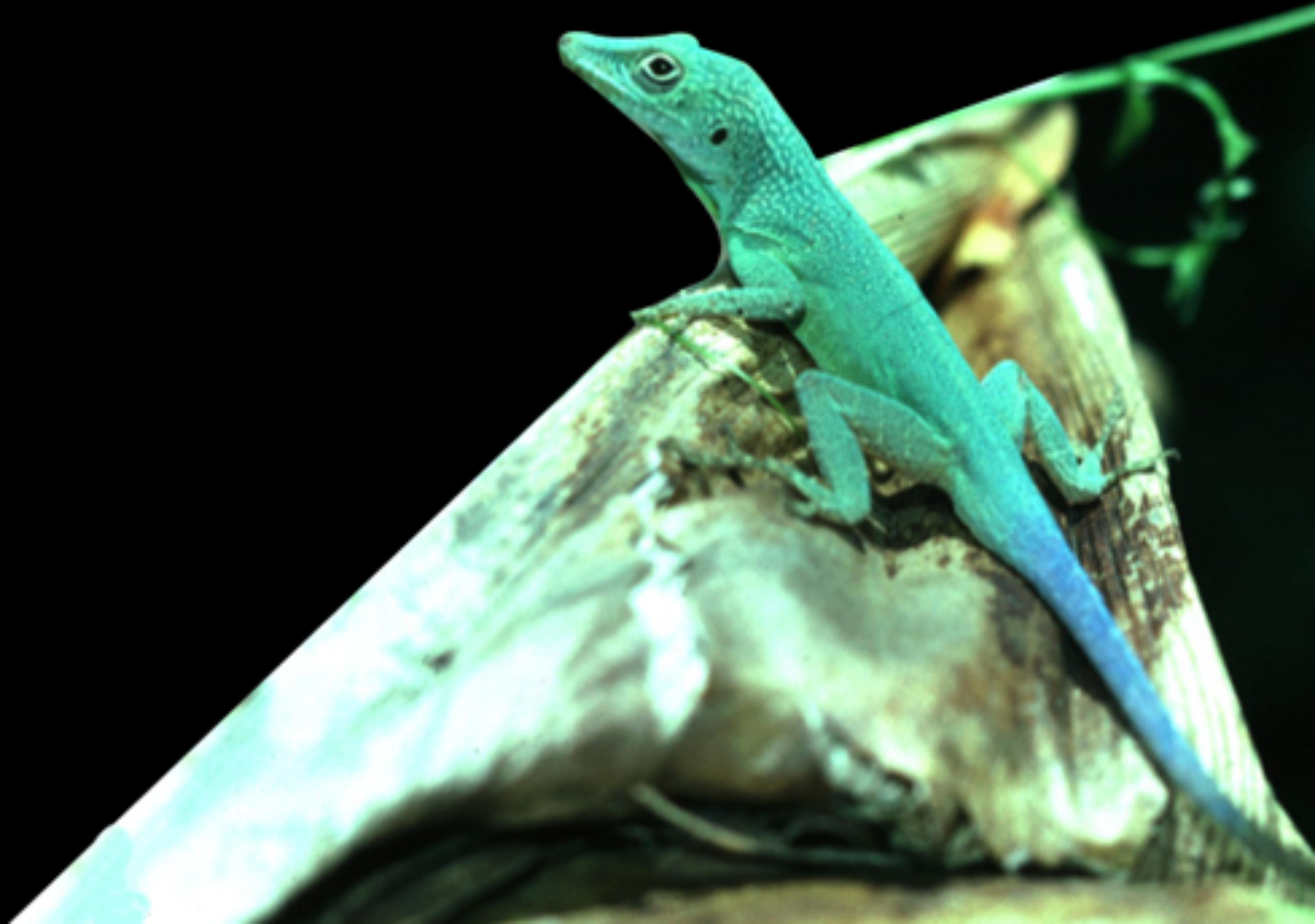




Rivera 2017

Darwin’s 3 explanations for Sexual Dimorphism:

- Intersexual competition for mates
- Differences in reproductive roles
- Independent adaptations in relation to “differences in their habits of life”



What can a Multivariate Approach tell us about Sexual Dimorphism and Biodiversity?

Competition

Adaptation to Resources

Interspecific Diversity

Sexual Dimorphism

Sexual Selection

Reproductive Differences

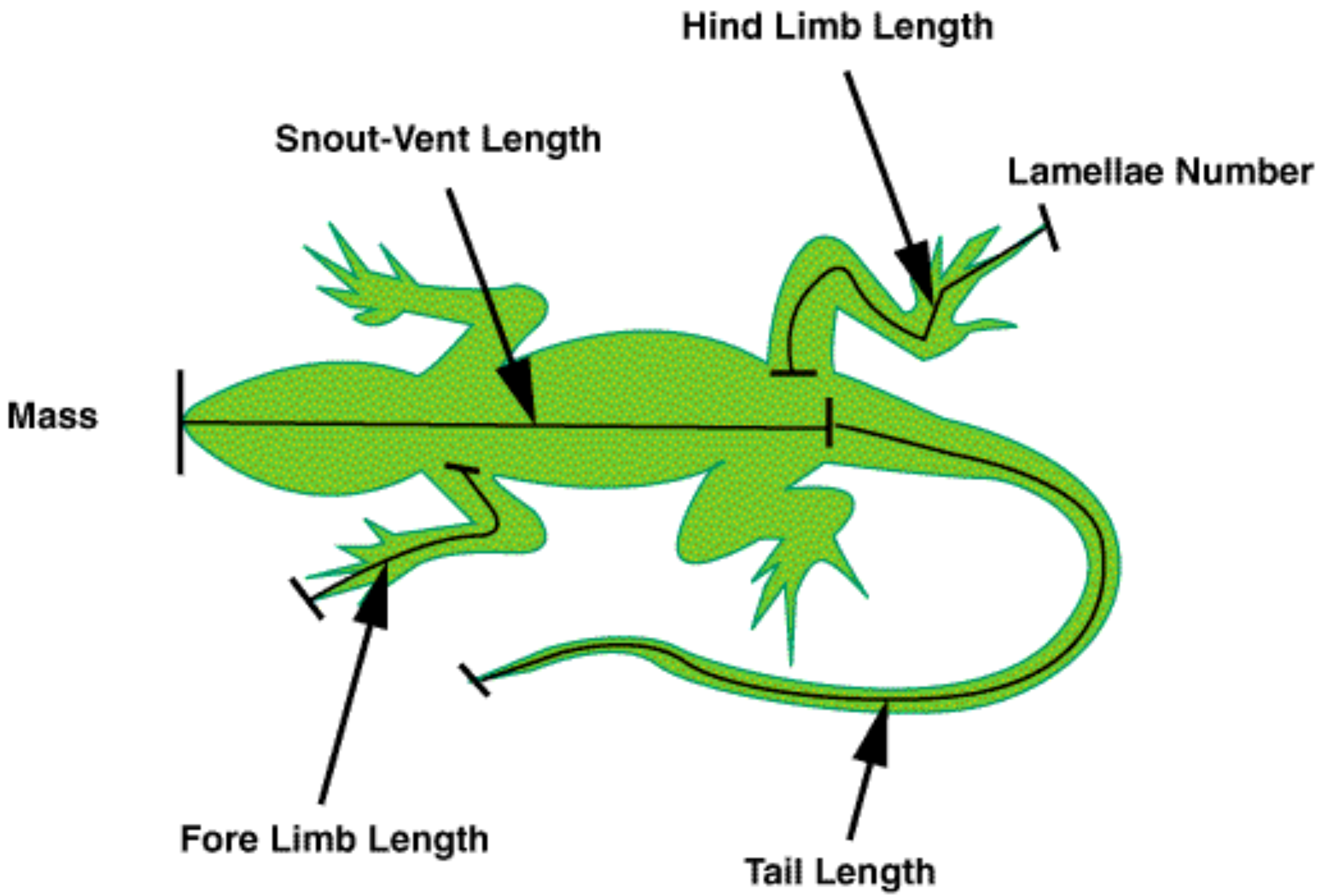
Most studies of interspecific diversity ignore sexual dimorphism

Can Sexual Dimorphism increase clade-level diversity?

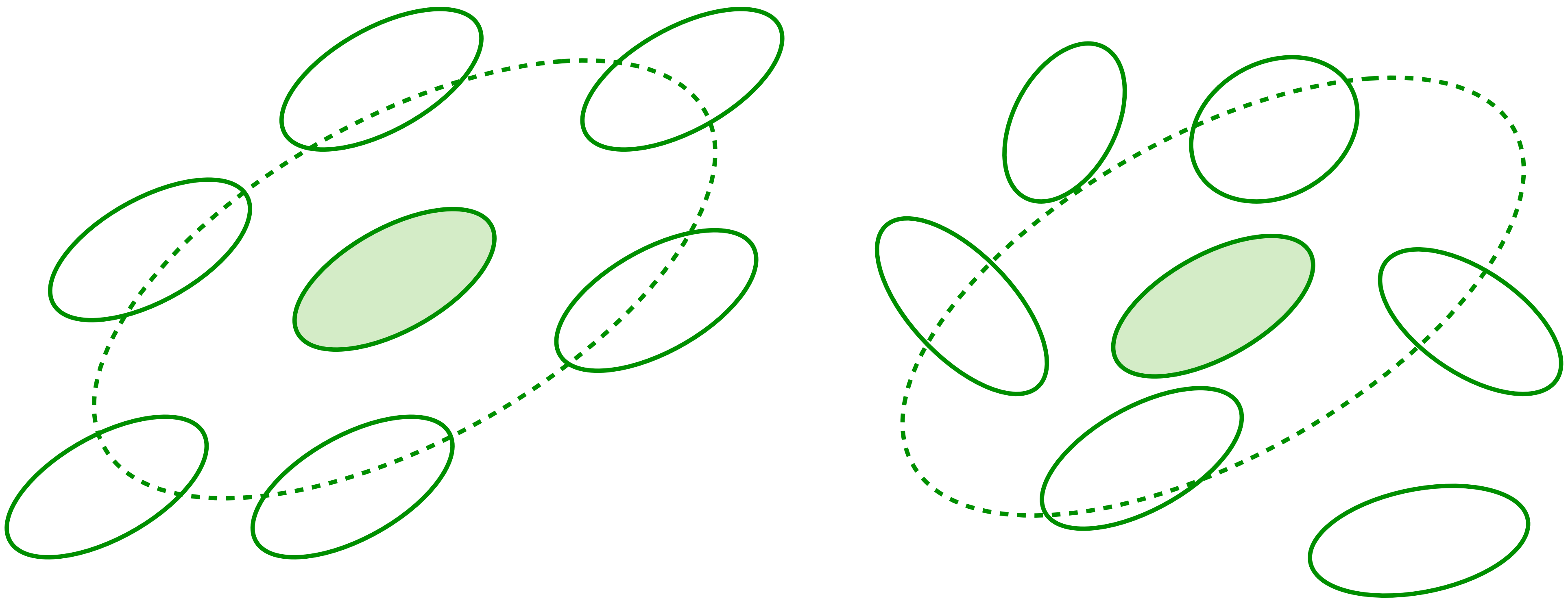
Can habitat variation affects sexual divergence?

Most studies of sexual dimorphism ignore environmental and interspecific variation

Morphology


Hind Limb Length
Snout-Vent Length
Lamellae Number
Mass
Fore Limb Length
Tail Length

Comparing Allometries



AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 59:139–149 (1982)

Relationships Among Ontogenetic, Static, and Evolutionary Allometry

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Flury's Hierarchy

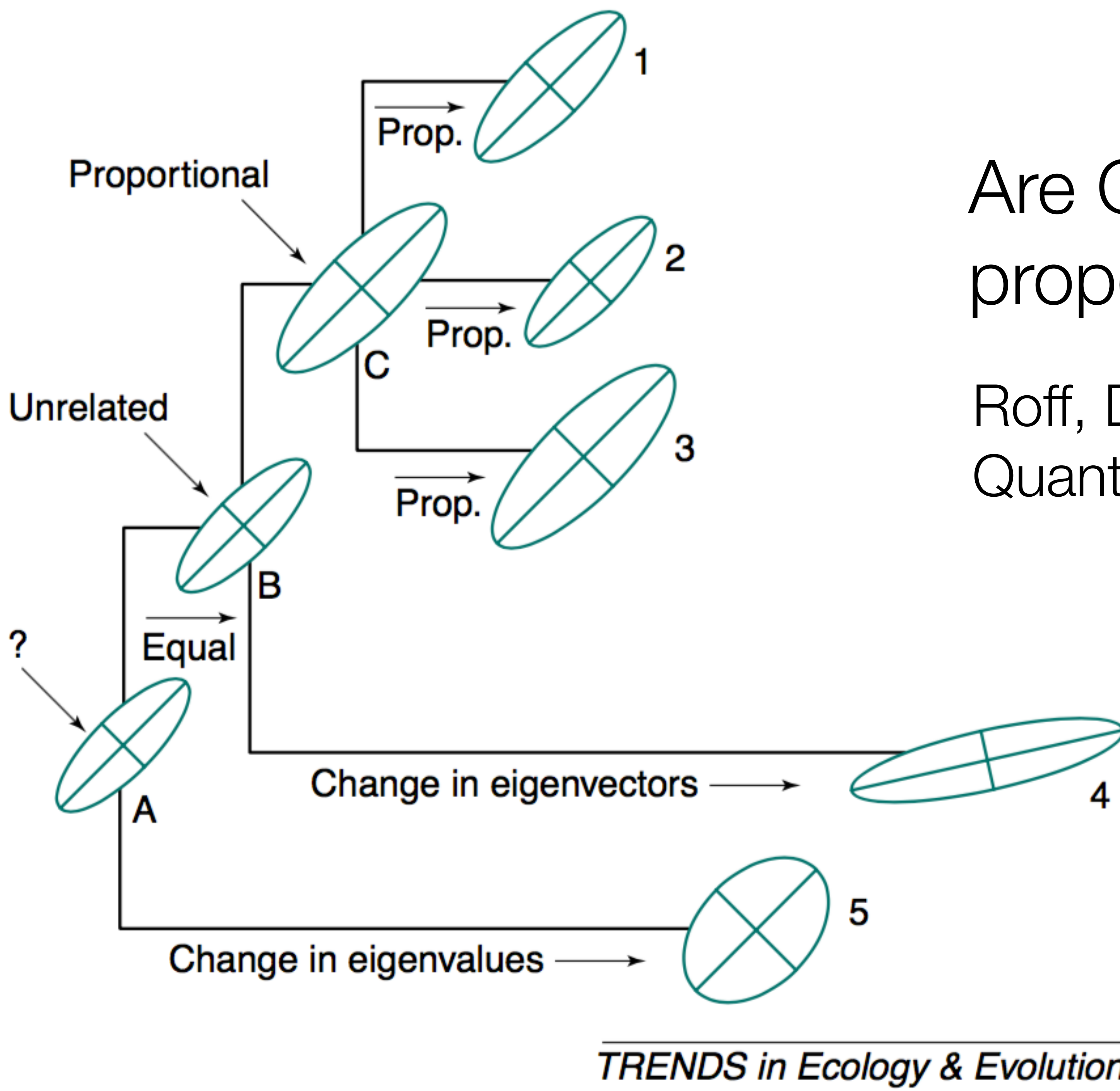

Fig. I. Hypothetical evolution of genetic variance–covariance matrices on a phylogeny. Text below branches summarizes changes

Are G and P correlated? proportional? Often yes

Roff, D.A. (1997) Evolutionary Quantitative Genetics, Chapman & Hall

Steppan et al. 2002 TREE

Sexual Dimorphism increases "Species Packing"

Sexes Contribute Substantially to Biodiversity

Table 1 | MANOVA results for shape morphology

Effect	Wilks' λ	F-value	P-value	p	q	r	η^2
Non-phylogenetic shape dimorphism							
Sex	0.599	78.78	<0.0001	5	1	1	40%
Ecomorph	0.00906	328.84	<0.0001	5	4	4	69%
Sex $\times$ ecomorph	0.838	5.35	<0.0001	5	4	4	4%
Species(ecomorph)	0.135	31.04	<0.0001	5	10	5	33%
Shape dimorphism adjusted for phylogeny							
Sex	0.594	80.52	<0.0001	5	1	1	41%
Ecomorph	0.0167	253.34	<0.0001	5	4	4	64%
Sex $\times$ ecomorph	0.794	7.07	<0.0001	5	4	4	6%
Species(ecomorph)	0.205	23.20	<0.0001	5	10	5	27%

All shape variables are entered into the model as dependent variables. Independent variables included in the model are listed under 'Effect'. 'F-value', value from F distribution; p, number of dependent variables; q, number of independent degrees of freedom; r, minimum of p or q; η^2, multivariate partial variance $= 1 - \lambda^{1/r}$ (refs 28, 29); Species(ecomorph), species nested within ecomorph.

Some Papers

Arnold, S.J. 1983. Morphology, Performance, and Fitness. Amer. Zool. 23:347-361.

Butler, M. A., and J. B. Losos. 2002. Multivariate sexual dimorphism, sexual selection, and adaptation in Greater Antillean Anolis lizards. Ecol. Monogr. 72, 541–559.

Butler, M. A., Sawyer, S. A., and J. B. Losos. 2007. Sexual dimorphism and adaptive radiation in Anolis lizards. Nature. 447, doi:10.1038/nature05774.

Cheverud, J. M. 1982. Relationships among ontogenetic, stat-ic, and evolutionary allometry. American Journal of Phys-ical Anthropology 59:139–149.

Klingenberg, C. P., and M. Zimmermann. 1992. Static, on-togenetic, and evolutionary allometry: a multivariate com-parison in nine species of water striders. American Natu-ralist 140:601–620.

Klingenberg, C. P. 1996. Multivariate allometry. Pages 23–49 in L. F. Marcus, M. Corti, A. Loy, G. Naylor, and D.E. Slice, editors. Advances in morphometrics. PlenumPress, New York, New York, USA.

Mosimann, J. 1970. Size allometry: size and shape variableswith characterizations of the lognormal and generalizedgamma distributions. Journal of the American StatisticalAssociation 65:930–945.

Revell, L.J. 2009. Size-correction and principal components for interspecific comparative studies. Evolution 63-12:3258–3268. doi:10.1111/j.1558-5646.2009.00804.x

Steppan, S. J., Phillips, P. C., and Houle, D. 2002. Comparative quantitative genetics: evolution of the G matrix. TREE. 17:320-327.

Wake, M. 1984. Science as a way of Knowing — Evolution: The Biology of Whole Organisms. Amer. Zool. 24:443-450.