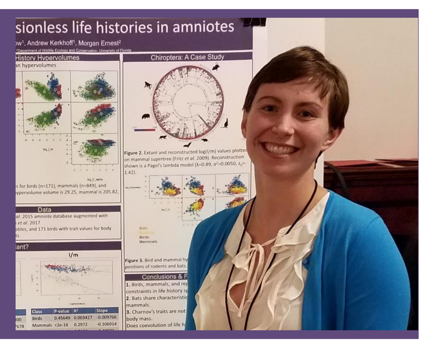
Macroevolution of dimensionless life histories in amniotes

Cecina Babich Morrow[1], Andrew Kerkhoff[1], Morgan Ernest[2]

[1]Department of Biology, Kenyon College; [2]Department of Wildlife Ecology and Conservation, University of Florida



Objectives

1. Use Charnov's dimensionless life history traits to visualize and quantify the life history strategies of amniotes

2. Compare life history strategies of birds, mammals, reptiles, and smaller clades by using hypervolumes

3. Investigate if these so-called invariant traits are actually invariant with body mass

4. Analyze the macroevolutionary patterns of the dimensionless traits and their components between clades

Motivation: How do evolutionary history and ecological roles interact to influence the trait combinations possible for a group of species?

Charnov's Dimensionless Traits

Most life history traits vary with body mass.

3 dimensionless variables hypothesized to be invariant with body mass (Charnov 2002):

1. **C·E = reproductive effort · average lifespan**
   - Fraction of body mass allocated to reproduction per unit death
   - Trade-off of reproductive effort and mortality rate
2. **E/α = average lifespan / age at female maturity**
   - Cost of aging to reproductive maturity relative to lifespan
   - Trade-off of reproductive age and overall lifespan
3. **I/m = mass at independence / adult body mass**
   - Size of independent offspring relative to adult
   - Trade-off of offspring size compared to adult size

These traits thus represent trade-offs that are presumably provide information beyond body mass.

Data

Used the Myhrvold *et al.* 2015 amniote database augmented with reptile data from Allen *et al.* 2017

849 mammals, 516 reptiles, and 171 birds with trait values for body mass and the invariants

Life History Hypervolumes

4-dimensional Gaussian hypervolumes: framework for classifying life histories

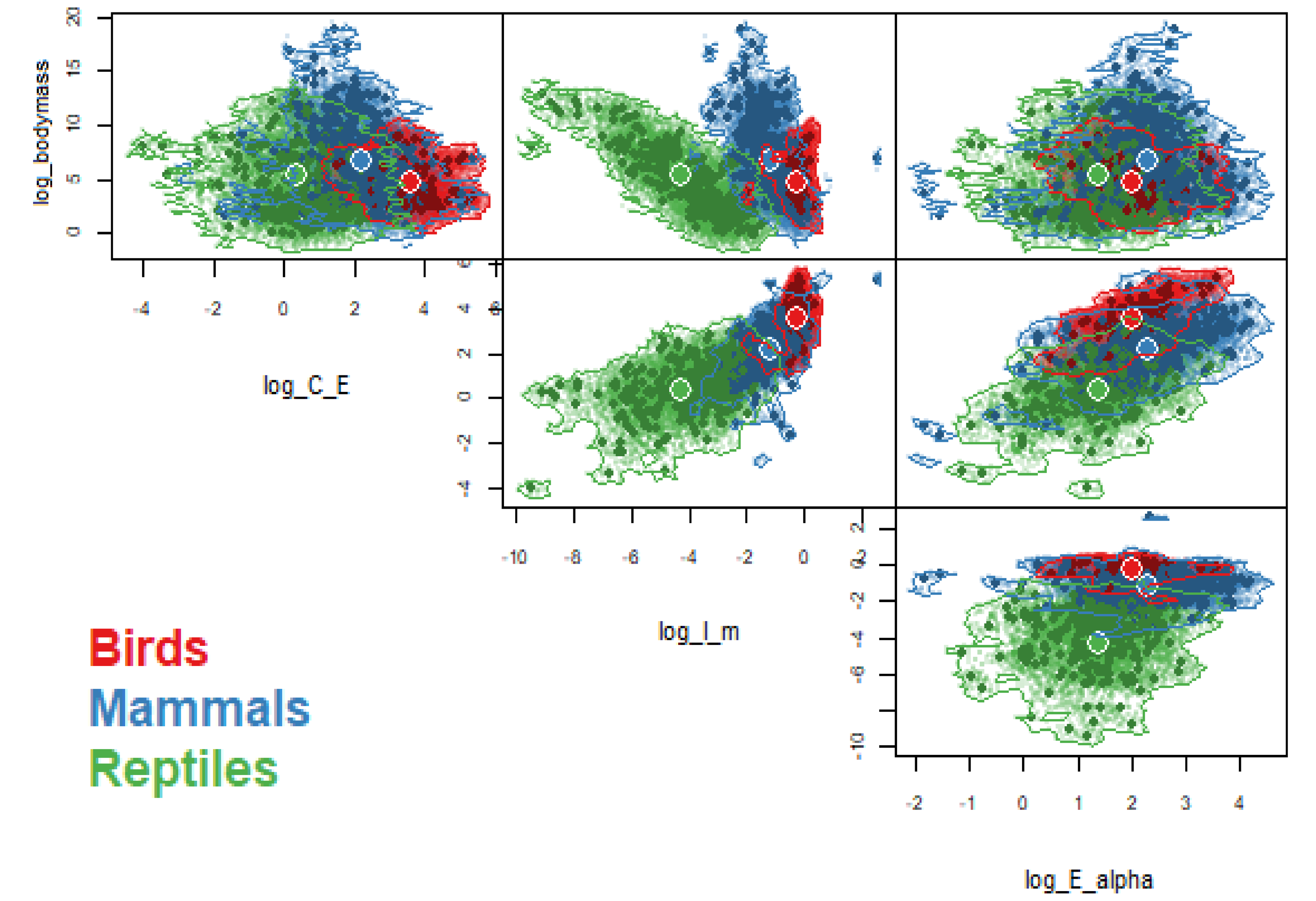


Figure 1. Hypervolumes for birds (n=171), mammals (n=849), and reptiles (n=516). Bird hypervolume volume is 29.25, mammal is 205.82, and reptile is 474.93.

Reptile Order Hypervolumes

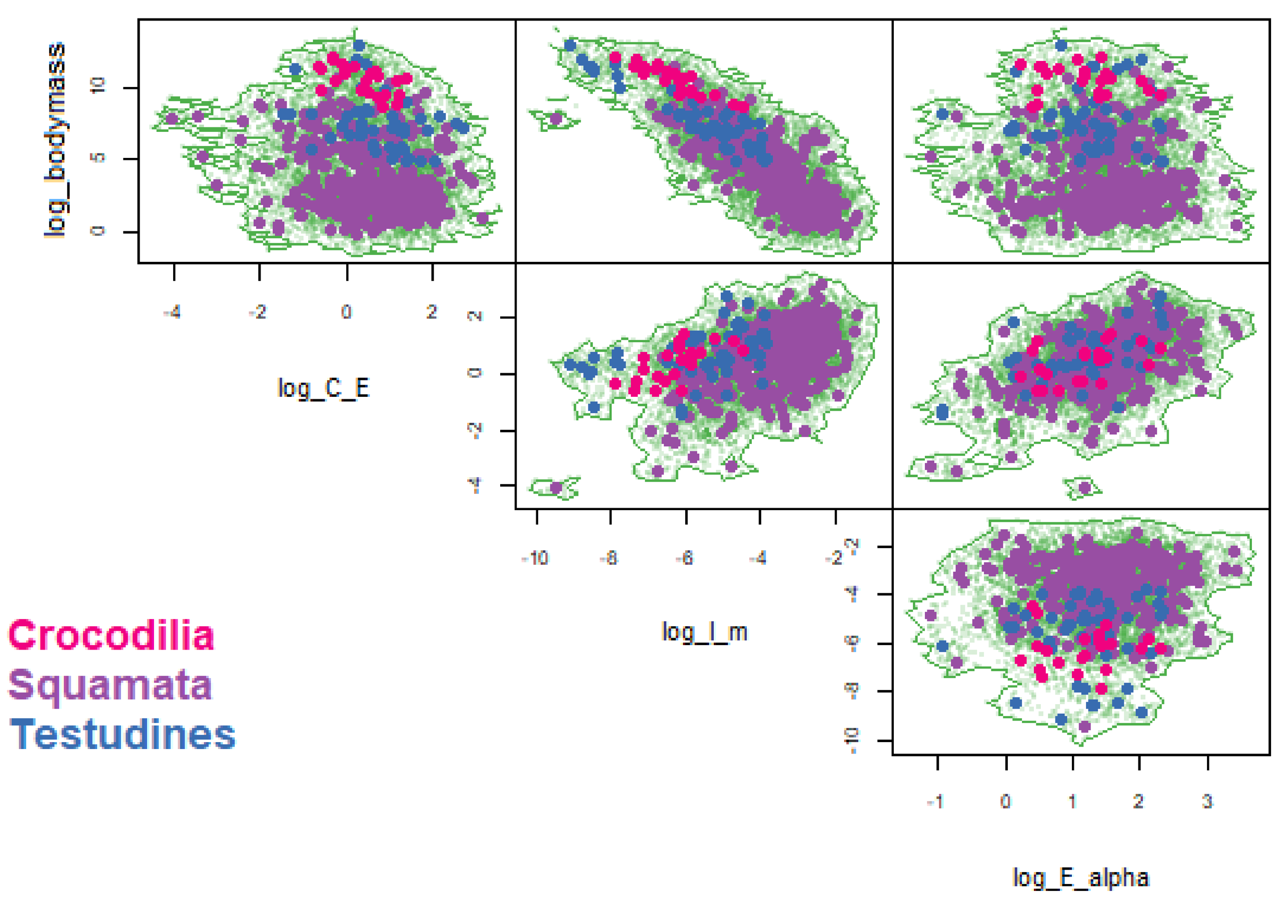


Figure 2. Reptile hypervolume showing the location of the three orders: Crocodilia (n=22), Testudines (n=54), and Squamata (n=440).

Chiroptera: A Case Study

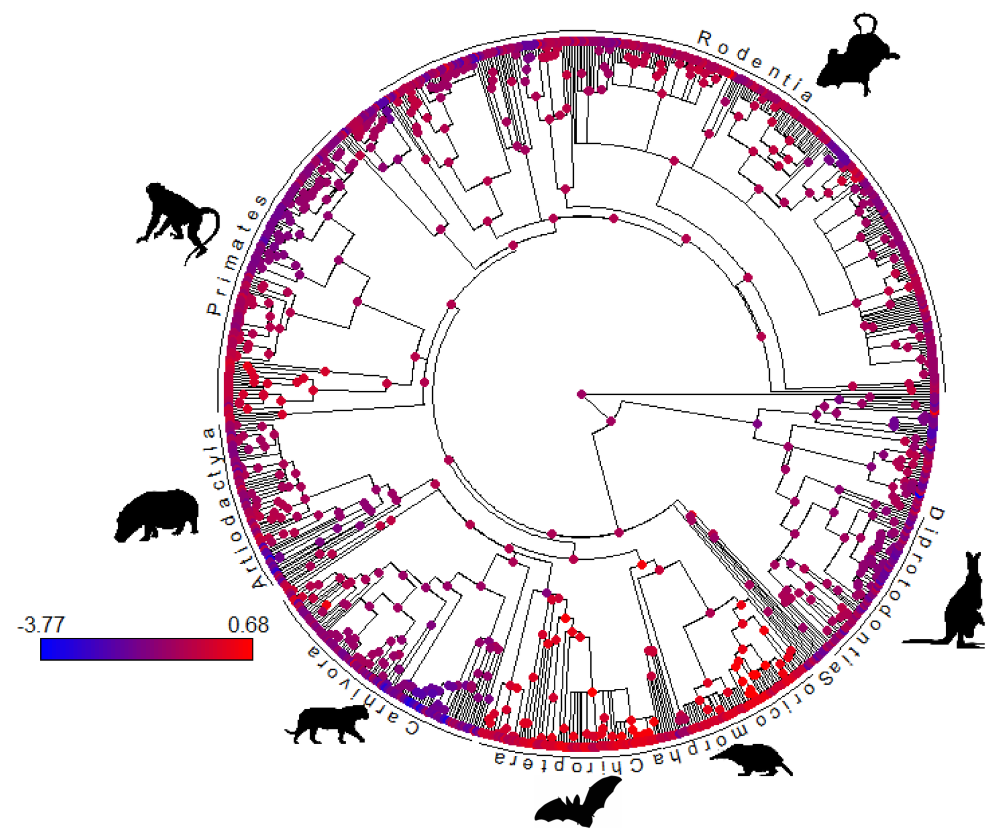


Figure 3. Extant and reconstructed log(I/m) values plotted on mammal supertree (Fritz *et al.* 2009). Reconstruction shown is a Pagel's lambda model (λ=0.89, σ^2=0.0050, z_0=-1.42).

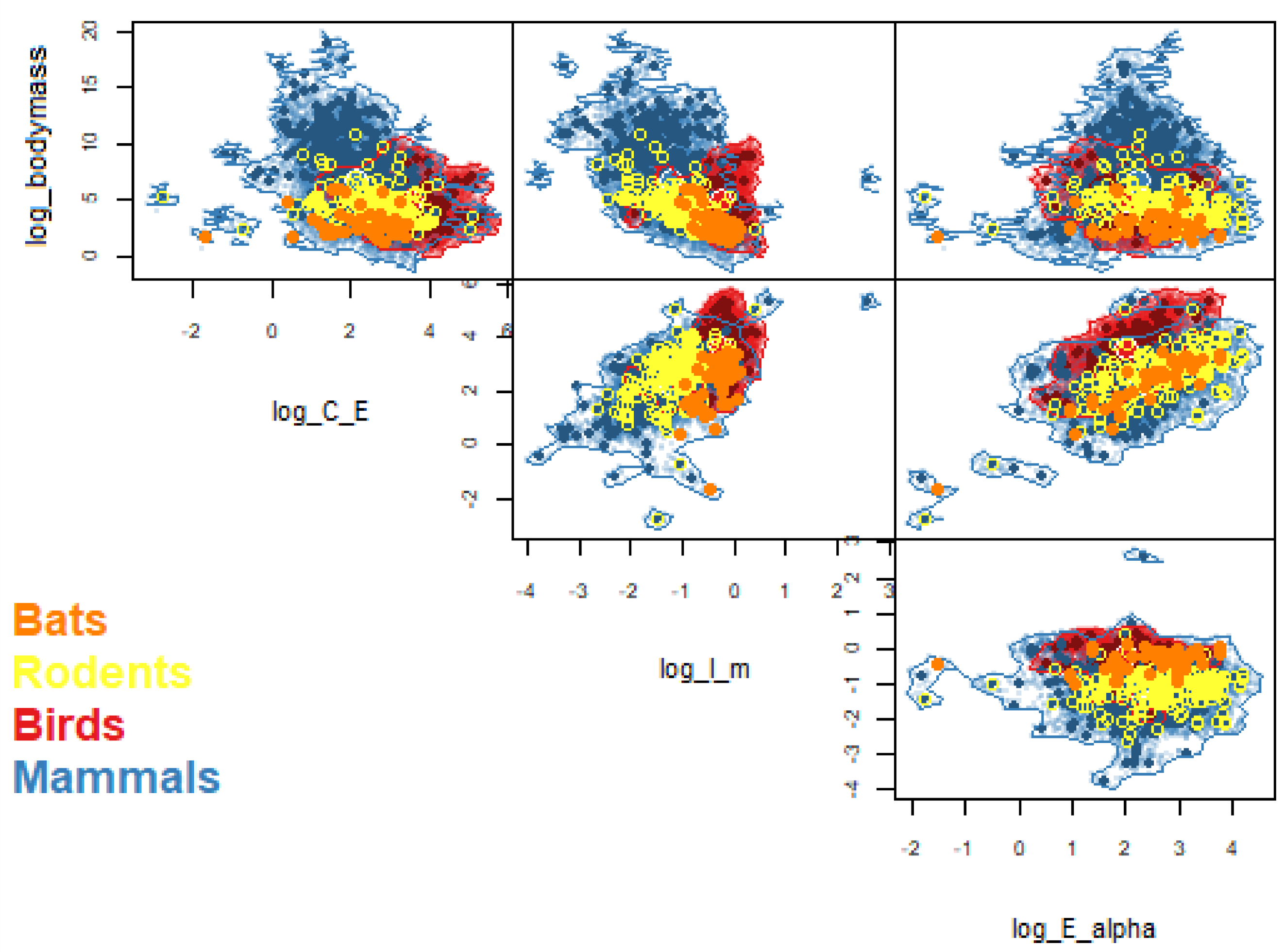
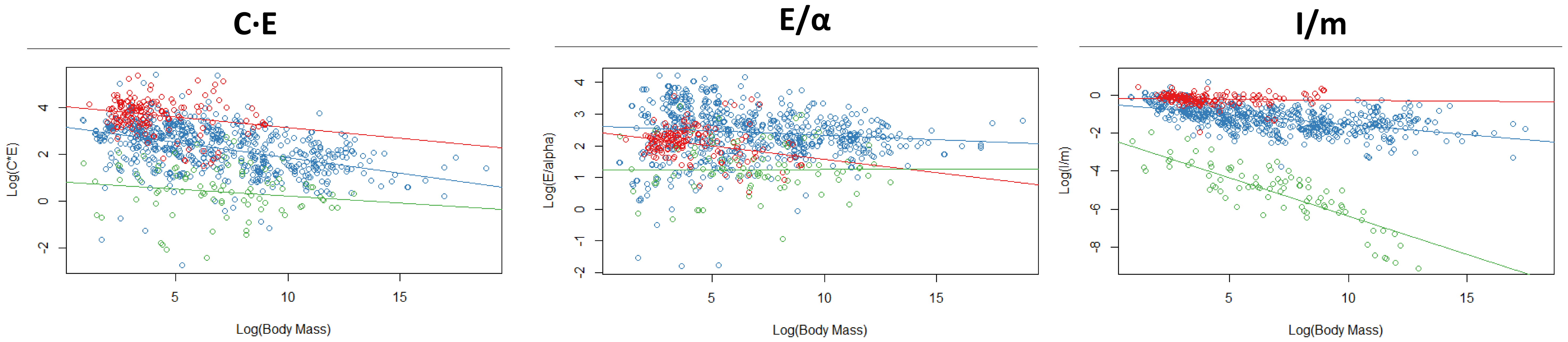


Figure 4. Bird and mammal hypervolumes displaying the positions of rodents and bats.

Are the invariants really invariant?

There are multiple ways to quantify invariance beyond p-value (Price *et al.* 2014), including R^2 and slope.



C·E

Class	P-value	R^2	Slope
Birds	0.003188	0.05242	-0.08924
Mammals	<2e-16	0.2048	-0.132068
Reptiles	0.11076	0.02197	-0.05874

E/α

Class	P-value	R^2	Slope
Birds	5.29e-05	0.09624	-0.08400
Mammals	0.00128	0.01239	-0.027678
Reptiles	0.954	2.907e-05	0.001521

I/m

Class	P-value	R^2	Slope
Birds	0.45649	0.003427	-0.009766
Mammals	<2e-16	0.2972	-0.106914
Reptiles	<2e-16	0.7138	-0.40072

Figure 4. Log-log regressions of the three invariant traits against body mass for the three classes of amniotes. Red points are birds, blue points are mammals, and green points are reptiles.

Conclusions & Future Directions

1. Birds, mammals, and reptiles have very different constraints in life history space.

2. Bats share characteristics with both birds and mammals, so flight may present unique constraints.

3. Charnov's traits are not always invariant with body mass for all groups of species.

Future Questions:

- Does ectothermy allow for a wider range of life history traits?
- What constraints do flight provide?
- Does coevolution of life history traits result in invariance?
- What differs in clades that do not exhibit invariance?

References

Allen, W. L., S. E. Street, and I. Capellini. 2017. Fast life history traits promote invasion success in amphibians and reptiles. Ecology Letters 20:222–230.

Charnov, E. L. 2002. Reproductive effort, offspring size and benefit–cost ratios in the classification of life histories. Evolutionary Ecology Research 4:749–758.

Myhrvold, N. P., E. Baldridge, B. Chan, D. Sivam, D. L. Freeman, and S. K. M. Ernest. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. Ecology 96:3109–3109.

Price, C. A., I. J. Wright, D. D. Ackerly, Ü. Niinemets, P. B. Reich, and E. J. Veneklaas. 2014. Are leaf functional traits 'invariant' with plant size and what is 'invariance' anyway? Functional Ecology 28:1330–1343.

Acknowledgments

This work was funded by NSF Grant DEB-1556651 and by the Kenyon College Summer Science Scholars Program.