

Ontogenetic and Interspecific Metabolic Scaling in Insects

James L. Maino* and Michael R. Kearney

Department of Zoology, University of Melbourne, Victoria 3010, Australia

Submitted March 26, 2014; Accepted July 18, 2014; Electronically published October 23, 2014

Online enhancement: appendix. Dryad data: <http://dx.doi.org/10.5061/dryad.3qv3p>.

ABSTRACT: Design constraints imposed by increasing size cause metabolic rate in animals to increase more slowly than mass. This ubiquitous biological phenomenon is referred to as metabolic scaling. However, mechanistic explanations for interspecific metabolic scaling do not apply to ontogenetic size changes within a species, implying different mechanisms for scaling phenomena. Here, we show that the dynamic energy budget theory approach of compartmentalizing biomass into reserve and structural components provides a unified framework for understanding ontogenetic and interspecific metabolic scaling. We formulate the theory for insects and show that it can account for ontogenetic metabolic scaling during the embryonic and larval phases, as well as the U-shaped respiration curve during pupation. After correcting for the predicted ontogenetic scaling effects, which we show to follow universal curves, the scaling of respiration between species is approximated by a three-quarters power law, supporting past empirical studies on insect metabolic scaling and our theoretical predictions. The ability to explain ontogenetic and interspecific metabolic scaling effects under one consistent framework suggests that the partitioning of biomass into reserve and structure is a necessary foundation to a general metabolic theory.

Keywords: metabolic theory, body-size scaling, allometry, insects, metabolic rates.

Introduction

In biology, metabolic rate is a fundamental property of organisms that governs the flow of energy and materials at all levels of biological organization (Schmidt-Nielsen 1984; Brown et al. 2004). Since Kleiber (1932), the metabolic rate in most plants and animals has been widely found to scale interspecifically with mass (M) as $\sim M^{3/4}$ when large body-size ranges are considered (Hemmingsen 1960; Savage et al. 2004; Chown et al. 2007; Ehnes et al. 2011). A major biological challenge is to find a general theory of metabolism to account for such scaling relationships (Kearney and White 2012). In the most prominent explanations of metabolic scaling, it is often implicitly assumed that the physical constraints responsible

for interspecific metabolic scaling are also responsible for ontogenetic patterns (West et al. 1997; Banavar et al. 1999; Darveau et al. 2002; Kozłowski et al. 2003; Hou et al. 2008; Glazier 2010; Kolokotronis et al. 2010). However, ontogenetic metabolic scaling is often found to deviate qualitatively and quantitatively from interspecific patterns (Wieser 1984; Glazier 2006; Chown et al. 2007; Moran and Wells 2007; Caruso et al. 2010; Yagi et al. 2010; Sears et al. 2012). This not only questions the universal power-law scaling of metabolic rate but also suggests that a completely different mechanism may underlie ontogenetic metabolic scaling. Here, using insects as a case study, we develop a framework that captures the diverse ontogenetic scaling of metabolism (fig. 1) as well as interspecific effects. As insects dominate the known diversity of animal life, any metabolic theory claiming to be universally general to life must also account for this important taxonomical group. We test our predictions against a data set we compiled on the respiratory metabolism of insects during various life-history stages.

A Mechanistic Model of Metabolism

The variety of respiration patterns during insect ontogeny cannot be captured using a single allometric function of the form $y = aM^b$, where a is the normalization constant and b is the scaling exponent. As allometric functions are monotonic, the U-shaped scaling of metabolic rate with mass during the pupation of holometabolous insects precludes their use and shows that mass is an unreliable indicator of metabolic state. Moreover, for insects in general (including nonholometabolous insects), embryonic respiration can vary by orders of magnitude while mass remains comparatively unchanged (Fink 1925; Rakshpal 1962), suggesting that mass-independent effects are an important, overlooked factor in metabolic scaling (Glazier 2005). A general framework for metabolic organization that can capture all of these patterns under a simple set of assumptions is dynamic energy budget (DEB) theory (Kooijman 2010). In addition, as most prominent theories are either applicable only to organisms with closed cir-

* Corresponding author; e-mail: jamesmaino@gmail.com.

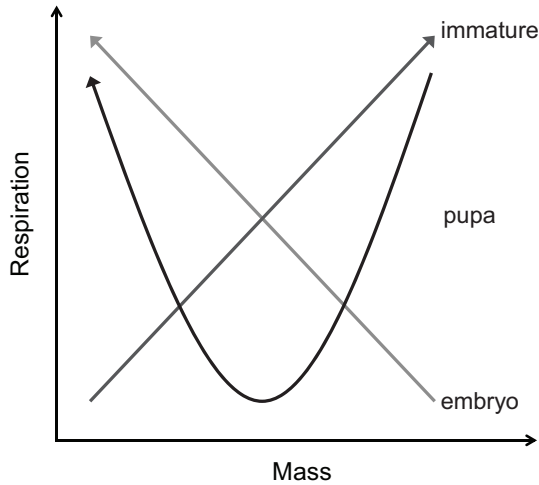


Figure 1: Throughout ontogeny, insects exhibit a range of metabolic scaling patterns. This schematic illustrates the variety of scaling patterns for key life-history stages, with the time course of development indicated by the arrows. Time moves from right to left for nonfeeding embryos and pupae, which lose mass as they develop.

culatory systems (West et al. 1997; Banavar et al. 1999; Kolokotronis et al. 2010) or do not make a priori predictions (Darveau et al. 2002; Glazier 2006; Kozłowski et al. 2010), DEB theory represents a general predictive framework in which to interpret metabolism for all organisms.

Dynamic energy budget theory departs from many prominent theories that consider mass to be the most important determinant of metabolism, by viewing body mass as a function of more fundamental quantities. In DEB theory, biomass is composed of “reserve” and “structure.” Reserve is defined as the sum of all intermediary materials between the uptake of food and the payment of costs incurred by general metabolism, which include the growth and maintenance of structure and reproduction (not considered here, but see Kooijman 2010). In this way, both the composition of biomass (proportion of reserve to structure) and the size of the organism (structure) can affect metabolism. This captures, for example, why two organisms of identical mass but different feeding histories are not equivalent in terms of their metabolism or why

organisms may continue to grow and reproduce under starvation.

Besides food availability, ontogeny can cause the ratio of reserve and structure to vary dynamically with time, which explains differences in respiration patterns. In a DEB framework, it is convenient to think of a fresh egg as almost entirely reserve, with an initially small amount of structure that increases with development. Under this view, due to the costs associated with the growing amount of structure, respiration is expected to increase as embryonic development proceeds in spite of any increase in total mass (Kooijman 1986). On the other hand, for growing larvae and nymphs (hereafter, jointly referred to as immatures), respiration is expected to increase with mass. Given that food is unrestricted, immatures are assumed to be constrained by pressures of stoichiometric homeostasis (Sterner and Elser 2002) and thus maintain a constant composition of reserve and structure (Kooijman 2010). Structure—and, therefore, maintenance metabolism—is then proportional to mass and increases with immature development. During pupation in Holometabola, there is no feeding and metabolism is fueled via the depletion of reserves. Larval structure is histolysed, and energy and materials are recuperated for the growth of adult structure. Pupal respiration would thus be expected to first decrease during the histolysis of larval structures and to then increase as adult structure is formed.

Allometric functions may adequately capture metabolic scaling for interspecific comparisons, but for reasons discussed above, they would not be able to capture these diverse ontogenetic patterns. We propose that a simple way to capture ontogenetic effects is to multiply the expected metabolic rate of a species by a dimensionless polynomial equation that adjusts the metabolic rate at ultimate size to the particular developmental stage:

$$B = paM^b.$$

In this way, the expression for metabolic rate (B) now consists of an interspecific component (aM^b) and an ontogenetic component (p). Three polynomials are presented to adjust for the stage of development during the embryonic, immature, and pupal phases (table 1). Developmental stages are represented by scaled time for eggs and pupae (time divided by emergence time) and scaled mass for

Table 1: Ontogenetic effect on respiration predicted by dynamic energy budget (DEB) theory compared to best-fit polynomials

Stage	Parameters determined by DEB theory	r^2	AIC	Parameters determined by best fit	r^2	AIC
Egg	$p_e = .12\tau^3 + .37\tau^2 + .38\tau + .13$.85	102.6	$p_e = 1.01\tau^3 - .94\tau^2 + .80\tau + .14$.86	95.3
Larva/nymph	$\log_{10} p_l = \log_{10} \mu^* + 0$.90	2,463	$\log_{10} p_l = .81 \log_{10} \mu^* - .15$.94	2,083
Pupa	$p_p = 2.75\tau^2 - 2.87\tau + 1$.40	458.3	$p_p = 2.14\tau^2 - 2.08\tau + .84$.50	425.5

Note: An asterisk indicates immature data, which spanned several orders of magnitude, that were log transformed to ensure errors were normally distributed. AIC = Akaike Information Criterion.

Table 2: Summary of insects that make up the data sets for each developmental stage

Insect species	Coverage of data over life cycle ^a		
	Egg	Immature	Pupa
Blattodea:			
<i>Blaberus discoidalis</i>	...	X	NA
<i>Blattella germanica</i>	...	X	NA
<i>Periplaneta americana</i>	...	X	NA
Coleoptera:			
<i>Aphodius rufipes</i>	...	X	...
<i>Callosobruchus analis</i>	...	X	...
<i>Crioceris asparagi</i>	X
<i>Cryptolestes ferrugineus</i>	...	X	X
<i>Hippodamia convergens</i>	X
<i>Leptinotarsa decemlineata</i>	X	...	X
<i>Paropsis charybdis</i>	X
<i>Popillia japonica</i>	X	...	X
<i>Rhyzopertha dominica</i>	...	X	X
<i>Sitophilus granarius</i>	...	X	...
<i>Tenebrio molitor</i>	X	...	X
<i>Tribolium confusum</i>	X
Diptera:			
<i>Chironomus riparius</i>	...	X	...
<i>Delia platura</i>	X
<i>Drosophila melanogaster</i>	X
<i>Glossina morsitans</i>	X
<i>Lucilia illustris</i>	...	X	...
<i>Musca domestica</i>	X
<i>Sarcophaga argyrostoma</i>	X
<i>Tipula abdominalis</i>	...	X	...
Hemiptera:			
<i>Anasa tristis</i>	X	...	NA
<i>Lygaeus kalmii</i>	...	X	NA
<i>Oncopeltus fasciatus</i>	X	X	NA
<i>Philaenus spumarius</i>	...	X	NA
<i>Rhodnius prolixus</i>	X	...	NA
<i>Trigonotylus coelestialium</i>	...	X	NA
Hymenoptera:			
<i>Apis mellifera</i>	...	X	X
<i>Macrocentrus ancylivora</i>	X
<i>Solenopsis invicta</i>	...	X	...
Lepidoptera:			
<i>Actias luna</i>	X
<i>Ancylis comptana</i>	X
<i>Bombyx mori</i>	X	X	X
<i>Galleria mellonella</i>	X
<i>Hyalophora cecropia</i>	X
<i>Manduca sexta</i>	X
<i>Ostrinia obumbratalis</i>	X
<i>Pachysphinx modesta</i>	...	X	...
Orthoptera:			
<i>Acheta domesticus</i>	...	X	NA
<i>Allonemobius socius</i>	X	...	NA
<i>Encoptolophus sordidus</i>	...	X	NA
<i>Gryllus pennsylvanicus</i>	X	...	NA
<i>Gryllus veletis</i>	X	...	NA
<i>Melanoplus differentialis</i>	X	...	NA
<i>Melanoplus sanguinipes</i>	...	X	NA
Phasmatodea:			
<i>Phyllium crurifolium</i>	...	X	NA
Trichoptera:			
<i>Potamophylax cingulatus</i>	...	X	...
<i>Sericostoma personatum</i>	...	X	...

Note: NA = not applicable.

^a For data sources, see supporting data set, available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3qv3p> (Maino and Kearney 2014).

immatures (mass divided by ultimate mass). We use scaled time for the embryonic and pupal stages, because compared to the immature phase, mass changes are small and, consequently, prone to measurement error. Polynomial functions are well suited to capturing ontogenetic changes because they are simple, nonmonotonic functions with desirable statistical properties. As polynomials reduce to a linear function, their parameters are easily estimated from data. More importantly, under special circumstances, DEB theory predicts ontogenetic respiration to follow a polynomial function of the developmental stage (appendix, available online), which offers a mechanistic interpretation and method to estimate polynomial coefficients from underlying biological processes.

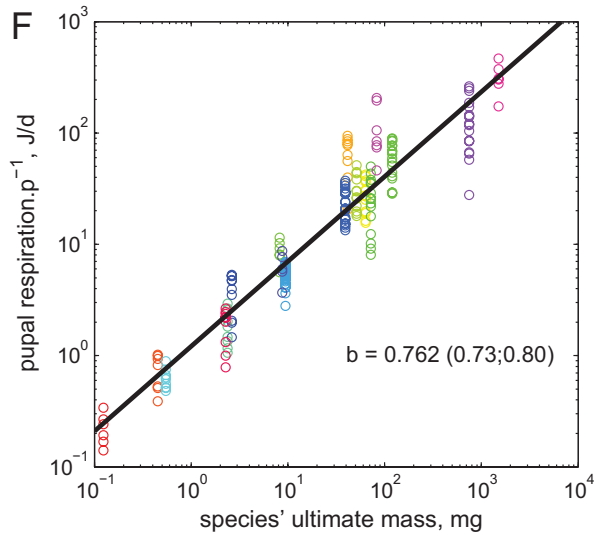
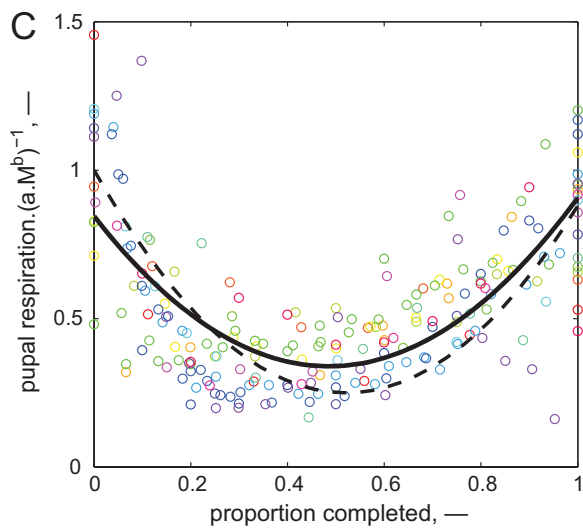
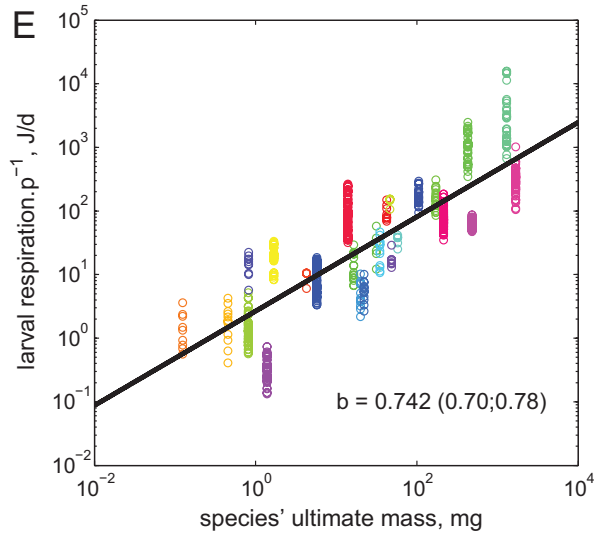
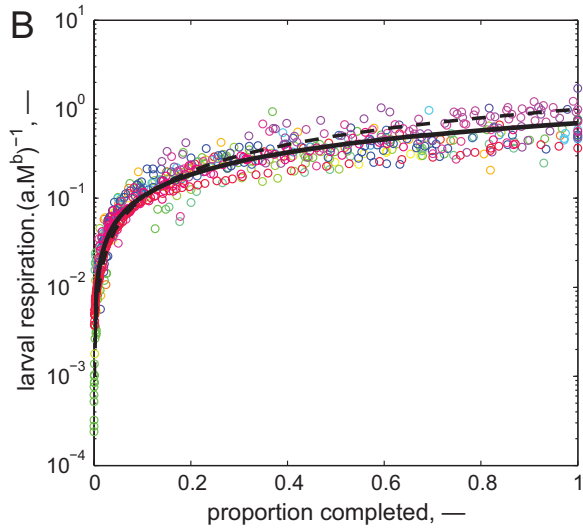
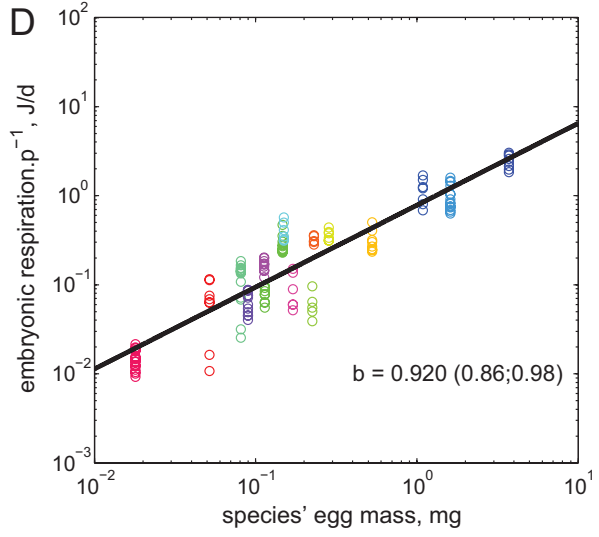
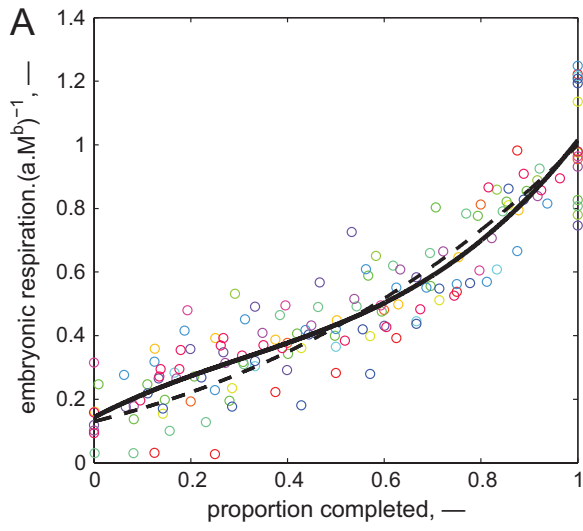
Some simplifying assumptions are required to derive polynomial correction factors from DEB theory. We take respiration to be proportional to somatic maintenance, which ignores the contributions from growth and feeding usually considered in a DEB framework. We also assume that the amount of reserve is not limiting development rate during the embryonic and pupal phases (see appendix). The result of these simplifying assumptions is that the effect of ontogeny p is separate from interspecific effects aM^b and that respiration can be divided by interspecific effects and plotted on universal curves:

$$\frac{B}{aM^b} = p.$$

Or conversely, the interspecific scaling of metabolism can be observed by adjusting respiration by the predicted ontogenetic effects shown in table 1 and plotting the result against species mass:

$$\frac{B}{p} = aM^b.$$

Theoretically derived polynomial equations are compared with the polynomial of the same degree estimated by least squares regression in terms of the variance explained and the Akaike Information Criterion (AIC; Burnham and Anderson 2002). Interspecific scaling exponents are estimated by applying an ordinary least squares regression to log-transformed data. Dynamic energy budget theory predicts the interspecific component of respiration aM^b to vary with species' mass raised to an exponent between three-quarters and one; DEB theory predicts Kleiber's three-quarters scaling rule at the limit of large mass, but at small masses, the exponent will be closer to one (Maino et al. 2014). This is because, at very small masses, reserve makes up a very small amount of biomass, and structure can be approximated by total mass. Structure and, thus, maintenance metabolism increase proportional to mass at very small sizes. At very large sizes, reserve contributes signif-



icantly to mass, meaning structure and, thus, maintenance metabolism scale sublinearly with size or with an exponent less than one. Readers are directed to Maino et al. (2014) for a detailed discussion and derivation of predictions for interspecific metabolic scaling.

Data Set

To demonstrate the unique ontogenetic and interspecific effects on respiration, we compiled ontogenetic respiration data for embryonic, immature, and pupal developmental stages. Data was retrieved from a comprehensive literature search of insect respiration through ontogeny, which resulted in 64 studies on insects from nine orders being included in our analysis (see table 2 for a summary of the data set). Where possible, data was extracted from tables or requested from the original authors of the study; otherwise, figures were digitized so that data points could be extracted. All respiration data was standardized to a common temperature of 20°C using the Arrhenius equation and an Arrhenius temperature of 8,000 K (Gillooly et al. 2001). Most respiration measurements were reported in $\mu\text{L O}_2$ consumption, which were converted to joules, assuming a conversion coefficient of 48.9 $\mu\text{L}/\text{J}$.

To make respiration of holometabolous larvae comparable with nonholometabolous nymphs, we excluded the prepupal period after the cessation of feeding. As we do not consider reproduction here, we also excluded data from reproductive stages. For all sources, when multiple data were given for one time point, the mean was taken. In addition, where females and males were separated, female data were used. For embryonic and pupal data that listed only mass-specific rates, absolute rates were recovered by assuming that eggs and pupae lose a negligible amount of dry weight before eclosion. This holds approximately for dry weights, which are used in all analyses. When only egg dimensions were given, weight was calculated from volume. Our full data set with references and comments is available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3qv3p> (Maino and Kearney 2014).

Results

Our results confirm that egg, immature, and pupal respiration follow generic patterns for a diverse range of insects (fig. 2). During embryonic development, respiration rate increases despite the lack of feeding or mass gain. In immatures, respiration increases with development, while during pupation, respiration exhibits both decreasing and increasing phases as emergence is approached.

Dimensionless polynomials derived from a simplified DEB framework were able to capture these broad ontogenetic patterns (fig. 2A–2C), explaining 40%–90% of the variation in the ontogenetic component of respiration (table 1). Furthermore, after controlling for ontogenetic effects on respiration, the interspecific metabolic scaling exponents were found to be within the expected range of three-quarters and one (fig. 2E, 2F).

Best-fit polynomials determined by least squares regression were able to explain 50%–94% of the variation in the ontogenetic component of respiration (table 1). Comparing least squares polynomials with the theoretically derived polynomials found that the least squares polynomials consistently explained more variance and had lower AIC scores, even after accounting for the fewer free parameters in the DEB polynomials. However, the theoretically derived polynomials explained comparable levels of variance (1%, 4%, and 10% less variance than the best-fit polynomials for the egg, immature, and pupal stages, respectively).

Discussion

Our presented framework is the first to explain not only the interspecific scaling of insect metabolism but also the distinct ontogenetic scaling, as most dramatically illustrated by the U-shaped time course of respiration during pupation. Interspecific scaling exponents recovered from the data after controlling for ontogenetic effects supported our theoretically predicted exponents for insect metabolic scaling. In addition to our theoretical predictions, our findings support past empirical studies. Addol-Bediako et al. (2002) found insect respiration to scale with an exponent of 0.77 but noted that the scaling exponent changed when flying and nonflying insects were separated. Studies conducted independently by Chown et al. (2007)

Figure 2: After normalizing interspecific effects, ontogenetic respiration for eggs (*a*), immatures (*b*), and pupae (*c*) is predicted to follow a dimensionless polynomial function of the proportion of the developmental stage completed (dashed line; see appendix, available online). The best-fit (least squares) polynomial of the same degree is also shown with a solid line. After accounting for these ontogenetic effects, respiration for eggs (*d*), immatures (*e*), and pupae (*f*) scaled interspecifically, with mass raised to an exponent between 0.74 and 0.92 (parentheses contain the 95% confidence interval). Unique shades represent unique species, with the legend given in the supporting data set, available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3qv3p> (Maino and Kearney 2014).

and Ehnes et al. (2011) found that respiration data on ~400 insects scaled with interspecific mass with an exponent indistinguishable from 0.75. Interestingly, Ehnes et al. (2011) found that estimated exponents for other non-insect invertebrate groups were significantly lower than 0.75, highlighting groups where simple models for metabolic scaling may need to be extended.

We have shown that dimensionless polynomials estimated from both DEB theory and by regression were able to correctly predict the diverse patterns in respiration that occur throughout insect ontogeny. Our theoretical approach departs from the prevalent view that the same mechanisms underlie both ontogenetic and interspecific patterns (West et al. 1997; Banavar et al. 1999; Darveau et al. 2002; Kozłowski et al. 2003; Hou et al. 2008; Glazier 2010; Kolokotronis et al. 2010). In explaining diverse scaling patterns in one consistent framework, we highlight the usefulness of a theoretical approach based on compartmentalizing biomass to capture mass-independent effects.

Although our theoretical curves lay close to the best-fit polynomials, it is important to emphasize the difference in approaches. The DEB polynomials were derived from underlying biological processes and have a mechanistic interpretation based on the energetic implications of the changing proportions of reserve and structure through ontogeny. In comparison, the best-fit polynomials are simple descriptors of data. Unlike the best-fit polynomials, whose parameters are constrained by the data, the DEB polynomials are constrained by our simple assumptions of the processes underpinning metabolic rate. Deviations from simple mechanistic models highlight when other processes may need to be considered. For example, the best-fit polynomial for immature respiration estimated an ontogenetic scaling exponent of less than one. This is likely due to the significant contribution to respiration of surface area-mediated processes such as nutrient absorption, which were not considered in the current study.

To capture these deviations, our simplified approach can be replaced by a more nuanced approach whereby differences between individuals can be represented through the addition of species-specific parameter values. This is the standard approach in typical studies implementing DEB models. Once parameters for different species have been determined, patterns in parameter values can then be tested for systematic variation. This approach has been used to explain divergent life-history traits in groups of related frogs (Mueller et al. 2012) and fish (Perciformes; Lika et al. 2014), as well as in more broadscale analysis that include several different phyla (Kooijman 2013). Estimated DEB parameters have physical dimensions, which allow natural interpretation and straightforward comparison. The downside of such approaches is that a large amount of data, including various energetic and devel-

opmental data, is required to estimate species parameters with confidence. Our present results show that in addition to more detailed studies, DEB theory can also be used to explore broadscale interspecific patterns in only one type of data—respiration, in this case.

Although here we focused on insects, the implications are far reaching and apply to animals in general. Size imposes constraints on metabolism that depend on whether the observed mass increase is ontogenetic or interspecific. In DEB theory, these constraints are reflected by changing proportions of reserve and structure, of which the relative quantities are predicted to vary in specific ways under different circumstances. The partitioning of biomass into reserve and structure predicts metabolic properties of biomass to change even when mass is (approximately) constant and is thus a necessary abstraction to capture the metabolic scaling of diverse organisms throughout various developmental stages.

Acknowledgments

We thank C. Bywater, A. Hoffmann, T. Jager, S. Kooijman, E. Pirtle, and anonymous reviewers for their comments. This work was supported by a Discovery Project (DP110101776) and Australian Research Fellowship (DP110102813) grant from the Australian Research Council and the University of Melbourne's Overseas Research Exchange Scholarships and Melbourne Abroad Travelling Scholarships schemes.

Literature Cited

- Addol-Bediako, A., S. Chown, and K. Gaston. 2002. Metabolic cold adaptation in insects: a large-scale perspective. *Functional Ecology* 16:332–338.
- Banavar, J. R., A. Maritan, and A. Rinaldo. 1999. Size and form in efficient transportation networks. *Nature* 399:130–132.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 96:858–873.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer, Berlin.
- Caruso, T., D. Garlaschelli, R. Bargagli, and P. Convey. 2010. Testing metabolic scaling theory using intraspecific allometries in Antarctic microarthropods. *Oikos* 119:935–945.
- Chown, S. L., E. Marais, J. S. Terblanche, C. J. Klok, J. R. B. Lighton, and T. M. Blackburn. 2007. Scaling of insect metabolic rate is inconsistent with the nutrient supply network model. *Functional Ecology* 21:282–290.
- Darveau, C. A., R. K. Suarez, R. M. Andrews, and P. W. Hochachka. 2002. Allometric cascade as a unifying principle of body mass effects on metabolism. *Nature* 417:166–170.
- Ehnes, R. B., B. C. Rall, and U. Brose. 2011. Phylogenetic grouping,

- curvature and metabolic scaling in terrestrial invertebrates. *Ecology Letters* 14:1–8.
- Fink, D. 1925. Metabolism during embryonic and metamorphic development of insects. *Journal of General Physiology* 7:527–543.
- Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. *Science* 293:2248–2251.
- Glazier, D. S. 2005. Beyond the “3/4-power law”: variation in the intra- and interspecific scaling of metabolic rate in animals. *Biological Reviews of the Cambridge Philosophical Society* 80:611–662.
- . 2006. The 3/4-power law is not universal: evolution of isometric, ontogenetic metabolic scaling in pelagic animals. *BioScience* 56:325–332.
- . 2010. A unifying explanation for diverse metabolic scaling in animals and plants. *Biological Reviews of the Cambridge Philosophical Society* 85:111–138.
- Hemmingsen, A. 1960. Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Reports of the Steno Memorial Hospital and the Nordisk Insulin Laboratorium* 9:1–110.
- Hou, C., W. Zuo, M. Moses, and W. Woodruff. 2008. Energy uptake and allocation during ontogeny. *Science* 322:736–739.
- Kearney, M. R., and C. R. White. 2012. Testing metabolic theories. *American Naturalist* 180:546–565.
- Kleiber, M. 1932. Body size and metabolism. *Hilgardia* 6:315–353.
- Kolokotronis, T., V. Savage, E. J. Deeds, and W. Fontana. 2010. Curvature in metabolic scaling. *Nature* 464:753–756.
- Kooijman, S. A. L. M. 1986. What the hen can tell about her eggs: egg development on the basis of energy budgets. *Journal of Mathematical Biology* 23:163–185.
- . 2010. *Dynamic energy budget theory for metabolic organisation*. Cambridge University Press, Cambridge.
- . 2013. Waste to hurry: dynamic energy budgets explain the need of wasting to fully exploit blooming resources. *Oikos* 122:348–357.
- Kozłowski, J., M. Czarnoleski, A. François-Krassowska, S. Maciak, and T. Pis. 2010. Cell size is positively correlated between different tissues in passerine birds and amphibians, but not necessarily in mammals. *Biology Letters* 6:792–796.
- Kozłowski, J., M. Konarzewski, and A. T. Gawelczyk. 2003. Cell size as a link between noncoding DNA and metabolic rate scaling. *Proceedings of the National Academy of Sciences of the USA* 100:14080–14085.
- Lika, K., S. A. L. M. Kooijman, and N. Papandroulakis. 2014. Metabolic acceleration in Mediterranean Perciformes. *Journal of Sea Research* (forthcoming).
- Maino, J. L., and M. R. Kearney. Data from: Ontogenetic and interspecific metabolic scaling in insects. *American Naturalist*, Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.3qv3p>.
- Maino, J. L., M. R. Kearney, R. M. Nisbet, and S. A. L. M. Kooijman. 2014. Reconciling theories for metabolic scaling. *Journal of Animal Ecology* 83:20–29.
- Moran, D., and R. M. G. Wells. 2007. Ontogenetic scaling of fish metabolism in the mouse-to-elephant mass magnitude range. *Comparative Biochemistry and Physiology A: Molecular and Integrative Physiology* 148:611–620.
- Mueller, C. A., S. Augustine, S. A. L. M. Kooijman, M. R. Kearney, and R. S. Seymour. 2012. The trade-off between maturation and growth during accelerated development in frogs. *Comparative Biochemistry and Physiology A: Molecular and Integrative Physiology* 163:95–102.
- Rakshpal, R. 1962. Respiratory metabolism during embryogenesis of *Gryllus veletis* (Alexander and Bigelow) (Orthoptera: Gryllidae). *Physiological Zoology* 35:47–51.
- Savage, V. M., J. F. Gillooly, W. H. Woodruff, G. B. West, A. P. Allen, B. J. Enquist, and J. H. Brown. 2004. The predominance of quarter-power scaling in biology. *Functional Ecology* 18:257–282.
- Schmidt-Nielsen, K. 1984. *Scaling, why is animal size so important?* Cambridge University Press, Cambridge.
- Sears, K. E., A. J. Kerckhoff, A. Messerman, and H. Itagaki. 2012. Ontogenetic scaling of metabolism, growth, and assimilation: testing metabolic scaling theory with *Manduca sexta* larvae. *Physiological and Biochemical Zoology* 85:159–173.
- Sterner, R. W., and J. J. Elser. 2002. *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton University Press, Princeton, NJ.
- West, G. B., J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276:122.
- Wieser, W. 1984. A distinction must be made between the ontogeny and the phylogeny of metabolism in order to understand the mass exponent of energy metabolism. *Respiration Physiology* 55:1–9.
- Yagi, M., T. Kanda, T. Takeda, A. Ishimatsu, and S. Oikawa. 2010. Ontogenetic phase shifts in metabolism: links to development and anti-predator adaptation. *Proceedings of the Royal Society B: Biological Sciences* 277:2793–2801.

Associate Editor: Tony D. Williams
 Editor: Judith L. Bronstein