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Ontogenetic and interspecific scaling of consumption in insects

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The uptake of resources from the environment is a basic feature of all life. Consumption rate has been found to scale with body size with an exponent close to unity across diverse organisms. However, past analyses have ignored the important distinction between ontogenetic and interspecific size comparisons. Using principles of dynamic energy budget theory, we present a mechanistic model for the body mass scaling of consumption, which separates interspecific size effects from ontogenetic size effects. Our model predicts uptake to scale with surface-area ($mass^{2/3}$) during ontogenetic growth but more quickly (between $mass^{3/4}$ and $mass^{1}$) for interspecific comparisons. Available data for 41 insect species on consumption and assimilation during ontogeny provides strong empirical support for our theoretical predictions. Specifically, consumption rate scaled interspecifically with an exponent close to unity (0.89) but during ontogenetic growth scaled more slowly with an exponent of 0.70. Assimilation rate (consumption minus defecation) through ontogeny scaled more slowly than consumption due to a decrease in assimilation efficiency as insects grow. Our results highlight how body size imposes different constraints on metabolism depending on whether the size comparison is ontogenetic or inter-specific.

Synthesis

One of the most robust patterns in biology is the effect of body size on metabolism – a relationship that underlies the rapidly emerging field of metabolic ecology. However, the precise energetic constraints imposed by body size have been notoriously difficult to entangle. Here we show that the constraints imposed on metabolism by body size are different depending on whether the size comparison is ontogenetic or interspecific. Using a single unifying theory of animal metabolism and a newly compiled data set on insect consumption and assimilation rates, we show that interspecific comparisons generally lead to the estimation of higher scaling exponents compared with ontogenetic comparisons. Our results help to explain large variation in estimated metabolic scaling exponents and will encourage future studies in metabolic ecology to make the important distinction between ontogenetic and evolutionary size changes.

Attention to the physico-chemical constraints on metabolic organisation has increasingly aided the interpretation of seemingly distinct biological phenomena (Brown et al. 2004). The consideration of cells, individuals, populations and ecosystems as simple 'energy processors' increases the comparability of biological units that span vast spatio-temporal scales. This approach is the hallmark of the emerging field of metabolic ecology (Humphries and McCann 2013). Diverse species implement a startling array of unique strategies when faced with the problem of resource acquisition but, importantly, are constrained by their shared need to fuel growth, somatic maintenance, and reproduction in the context of a body comprised of cells. Thus, understanding constraints on the resource consumption rates of individuals should elucidate constraints on overall ecosystem functioning.

Surface areas often mediate the passage of food from the environment into an organism, for example, a spider's web, the mouth of a filter feeder, the gut of caterpillar, or the plasma membrane of a prokaryote. This has led some to argue that, all other things being equal, consumption should scale in proportion to a relevant surface area and hence with $mass^{2/3}$ (von Bertalanffy 1957, Kooijman 2010). Others have claimed a 3/4 power scaling of consumption on the basis of the 3/4 power scaling of metabolic rate, arguing that supply matches demand (Calder 1984, Peters 1986, West et al. 2001). Recently it has been found that consumption scales higher than 3/4 across diverse organisms (Pawar et al. 2012). This claim was made on the basis of a large dataset including 376 species of juveniles and adults, with body masses ranging from 5.24×10^{-14} kg to 800 kg. However, as the scaling exponent and underlying mechanism may differ between ontogenetic and interspecific comparisons, pooling juveniles and adults in allometric analyses may be inappropriate (Maino and Kearney 2014).

Here, we quantify the difference between the ontogenetic and interspecific scaling of consumption among insects (Fig. 1). We explain these differences using a parameter-sparse, generic dynamic energy budgeting approach (Kooijman 2010), which predicts different scaling exponents depending on whether the analysis is ontogenetic or interspecific. A single mechanistic equation for the scaling of consumption with size that partitions these distinct ontogenetic and

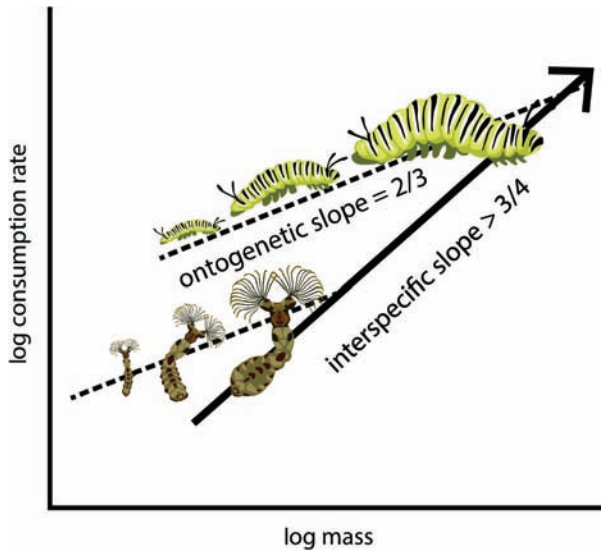

Figure 1. Theoretical predictions of the body mass scaling exponent of consumption for ontogenetic and interspecific size comparisons. Interspecific scaling of consumption is predicted to be steeper than the ontogenetic scaling of consumption.

interspecific effects is presented and tested against a newly compiled data set on ontogenetic consumption rates for over 41 insects (Supplementary material Appendix 1). Insects are an important case study as they 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. In addition, as many models make the simplifying assumption that consumption is proportional to assimilation (consumption minus defecation), we also compare the scaling of assimilation.

Model formulation and methods

Following Kooijman (2010) biomass is taken as being comprised of 'reserve' and 'structure' components where reserve consists of intermediate chemical substrates between the transformation of food to production (structural biomass and reproductive outputs), and dissipation (payment of structural overhead and maintenance costs). The reserve concept is motivated by the observation that nutritional history affects the quality (composition) of biomass, which in turn has metabolic consequences. The presence of reserve in biomass explains why organisms continue to function when their guts are empty, and may continue growth and reproduction under starvation (via the depletion of reserve).

In DEB theory the concept of 'reserve' differs from more classical use in bioenergetics studies where reserve typically relate to storage compounds. Likewise, 'structure' does not relate only to 'support structures' in organisms such as chitin or cellulose. Molecules are assigned to reserve and structure on the basis of their dynamics. Molecules that can be considered as having a constant turnover, irrespective of nutritional history, are assigned to structural compartment, while molecules that turnover at different rates should be considered reserve. Thus, structural lipids in cell walls would be considered structure, while lipids comprising the fat body are reserve. Of course, not all biomass components can be classed easily into structure or reserve compartments. Indeed, DEB models can be extended to include more compartments as necessary (Kooijman 2010). Taken to the extreme each molecule could be modelled as a separate compartment with its own dynamics. The key point is that allowing components of biomass to exhibit two dynamics (reserve and structure) is closer to reality than treating mass as one homogenous compartment as in the case in most allometric studies.

Within a species, DEB theory assumes that the rates of maximum consumption and assimilation are each proportional to structural mass$^{2/3}$. This is supported by the observation that surface areas almost always mediate consumption and absorption processes and that, during growth, shape remains approximately constant. The relevant surface is taken proportional to structure$^{2/3}$ rather than mass$^{2/3}$, as mass also includes reserve, which can decrease under food restriction. The higher structure to reserve ratio that is predicted after a period of starvation captures compensatory feeding responses (Carvalho et al. 2005). Motivated by the importance of stoichiometric homeostasis in life processes (Sterner and Elser 2002), the chemical constituents of reserve are assumed proportional to those of structure under constant food levels (e.g. ad libitum feeding) known as the assumption of 'weak homeostasis'. This results in the expression for ontogenetic consumption rate $\dot{p}_X$ in terms of structure V:

$$\dot{p}_X = \{\dot{p}_{Xm}\} V^c \quad (1)$$

where $\{\dot{p}_{Xm}\}$ is the maximum surface-specific consumption rate and $c = 2/3$. Under constant feeding conditions, structure is proportional to mass (due the weak homeostasis assumption) so we can substitute V for μV_m where μ is the ratio of mass to ultimate mass and V_m is ultimate structure ($V \propto M$ so $\mu = V/V_m = M/M_m$ during ontogeny, where M_m is ultimate mass).

The surface-specific consumption rate $\{\dot{p}_{Xm}\}$ is constant during the growth of an individual, but varies between individuals of different size. The reason for this is because if consumption scales as $V^{\frac{2}{3}}$, with maintenance scaling more quickly as V^1, size with eventually reach an asymptotic limit of V_m. This asymptotic size can be increased by decreasing volume specific maintenance or increasing surface-specific consumption. DEB theory assumes the latter on the basis that density-based (or 'intensive') parameters are approximately invariant (Kooijman 2010), such as the energetic requirement of cells in vitro (West et al. 2002). Thus, uptake per volume of structure $[\dot{p}_{Xm}] = \{\dot{p}_{Xm}\}/V_m^{\frac{1}{3}}$ is taken to be constant between species. Importantly, this does not imply maintenance metabolism or uptake scale as mass^1 between species due to the contribution of reserve to mass (Maino et al. 2014). We now substitute $\{\dot{p}_{Xm}\}$ for $[\dot{p}_{Xm}]\ V_m^{\frac{1}{3}}$, which yields:

$$\dot{p}_X = [\dot{p}_{Xm}] V_m \mu^c \quad (2)$$

The expression consists of two components: the rate of consumption at ultimate size $[\dot{p}_{Xm}]V_m$ (interspecific size effect), which is scaled by the dimensionless component for developmental stage μ^c (ontogenetic size effect). As μ scales

proportional to ontogenetic mass, any scaling exponent calculated using the quantity μ will be the same as that calculated for ontogenetic mass. However, the intercept with be different due to the (hypothesised) interspecific effect of $[\dot{p}_{Xm}]V_m$. Consumption rate at ultimate size $[\dot{p}_{Xm}]V_m$ can be substituted by a more usual allometric function of body mass aM^b.

$$\dot{p}_X = aM^b \mu^c \quad (3)$$

Ultimate size is now reflected by ultimate body mass M. Ultimate body mass is not proportional to ultimate structure V_m because larger organisms have less structure and more reserve (Kooijman 2010, Maino et al. 2014). The scaling exponent b reflects this non-proportionality and is expected to take values between to 3/4 to 1 (Maino et al. 2014) whereas the ontogenetic exponent c is predicted to be close to 2/3. Thus, ontogenetic consumption is expected to scale more slowly than interspecific size comparisons (Fig. 1).

The effect of temperature can be introduced by using the Arrhenius–Boltzman correction factor exp (–E/RT), where R is the gas constant, E is the effective activation energy and T is body temperature in Kelvin (Gillooly et al. 2001). This simplistically assumes that temperature independently effects consumption rate, even though studies exist showing that there may be a more subtle interaction between body size and temperature (Ivleva 1980, Glazier 2005, Killen et al. 2010). Including this temperature correction factor into the previous equation gives:

$$\dot{p}_X = e^{-E/RT} aM^b \mu^c \quad (4)$$

To test these predictions, we compiled a data set of consumption and assimilation rates through ontogeny for different insects. Data was retrieved from a comprehensive literature search of insect consumption and assimilation through ontogeny, which resulted in data for 41 insects from six orders being included in the present analysis (Coleoptera (n = 14), Lepidoptera (n = 14), Hemiptera (n = 6), Orthoptera (n = 5), Diptera (n = 1) and Neuroptera (n = 1)). 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.

Assimilation was calculated either as consumption minus defecation, or biomass production plus energy dissipation (usually measured as oxygen consumption) as per Klekowski et al. (1967). All weight measurements were standardised to dry weight milligrams. Rates were standardised to milligrams per day. Units of mass was chosen for the analysis rather than energy as they were most commonly used in the studies comprising the compiled data set. This minimised the amount of conversion required to standardise units and thus minimised the error introduced into the analysis. Of the data on 40 insects used in this study, 26 sources were reported in units of mass, nine used a combination of mass and energy units, three used only energy units, while only two used respiration and growth measurement to recover assimilation (assimilation = respiration + growth). In the majority of the studies using energy units, energy densities of food and insect biomass were given. When not given, we assumed the energy content of biomass (food and insect) to be 25 J mg^{-1}. As this latter assumption was employed in only the small minority of studies using energy units the analysis is not sensitive to small changes around this value. Weights associated with a given consumption or uptake rate correspond to the end of the measured feeding period. Data always spanned multiple instars and did not include feeding in the adult phase. This was done to minimise the effect of senescence, and also because diets often change markedly upon sexual maturity (Grimaldi and Engel 2005). Terminal mass is taken as the maximum larval weight for holometabola, or adult weight otherwise. When data on multiple diets or temperatures were given we used the most optimal conditions, i.e. largest body sizes. Where sexes were separated, female values were used.

We use this data to test the hypotheses that interspecific mass exerts a larger effect on the scaling of uptake (observed as higher exponent) compared to ontogenetic mass. Taking the logarithm of Eq. 4 multiplied by the temperature correction factor yields:

$$\log_{10}\dot{p}_X = \log_{10}a + b\log_{10}M + c\log_{10}\mu + d/T \quad (5)$$

where $d = E/R\log_{10}e$. The result is simple linear equation that allows interspecific and ontogenetic scaling effects to be estimated simultaneously. For comparison, we test this model against the null model which does not separate the effect of ontogenetic mass from interspecific mass and uses a single scaling exponent:

$$\log_{10}\dot{p}_X = \log_{10}a + B\log_{10}m + d/T \quad (6)$$

where m is the mass of the insect at the time of measurement, and B is the scaling exponent of mass (pooled for all species despite different ontogenetic stage). Models are compared in terms of the explained variance (R^2) and AIC values (Burnham and Anderson 2002). Unlike R^2 values, AIC values take into account the number of model parameters and can be used quantify the probability of competing models, based on the ratio of their likelihoods (Akaike weights). We also test the frequently made assumption that consumption rate scales proportional to assimilation rate by repeating the analysis for assimilation rate $\dot{p}_A$ where $\dot{p}_A = [\dot{p}_{Am}]V_m\mu^c$.

Data available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.35n9f>. (Maino et al. 2015).

Results

The results of the multiple linear regression analysis (Table 1) confirm that the full model (Eq. 5) performed better than the null model (Eq. 6) in terms of explained variance and Akaike weights. For consumption rate, the proportion of variance explained by the full model was 0.82 compared to 0.81 explained by the null model. Likewise, for assimilation rate, the proportion of variance explained by the full model was, again, higher at 0.83 compared to 0.81 explained by the null model. While the explained variance may seem comparable, the small Akaike weights of the null model for consumption and assimilation show a very low relative likelihood of the null model and strongly support the full model. The AIC results suggest that the weight of evidence for the full model is almost one (= 1.00 at two significant figures) compared to a weighting of nearly 0 for the null model, which did not separate ontogenetic mass from interspecific mass.

More importantly, the full model strongly suggests that the phenomenon of ontogenetic scaling is distinct from

Table 1. Multiple linear regression parameter estimates for consumption and assimilation models.

	Parameter estimates								
	$\log_{10}(a)$	b	B	c	d	R^2	AIC	Δ_i	w_i
Consum. rate									
Null model	−0.635 (−4.92, 3.65)		0.842 (0.794, 0.89)		236 (−1046, 1518)	0.812	441.3	16.76	0.00
Full model	−0.836 (−4.99, 3.31)	0.894 (0.842, 0.945)		0.695 (0.615, 0.776)	233 (−1010, 1475)	0.824	424.5	0.00	1.00
Assim. rate									
Null model	0.184 (−5.72, 6.09)		0.762 (0.711, 0.813)		−74.8 (−1850, 1701)	0.806	333.4	28.16	0.00
Full model	1.36 (−4.18, 6.9)	0.834 (0.781, 0.888)		0.564 (0.48, 0.648)	−522 (−2189, 1146)	0.831	305.2	0.00	1.00

Notes: the full and null model refers to Eq. 5 and 6 respectively. Parentheses contain 95% confidence intervals of estimates. Δ_i is the change in AIC values of the competing models, while w_i signifies Akaike weights (Burnham and Anderson 2002).

interspecific scaling. As predicted by theory the interspecific exponent (b) for the full model was higher than the ontogenetic exponent (c) for both consumption and assimilation (Fig. 2, 3). This result is statistically robust as the 95% confidence intervals of the ontogenetic and interspecific exponents do not overlap (Table 1). Interspecific scaling exponents for both consumption and assimilation were within the theoretical bounds of 3/4 to 1. Consumption rate scaled interspecifically with an exponent of 0.894, but scaled ontogenetically with an exponent of 0.695. Likewise, assimilation rate scaled interspecifically with an exponent of 0.834, but scaled ontogenetically with an exponent of 0.564. As predicted, the ontogenetic exponent for consumption could not be distinguished from 2/3 at the 95% confidence level. However, the lower ontogenetic exponent for assimilation excluded 2/3 at the 95% confidence level.

The lower ontogenetic scaling exponent of assimilation compared with consumption was explained by the decrease in assimilation efficiency (assimilation/consumption × 100%) that occurred during development. A pairwise student t-test of the change in assimilation efficiency from early to late in the growth period (for those insects where consumption and assimilation data was available) revealed an average decrease of 29% ($n = 26$, $t = 5.42$, $p = 1.25 \times 10^{-5}$). These results are summarised in Fig. 5.

Consumption rate was estimated to scale with an exponent indistinguishable from 2/3 through ontogeny, however, this estimate was based on pooled data for a number of species. Estimating the scaling exponent for individual insects reveals that, within species, consumption scales with exponents that exclude 2/3 at the 95% confidence level (Fig. 4). However, 2/3 still adequately describes the central tendency of all exponents, with a mean exponent of 0.676 ± 0.076 (95% CI).

Discussion

The mechanistic basis for the scaling of consumption with size differs depending on whether the comparison is ontogenetic or interspecific, as supported by the superior fit of the full model and the different ontogenetic and interspecific scaling exponents. The interspecific scaling exponent was closer to that found by Pawar et al. (2012) in their larger study that extended outside the insects, than 2/3 or the canonical 3/4 power law. Pawar et al. further divided their analysis based on the dimensionality of the interaction between the organism and its food resources. They found (at abundant resources) consumption for 2D interacting organisms (e.g. in benthic habitats) scaled with a mass exponent of 0.85 ± 0.5 (95% confidence interval) and for 3D interacting organisms (e.g. in pelagic habitats) scaled with an exponent of 1.06 ± 0.6 (95% confidence interval). While dimensionality did effect the interspecific scaling of consumption as they predicted, all estimated exponents were close to the range of 3/4 to 1, as we predict for interspecific scaling, and were significantly higher than the canonical 3/4.

In contrast, the ontogenetic scaling of consumption was better approximated by a less steep, surface area or $\text{mass}^{2/3}$ scaling. DEB theory explains the scaling as a result of organisms being more similar in shape to a larger conspecific than to one of a different species. If maintenance scales with volume and uptake scales with a surface area, organisms will reach an asymptotic size where energy uptake matches maintenance demand with nothing remaining for growth. To overcome this limit in ontogenetic size, uptake is expected to scale greater than $\text{mass}^{2/3}$ between species (Maino et al. 2014). It turns out that between species, maintenance is expected to scale with a mass exponent between 3/4 and 1, from which it follows that interspecific consumption must scale with a similar exponent.

Given the wide interest in determining metabolic scaling exponents from data (Isaac and Carbone 2010) it will be important for future studies to acknowledge the distinct effect of ontogeny, as failing to make this distinction will bias estimates of exponents. For example, when the effect of ontogeny was ignored for the body mass scaling of consumption and assimilation rates (null model), the interspecific scaling exponent was lower than the case where ontogenetic effects were considered (full model).

In insects, metabolic rate has been shown to scale with exponents higher than 2/3. Addol-Bediako et al. (2002) found insect respiration to scale with interspecific mass with an exponent of 0.77, while more recent and larger studies (~400 insects) conducted independently by Chown et al. (2007) and Ehnes et al. (2011), found metabolic rate scaled with an exponent between 0.75 and 0.81. This range overlaps with the 95% confidence interval of our estimate for the interspecific scaling of assimilation rate and supports the expectation based on the energetic balancing of supply and demand in insects. As assimilated energy is the energy available for metabolic processes, an organism's energetic supply corresponds more closely to assimilation than to consumption. This highlights when it may be problematic to assume

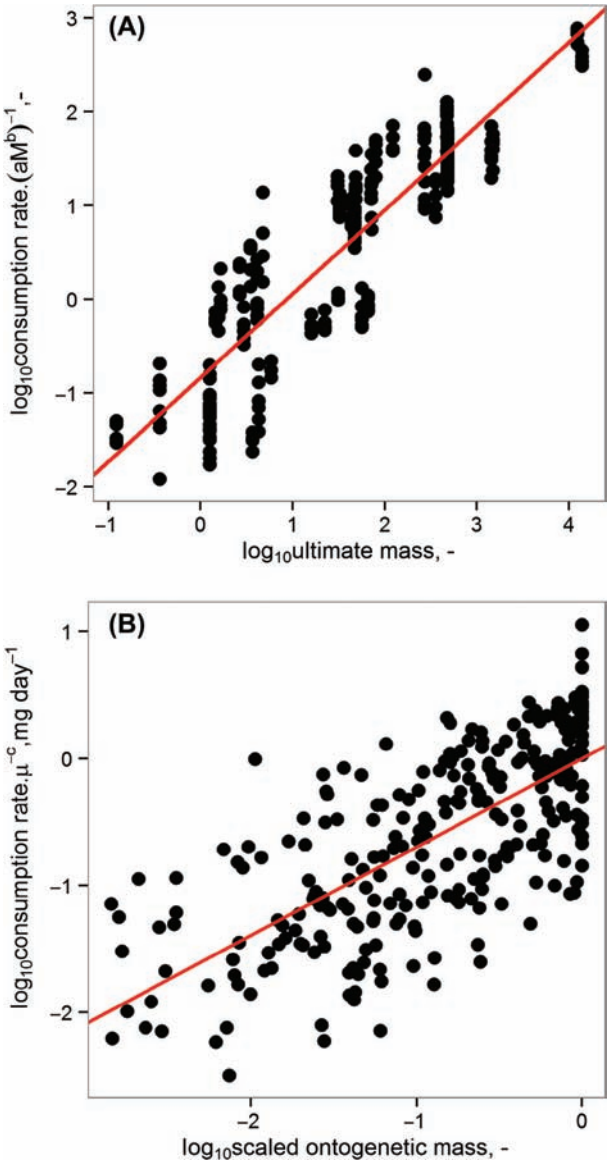

Figure 2. Partial residual plots showing the temperature corrected effects of interspecific mass and ontogenetic mass on consumption rate. (A) After normalising for ontogenetic effects, consumption scales with the species' ultimate mass with an estimated exponent of 0.894. This is significantly higher (95% confidence level) than the ontogenetic exponent of 0.695. (B) After normalising for interspecific effects, consumption as a function of scaled ontogenetic mass μ (mass divided by ultimate mass) is predicted to scale with $\mu^{2/3}$. The estimated ontogenetic scaling exponent includes 2/3 at the 95% confidence level. Axes units given as a dash indicate dimensionless variables.

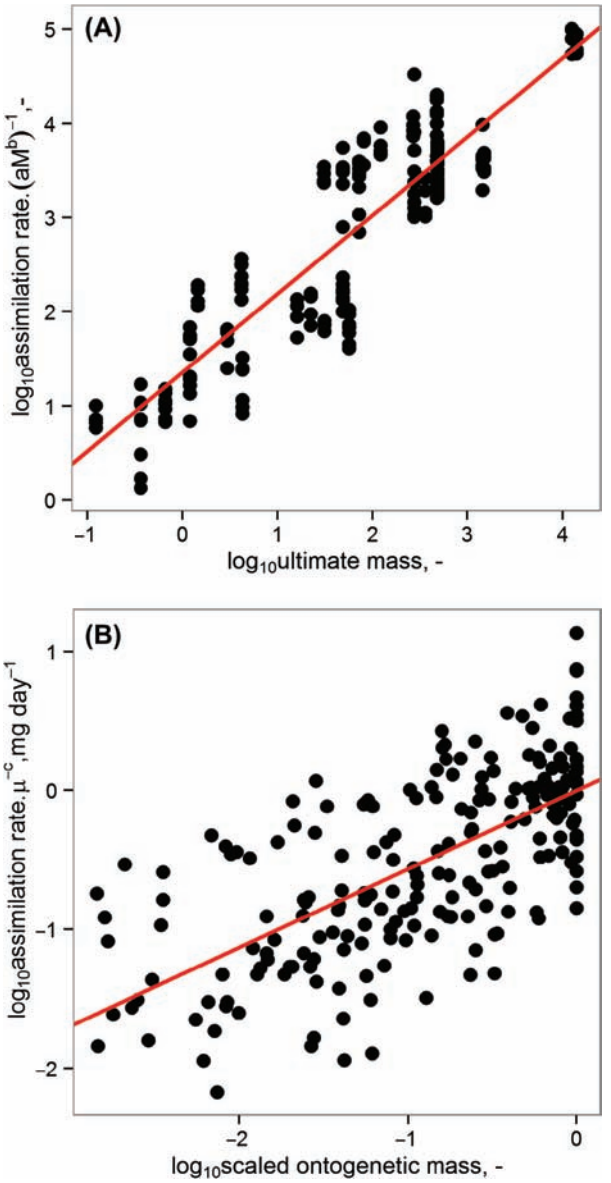

Figure 3. Partial residual plots showing the temperature corrected effects of interspecific mass and ontogenetic mass on assimilation rate. (A) After normalising for ontogenetic effects, assimilation scales with the species' ultimate mass with an estimated exponent of 0.834. This is significantly higher (95% confidence level) than the ontogenetic exponent of 0.564. (B) After normalising for interspecific effects, assimilation as a function of scaled ontogenetic mass μ (mass divided by ultimate mass) is predicted to scale with $\mu^{2/3}$. The estimated ontogenetic scaling exponent excludes 2/3 at the 95% confidence level. Axes units given as a dash indicate dimensionless variables.

that consumption rate scales in proportion to assimilation rate. For example, Pawar et al. (2012) based their analyses on consumption rather than assimilation, which may help to explain why their estimated exponents were higher than that expected on the basis of simple supply and demand arguments.

During ontogeny, assimilation was found to scale more slowly than consumption. The lower ontogenetic scaling of assimilation compared with consumption can be explained by the decline in assimilation efficiency that was found to occur in insects in our data set. Indeed, past studies have also found this to be a general phenomenon in insect nutrition (Scriber 1977). In insects, a number of intrinsic and extrinsic factors may account for this decrease in assimilation efficiency. First, as an organism grows, its mouthparts also increase in size, which decreases food selectivity (Hochuli 2006). This can lead to an increased consumption of lower quality foods, such as the ingestion of older and larger leaves, which contain less nitrogen and water and more indigestible cellulose. Second, as an insect ages so too may its food source, which in turn may be associated with a decrease in food quality (Scriber and Slansky 1981). This can involve decreases in nitrogen and water content, and increases in

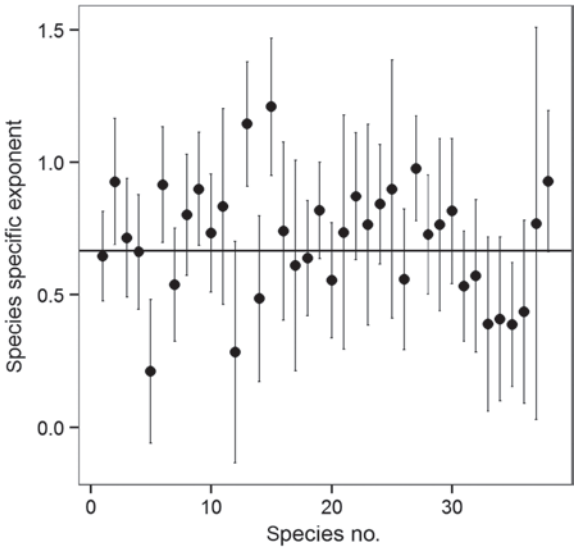

Figure 4. Estimates of the ontogenetic scaling of consumption for individual species shows that some species reject a surface-area rule. However, a surface scaling law (horizontal line) still describes the central tendency; the mean of all individual exponents is equal to 0.676 ± 0.076 (95% confidence interval). The error bars denote 95% confidence intervals.

defensive allelochemicals of plants – all of which have been shown to negatively impact assimilation efficiency (Scriber and Slansky 1981, Muthukrishnan and Pandian 1987). Third, the nutrient demands of an insect may change with age rendering the food source lower quality relative to the new nutritional target. For example, insects preparing for reproduction require greater energy reserves and specific fatty acids (Stockhoff 1993). Fourth, as holometabolic insects prepare for pupation, decreased production of hormones from brain neurosecretory cells, the corpora cardiaca and corpora allata causes a decrease in digestive enzyme production and, as a consequence, assimilation efficiency drops (Sindhu and Nair 2004).

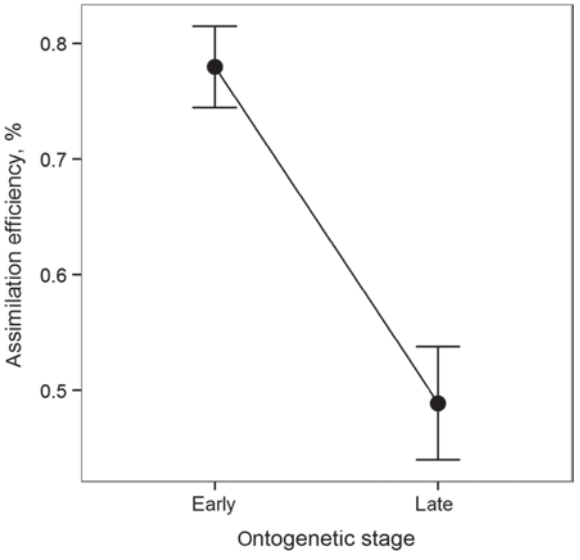

Figure 5. As insects grow, there is typically a decrease assimilation efficiency (as measured as the ratio of assimilation to consumption $\times 100\%$). The declining efficiency explains why ontogenetic consumption scales more quickly than assimilation in insects. Error bars denote standard errors.

Our results support the assumption of a surface area scaling of consumption made by some prominent mechanistic growth models (von Bertalanffy 1957, Kooijman 2010). However, we highlight that the simplifying assumption that consumption is proportional to assimilation should be used with caution.

Interestingly, insects often exhibit exponential or near-exponential growth (von Bertalanffy 1951, Tammaru and Esperk 2007), which is a faster growth rate than predicted by popular mechanistic models for growth (von Bertalanffy 1957, West et al. 2001, Hou et al. 2008, Kooijman 2010). If the assumption of uptake scaling with a surface area broadly holds, this suggests that the other core assumption of somatic maintenance (or rate of catabolism) scaling with mass^1 may not be valid in general. Indeed, as insects develop, a greater proportion of biomass consists of lipids with low maintenance costs (Elia 1992, Hayes et al. 1992). This lower cost of maintaining biomass in later instars may also explain higher biomass production efficiencies in later instars (Scriber and Slansky 1981).

Although the broad scaling pattern of ontogenetic consumption can be well approximated by a surface area rule, there exists substantial unexplained variation in the data. In addition, while the central tendency of individual species' exponents does not reject a 2/3 power scaling of consumption within species, many exhibit a scaling that is significantly different from 2/3 (Fig. 4). It is not surprising that such deviations exist as the implemented model is simple and focuses only on a small number of processes. However, such deviations from broad trends may be as instructive as congruence, and demonstrate that we must look to an organism's life history to explain departures from simple bio-physical expectations. According to DEB theory, relaxing the invariance of parameter values can capture deviations from simple biophysical expectation, such that each species (or even individual) has a unique parameter set specifying its metabolic architecture. With enough data, parameters of diverse species can then be explored for systematic variation (Kooijman 2013). A recent study that applied a full life-cycle DEB models to nine species of Perciformes captured differences in the evolution of metabolic rate for growing larval by relaxing the parameters held constant in the present study (Lika et al. 2014). The authors suggested that differences in parameter values could be largely explained by differences in the spawning season and food availability. Demersal fish spawning in the autumn and winter experience higher temperatures and lower food availability and benefit from lower metabolic rates and delayed development.

Alternatively, deviations from the constant shape assumption (isometric growth) of DEB theory can be measured empirically and related to changes in metabolic parameters. A recent study by Hirst et al. (2014) found that the degree of shape flattening exhibited by growing marine invertebrates explained deviations from simple Euclidean expectations for perfectly isometric organisms. In the same way, shape changes that are known to occur in growing insects (Shingleton et al. 2007) may account for some of the large interspecific variation in the scaling of consumption (Fig. 4).

Previous work has shown that dynamic energy budget theory offers a consistent framework to explore differences

in the ontogenetic and interspecific scaling of a number of physiological attributes (Maino and Kearney 2014, Maino et al. 2014). We have shown here that this explanatory power extends to the scaling of consumption and assimilation, which will help refine assumptions currently used in models ranging from individual growth (Hou et al. 2008, Kooijman 2010) to ecosystem dynamics (Yodzis and Innes 1992, Brown et al. 2004, Jetz et al. 2004, Brose et al. 2006).

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Supplementary material (available online as Appendix oik.02341 at <www.oikosjournal.org/appendix/oik-02341>). Appendix 1.

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