

Does consumption rate scale superlinearly?

ARISING FROM S. Pawar, A. I. Dell & V. M. Savage *Nature* **486**, 485–489 (2012)

A recent paper by Pawar and colleagues¹ has provided important insights into the consequences of foraging behaviour for food-web dynamics. One notable pattern predicted by their analysis is that consumption rate (c) scales superlinearly ($c \propto m^{1.16}$) with consumer body mass (m) in three-dimensional (3D), but not two-dimensional (2D), foraging spaces. Although we feel that the authors should be applauded for this interesting contribution, we argue that their result is not consistent with established life-history theory. To resolve this contradiction, progress in both fields is probably required, including new empirical studies in which consumption rate, metabolism and dimensionality are examined directly under natural conditions.

One inconsistency is that, under a superlinear scaling of consumption rate, most models of ontogenetic growth and life-history optimization would predict infinitely large body sizes^{2–6}. To obtain realistic ranges in maturation and maximum sizes, an equally superlinear scaling of metabolism and/or a positive scaling of mortality rate with body size would be required, but these are not generally found in nature^{7,8}. Although biomechanical factors may set an ultimate limit to body size, such ‘universal’ constraints cannot account for body-size variation among species with similar body plans living in environments with similar physical properties (for example, pelagic fish). However, biomechanical constraints can explain differences in the sizes of organisms between habitats (that is, pelagic organisms can be larger than terrestrial organisms because they are less constrained by gravity) and can also explain why terrestrial organisms foraging in 3D (for example, flying or canopy-dwelling species) are more limited in size than ground-dwelling organisms that forage in 2D — a pattern that contradicts the predictions of Pawar *et al.* concerning size and dimensionality.

Another inconsistency is that substantial difference in scaling between realized and maximum consumption ($m^{0.75}$)^{1,9,10} implies that the superlinear model must be violated; first, for body sizes larger than the point at which these two relationships intersect (that is, realized consumption cannot be greater than maximum consumption); and second, for body sizes smaller than the point at which growth is prohibited because realized consumption is equal to or lower than maintenance consumption (that is, the minimum consumption required to cover metabolic costs) (Fig. 1, Methods). One possible explanation for this unrealistic behaviour at small body sizes is that the model was designed for consumption rates per trophic link¹, such that in nature small consumers would meet their needs by eating additional resources. However, narrowing the focus of the model in this way would necessarily limit its ability to describe the behaviour of natural ecosystems, as most consumers eat more than one prey species and there is no reason to expect that small consumers would be more generalist than large consumers¹¹.

These inconsistencies raise questions regarding both model mechanisms and analyses of empirical data. First, the model does not include the ability of prey to evade predators as a function of the prey’s reaction distance. Instead, capture success per predator–prey encounter is assumed as a constant¹, although it can vary by orders of magnitude in nature¹² and substantially reduce consumption rates for larger predators. Second, the consumption-rate data consist mainly of laboratory experiments, which can overestimate field consumption rates through container effects (in the 3D data, foraging arenas are proportionally smaller for larger consumers; that is, container size scales sublinearly with consumer size, see Methods) that allow large consumers to feed unhindered by fear of predation¹³ while reducing

the efficacy of predator evasion by prey¹². Finally, the authors implicitly emphasize interspecific patterns, but their model is based on principles equally applicable to intra- and interspecific size variation, and both were included in their empirical data. Combining intra- and interspecific variation in one analysis (for example, in the 3D data, life stage changed systematically with species size) can introduce a bias to estimates of scaling exponents (Fig. 2, Methods).

Limitations notwithstanding, 3D consumption rates remain higher than 2D rates. Other studies have shown that metabolism scales more steeply in pelagic (3D) than in surface-dwelling (2D) animals^{8,14}, thus raising the fundamental question of whether consumption rates are driven internally by consumer energetic demand or externally by resource availability. In addition, the important role of predator–prey size relations in this work suggests that the effects of dimensionality

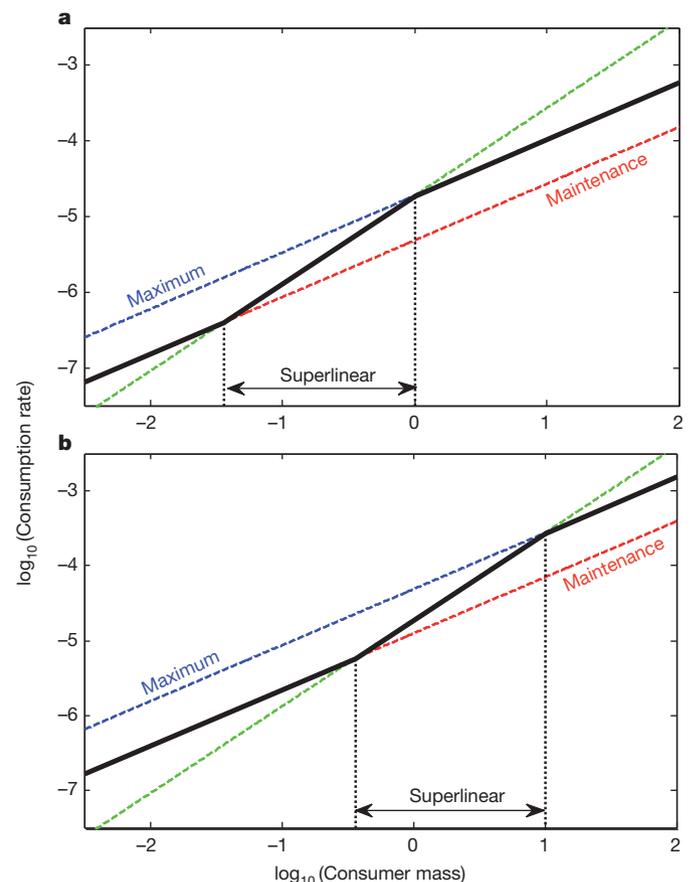


Figure 1 | Scaling of consumption rates with consumer mass. **a**, Superlinear scaling (green line, $c \propto m^{1.16}$)¹ is only feasible (black line) between the interceptions with maintenance and maximum consumption ($c \propto m^{0.75}$)⁹. The upper intercept was arbitrarily set at 1 kg, the lower intercept (36 g) is based on maintenance consumption of ectothermic vertebrates (see Methods). Consumption rates are in kg s^{-1} , consumer mass in kg. **b**, As maintenance consumption is a constant proportion of maximum consumption, changing the upper intercept (10 kg) has no effect on the feasible range of superlinear scaling, which encompasses only 1.4 orders of magnitude of body size (or 3.1 and 0.5 orders of magnitude in invertebrates and endothermic vertebrates, respectively).

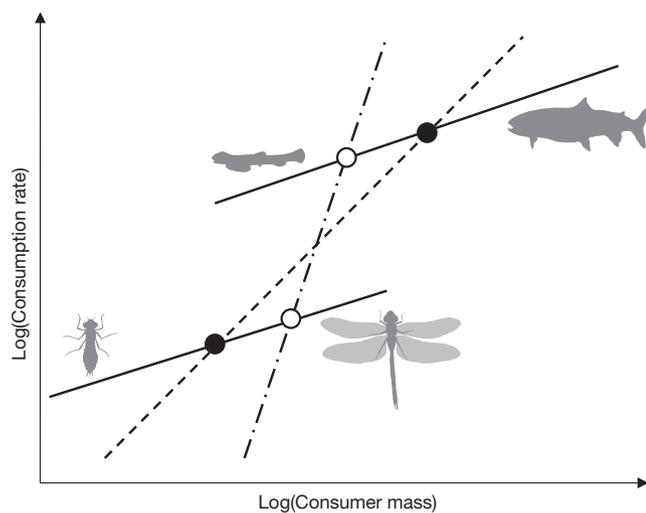


Figure 2 | Effect of biased sampling of stages of development on the scaling of consumption. Continuous lines represent intraspecific scaling, black circles mark the average or typical body mass for each species, and the dashed line is the resulting true interspecific scaling. When sampling from larger species is biased towards immature stages and vice versa, the resulting scaling estimate (dashed-dotted line) exceeds both the true intra- and interspecific scalings.

on these relations for intra- versus interspecific size variation would be a fruitful focus for future study.

METHODS SUMMARY

Maintenance consumption was estimated by dividing maximum consumption by the ecological scope (defined as maximum consumption/metabolism, whose values are typically 19.4, 3.9 and 1.6 for invertebrates, ectothermic vertebrates and endothermic vertebrates, respectively¹⁵). We assumed scaling exponents of 1.16 (ref. 1) and 0.75 (refs 1, 9, 10) for realized and maximum consumption.

Sublinear scaling of container size was tested by a log-log regression ($b = 0.50$, 95% CI = 0.41–0.60) on 3D data from the paper by Pawar *et al.*¹ We tested the association between species size (using invertebrates versus vertebrates as a surrogate) and life stage (juvenile versus adult) through chi-squared tests ($P = 0.27$ for 2D and $P < 0.001$ for 3D).

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Pawar *et al.* reply

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Current studies assume that per-capita consumption rates always scale with body mass to an exponent of 0.75. We showed that, contrary to this assumption, consumption rates scale sublinearly (exponent of approximately 0.85) when organisms forage in two dimensions (2D), and superlinearly (exponent of approximately 1.06) when they forage in 3D¹. Giacomini *et al.* argue that the superlinear scaling in 3D interactions we observed cannot be reconciled with life-history theory for maximal body size². Consequently, they search for biases in our study that might cause this superlinear scaling. However, their comments do not challenge our central result that consumption rates scale superlinearly in 3D, and significantly more steeply than in 2D. We propose instead that life-history theory may need revision to include interaction dimensionality.

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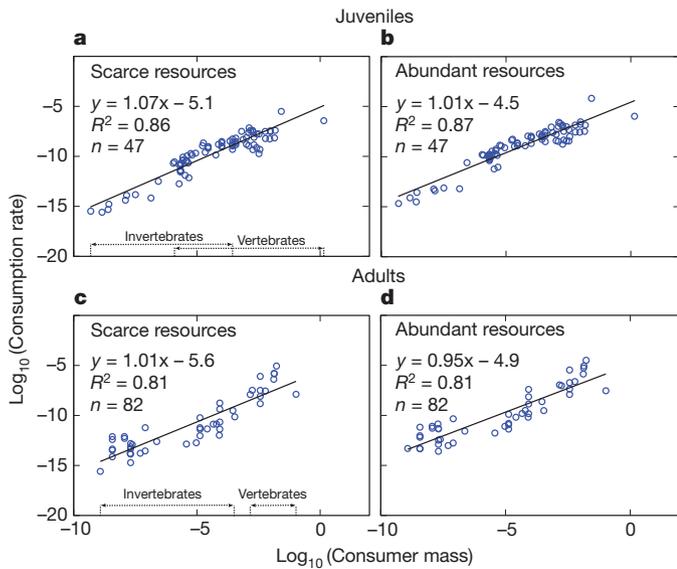


Figure 1 | Effect of ontogeny on scaling of 3D per-capita consumption rates. **a, b,** Scaling of juvenile consumption rate (kg s^{-1}) with consumer body mass (kg) at scarce and abundant resource densities. **c, d,** Scaling of adult consumption rate. These data are the same as in Fig. 3 of our paper¹, but separated by life stage. Solid black lines were fitted using ordinary least-squares regression. Both scaling exponents (slopes) with scarce resources are superlinear (exponent \pm 95% confidence intervals; 1.07 ± 0.10 for juveniles and 1.01 ± 0.15 for adults) and significantly steeper than the 2D exponent of 0.85 (excluded from both confidence intervals), showing that our original results¹ remain unaltered.

results using a schematic (their Fig. 2) that has no relation to values in our data. To test directly for this bias, we analysed our data for juvenile and adult stages separately and found no significant difference in 3D scaling (1.07 ± 0.10 for juveniles and 1.01 ± 0.14 for adults) between juveniles and adults (Fig. 1).

The first theoretical concern of Giacomini *et al.* is that we assume capture success per predator–prey encounter is constant. This claim is incorrect. We assume only that capture success does not vary systematically with body size³, so our model is consistent with variation in capture success that does not correlate with size. Second, they state that biomechanical constraints can explain why terrestrial organisms foraging in 3D (for example, flying species) are more limited in size than ground dwelling (2D) species, and that our predictions contradict this pattern. This is also incorrect because we make no predictions about maximum body size, and we certainly do not contrast sizes of flying and ground-dwelling species. Maximum body size is a prediction best made by biomechanical theories, whereas our theory makes predictions about the feasible size ratios of consumer–resource pairs. Third, they state that differential scaling for realized and maximal consumption rate implies that organisms above and below certain sizes are not energetically viable. However, their argument is based on the assumption that maximal consumption rate scales as $m^{0.75}$. Our database and analysis are more extensive than those in studies cited^{4,5} by Giacomini *et al.*, and indeed a key conclusion of our work is that consumption

rates do not scale as $m^{0.75}$, even when there are abundant resources and a maximal consumption rate is expected. To assume that maximal consumption rate scales as $m^{0.75}$ is inconsistent with available data and is counter to our main findings. Attempting to reconcile this assumption with our study will inevitably lead to inconsistent predictions. Fourth, Giacomini *et al.* suggest that superlinear scaling of consumption rate would predict infinitely large body sizes when integrated into life-history models. Apart from the fact that biomechanical and physiological constraints do indeed set strict upper bounds on organismal sizes⁶, current life-history theory^{7–9} does not incorporate mechanistic models of consumption rate. By revealing a surprising dependence of consumption rate on interaction dimensionality, our study shows why integration of such models is necessary.

Life-history models also cannot account for organisms that shift between 2D and 3D foraging during ontogeny. Such shifts are common¹⁰ and should be considered before combining life-history theory with the superlinear scaling of consumption rate. Moreover, as we emphasized¹, and as Giacomini *et al.* acknowledge², our theory is for consumption rate per trophic link, whereas consumers rarely feed exclusively on a single resource. For example, 3D consumers may compensate for the disadvantage of being small through ontogenetic shifts in foraging behaviour or by feeding on multiple resource types. These are interesting areas for future study but do not call into question our original findings¹.

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