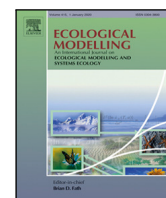


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The aerobic scope is clearly linked to the supply–demand spectrum as quantified by DEB theory[☆]

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ABSTRACT

Supply-species typically eat what is available, while demand-species eat what they need, almost independently of what is available. The trait ‘supply stress’ quantifies the supply–demand spectrum, in the context of the Dynamic Energy Budget (DEB) theory. This dimensionless trait is defined as the maturity maintenance times the squared somatic maintenance, divided by the cubed assimilation. This function of DEB parameters is mostly estimated from data on growth, reproduction and life history, typically applied for fully grown individuals. Only a minority of the over 7300 species in the Add-my-Pet collection also have respiration data, combined with other data. Consistent with a set of traits that characterizes the supply/demand spectrum, birds and mammals score high on the supply stress, reptiles, amphibians, cartilaginous fish score moderate and ray-finned fish and invertebrates score low. The structure of the standard DEB model explains why species must have a low supply stress to allocate a large fraction of their assimilation to reproduction. We show this for large taxa, but also for rodents, compared to carnivores, where rodents have a lower position in the food chain. We list and discuss ecophysiological properties that characterize the spectrum. A decade ago, the factorial aerobic scope (FAS), i.e. the ratio of the maximum and basal metabolic rate (MMR and BMR), was predicted to be high for species at the demand-end of the spectrum, and low for those at the supply-end. The aim of this paper is to test this prediction for respiration data from the literature. Our conclusion is that the FAS indeed increases for increasing supply stress, but the scatter is substantial. The FAS roughly increases from 3.2 at zero supply stress to 32 at maximum supply stress. We discuss an application of this finding for the estimation of the maturity maintenance rate coefficient from data, which is otherwise difficult with simple data. We also discuss the large scatter of respiration rates and show, with a computer simulation study of the standard DEB model, that a little scatter in food intake translates into a much larger scatter of respiration rates. Despite the scatter, the measured BMR was found to be close to the DEB-predicted field metabolic rate. This is remarkable because DEB theory makes no direct assumptions about respiration, but can still predict it exploiting the conservation laws for the chemical elements C, H, O and N. Our findings not only suggest functionalities of the aerobic scope in a wider context, but also support the concept of maturity maintenance, which is key to DEB theory, but hard to make concrete.

1. Introduction

Metabolic rate is the rate of chemical transformations occurring within an organism’s body. Common empirical methods for quantifying metabolic demands or limitations—such as dioxygen consumption, heat production, and isotope incorporation—are sensitive, but rely on assumptions about the relationships between measured variables and underlying biochemical processes. Depending on the system, these assumptions can lead to misleading conclusions about an individual’s ecological physiology. From a thermodynamic perspective, metabolic

rate should be quantified by entropy production, which requires a comprehensive quantification of all energy fluxes and chemical transformations within the organism. These fluxes can be deduced from accurate measurement of quite a list of traits under controlled feeding levels and temperature - a technically demanding approach; Sousa et al. (2006) give a numerical example for *Klebsiella* in chemostats. Dynamic Energy Budget (DEB) theory offers a mechanistic framework to theoretically track these energy fluxes and transformations, applying mass and energy conservation laws to estimate metabolic rate and its

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life-history consequences. Aiming to capture the full life cycle, from start of egg development to death by aging, the primary focus of DEB theory is on relatively long time scales (hours in bacteria to years in whales), whereas empirical metabolic rate measurements typically operate on shorter time scales (minutes to days). Thus, while DEB modeling can overcome some limitations of empirical approaches, it does so at the cost of temporal resolution, potentially missing short-term fitness-limiting energetic challenges. Therefore, this work aims to explore the connections between metabolic rate estimates derived from DEB model predictions and those obtained through empirical measurements (specifically dioxygen consumption) with the goal of improving the applicability and integration of both approaches. Although DEB theory is meant to apply to all organisms, we here focus on animals only.

Dioxygen consumption is a common and sensitive method to estimate metabolic demands and limits in aerobic animals, though it has shortcomings. Its use as a proxy for metabolic rate is grounded in the central role of ATP as the energy currency in vertebrates and the reliance on oxidative phosphorylation for efficient and sustainable ATP production. A variety of processes contribute to dioxygen consumption (Hulbert and Else, 2000; Treberg et al., 2016). While anaerobic pathways—such as ATP and creatine phosphate reserves and glycolysis—can significantly elevate metabolic rate over short time scales, their limited capacity, inefficiency, and accumulation of metabolic byproducts render them unsustainable in aerobic metabolism. Animal life can also be abundant in anaerobic or micro-aerobic environments, such as mud, guts, endo-parasites (Fenchel and Finlays, 1980; Hochachka, 1980). Five different patterns/mechanisms have been identified that can elevate metabolic rate, but not all result in increased dioxygen consumption (Kooijman, 2014). Increasing surface area of an individual faster than volume^{2/3} over ontogeny affects the change in dioxygen consumption, but not the instantaneous dioxygen consumption at a single time point itself. Reproduction, for instance, is a metabolically intensive activity, but hardly contributes to maternal dioxygen consumption. This is because embryos start with exported (read transported) reserve from the mother, a process that requires little chemical transformation and thus minimal oxygen use. Although Ginther et al. (2024) suggest considerable reproduction overheads, their conclusions are contested due to methodological flaws and misinterpretations (see the eletters at the site of the paper). Many species exhibit temporary reductions in dioxygen use or switch to anaerobic metabolism during torpor. Examples include daily torpor in hummingbirds, bats, dasyurids, didelphids, golden and marsupial moles, tenrecs as well as seasonal torpor (hibernation) in non-migratory mammals and poorwills (Hochachka, 1980). This paper is about a sudden short-term increase in respiration, so over a short time period only, minutes to hours, known as maximum or peak metabolic rate.

Metabolic demands associated with basal maintenance processes (referred to as standard metabolic rate (SMR) in ectotherms and basal metabolic rate (BMR) in endotherms) are assumed fully supported by aerobic ATP production. BMR and SMR are taken to be equivalent in this paper. Dioxygen uptake rates required to fuel maintenance are typically quantified in animals performing only essential homeostatic activities for cells and whole organisms excluding movement, digestion, somatic growth, or gonadal growth (Chabot et al., 2016). However, this definition is rather academic. Although the Add_my_Pet (AmP) collection (AmP, 2025) includes many examples where growth depends on food, complete growth cessation via starvation is rarely observed in healthy individuals, especially in demand species or very young individuals. Additionally, excluding contributions from digestion (Chabot et al., 2016) can be challenging for species that depend on gut flora for nutrient processing (White and Seymour, 2003). The concept Resting Metabolic Rate (RMR) includes a bit more activity, and some digestion work, relative to BMR. Limits to sustained metabolic rate are frequently estimated via measurements of dioxygen uptake in

individuals undergoing maximal locomotion or digestion or thermoregulation in sub thermoneutral zone for endotherms. These estimates are referred to as maximum metabolic rate (MMR), peak metabolic rate (PMR), or summit metabolic rate, and represent the highest rate of oxygen transfer from the environment to mitochondria within body cells. Although anaerobic pathways (e.g., ATP and creatine phosphate reserves and glycolysis) can significantly elevate metabolism without increasing dioxygen uptake over short time scales, their limited capacity, inefficiency, and accumulation of metabolic byproducts render them unsustainable. This supports the use of dioxygen consumption as a proxy for MMR (Hedrick et al., 2015), with some exceptions in organisms that have evolved alternative metabolic strategies, such as lactate fermentation in carp. MMR may be sustainable over varying durations depending on species, with shorter durations often referred to as PMR. However, the timeframes used to distinguish these terms are not standardized and are highly species-dependent. While metabolic processes not directly associated with dioxygen demand likely occur at low enough rates to avoid introducing significant error into MMR estimates, methodological limitations pose risks of underestimation. These include failure to elicit activities that require maximal dioxygen flux from the environment into the body, and failure to account for depletion of internal oxygen stores when steady-state conditions are not achieved.

Metabolic scopes are more relevant estimates to fitness and life history of animals in nature. The factorial aerobic scope (FAS) is defined as the ratio of MMR and BMR and represents the metabolic rate available for processes above and beyond BMR normalized to BMR. DEB theory does not produce estimates directly comparable to MMR or FAS. However, DEB theory can predict dioxygen consumption by closing the mass balance for key chemical elements (carbon, hydrogen, oxygen, and nitrogen). This uniquely determines what are called mineral fluxes: water, carbon dioxide, and nitrogenous waste (e.g., ammonia) production and dioxygen use (Kooijman, 2010, 2013). In view of the typical time scale of DEB predictions, its dioxygen consumption production can best be identified with the Field Metabolic Rate (FMR), or Daily Energy Expenditure (DEE), which is the energy expenditure of free-living animals over an extended period. The theory allows partitioning of the total energy flux into its components: digestion and assimilation of food (specific dynamic action, SDA), maturity maintenance (including immune and other defense functions), somatic maintenance, and growth and reproduction overheads. Unlike BMR, MMR, and RMR, FMR is not typically measured as dioxygen uptake, but computed from measurements on isotope incorporation from double-labeled water (Kooijman, 2010). The FMR typically increases BMR with a factor 2.5–3.5 for birds and mammals (Nagy, 1987, 2005).

A general problem with the interpretation of respiration data is to what extent does metabolic memory matter? DEB theory accounts for long-term memory via reserve, but short-term mechanisms are not included in the standard DEB model. Measured respiration depends on the recent metabolic history (food, temperature) of the subject. But what is recent? For example, to what extent do environmental food limitations (or feeding rations in captivity) impact dioxygen consumption rate measurements and for how long?

The supply–demand spectrum is one of the recognized patterns in parameter values of Dynamic Energy Budget (DEB) theory. It is first described by Lika et al. (2014) as a set of coherent traits. One of these traits is a high peak metabolic rate for demand-species, compared to supply-species, see Table 1. However, this has not yet been tested against data. The aim of this paper is to provide such a test. To this end, we first introduce the supply–demand spectrum, then the aerobic scope, and finally present and discuss the test.

2. Supply–demand spectrum

As side-result of research on the boundaries of the data and the parameter space in DEB models, we found that the ability to reach puberty

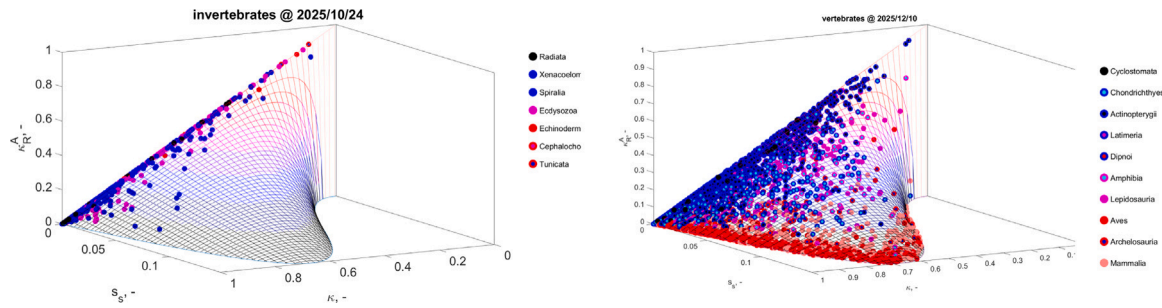


Fig. 1. The fraction of mobilized reserve to soma κ (x-axis), the supply-stress s_s (y-axis) and the fraction of assimilation to reproduction κ_R^A (z-axis) at abundant food for the invertebrates (left) and the vertebrates (right) in the AmP collection. The mesh is the surface defined by $\kappa_R^A = 1 - \kappa - s_s/\kappa^2$; see Appendix A. All points are on that surface; the 3D graphs in the SI can be rotated.

Table 1

Stylized eco-physiological properties that relate to the position of a species in the supply–demand spectrum. From Lika et al. (2014).

Supply	Demand
eat what is available	eat what is needed
large half saturation coefficient	small half saturation coefficient
rather passive, simple behavior	rather active, complex behavior
sensors less developed	sensors well developed
can handle large range of intake	can handle small range of intake
low peak metabolic rate	high peak metabolic rate
open circulatory system	closed circulatory system
iso- & centro-lecithal eggs	a- & telo-lecithal eggs
typically ectothermic	typically endothermic
reserve density varies strongly	reserve density varies little
large range of ultimate sizes	small range of ultimate sizes
survives some shrinking well	survives shrinking badly
survives rejuvenation well	survives rejuvenation poorly
energetic birth control	behavioral birth control
no upregulation for reproduction	upregulation for reproduction
no acceleration of aging	acceleration of aging
evolutionary original	evolved from supply systems
has demand components (maintenance)	has supply components (some food must be available)

is controlled by a particular statistic, called the supply stress s_s (Lika et al., 2014). This statistic is defined as $s_s = \dot{p}_J \dot{p}_M^2 / \dot{p}_A^3$, with $\dot{p}_J$ and $\dot{p}_M$ being the maturity and somatic maintenance rates, and $\dot{p}_A$ being the assimilation rate, typically (but not necessarily) evaluated at abundant food and maximum size. Theoretically, it can take values between 0 and 4/27 in DEB models. The value 4/27 minus the supply-stress can be called demand-stress. As far as we know, the supply stress does not have a direct physiological interpretation, other than that it is a dimensionless ratio between maintenance and assimilation. DEB theory takes $\dot{p}_A$ proportional to squared length and $\dot{p}_M$ to cubed length, so s_s is independent of length. Multiplying by $\dot{p}_J$, it also becomes independent of energy and time. The motivation for its name is that, when applied to the many species in the AmP collection (AmP, 2025; Marques et al., 2018), it turned out that mammals and birds score high for s_s , amphibians, reptiles and cartilaginous fish score moderate, and ray-finned fish and invertebrates score low; see Fig. 1. The eco-physiological traits of these taxonomic groups match the supply–demand pattern as stylized in Table 1. Several eco-physiological properties turn out to be linked to the position of species in the spectrum.

Unlike the suggestion implied by Fig. 1, invertebrate species greatly outnumber vertebrates, some 2 million versus 76 thousand extant species. Data availability in the literature has a strong taxonomic bias. Fig. 1 shows that invertebrates behave very differently from vertebrates quantitatively. To understand why, we briefly discuss the properties in Table 1 to reveal their coherence. We treat this table as a conceptual definition of the supply–demand spectrum and the supply stress as a quantifier for the spectrum.

Demand species can be seen as having a relatively high level of acquisition homeostasis: their feeding rate is less dependent on food

availability as a result of a small half saturation constant. It would be ideal to test this against data, but the huge diversity of food items, food searching methods, habitat types and lack of data render that impossible. Endothermy, a property of demand species, can be seen as a high level of thermal homeostasis (Polymeropoulos et al., 2018), with homeothermy as a less extreme form. This allows them to be active at environmental temperatures at which ectotherms cannot be active, or much less so, which is useful for food acquisition. Endotherms use thermal insulation (feathers, hair, fat layers), migration, and torpor to keep the metabolic costs down.

The effects of metabolic history may vary with a species' position on this spectrum. Demand species experiencing low food availability may experience a drive to guard against fluctuations in reserve density and breakdown of somatic structures by increasing energy expenditure into searching and acquisition of food. Demand species are thought to have higher peak metabolic rates than supply species due to the energetic demands of maintaining energy assimilation rates regardless of food abundance.

Apart from annelids and cephalopods, invertebrates do not have capillaries, but vertebrates do. With capillaries, the effect of fluctuations in cardiac output is felt directly in the most remote corners of the body; with an open circulatory system, this is much less the case. Nonetheless, all animals more or less follow Kleiber's law: dioxygen consumption is about proportional to the body mass to the power 3/4. So, it is very unlikely that the explanation has anything to do with capillaries, despite suggestions from frequently-cited literature (West et al., 1997; Brown et al., 2004; Barbosa et al., 2006; Clarke, 2025). The explanation for Kleiber's law given by DEB theory is (1) large-bodied species have relatively more reserve, which does not need maintenance (Kooijman, 1986) and (2) small-bodied species more likely follow the waste-to-hurry strategy (Kooijman, 2013; Augustine et al., 2019). Table 1 shows that capillaries make already the difference in the embryo-stage. Vertebrate embryos in telo-lecithal eggs develop near the outer egg membrane on one side of the egg, so close to where dioxygen is available, sending their capillaries inside the yolk for mobilization. They keep yolk separated from reserve and structure and absorb the last bit of yolk at birth, i.e. the start of feeding. Invertebrate embryos in iso- and centro-lecithal eggs undergo repeated cleaving and do not keep yolk separated from reserve and structure. Dioxygen needs to diffuse in through tissues, which limits their maximum development rate. Foetal development is a variation on embryo development that shares many quantitative aspects with egg development in DEB theory (Zonneveld and Kooijman, 1993), and occurs also in some invertebrates (e.g. peripatus).

With the property “behavioral birth control” of demand species, Table 1, we think of territorial defense. Species that sport this behavior do this typically only during the breeding season, which points to its function: the parents try to ensure that their offspring will have sufficient food. The fact that territories tend to be smaller in years when food is abundant further supports this interpretation. The unlucky ones

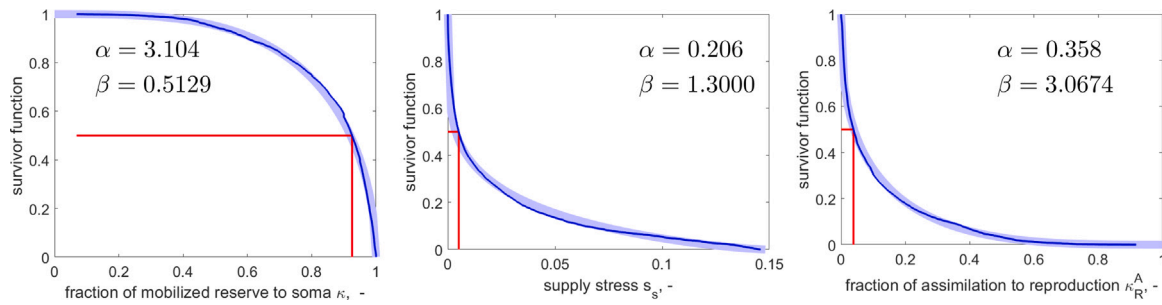


Fig. 2. The survivor functions of the fraction of mobilized reserve to soma κ_s (left), of the supply-stress s_s (middle) and of the fraction of assimilation to reproduction κ_R^A (right) for all the 6540 entries in the AmP collection at 2025/10/02. The light-blue broad curves are fitted beta distributions: $S(\kappa) = 1 - I_\kappa(\alpha, \beta)$, but that for s_s is the truncated beta distribution for the interval (0,4/27). The parameter values are given in the figures and their computation in the SI.

that fail to find and defend a territory simply do not breed that season; this combines beautifully with the fact that birds have (potentially) a long life span, compared to other species, so more opportunities to try their luck. Birds are well known for this behavior and the number of breeding pairs in a given area is typically monitored by counting singing birds. If a defending pair drops out for some reason, their place is rapidly occupied by individuals who previously failed to find a territory. This situation strongly selects for high somatic maintenance (typical for birds; Appendix C comes back to this). Since the von Bertalanffy growth rate is proportional to the specific somatic maintenance (Kooijman, 2013; Lika and Kooijman, 2024), the high somatic maintenance of birds results in rapid growth and a short period required for parental care, including territorial defense. So birds, and to a slightly less extent mammals, are on their asymptotic weight for a large part of their life span and have less opportunity to compensate for starvation by reducing growth during low food availability. Ectotherms typically hardly reach their asymptotic weight under field conditions and have more opportunities to reduce growth in response to starvation, so they can handle a wider range of food availability. In conclusion, there is a lot of logic in the coherence of the traits listed in Table 1.

Fig. 1 shows that, although birds score low in the allocation to reproduction as a fraction of assimilation κ_R^A , they occupy almost the full range of supply stress values. Appendix C returns to this. The link between supply stress, s_s , and allocation fraction of mobilized reserve to soma (= somatic maintenance plus growth), κ_s , becomes clear after realizing that, for fully-grown individuals, somatic maintenance equals fraction κ of assimilation, so $s_s = \dot{p}_J \dot{p}_M^2 / \dot{p}_A^3 = \kappa^2 \dot{p}_J / \dot{p}_A$. Another important observation is that ray-finned fish score high in κ_R^A , but their total neonate mass, cumulated over their life span, more or less equals the ultimate mass of the mother, like for almost all animal taxa (Augustine et al., 2022). The mesh on which all points lie in Fig. 1, defined by $\kappa_R^A = 1 - \kappa - s_s / \kappa^2$, see Appendix A, shows that only species with a small supply stress can allocate a large fraction of their assimilation to reproduction; having a small κ is not enough. With a high κ the adult individual allocates little to reproduction, but with a low κ it allocates little to growth, while the feeding rate is proportional to surface area (Kooijman and Lika, 2014b) and reproduction is ultimately paid from feeding. The present relationship between κ_R^A and s_s shows that supply stress also needs to be considered to understand reproduction in an ecological context. So, a large supply stress comes with strong ecological restrictions for predator–prey relationships.

Fig. 2 shows that κ_s , s_s and κ_R^A all follow the beta distribution accurately (see Appendix B); the distribution of the supply stress is truncated to the interval (0,4/27). The reasons for the beta-distributions are well-understood (Lika et al., 2019): these quantities are particular ratios of Weibull-distributed energy fluxes and Weibull distributions for energy fluxes result if a large number of causing factors contribute, for the same reason why allometric functions frequently fit biological data well. This can be seen as an empirical equivalent to the central limit theorem in probability theory, but for biological traits.

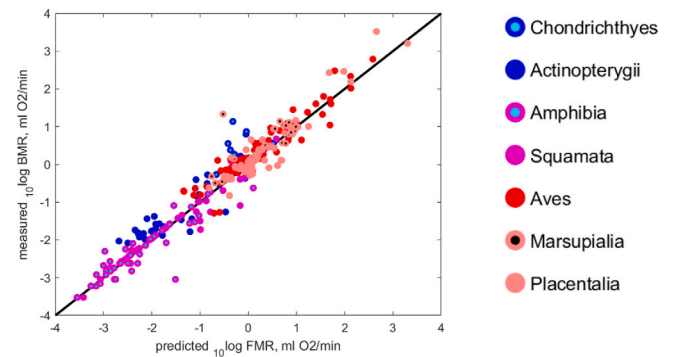


Fig. 3. The measured basal metabolic rate (BMR), as function of the DEB-predicted field metabolic rate (FMR). The references are given in the SI. The line indicates equality.

3. Factorial aerobic scope

DEB theory makes no direct assumptions about respiration but can still predict it, using the conservation law for chemical elements (C, H, O, N). This respiration rate corresponds to the field metabolic rate (Lika et al., 2019), but the various contributions to respiration can be evaluated separately. DEB theory provides no direct predictions for the maximum metabolic rate. The aerobic scope can be expressed as absolute (AAS), i.e., the difference between the maximum and standard metabolic rate, or factorial (FAS), i.e., their ratio (Bishop, 1993; Halsey et al., 2018). We here use the FAS, rather than AAS, because it is insensitive to differences in units and is less sensitive to temperature and mass (Bishop, 1999). Although FAS does vary with body temperature (e.g. Farrell (2013)), it is maintained relatively constant across a range of body temperatures near an organism's optimal performance. In the published literature, dioxygen consumption measurements are often reported as weight-specific, without specifying the weight itself. The values of FAS are frequently linked to feeding behavior (Auer et al., 2015; Fu et al., 2022; Clark et al., 2013). This implies that the FAS for embryos and early juveniles is likely to differ from those of late juveniles and adults, since they typically differ in the type of food. Thus, we focus our analyses on late juveniles/adults in a temperature window around the optimum one for FAS.

4. Results

All values for the basal metabolic rate and the predicted field metabolic rate in Fig. 3 were at approximate optimal ambient temperature for ectotherms and within the thermoneutral zone for endotherms and for specified body weight. For BMR measurements, food was restricted according to species-specific standard protocols; and for FMR predictions, food availability is assumed to be abundant. Figs. 3 and 4

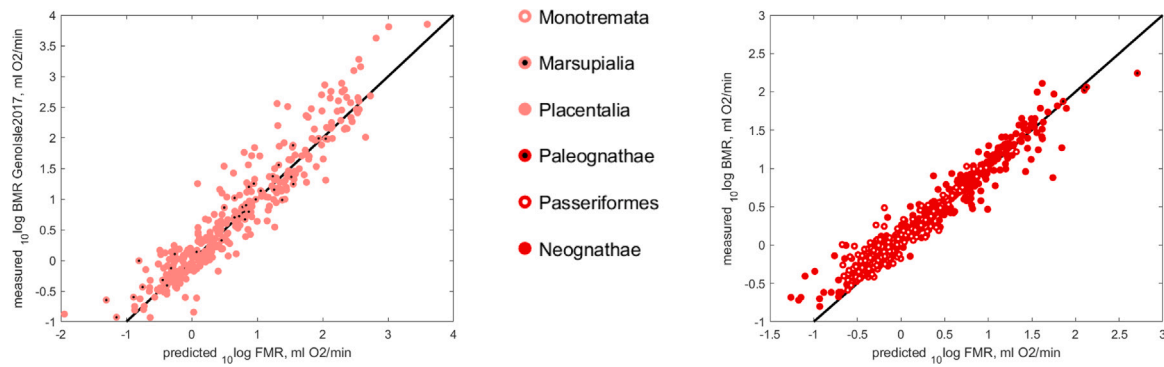


Fig. 4. The measured basal metabolic rate (BMR), as function of the DEB-predicted field metabolic rate (FMR) for mammals (left, data reported in [Genoud et al. \(2018\)](#)) and birds (right, data reported in [Gavrilov et al. \(2013\)](#)). The Neognathae here exclude the Passeriformes. The lines indicate equality.

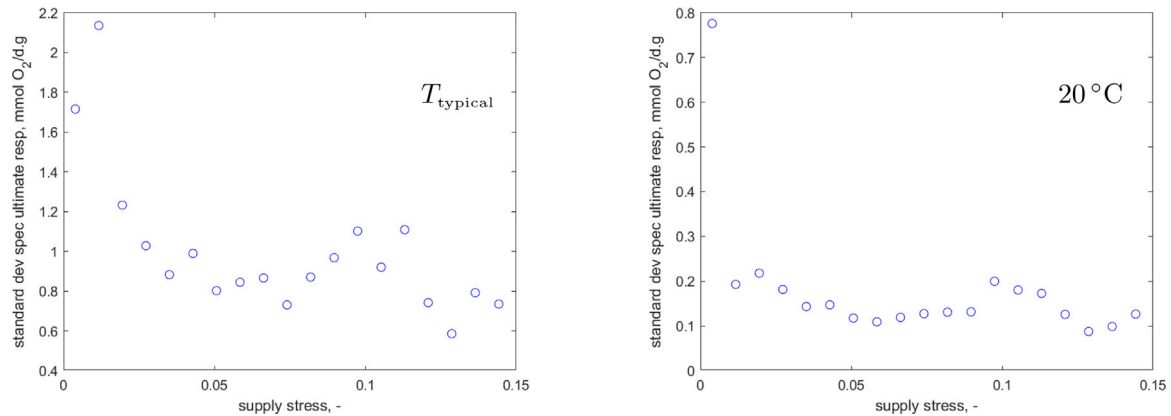


Fig. 5. The standard deviation of the weight-specific Field Metabolic Rate (FMR) predicted by DEB theory at ultimate weight and abundant food as function of the supply stress s_s . Left: at the body temperature (T_{typical}); Right: corrected for a body temperature of 20 °C. The number of species over which the standard deviation is calculated decreases from 3400 for low s_s to 50 for high s_s . The sharp decrease of the survivor function of s_s explains this strong decay in numbers, see [Fig. 2](#).

show that the measured BMR is in reasonable agreement with the DEB-predicted FMR for species in the AmP collection. This is remarkable since for most AmP entries, DEB parameters are estimated without using dioxygen consumption data. The procedure is that DEB parameters are estimated from a set of data sets (mainly on growth, reproduction, lifespan, and life history events), and these parameters are used for the FMR predictions, given body weight and temperature. Notably DEB-based FMR predictions include a contribution from digestion, based on default values for digestion efficiency, in most cases; they also include growth overheads.

The standard deviation of the specific FMR predicted by DEB models tends to decrease with increasing supply stress; see [Fig. 5](#); see the SI for computational details. The initial sharp decrease is caused by the large biodiversity at low supply stress (especially for the invertebrates which differ much more from each other than the vertebrates), compared to the much smaller biodiversity at higher values. The gradual decrease (from supply stress values of 0.05 to 0.15) is mostly due to the body temperature that tends to increase with the supply stress (cartilaginous fish, amphibians and reptiles have moderate supply stresses and have low body temperature; the endotherms birds and mammals dominate at the demand-end with relatively high supply stresses and body temperatures).

[Fig. 6](#) gives the factorial aerobic scope (FAS) as the ratio of empirically measured MMR to BMR as found in the literature, in relation to the supply-stress, see SI. It also gives the FAS as ratio of the measured MMR and the DEB-predicted FMR; it has more points because we could not find measured values for BMR for quite a few species in the literature. For all data points, we checked metabolic rate measurement

methodologies. For MMR, only data acquired through methods that provoked elevated metabolism via locomotion (for endotherms and ectotherms) or hypothermia (for endotherms) were included. Data for which peak metabolic rate was measured via the diet were omitted. The general pattern is what we expected, a covariation of FAS with the supply stress, although the scatter is very high. [Bundle et al. \(1999\)](#), [Taylor et al. \(1980\)](#) mention that the typical FAS for mammals is 10.

The supply stress seems to be independent of BMR itself, so the increase of the FAS with the supply stress is due to the increase of PMR with supply stress (as mentioned in [Table 1](#)); data and plots provided in the SI. As aging directly relates to respiration, in the DEB context, no surprise that the supply stress was also found to be independent of life span; see the SI Consistent with the findings of [Taylor et al. \(1980\)](#), we found that the FAS is independent of (ultimate) body weight for placentals; this also holds for birds. This means that PMR depends on body weight, similar to BMR, so roughly complies with Kleiber's law. Results are provided in the SI.

5. Discussion

A fundamental difference between assimilation models for the energetics of an individual, such as DEB models ([Kooijman, 2010](#)), and production models, such as the Scope for Growth model and the Wisconsin bioenergetics model ([Kitchell et al., 1977](#); [Stewart et al., 1983](#)), is the way respiration is treated ([Lika and Kooijman, 2011](#)).

Production models lump all contributions to respiration into a single allometric function of body mass, treat it, along with digestion overheads, as losses from food energy, and distribute the remainder

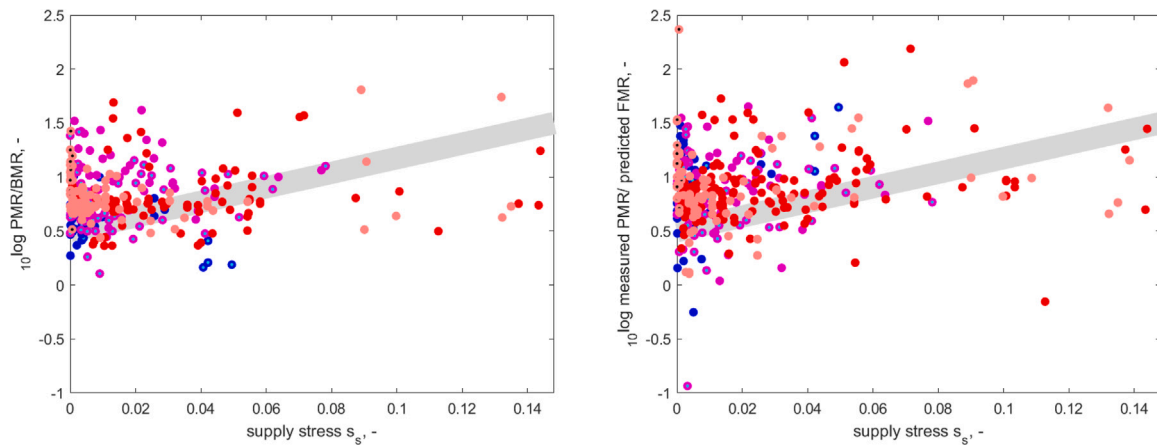


Fig. 6. Left: The log of the ratio of the peak over the basal metabolic rate as function of the supply-stress for data from the literature; values and references are given in the SI. The values of the supply-stress come from the AmP collection. Right: The log of the ratio of the peak over the DEB-predicted field metabolic rate. A stylized linear relationship is indicated. Legend as in Fig. 3.

over production: growth and reproduction. The problem with that is that growth and reproduction overheads, which are included in respiration, no longer depend on actual growth and reproduction: the scheme is thermodynamically inconsistent. Moreover, production models cannot conserve energy and mass of chemical elements at the same time and violate indirect calorimetry by taking dioxygen consumption proportional to energy fluxes; which would strongly constrain budget models (Kooijman, 2020). The growth overhead is not tiny and the reason why respiration of a single individual during ontogeny is about proportional to its mass to the power $3/4$; the similarity of this scaling exponent for fully grown adult respiration across species has caused, and still causes, considerable confusion in the literature, despite early warnings (Zeuthen, 1947).

Assimilation models, at least DEB models, do not use allometric functions and exploit the conservation of chemical elements to quantify respiration and energy conservation to quantify dissipating heat. By decomposing metabolism into a small number of macro-chemical reaction equations, the various contributions to respiration remain separated, as typically done in the classic physiological literature. Growth and reproduction overheads are among these contributions. Variations in metabolism, such as BMR, RMR, FMR, MMR, PMR can, therefore, be accommodated naturally in assimilation models, contrary to production models.

We could not find measured BMR values for all species for which we could find MMR/PMR values in the literature. We therefore replaced BMR by DEB-predicted FMR (which is available for all AmP species) and checked that these values correspond to the measured BMR data, when given. The correspondence is very good, but we were surprised that the predicted FMR were occasionally lower than or similar to the measured BMR. An extreme case of this mismatch occurred for the hummingbirds. Empirical measurements of BMR for every hummingbird species (Median = $0.308 \text{ mgO}_2\text{min}^{-1}$, Minimum = $0.192 \text{ mgO}_2\text{min}^{-1}$, Maximum = $0.576 \text{ mgO}_2\text{min}^{-1}$) reported in Gavrilov et al. 2013 were lower than DEB FMR predictions for the same species (Median = $0.103 \text{ mgO}_2\text{min}^{-1}$, Minimum = $0.055 \text{ mgO}_2\text{min}^{-1}$, Maximum = $0.396 \text{ mgO}_2\text{min}^{-1}$). This might point to contributions to measured BMR linked to growth, digestion or stress in practice, despite the formal definition of BMR or, at least for the hummingbirds that have a complex life style with daily torpor, may reflect a need to fine tune DEB model parameterization. As would be expected, in the minority of cases where respiration data are among the data from which DEB parameters have been estimated, the goodness of fit is very good; see AmP (2025).

Our general conclusion is that the factorial aerobic scope, and more specifically the peak metabolic rate, indeed tends to increase

with the supply stress, at least for vertebrates. We can stylize the relationship between supply stress and FAS to $_{10}\log(\text{FAS}/\text{FAS}_s) = s_s/s_s^d$, with $_{10}\log \text{FAS}_s = 1/2$, being the log of FAS at the supply-end of the spectrum, and s_s^d is the maximum value of s_s , $4/27$, at the demand-end of the spectrum; see Fig. 6. The somatic maintenance relates to FAS as $\dot{p}_M^2 = _{10}\log(\text{FAS}/\text{FAS}_s)s_s^d\dot{p}_A^3/\dot{p}_J$, where $\dot{p}_J$ is the maturity maintenance rate and $\dot{p}_A$ the assimilation rate. So, the FAS roughly increases from $10^{0.5} = 3.2$ at zero supply stress, to 32 at maximum supply stress, see Fig. 12. The FAS applies only to very short periods and hardly has an effect on the whole lifetime budget. The ratio of PMR and measured BMR has a less clear relationship with supply-stress, which suggests a possible problem with measuring BMR, as discussed in the introduction. A remarkable aspect of our conclusion is that the quantities FAS and s_s are obtained from very different measurements and place the FAS in a wider ecological context, where interactions with food/prey and predators play important roles and, for endotherms, keeping the body at target temperature outside the thermal neutral zone.

The huge scatter in metabolic rates is due to a variety of reasons. First, there is measurement error in the data, including the definitions of the various types of metabolism (BMR, RMR, FMR, PMR), which cannot always be standardized or achieved through experimental manipulations; the huge biodiversity does not help to make them sharper. For example, MMR and PMR are defined to be maximum 'sustainable' metabolic rate, but there is no standard definition of 'sustainable' applicable across taxa.

Second, not all DEB parameters are very well determined by the data that is used, which certainly applies to the supply stress, but differs from case to case. The various AmP entries differ greatly in the amount of data from which the DEB parameters were estimated.

Third, a rather deep reason that has never been highlighted to our knowledge: respiration data have intrinsically a large scatter, as illustrated in Fig. 7. The figure illustrates a computer simulation of a single individual that follows the standard DEB model at constant food density, with only two stochastic elements: food searching and survival. Starvation during long searching spells can cause rejuvenation, i.e. a reduction in maturity, but this increases the hazard rate; it can also cause shrinking of structure resulting in death if too much. The food particles all have the same mass; the searching time to find the next particle follows a time-inhomogeneous Poisson process, so the searching spells are exponentially distributed, with a parameter that (slowly) changes in time to account for individual growth and associated increases in food consumption. We see that the scaled reserve density initially varies a lot when the individual is still small, but these fluctuations dampen with increasing length. Variables, such as length, maturity, aging acceleration, hazard rate linked to aging, cumulated reproduction and feeding

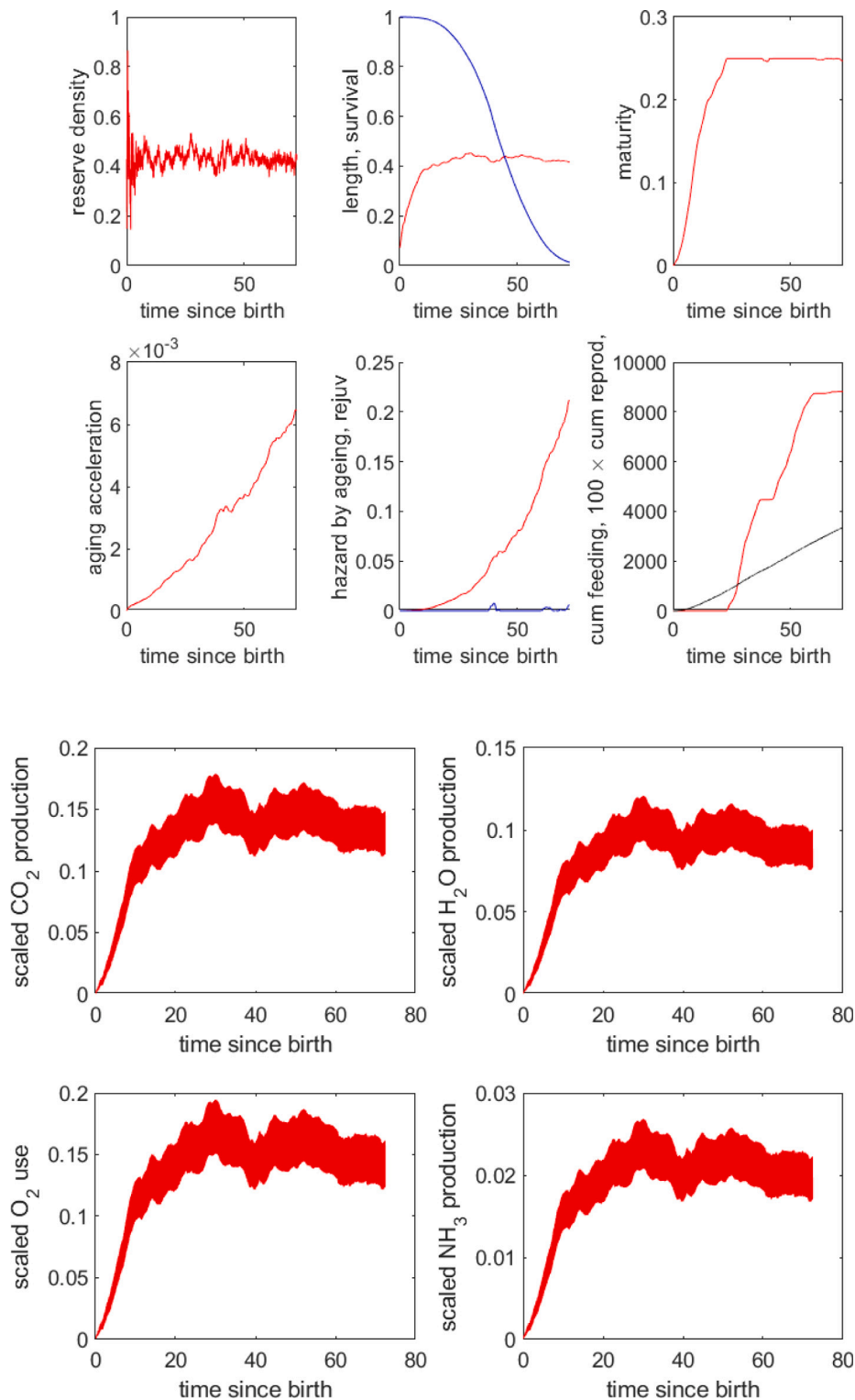


Fig. 7. The simulated trajectories for a single individual that follows the standard DEB model at constant food density, but stochastic food searching (and survival). All quantities are given in scaled form, including time. The red curve in subplot (1,2) is the scaled length, the blue one the survival probability. The red curve in subplot (2,2) is the aging hazard rate, the blue one the rejuvenation hazard. The red curve in subplot (2,3) is cumulated reproduction, the blue one is cumulated feeding. Explanation is in the text and in the SI.

rate suffer much less from stochasticity in food searching. However, mineral fluxes, such as dioxygen consumption, show quite a bit more scatter, given the previous trajectories. With the chosen parameter settings, the fluxes of water, dioxygen, carbon dioxide and ammonia are all proportional to each other, but with different parameter values

this does not need to be the case. Parameters are easy to change, see SI. Part of this scatter is smoothed out in practice due to the digestion process, which is here assumed to be instantaneous. On the other hand, variation in food particle size will increase the scatter. The simulation details and the parameter values are given in the SI. [Kooijman \(2009\)](#)

discusses a related case of effects of social interaction on stochastic inputs in an otherwise deterministic standard DEB model, which can enhance differences between individuals that were identical at birth, including all parameters and state variables.

Despite being mammals, which generally have a high supply stress, marsupials have a very low supply stress, which is due to puberty being early in their life cycle in combination with a small reproductive output (= reproduction rate times mean mass of a neonate). The costs for maturation and maturity maintenance are estimated from the reproductive output after puberty. The main reproduction investment of marsupials is via lactation, which is paid from up-regulated assimilation, but not included in these computations. The mean ratio of weight at puberty and ultimate weight is 0.71 for the marsupials (106 AmP species) and 0.83 for the placentals (1094 AmP species). More impressive is that the mean maturity at puberty is 1.3MJ for the AmP marsupials and 98.9MJ for the AmP placentals, so a factor 76 difference. Maximum body weight strongly contributes to this result. To exclude that, the mean maturity maintenance as fraction of assimilation is 0.0144 and 0.0947 for marsupials and placentals, respectively, so a factor 6.6 difference. After puberty, maturity no longer increases, so does maturity maintenance, which is proportional to maturity with similar proportionality constants for the two groups of mammals. Maturity maintenance dominates the supply stress, since κ is close to 1 for most species, see Fig. 2; somatic maintenance as fraction of assimilation when fully grown is quite similar in both groups, around 0.9.

Birds have the problem that, when kept in aviaries, many species prove to be able to start a nest rather soon after fledging. They do not do this in the field, probably for environmental (seasonal) and/or social reasons. Breeders know that they weaken the health of their birds in this way, challenging the idea that maturity reached its maximum level at first brooding in aviaries. This bird-problem probably directly relates to birds spanning the full range of supply-stress values, despite of high supply stress values only. The Appendix C discusses this problem in more detail and proposes a modified supply stress that might be more appropriate for birds. Birds like tinamous have a small heart, which probably excludes the high peak metabolic rates that are required for sustained flight (Altamiras et al., 2017).

Unfortunately, we could not find FAS values for (flying) insects for which we have s_s values. Given their ability to substantially increase their body temperature during flight (Heinrich, 1993; B., 1996), we expect high FAS values for them. Holometabolic insects combine this with very low values for the supply stress, since many species almost skip the juvenile stage (e.g. butterflies); the larval stage already allocates to reproduction, i.e. storing reserve for later egg production. Puberty occurs in them soon after birth at a very low maturity level. The task of the imago is then reduced to depositing eggs at the proper sites. The imago of (some) beetles, for instance, start as juvenile, so for them, the supply stress will probably be larger.

An interesting application of the (empirical) relationship between FAS and supply stress is in the estimation of DEB parameters from the data, and especially the maturity maintenance rate coefficient k_J . This parameter is rarely well-determined by data, due to the lack of data. This is less problematic than might seem because maturity maintenance is typically a (very) small component of the whole energy budget. The common practice is to fix it at 0.002 d^{-1} at 20°C as long as the volume-specific somatic maintenance rate $[\dot{p}_M]$ is greater than 20 J/d cm^3 , since in that case the maintenance ratio k remains well below 1. If $k = 1$, the maturity density (the maturity per structural volume) remains constant, with strange implications for embryo development. For $k < 1$, the maturity density increases until puberty. The maintenance ratio is defined as $k = k_J/k_M$ with $k_M = [\dot{p}_M]/[E_G]$ and $[E_G]$ is the volume-specific cost of the structure. If $[\dot{p}_M]$ is lower than 20 J/d cm^3 , the parameter k_J is released and $k = 0.3$ is taken as a pseudo-data point, i.e. a data point that is given a low weight coefficient (Lika et al., 2011a,b; Marques et al., 2018). The relationship between FAS and s_s , in combination with knowledge of the value of FAS, can be used to

assign a likely value to s_s and treat this as a pseudo-data point. The AmP estimation guidance in Kooijman (2025) provides details in the section “Elusive parameters”. This will substantially help in estimating k_J , despite the fact that we do not have a mechanistic theory for FAS.

Our results highlight connections between empirical measurements of dioxygen consumption rates and DEB predictions and some limitations of these connections. They emphasize the broader functionalities of aerobic scope in ecological and physiological contexts and reinforce the central role of DEB theory, particularly the concept of maturity maintenance, which is key to DEB theory and especially relevant to supply stress, but hard to make concrete and to quantify; maturity has no mass or energy. To our knowledge, only DEB models deal with maturity and maturity maintenance, so these findings are unique for DEB theory. Although not all traits that characterize the supply/demand-spectrum have been discussed in this paper, see Table 1, our findings so far do support their natural coherence. The finding that the fraction of assimilation that is allocated to reproduction amounts to $\kappa_R^A = 1 - \kappa - s_s/\kappa^2$, so s_s needs to be small for κ_R^A to be high, is in beautiful harmony with Fig. 1: invertebrates have a low s_s and vertebrates other than ray-finned fish have a higher s_s ; vertebrates generally have a higher trophic position in the food chain than invertebrates and the latter have the capability to deal with high predation rates by investing more of their assimilation in offspring. Ray-finned fish are special; as tiny neonates they are in a low trophic position, but they can be in a much higher position as adults (Lika et al., 2022; Kooijman and Lika, 2014a). Fig. 8 shows that the relationship between trophic level, supply stress and allocation to reproduction also holds for more related taxa: Although not all carnivores are carnivores (Kooijman and Augustine, 2022), and certainly not all consume rodents, rodents generally occupy a lower trophic position in the food chain than carnivores. This is in harmony with rodents allocating only slightly more mobilized reserve to soma, but their median supply stress is less than half and the fraction of assimilation to reproduction more than double, compared to carnivores. We see this as strong support for the ideas in this paper.

CRedit authorship contribution statement

Christine E. Verhille: Methodology, Data curation, Conceptualization. **Sebastiaan A.L.M. Kooijman:** Writing – original draft, Visualization, Methodology, Investigation, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. The relationship between κ_R^A , κ and s_s

This section explains why the points $(\kappa_R^A, \kappa, s_s)$ for each species are on a particular parameter-free surface, see Fig. 1. For a fully grown individual that follows the standard DEB model at constant food, reserve and structure no longer change and assimilation $\dot{p}_A^\infty$ equals reserve mobilization $\dot{p}_C^\infty$, else reserve will change. The κ -rule of DEB theory states that a fraction $1 - \kappa$ of the mobilized reserve flux is allocated to maturity maintenance $\dot{p}_J^\infty$ plus reproduction $\dot{p}_R^\infty$. So $\dot{p}_R^\infty = (1 - \kappa)\dot{p}_C^\infty - \dot{p}_J^\infty = (1 - \kappa)\dot{p}_A^\infty - \dot{p}_J^\infty$. The fraction of assimilation that is allocated to reproduction becomes $\kappa_R^A = \frac{\dot{p}_R^\infty}{\dot{p}_A^\infty} = 1 - \kappa - \kappa_J^A$ for $\kappa_J^A = \frac{\dot{p}_J^\infty}{\dot{p}_A^\infty}$ is the fraction of assimilation that is allocated to maturity maintenance.

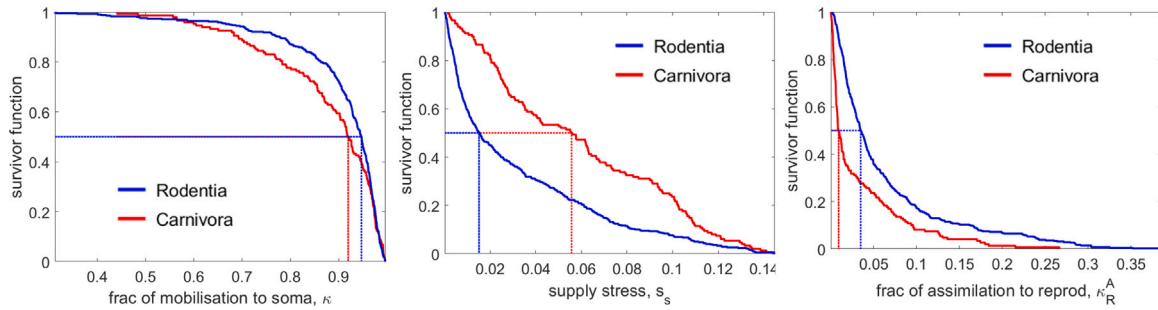


Fig. 8. The survivor functions of the fraction of mobilized reserve to soma (left), of the supply-stress s_s (middle) and of the fraction of assimilation to reproduction κ_R^A (right), for rodents (418 species) and carnivorans (148 species). The data come from the AmP collection.

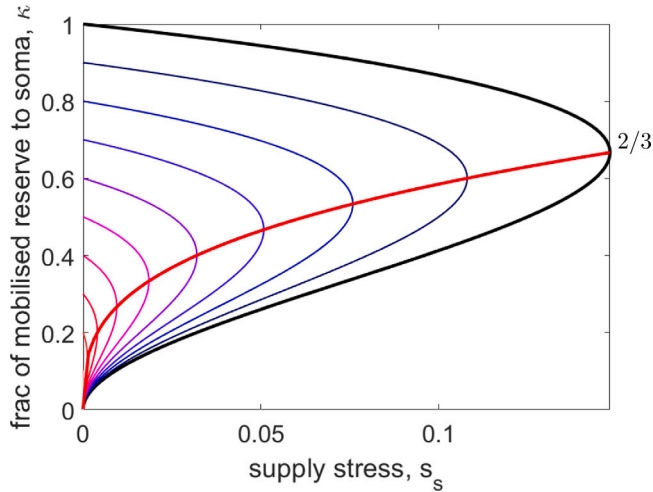


Fig. 9. The isoclines of $\kappa(s_s)$ for $\kappa_R^A = 0, 0.1, \dots, 0.9$ and the values of $\kappa(s_s) = (2s_s)^{1/3}$ for which κ_R^A is at maximum (red curve).

The supply stress is defined as $s_s = \frac{\dot{p}_J^\infty \dot{p}_M^{\infty 2}}{\dot{p}_C^\infty \dot{p}_A^\infty} = \kappa_J^A \kappa_M^A$, for $\kappa_M^A = \frac{\dot{p}_M^\infty}{\dot{p}_A^\infty}$ is the fraction of assimilation that is allocated to somatic maintenance. In this case $\kappa \dot{p}_C = \dot{p}_M$, else the individual will grow or shrink. So $\kappa \dot{p}_A = \dot{p}_M$ and we can rewrite the supply stress as $s_s = \kappa_J^A \kappa^2$. Substitution of $\kappa_J^A = s_s / \kappa^2$ into the expression for κ_R^A gives $\kappa_R^A = 1 - \kappa - s_s / \kappa^2$. This expression defines the surface on which all points lie, see Fig. 9.

Appendix B. The distribution of κ_R^A , κ and s_s

This section explains why κ_R^A , κ and s_s for the various species all follow a beta distribution, see Fig. 2. In probability theory it is known that if X and Y are independently gamma distributed, the quantity $\frac{X}{X+Y}$ is beta distributed and the product of independently beta distributed variables is again beta distributed. Lika et al. (2019) found that ultimate reproduction $\dot{p}_R^\infty$, maturity and somatic maintenance, $\dot{p}_J^\infty$ and $\dot{p}_M^\infty$, for the AmP species are all Weibull distributed in the AmP collection, not gamma distributed. In that time, in 2019, the AmP collection had 875 entries, now 6540, but Fig. 10 shows that the fit is still good, although somewhat less than in 2019. Lika et al. (2019) also found that $\frac{X}{X+Y}$ is then not beta distributed mathematically, but it is so by a very good numerical approximation. The squared values from a beta-distribution are not mathematically beta distributed, but are so again by a very good numerical approximation; the sum of Weibull distributed variables is not Weibull distributed, but is so by a good approximation if the scaling parameters do not differ much. The numerical approximations were checked with Monte Carlo studies.

The final task of this section is to show that κ_R^A , κ and s_s can be written in the required form for a beta distribution for fully grown

individuals who follow the standard DEB model at constant food. As shown in the previous section, $\kappa = \frac{\dot{p}_M^\infty}{\dot{p}_C^\infty} = \frac{\dot{p}_M^\infty}{\dot{p}_A^\infty} = \frac{\dot{p}_M^\infty}{\dot{p}_M^\infty + \dot{p}_J^\infty + \dot{p}_R^\infty}$. Given the above-listed properties, κ has the required form for a beta distribution. Then $\kappa_R^A = \frac{\dot{p}_R^\infty}{\dot{p}_A^\infty} = \frac{\dot{p}_R^\infty}{\dot{p}_R^\infty + \dot{p}_J^\infty + \dot{p}_M^\infty}$, so also has the required form for a beta distribution. This also applies to $s_s = \kappa_J^A \kappa^2$, being a product of beta distributed quantities, but with the condition that it can only assume values between 0 and 4/27, meaning that it does not follow a beta-distribution, but a truncated one.

It is remarkable that the small deviations from Weibull distributions for powers in Fig. 10 do not translate into deviations from beta distributions for fractions in Fig. 2.

Appendix C. Care-corrected supply stress for birds

The 1724 species of birds in the AmP collection occupy the full range of possible supply stress values and the fraction of assimilation that is allocated to reproduction, κ_R^A , is low; see Fig. 1. This is not what we expect with the idea that birds are demand species. Our explanation is that the ecological bottleneck for birds is not egg production, but parental care just prior to the fledging of the offspring, i.e. when they have to eat most, but still depend on their parents for food. Shoebills, for example, live in the White Nile area of lungfish. They lay two eggs per litter, but can raise only one chick until fledging; the weak chick is cannibalized by the strong one. Chicken-farmers know that they can egg-milk their chickens for a year by removing eggs just after laying (after which they are dumped). In the context of DEB theory, parental care is paid for by somatic maintenance. To account for this behavioral investment in reproduction, we corrected the expression for supply stress for birds by adding a small fraction of somatic maintenance, say κ_J^M , to maturity maintenance to mimic the real investment in offspring. To avoid any change in energy fluxes, we reduced the remaining somatic maintenance to compensate. So, the care-corrected supply stress becomes $s_s^c = (\dot{p}_J + \kappa_J^M \dot{p}_M)(1 - \kappa_J^M)^2 \dot{p}_M^2 / \dot{p}_A^3$. Notice that for $\kappa_J^M = 0$, the care-corrected supply stress reduces to the uncorrected one, $s_s = \dot{p}_J \dot{p}_M^2 / \dot{p}_A^3$. Fig. 11 shows that the effect of $\kappa_J^M = 0.025$ on s_s is considerable for bird species that have a low s_s and high κ ; other species are hardly affected. For low values of κ , maturity maintenance is substantial and a small addition from somatic maintenance hardly changes the total. If κ_J^M had been chosen 0.05, rather than 0.025, no s_s would be smaller than 0.04 for large κ , but the FAS as function of s_s in the right panel of Fig. 12, would be more frequently below the prediction by the empirical model. This can be seen as an estimation procedure for κ_J^M .

Fig. 12 shows the effect of care-correction on the relationship between FAS and supply stress. The uncorrected figure (left) is identical to Fig. 6, but then only for birds.

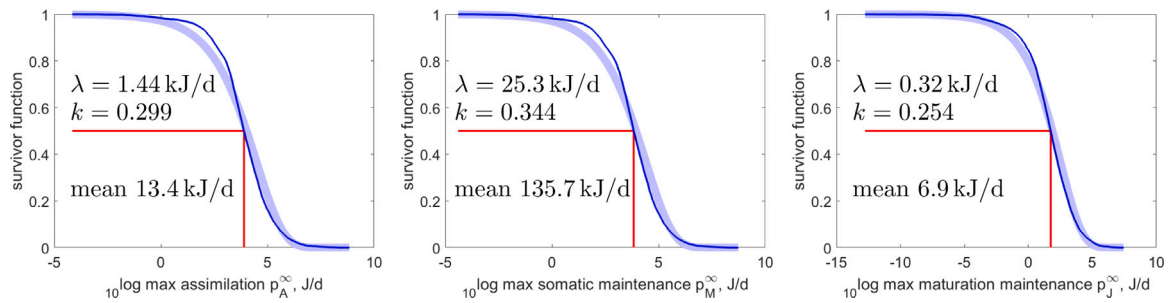


Fig. 10. The survivor functions of ultimate assimilation $\dot{p}_A^\infty$ (left), of somatic maintenance $\dot{p}_M^\infty$ (middle) and of maturity maintenance $\dot{p}_J^\infty$ (right) for all the 6839 entries in the AmP collection at 2025/10/24. The temperatures are correct for a body temperature of 20 °C. The light-blue broad curves are fitted Weibull distributions: $S(p) = \exp(p/\lambda)^k$. The parameter values are given in the figures and their computation in the SI.

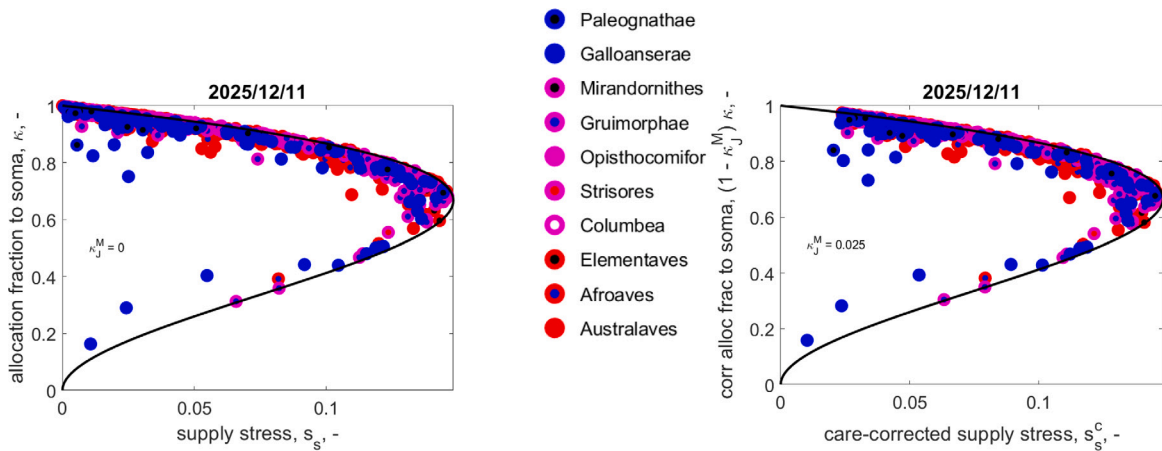


Fig. 11. The allocation fraction to soma as function of the supply stress for birds. Left: the uncorrected supply stress; right: the care-corrected supply stress when the fraction of somatic maintenance that is added to maturity maintenance is $\kappa_J^M = 0.025$. The curve represents $s_s = \kappa^2(1 - \kappa)$.

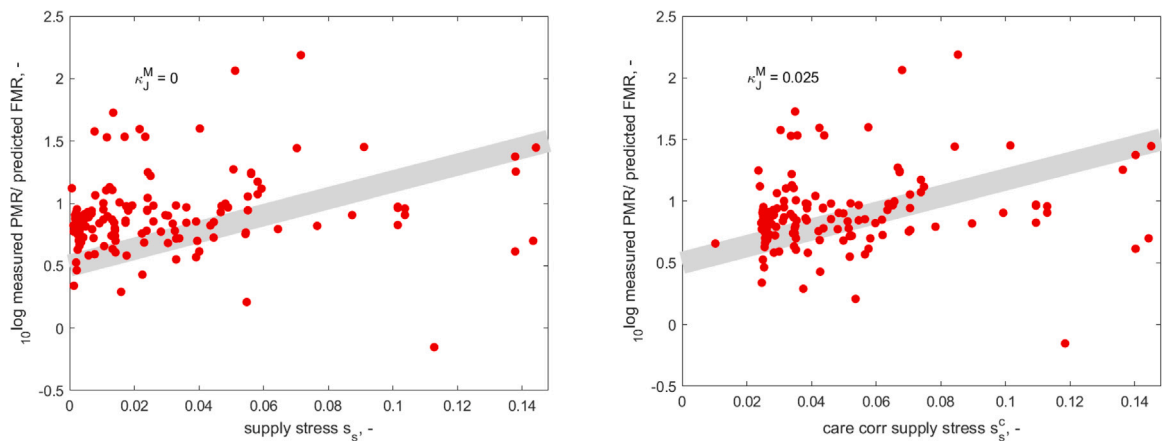


Fig. 12. The $_{10} \log$ FAS as function of the supply stress for birds. Left: the uncorrected supply stress; right: the care-corrected supply stress when the fraction of somatic maintenance that is added to maturity maintenance is $\kappa_J^M = 0.025$. The line represents $_{10} \log(\text{FAS}/\text{FAS}_s) = s_s/s_s^d$, like in Fig. 12.

Data availability

The data in this paper and the code to produce the figures in this paper are given in <https://github.com/add-my-pet/SI/tree/main/VerhKooy2026/>. The supply stress values and the data on which they are based are available in the AmP collection (AmP, 2025).

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