Structuring animal biodiversity according to five patterns

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Background

The Dynamic Energy Budget (**DEB**) theory provides a quantitative framework to explore the interaction between an organism's metabolism and its environment throughout its entire life cycle, within its eco-evolutionary history.

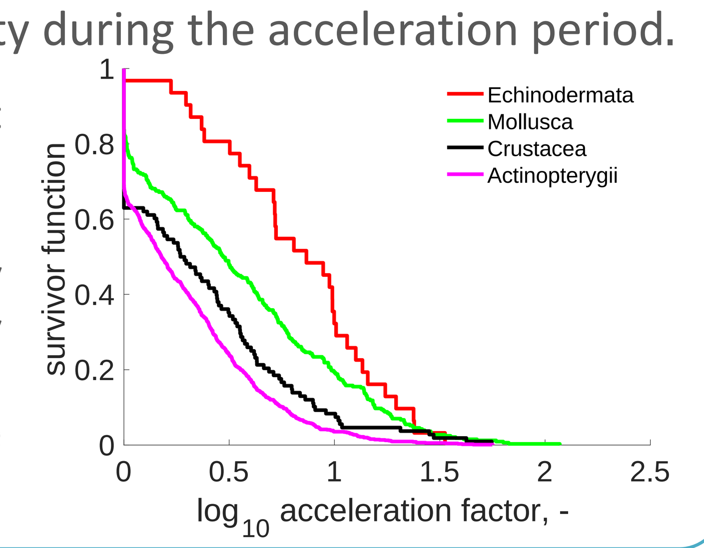
DEB offers practical applications for assessing the quality of measurements and handling missing data in unmeasured traits. To demonstrate practical implementation, a dedicated database called **AmP** was established in 2009, currently encompassing 4035 animal species from all major phyla.

This poster provides a concise overview of research that connects bioenergetic patterns, as quantified by DEB models, with observable functional traits. These connections involve underlying physical principles governing trait co-variations, waste-to-hurry (bloomers), quantifiers for supply-demand and altricial-precocial spectra, and interconnections between different life stages, exemplified by morph (M)-type metabolic acceleration.

M-type metabolic acceleration

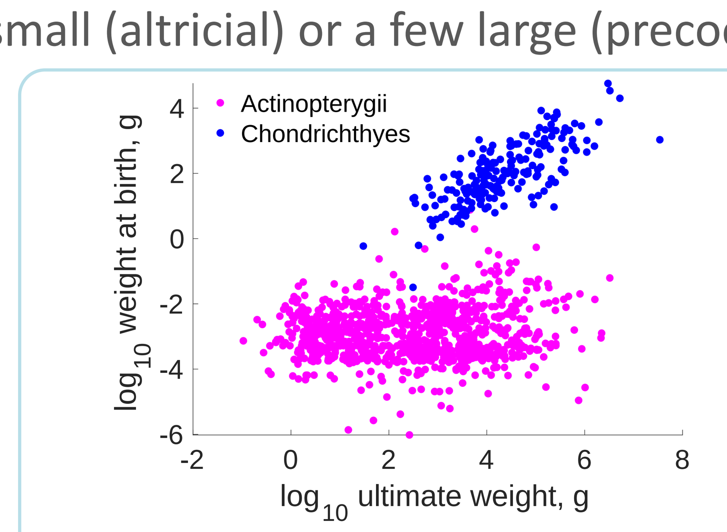
DEB theory links assimilation to surface area and maintenance to volume but has no assumption for how surface area relates to volume. Many animal species are isomorphic (so surface area ∝ volume$^{2/3}$), but some have surface area proportional to volume during a short period after birth. This affects both specific assimilation $\{\dot{p}_{Am}\}$ and energy conductance $\dot{v}$. M-type acceleration is defined as an increase in both $\{\dot{p}_{Am}\}$ and $\dot{v}$, resulting in no change in reserve capacity. It is quantified by the **acceleration factor** $s_M = L_j/L_b$, where L_b and L_j are the structural lengths at birth and end of acceleration, respectively. The acceleration factor depends on food availability during the acceleration period.

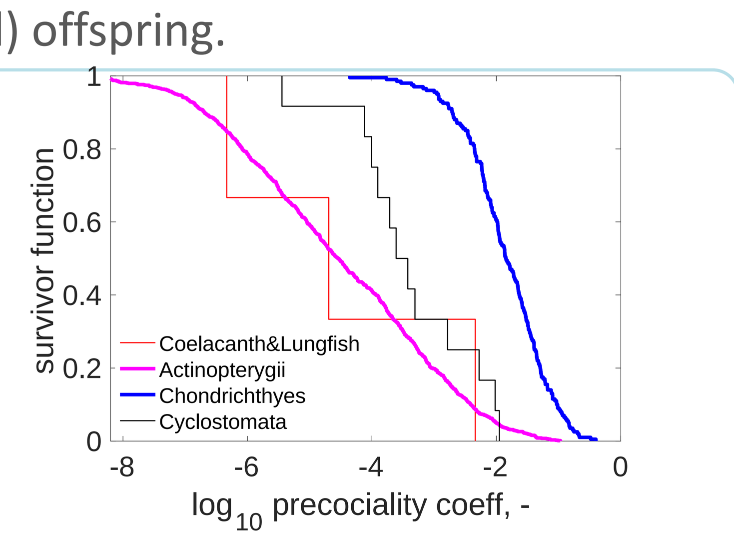
M-type acceleration is observed in most invertebrate species with morphological metamorphosis, but also to some taxa without. Some **molluscs** and **ctenophores** may have a delay in acceleration. The **actinopterygians** are the only vertebrates that show metabolic acceleration. Some species, like amphibians, have metamorphosis, but no acceleration.



Altricial-precocial spectra

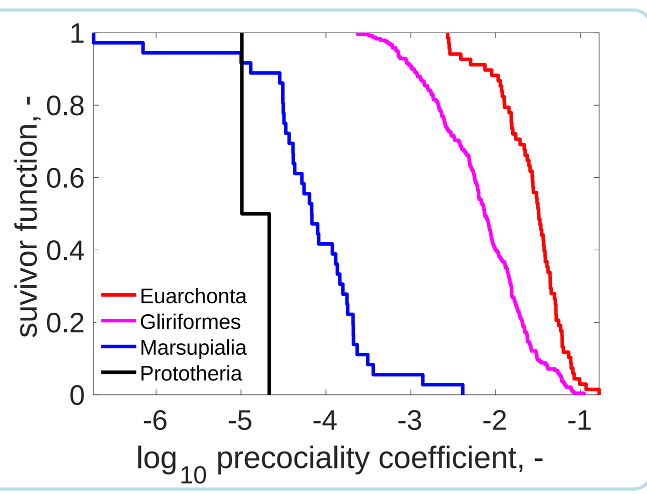
The altricial-precocial spectrum, akin to M-type metabolic acceleration, quantifies an interconnection between stages in the ontogeny of an individual. It is quantified by the **precociality coefficient**, $s_H^{bp} = E_H^b/E_H^p$, the ratio of maturity levels at birth and puberty. Evolution shapes parameter values of the energy budget independent of the offspring size. The choice is between many small (altricial) or a few large (precocial) offspring.





Actinopterygians lay small eggs independent of the ultimate weight, as an adaptation to planktonic larvae stage. In contrast, **chondrichthyans** produce large offspring that is proportional to ultimate weight. Chondrichthyans have s_H^{bp} larger than that for actinopterygians.

Birds evolved from precocial to altricial; mammals did the opposite. **Euarchonta** (mostly primates) are the most derived, while **Prototheria** (egg-laying mammals) are most ancestral. Since their origin, 250 Ma ago, all mammals laid eggs till some 30 Ma ago.



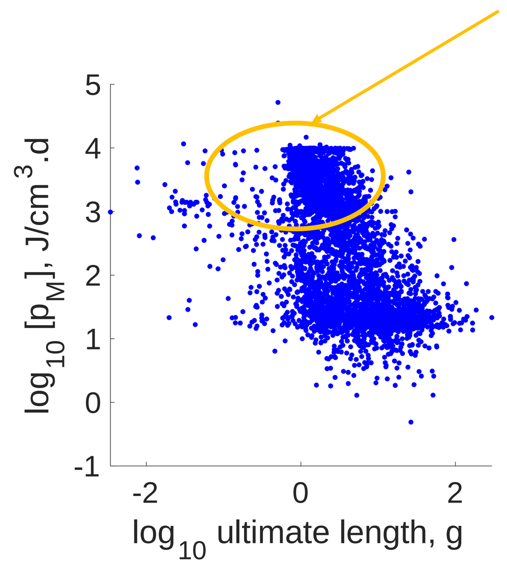
Physical co-variation rules

Since all DEB parameters have a clear physical interpretation, they can be classified as either **intensive** (i.e. size-independent) or **extensive** (i.e. size-dependent). Appropriate ratios of extensive parameters are intensive. The rules assume that intensive parameters do not vary among species. This links all parameters, leaving only a one-dimensional degree of freedom for co-variation. Many traits, such as specific respiration rate and feeding rate, are functions of DEB parameters and show predicted co-variation with maximum weight across species. Adaptation causes deviations from the assumption that intensive parameters are the same for all species.
This is the topic of the other four patterns.

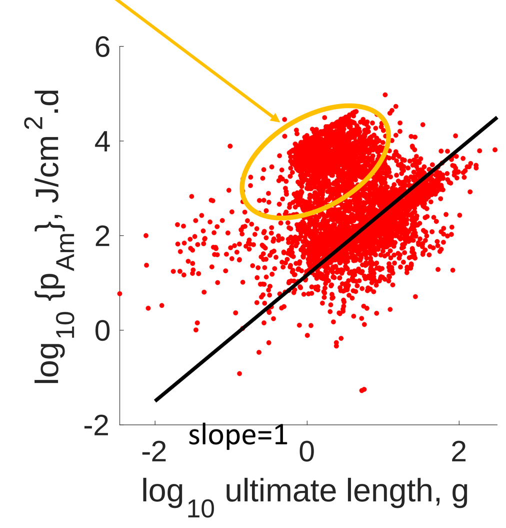
Waste-to-hurry

The waste-to-hurry strategy refers to the simultaneous increase in both specific somatic maintenance $[\dot{p}_M]$ and specific assimilation $\{\dot{p}_{Am}\}$. The κ-rule of DEB theory implies that this strategy enhances growth and to some extent also reproduction. Small-bodied species that experience seasonal short periods of food abundance typically evolve this strategy, effectively coping with food scarcity between these periods by combining it with other adaptations like torpor, migration, and rest stages.

waste-to-hurry strategists



Waste to hurry species achieve high growth (and reproduction) by being wasteful (high maintenance, so dissipation).

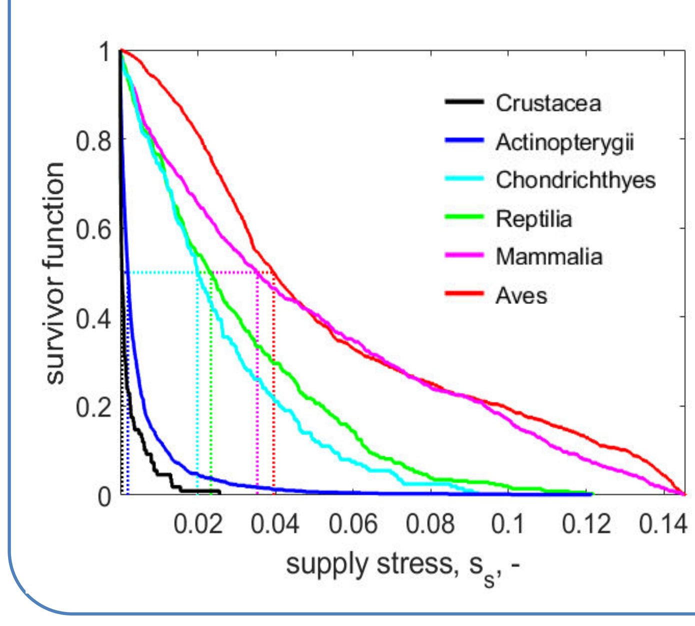


Supply–demand spectra

Species can be ordered based on a supply–demand spectrum, which provides a rough approximation of where the control of energy flows are: from environmental to internal processes. The structure of the DEB models is a mix of components with supply (growth, maturation/reproduction) and demand (somatic and maturity maintenance) organization. The table lists inter-linked stylized traits.

The supply-demand spectrum is quantified by the dimensionless **supply stress** $s_s = \frac{p_J p_M^2}{p_A^3}$, the ratio of the maturity maintenance times the squared somatic one and the cubed assimilation rate. It takes values between 0 (extreme supply) and 4/27 (extreme demand), and is independent of structural length.

Supply	Demand
Eat what is available	Eat what is needed
Large half saturation coefficient	Small half saturation coefficient
Rather passive, simple behaviour	Rather active, complex behaviour
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	Behavioural birth control
No upregulation for reproduction	Upregulation for reproduction
No acceleration of ageing	Acceleration of ageing
Evolutionary ancestral	Evolved from supply systems
Has demand components (maintenance)	Has supply components (some food must be available)



Mammals and **birds** are near the demand-end of supply–demand spectrum, **chondrichthyans** and **reptiles** clearly show demand properties. **Actinopterygians** and **crustaceans** are near the supply-end.

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DEB papers on parameter patterns

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