DEB model description: 'hex'

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This document specifies the typified DEB model 'hex' (Marques et al., 2018). The 'hex' typified model is a DEB model for holometabolic insects (and some other hexapods). Its characteristics are

○ morphological life stages: egg, larva, (pupa), imago; functional stages: embryo, adult, (pupa), imago

○ the embryo still behaves like the std-model

○ the larval stage accelerates (V1-morph) and behaves as adult, i.e. no maturation, allocation to reproduction and $E_H^b = E_H^p$.

○ pupation occurs when reproduction buffer density hits a threshold, $E_R/L^3 = [E_R^j]$

○ pupa behaves like an isomorphic embryo of the std-model, emergence occurs at $E_H = E_H^e$; larval structure rapidly transforms to pupal reserve just after start of pupation, and sets $E_H = 0$ at j.

○ the reproduction buffer remains unchanged during the pupal stage

○ the imago does not grow or allocate to reproduction. Imago's reserve mobilisation matched somatic plus maturity maintenance $\dot{p}_C = \dot{p}_M + \dot{p}_J$.

Hemi-metabolic insects skip the pupal stage, don't convert larval structure to reserve. Imago structure equals larval structure when reproduction buffer density hits a threshold. The model is discussed in the comments for Section 7.8.

For $\dot{k}_E = \dot{v}/L_b$, reserve mobilisation prior to pupation (i.e. during acceleration) is $\dot{p}_C = E(\dot{k}_E - \dot{r})$ with $\dot{r} = \frac{\kappa[E]\dot{k}_E - [\dot{p}_M]}{\kappa[E] + [E_G]} = g\dot{k}_M \frac{e/l_b - 1}{e + g}$. The larva allocates to reproduction as $\dot{p}_R = (1 - \kappa)\dot{p}_C - \dot{p}_J$, with $\dot{p}_J = \dot{k}_J E_H^p$. $[E_R]$ has a maximum at $[E_R^m] = [E_R^{\text{ref}}]f\frac{1-l_b}{f-l_b}$ with$[E_R^{\text{ref}}] = (1 - \kappa)[E_m]\frac{g+l_b}{1-l_b}$, so pupation occurs when $[E_R] = s_j[E_R^{\text{ref}}]$, with $s_j = [E_R^j]/[E_R^{\text{ref}}]$.

Reserve mobilisation of the imago is $\dot{p}_C = \dot{p}_M^e + \dot{p}_J^e$, where $\dot{p}_M^e = [\dot{p}_M]L_e^3$ and $\dot{p}_J^e = \dot{k}_J E_H^e$.

1 Background

1.1 Life-stages

It serves to understand the difference between morphological life-stages and functional lifestage. Morphological life-stage are attributed based on a description of the species or group. For example an insect might have the following morphological life stages: egg, larva, (sub)imago. A bird could have: egg, chick, (immature)adult. A human mammal: fetus, baby, child, teenager, adult. Something like a cheetah has a fetus, cubs, juveniles and adults. There are many reproductive strategies, and some groups have species with a fetus-like development and others who lay eggs.

So one could make a rather long list of all types of morphological life-stages used to describe different part of the life-cycle across all animal kingdom. Dynamic energy Budget theory provides a synthetic description of the life-cycle of all animals using a reduced list of functional stages:

embryo, juvenile, adult, and imago. A single model captures the full life-cycle from conception to death and transitions between functional life-stages are construed as switches.

Fetuses and eggs are embryo's: they grow, mature and do not feed. Babies, children, cubs, (some) larvae are all "juveniles": the grow, feed and mature but do not yet reproduce. Sometimes finding out what functional life stage best describes a morphological life-stage is the result of some investigation.

1.2 A unified energetic basis captures animal biodiversity

As the number of species grew, for which DEB models were applied to animal taxa (over 3000 from all major phyla as of (2022/02/01) it became evident that the standard DEB model, 'std' required simple extensions for particular taxa, e.g. to accommodate larval life stages, foetal development, various forms of metabolic acceleration Kooijman (2014), substantial programmed shrinking (observed for Elopocephalai a mega cohort of ray-finned fish that includes eels) etc.

A typified model can now be selected from a set, see the **Typified models** page of the DEBwiki: . The choice of typified model depends on higher-level classifications, not on the species-level. These related models belong to three families **s** , **a** and **h**. Their relative frequency within the online AmP database is updated with each new entry:

The **s**–models apply to most animal species without larval phases, like birds or some crustaceans. Models for mammals are part of this model family but deviate from the standard model by having a fetus, the production of milk mostly by females and a diet-switch of the juvenile at weaning. Most mammals also delay start of fetal development during gestation (so-called diapause).

The **a**–models apply to most species with a larval phase. The analysis of data for thousands of animals revealed that these species show metabolic acceleration at, or soon after, birth; the end of acceleration frequently coincides with morphological metamorphosis. Enthognaths, (which include springtails) and arachnids (spiders) are examples of species who can sometimes substantially accelerate their metabolism while they do not have clear larval stages nor morphological metamorphosis. Since the oldest animal group, the Radiata, and the oldest deuterostomes, the echinoderms, accelerate, it might well be that acceleration became suppressed in several other groups and this suppression evolved several times in evolution Kooijman (2014).

The **h**–models mostly apply to insects (also included in the hexapods). Most insects seem to skip the juvenile phase and allocate to reproduction as larvae, which classifies them as adult in DEB terms, while the imago neither grows, nor eats (frequently). Holometabolic insects insert a pupal phase between the larval and imago phases that behaves like an embryo with a reproduction buffer, where most of the larval structure is first converted to reserve Llandres et al. (2015) and imago structure is build from reserve.

Delayed stage transitions are also accounted for in the different model families. Most mammals delay start of fetal development during gestation. Some bivalves delay the start of metabolic acceleration; this phenomenon can prove to be more common with the increase of available data.

1.3 ressources

This small movie provides the overview of the related family of DEB models for animals: `https://youtu.be/E4ag2-WzhmQ`.

2 Notation and units

All if the symbols, and their dimensions, used herein are defined in the DEB notation document. The AmP collection contains 11 related DEB models.

Table 1: The assumptions that specify the standard DEB model quantitatively. This is a copy of Table 2.4 from Kooijman (2010)
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1 The amounts of reserve, structure and maturity are the state variables of the individual; reserve and structure have a constant composition (strong homeostasis) and maturity represents information.

2 Substrate (food) uptake is initiated (birth) and allocation to maturity is redirected to reproduction (puberty) if maturity reaches certain threshold values.

3 Food is converted into reserve and reserve is mobilised at a rate that depends on the state variables only to fuel all other metabolic processes.

4 The embryonic stage has initially a negligibly small amount of structure and maturity (but a substantial amount of reserve). The reserve density at birth equals that of the mother at egg formation (maternal effect). Foetuses develop in the same way as embryos in eggs, but at a rate unrestricted by reserve availability.

5 The feeding rate is proportional to the surface area of the individual and the food–handling time is independent of food density.

6 The reserve density *at constant food density* does not depend on the amount of structure (weak homeostasis).

7 Somatic maintenance is proportional to structural volume, but some components (osmosis in aquatic organisms, heating in endotherms) are proportional to structural surface area.

8 Maturity maintenance is proportional to the level of maturity

9 A fixed fraction of mobilised reserves is allocated to somatic maintenance plus growth, the rest to maturity maintenance plus maturation or reproduction (the κ-rule).

10 The individual does not change in shape during growth (isomorphism). This assumption applies to the standard DEB model only.

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3 Specification of the 'std' model

All models are variations on the standard ('std') model which is specified as follows, where the environmental variables, temperature $T(t)$ and food density $X(t)$, can change in time t. All models handle environmental variables in the same way:

Effect of temperature on any rate $\dot{k}$:

Basic: $\quad \frac{\dot{k}(T)}{\dot{k}(T_{\text{ref}})} = \exp\left(\frac{T_A}{T_{\text{ref}}} - \frac{T_A}{T}\right)$

Extended: $\quad \frac{\dot{k}(T)}{\dot{k}(T_{\text{ref}})} = \exp\left(\frac{T_A}{T_{\text{ref}}} - \frac{T_A}{T}\right) \frac{1 + \exp\left(\frac{T_{AL}}{T_{\text{ref}}} - \frac{T_{AL}}{T_L}\right)_+ + \exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_{\text{ref}}}\right)_+}{1 + \exp\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right)_+ + \exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right)_+}$

Effect of food on assimilation:

if $E_H < E_H^b$, $\dot{p}_X = 0$, else $\dot{p}_X = f\{\dot{p}_{Xm}\}L^2$ with $f = \frac{X}{K+X}$ and $K = \frac{\{\dot{J}_{Xm}\}}{\{\dot{F}_m\}}$ and $\{\dot{p}_{Xm}\} = \{\dot{p}_{Am}\}/\kappa_X$

3.1 std model

The std-model follows from the assumptions as listed in Table 1.

Within the family of DEB models, the std-model can be seen as a canonical form.

Main characteristics:

○ 1 type of food X, 1 type of structure V, 1 type of reserve E, 1 type of feces P

○ 4 minerals (carbon dioxide C, water H, dioxygen O, N-waste N); O is not limiting

- 3 life stages (embryo, juvenile, adult) triggered by maturity thresholds
  - birth is defined as start of assimilation via food uptake
  - puberty as end of maturation and start of allocation to reproduction
- If mobilisation is not fast enough to cover maturity and/or somatic maintenance, rejuvenation and/or some shrinking can occur, but only after use of the reproduction buffer
- The reproduction buffer is continuously converted to a spawning buffer, which is instantaneously converted to exported eggs, if the spawning buffer exceeds a density threshold

Parameters:

Temperature: $T_A, T_L, T_H, T_{AL}, T_{AH}$

Hazard: $\ddot{h}_a, s_G, \delta_L, \dot{h}_J, \dot{h}_0, \dot{h}_0^e$

Life stage: E_H^b, E_H^p

Core: $\{\dot{F}_m\}, \{\dot{p}_{Am}\}, [\dot{p}_M], \{\dot{p}_T\}, \dot{k}_J, \dot{k}_J', \dot{v}, [E_G], \kappa, \kappa_X, \kappa_P, \kappa_R, [E_R^s]$

Chemical: $[M_V], \boldsymbol{d}_\mathcal{O} = (\begin{array}{cccc} d_X & d_V & d_E & d_P \end{array}), \boldsymbol{\mu}_\mathcal{O} = (\begin{array}{cccc} \overline{\mu}_X & \overline{\mu}_V & \overline{\mu}_E & \overline{\mu}_P \end{array}), \boldsymbol{n}_\mathcal{M}, \boldsymbol{n}_\mathcal{O}^d,$
where the chemical coefficients for minerals and (dry) organic compounds are

$$\boldsymbol{n}_\mathcal{M} = \begin{pmatrix} 1 & 0 & 0 & n_{CN} \\ 0 & 2 & 0 & n_{HN} \\ 2 & 1 & 2 & n_{ON} \\ 0 & 0 & 0 & n_{NN} \end{pmatrix} \text{ and } \boldsymbol{n}_\mathcal{O}^d = \begin{pmatrix} 1 & 1 & 1 & 1 \\ n_{HX}^d & n_{HV}^d & n_{HE}^d & n_{HP}^d \\ n_{OX}^d & n_{OV}^d & n_{OE}^d & n_{OP}^d \\ n_{NX}^d & n_{NV}^d & n_{NE}^d & n_{NP}^d \end{pmatrix}.$$

If the N-waste is ammonia, we have $n_{CN} = 0, n_{HN} = 3, n_{ON} = 0, n_{NN} = 1$.

Help quantities (for the specification of changes in state):

wet/dry mass: The chemical coefficients of wet organic mass $n_{*_1*_2}^w$ relate to that of dry mass $n_{*_1*_2}^d$ for $*_1 \in \{H, O\}$ and $*_2 \in \{X, V, E, P\}$ as $n_{H*_2}^w = 2x_{*_2} + n_{H*_2}^d$ and $n_{O*_2}^w = x_{*_2} + n_{O*_2}^d$, while $n_{C*_2}^w = n_{C*_2}^d$ and $n_{N*_2}^w = n_{N*_2}^d$, where $x_{*_2} = \frac{1 - d_{*_2}^d/d_{*_2}^w}{18}$, while $d_{*_2}^w \simeq 1\,\mathrm{g/cm^3}$.

mass fluxes: $\boldsymbol{\dot{J}}_\mathcal{O} = (\begin{array}{cccc} \dot{J}_X & \dot{J}_V & (\dot{J}_E + \dot{J}_{E_R}) & \dot{J}_P \end{array})$ relate to energy fluxes $\boldsymbol{\dot{p}} = (\begin{array}{ccc} \dot{p}_A & \dot{p}_D & \dot{p}_G \end{array})$, as

$$\boldsymbol{\dot{J}}_\mathcal{O} = \boldsymbol{\eta}_\mathcal{O}\boldsymbol{\dot{p}} \text{ with } \boldsymbol{\eta}_\mathcal{O} = \begin{pmatrix} -\frac{1}{\kappa_X \overline{\mu}_X} & 0 & 0 \\ 0 & 0 & \frac{\kappa_G}{\overline{\mu}_V} \\ \frac{1}{\overline{\mu}_E} & -\frac{1}{\overline{\mu}_E} & -\frac{1}{\overline{\mu}_E} \\ \frac{\kappa_P}{\kappa_X \overline{\mu}_P} & 0 & 0 \end{pmatrix} \text{ and } \kappa_G = \overline{\mu}_V \frac{[M_V]}{[E_G]}$$

assimilation: $\dot{p}_A = \kappa_X \dot{p}_X$

somatic maintenance: $\dot{p}_S = [\dot{p}_S]L^3$. If $E_H < E_H^b$, $[\dot{p}_S] = [\dot{p}_M]$, else $[\dot{p}_S] = [\dot{p}_M] + \{\dot{p}_T\}/L$

maturity maintenance: if $(1 - \kappa)\dot{p}_C > \dot{k}_J E_H$ (no rejuvenation), $\dot{p}_J = \dot{k}_J E_H$, else $\dot{p}_J = \dot{k}_J' E_H$

mobilization: $\dot{p}_C = E(\dot{v}/L - \dot{r})$. If $[E] \geq \frac{[\dot{p}_S]L}{\dot{v}\kappa}$ (no shrinking), $\dot{r} = \frac{[E]\dot{v}/L - [\dot{p}_S]/\kappa}{[E] + [E_G]/\kappa}$, else if $E_R > 0$, $\dot{r} = 0$, or if $E_R \leq 0$, $\dot{r} = \frac{[E]\dot{v}/L - [\dot{p}_S]/\kappa}{[E] + [E_G]\kappa_G/\kappa}$ (shrinking)

growth: $\dot{p}_G = \kappa\dot{p}_C - \dot{p}_S$, but if $\kappa\dot{p}_C < \dot{p}_S$ and $E_R > 0$: $\dot{p}_G = 0$

maturation/reproduction: $\dot{p}_R = (1 - \kappa)\dot{p}_C - \dot{p}_J$, but if $(1 - \kappa)\dot{p}_C < \dot{p}_J$ and $E_R > 0$: $\dot{p}_R = 0$

dissipation: if $E_H < E_H^p$, $\dot{p}_D = \dot{p}_S + \dot{p}_J + \dot{p}_R$, else $\dot{p}_D = \dot{p}_S + \dot{p}_J + (1 - \kappa_R)\dot{p}_R$

Initial states: $L(0) = 0, E_H(0) = 0, E_R(0) = 0, \ddot{q}(0) = 0, \dot{h}_A(0) = 0$ and $E(0) = E_0$ such that $[E](a_b)$ equals that of mother at egg production

Changes in state:

structure: $\frac{d}{dt}L = L\dot{r}/3$. So, initial change is $\frac{d}{dt}L(0) = \dot{v}/3$

reserve: If $E_H < E_H^b$ (embryo), $\frac{d}{dt}[E] = -[E]\dot{v}/L$, else $\frac{d}{dt}[E] = (\{\dot{p}_{Am}\}f - [E]\dot{v})/L$

maturity: If $E_H < E_H^p$ (embryo or juvenile), $\frac{d}{dt}E_H = \dot{p}_R$, else $\frac{d}{dt}E_H = 0$. However, if $\dot{p}_J < 0$ and $E_R = 0$ (rejuvenation), $\frac{d}{dt}E_H = \dot{p}_J'$ with $\dot{p}_J' = \min(0, \dot{p}_J\dot{k}_J'/\dot{k}_J)$

buffer: If $E_H = E_H^p$ (adult), $\frac{d}{dt}E_R = \dot{p}_R - \dot{p}'_J - \dot{p}'_G$, else $(E_H < E_H^p)$ $\frac{d}{dt}E_R = 0$. If adult and $E_R > 0$, $\dot{p}'_G = \max(0, [\dot{p}_S]L^3 - \kappa\dot{p}_C)$, else $(E_R \leq 0)$ $\dot{p}'_J = 0$ and $\dot{p}'_G = 0$. The buffer is partitioned as $E_R = E_R^0 + E_R^1$, where E_R^0 converts, for positive E_R^0, to E_R^1 at rate $\dot{p}_R^{\max} = \frac{1-\kappa}{\kappa}L^3\frac{[E_G]\dot{v}/L+[\dot{p}_S]}{1+g} - \dot{p}_J$ and $g = \frac{[E_G]\dot{v}}{\kappa\{\dot{p}_{Am}\}}$.

hazard: $\dot{h} = \dot{h}_A + \dot{h}_X + \dot{h}_B + \dot{h}_P$

- aging: $\frac{d}{dt}\ddot{q} = (\ddot{q}\frac{L^3}{L_m^3}s_G + \ddot{h}_a)e(\frac{\dot{v}}{L} - \dot{r}) - \dot{r}\ddot{q};$ $\frac{d}{dt}\dot{h}_A = \ddot{q} - \dot{r}\dot{h}_A$

- starving (food): If $E_H < E_H^b$, $\dot{h}_X = 0$, else if $\dot{p}_C < \frac{\dot{k}_J E_H}{1-\kappa}$, $\dot{h}_X = \dot{h}_J(1 - \frac{\dot{p}_C(1-\kappa)}{\dot{k}_J E_H})$.
  Let L_0 be the length at which $\dot{r} = 0$ for the last time.
  If $L = \delta_L L_0$, $h_X\,dt = \infty$ (instant death due to shrinking)

- accidental (background): If $E_H < E_H^b$, $\dot{h}_B = \dot{h}_B^{0b}$, else $\dot{h}_B = \dot{h}_B^{bi}$; both constant

- thinning (predation): If $E_H \geq E_H^b$, $\dot{h}_P = \frac{2}{3}\dot{r}$, else $\dot{h}_P = 0$

Input/output fluxes:

food: $\dot{J}_X = \frac{\dot{p}_A}{\kappa_X\overline{\mu}_X}$

feces: $\dot{J}_P = \frac{\kappa_P\dot{p}_A}{\kappa_X\overline{\mu}_P}$

eggs: If $E_R^1 = [E_R^s]L^3$: $\dot{R}\,dt = \kappa_R[E_R^s]L^3/E_0$ eggs are produced and E_R^1 is set to 0

minerals: $\dot{\boldsymbol{J}}_\mathcal{M} = -\boldsymbol{n}_\mathcal{M}^{-1}\boldsymbol{n}_\mathcal{O}^w\dot{\boldsymbol{J}}_\mathcal{O}$, where $\dot{\boldsymbol{J}}_\mathcal{M} = (\begin{array}{cccc} \dot{J}_C & \dot{J}_H & \dot{J}_O & \dot{J}_N \end{array})$

heat: $\dot{p}_{T+} = -\overline{\boldsymbol{\mu}}_\mathcal{O}^T\dot{\boldsymbol{J}}_\mathcal{O}$

death: at death, $[M_V]L^3$ moles of structure and $(E + E_R)/\overline{\mu}_E$ moles of reserve become available in the environment

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