

Supporting Information for “The dynamics of starvation and recovery”

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Explicit Consumption Derivation

If I were to write out an explicit mass balance for our system in a dimensional system it would be:

$$\begin{aligned}\dot{F} &= \lambda(R) F + \rho(R) H - \sigma \left(1 - \frac{R}{C}\right) F, \\ \dot{H} &= \sigma \left(1 - \frac{R}{C}\right) F - \rho(R) H - \mu H, \\ \dot{R} &= \alpha R \left(1 - \frac{R}{C}\right) - \left[\left(\frac{\rho(R)}{Y} + P\right) H + \left(\frac{\lambda(R)}{Y} + P\right) F\right]\end{aligned}\quad [1]$$

(note this is not fully explicit because I don't know how to deal with the response of σ to resources, although I have an idea for a derivation which may be necessary given the following approximations), where $\lambda(R)$ and $\rho(R)$ are the growth and recovery functions dependent on resource availability. Typically these can be written as $\lambda(R) = \lambda_{max} S(R)$ where λ_{max} is the maximum growth rate which changes with size, and $S(R)$ is a saturating function of resources, for example a Michealis-Menten or Monod function of the form $\frac{R}{k_H + R}$. In these equations Y represents the quantity of resources required to build a unit of organism (e.g. gram of mammal produced per gram of grass consumed) and P is the specific maintenance rate of resource consumption (g resource \cdot s⁻¹ \cdot g organism). If we pick F and H to have units of (g organisms \cdot m⁻²), then terms like $\frac{\rho(R)}{Y} H$ have units of (g resource \cdot m⁻² \cdot s⁻¹) which is just the net primary productivity (NPP), a natural unit for \dot{R} , and this also gives us the units of R as (g \cdot m⁻²) which is also a natural unit and is just the biomass density. In this system of units α is the growth rate of R . First, before diving into the constant values and a general nondimensionalization, let's look at the limits of the above equations in relationship to our two-state model: The saturation function should be defined by a linear regime proportional to R when $R \ll k$ and a constant value for $R \gg k$. Thus for starving individuals, where $R \ll k$, we have that $\rho(R) = \rho_{max} R/k$, and for the full class or organisms $\lambda(R) = \lambda_{max}$ such that the above relationships reduce to

$$\begin{aligned}\dot{F} &= \lambda_{max} F + \rho_{max} R H/k - \sigma \left(1 - \frac{R}{C}\right) F, \\ \dot{H} &= \sigma \left(1 - \frac{R}{C}\right) F - \rho_{max} R H/k - \mu H, \\ \dot{R} &= \alpha R \left(1 - \frac{R}{C}\right) - \left[\left(\frac{\rho_{max} R}{Y k} + P\right) H + \beta F\right]\end{aligned}\quad [2]$$

where $\beta = \frac{\lambda_{max}}{Y} + P$ which is just a constant that depends on the size of an organisms via the allometries for λ_{max} and P .

Now consider the following nondimensionalization (ignoring the $\sigma(1 - R)F$ terms which I don't have a dimensional form for yet): $F^* = fF$, $H^* = fH$, $R^* = qR$, $t^* = st$ then we would

have:

$$\begin{aligned}\dot{F}^* &= \frac{1}{s} \left[\lambda_{max} F^* + \rho_{max} \frac{R^*}{qk} H^* - \sigma \left(1 - \frac{R^*}{qC}\right) F^* \right], \\ \dot{H}^* &= \frac{1}{s} \left[\sigma \left(1 - \frac{R^*}{qC}\right) F^* - \rho_{max} \frac{R^*}{qk} H^* - \mu H^* \right], \\ \dot{R}^* &= \frac{1}{s} \left[\alpha R^* \left(1 - \frac{R^*}{qC}\right) - \frac{q}{f} \left[\left(\frac{\rho_{max} R^*}{Y k q} + P \right) H^* + \beta F^* \right] \right]\end{aligned}\quad [3]$$

Now there is a choice of factors that provides us with our original set of equations: if we pick $s = 1$, $q = 1/C$, and $f = 1/Yk$, then we are left with

$$\begin{aligned}\dot{F}^* &= \lambda_{max} F^* + \rho_2 R^* H^* - \sigma (1 - R^*) F^*, \\ \dot{H}^* &= \sigma (1 - R^*) F^* - \rho_2 R^* H^* - \mu H^*, \\ \dot{R}^* &= \alpha R^* (1 - R^*) - (\rho_2 R^* + P_2) H^* - \beta_2 F^*\end{aligned}\quad [4]$$

where $\rho_2 = C\rho_{max}/k$, $P_2 = YkP/C$, and $\beta_2 = Yk\beta/C$. Typically the value of C/k should roughly be 2. A summary of the parameters values is then: $\rho_2 = 2$ times our old ρ ; λ , σ , μ and α are all unchanged (the max notation can be dropped here and equated with the old values). Now $P = B_0 m^{3/4}$, and $Y = 18200$ (J g⁻¹) for grass [9] which allows us to calculate $P_2 = YB_0 m^{3/4}/2$ and $\beta_2 = Y/2$ (note again that $\beta = \frac{\lambda_{max}}{Y} + P$, and λ_{max} is our old value for λ). Finally, the value of α is given by the NPP divided by the corresponding biomass densities which I find to be $\alpha = 2.10 \times 10^{-9}$ (s⁻¹) in a database that I have.

Parameter Values and Estimates

Many of the parameter values employed in our model have either been directly measured in previous studies or can be estimated from combining several previous studies. Here we outline previous measurements and simple estimates of the parameters.

Standard synthesis and metabolic parameters Metabolic rate has been generally reported to follow an exponent close to $\eta = 0.75$ (e.g. [1, 2] and the supplement of [3]). We make this assumption in the current paper, although alternate exponents, which are known to vary between roughly 0.25 and 1.5 for single species

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[2], could be easily incorporated into our framework, and this variation is effectively handled by the 20% variations that we consider around mean trends. It is important to note the exponent, because it not only defines several scalings in our framework but also the value of the metabolic normalization constant, B_0 , given a set of data. For mammals the metabolic normalization constant has been reported to vary between 0.018 ($\text{W g}^{-0.75}$) and 0.047 ($\text{W g}^{-0.75}$) [3, 1], where the former value represents basal metabolic rate and the latter represents the field metabolic rate. We employ the field metabolic rate for our NSM model which is appropriate for active mammals (Table 1).

The energy to synthesize a unit of biomass, E_m , has been reported to vary between 1800 to 9500 (J g^{-1}) (e.g. [1, 2, 3]) in mammals with a mean value across many taxonomic groups of 5,774 (J g^{-1}) [2]. The unit energy available during starvation, E' , could range between 7000 (J g^{-1}), the return of the total energy stored during ontogeny [3] to a biochemical upper bound of $E' = 36,000$ (J g^{-1}) for the energetics of palmitate [4, 3]. For our calculations we use the measured value for bulk tissues of 7000 which assumes that the energy stored during ontogeny is returned during starvation [3].

For the scaling of body composition it has been shown that fat mass follows $M_{\text{fat}} = f_0 M^\gamma$, with measured relationships following $0.018M^{1.25}$ [5], $0.02M^{1.19}$ [6], and $0.026M^{1.14}$ [7]. We use the values from [6] which falls in the middle of this range. Similarly, the muscle mass follows $M_{\text{musc}} = u_0 M^\zeta$ with $u_0 = 0.383$ and $\zeta = 1.00$ [7].

The final parameters that we must consider connect the resource growth rate to the total metabolic rate of an organism. That is, we are interested in the relative rates of resource recovery and consumption by the total population. From [8] the total resource use of a population with an individual body size of M is given by $B_{\text{pop}} = 0.00061x^{-0.03}$ (W m^{-2}). Considering an energy density of 18200 (J g^{-1}) of grass [9] and an NPP between and 1.59×10^{-6} and 7.92×10^{-5} ($\text{g s}^{-1} \text{m}^{-2}$) would give a range of resource rates between 0.029 and 1.44 (W m^{-2}). This gives a ratio of total resource consumption to supply rates

between 0.00042 and 0.021, and we used a value of 0.002 in our calculations and simulations.

Table 1: Parameter values for mammals

Parameter	Value	References
η	3/4	(e.g. [1, 2, 3])
E_m	5774 (J gram^{-1})	[2, 1, 3]
E'_m	36,000	[4, 3]
B_0	0.047 ($\text{W g}^{-0.75}$)	[3]
γ	1.19	[6]
f_0	0.02	[6]
ζ	1.00	[7]
u_0	0.38	[7]

Rate equations for invaders with modified body mass If an invading subset of the resident population of mass M has an altered mass $M' = M(1 + \chi)$ where χ varies between $[-1, 1]$ ($\chi < 0$ denotes a leaner invader; $\chi > 0$ denotes an invader with more endogenous reserves), the invading population will have the following modified rates: $\sigma' = \sigma(M')$, $\rho' = \rho(M')$, $\beta' = \beta(M')$. Because we are assuming that the invading population is only modifying its endogenous energetic stores, we assume that the proportion of body mass that is non-adipose tissue remains the same as the resident population. This assumption leads to the following modified timescales:

$$\begin{aligned} t_{\sigma'} &= \frac{-M^{1/4}}{B_0/E'_m} \log \left(\frac{\epsilon_\sigma}{\chi + 1} \right), \\ t_{\rho'} &= \frac{-4M^{1/4}}{B_0/E'_m} \log \left(\frac{1 - (\epsilon_\lambda(\chi + 1))^{1/4}}{1 - (\epsilon_\lambda\epsilon_\sigma)^{1/4}} \right), \\ t_{\beta'} &= \xi B_0 (M(\chi + 1))^{3/4}. \end{aligned} \quad [5]$$

1. West GB, Brown JH, Enquist BJ (2001) A general model for ontogenetic growth. *Nature* 413:628–631.
2. Moses ME, et al. (2008) Revisiting a Model of Ontogenetic Growth: Estimating Model Parameters from Theory and Data. <http://dx.doi.org.proxy.lib.sfu.ca/10.1086/679735>
3. Hou C, et al. (2008) Energy Uptake and Allocation During Ontogeny. *Science* 322:736–739.
4. Stryer L (1995) *Biochemistry, Fourth Edition* (W.H. Freeman and Company, New York), pp 608–611.
5. Dunbrack RL, Ramsay MA (1993) The Allometry of Mammalian Adaptations to Seasonal Environments: A Critique of the Fasting Endurance Hypothesis. *Oikos* 66:336–342.

6. Lindstedt SL, Boyce MS (1985) Seasonality, Fasting Endurance, and Body Size in Mammals. *Am. Nat.* 125:873–878.
7. Lindstedt SL, Schaeffer PJ (2002) Use of allometry in predicting anatomical and physiological parameters of mammals. *Lab. Anim.* 36:1–19.
8. Allen AP, Brown JH, Gillooly JF (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* 297:1545–1548.
9. Estermann BL, Wettstein HR, Sutter F, Kreuzer M (2001) Nutrient and energy conversion of grass-fed dairy and suckler beef cattle kept indoors and on high altitude pasture. *Animal Research* 50:477–493.