

Supporting Information for “The dynamics of starvation and recovery”

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Mechanisms of Starvation and Recovery

Our overall goal is to understand the dynamics of starvation, recovery, reproduction, and resource competition, where our framework partitions starvation and reproduction into two classes of the consumer: a full class that is able to reproduce and a hungry class that experiences mortality at a given rate and is unable to reproduce. For the dynamics of growth, reproduction, and resource consumption past efforts have combined the overall metabolic rate as dictated by body size with a growth rate that is dependent on resource abundance and in turn dictates resource consumption (see Refs. (1, 2) for a brief review of this perspective). This approach has been used to understand a range of phenomena including a derivation of ontogenetic growth curves from a partitioning of metabolism into maintenance and biosynthesis (e.g. (1, 3–5)) and predictions of the steady-state resource abundance in communities of cells (2). Here we can leverage these mechanisms with several additional concepts to define our nutritional state model.

We consider the following generalized set of explicit dynamics for starvation, recovery, reproduction, and resource growth and consumption

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

where each term has a mechanistic meaning that we detail below (we will denote the dimensional equations with d before introducing the nondimensional form which is what is later derived and presented in the main text). In this set of equations $\lambda(R_d)$ and $\rho(R_d)$ are the growth and recovery functions as functions of the current resource availability. Typically these can be written as $\lambda(R_d) = \lambda_{max} S(R_d)$ or $\lambda(R_d) = \lambda_{max} S(R_d)$ where λ_{max} and ρ_{max} are the maximum growth and recovery rates respectively (each which scale with body size as discussed later), and $S(R_d)$ is a saturating function of resources, for example a Michaelis-Menten or Monod function of the form $\frac{R_d}{k + R_d}$, where k is the half-saturation constant. A simplified version of the Michaelis-Menten or Monod functional form, which captures the essential features, is a linear function that saturates to a constant value above a certain abundance of R_d . In these equations Y represents the yield coefficient (e.g. (6, 7)) which is 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_d and H_d to have units of (g organisms \cdot m⁻²), then all of the terms of \dot{R}_d , such as $\frac{\rho(R_d)}{Y} H_d$, have units of (g resource \cdot m⁻² \cdot s⁻¹) which are the units of net primary productivity (NPP) a natural choice

for \dot{R}_d . This choice also gives R_d as (g \cdot m⁻²) which is also a natural unit and is simply the biomass density. In this system of units α (s⁻¹) is the specific growth rate of R_d and C is the carrying capacity or maximum density of R_d in a particular environment.

Before describing the values of each of these constants and a general nondimensionalization of the system of equations, it is important to consider the resource regimes associated with the above equations as this leads to a simplification. As discussed above, the resource saturation function should be defined by a linear regime proportional to R_d when $R_d \ll k$ and a constant value for $R_d \gg k$. Thus for hungry individuals, H_d , where $R_d \ll k$, we have that $\rho(R_d) \approx \rho_{max} R_d/k$, and for the full class, F_d , of organisms $\lambda(R_d) \approx \lambda_{max}$ such that the above relationships reduce to

$$\begin{aligned}\dot{F}_d &= \lambda_{max} F_d + \rho_{max} R_d H_d/k - \sigma \left(1 - \frac{R_d}{C}\right) F_d, \\ \dot{H}_d &= \sigma \left(1 - \frac{R_d}{C}\right) F_d - \rho_{max} R_d H_d/k - \mu H_d, \\ \dot{R}_d &= \alpha R_d \left(1 - \frac{R_d}{C}\right) - \left[\left(\frac{\rho_{max} R_d}{Y_H k} + P_H \right) H_d + \left(\frac{\lambda_{max}}{Y_F} + P_F \right) F_d \right].\end{aligned}\quad [2]$$

We can formally nondimensionalize this system by choosing the general rescaling of $F = f F_d$, $H = f H_d$, $R = q R_d$, $t = s t_d$, in which case our system of equations becomes

$$\begin{aligned}\dot{F} &= \frac{1}{s} \left[\lambda_{max} F + \rho_{max} \frac{R}{qk} H - \sigma \left(1 - \frac{R}{qC}\right) F \right], \\ \dot{H} &= \frac{1}{s} \left[\sigma \left(1 - \frac{R}{qC}\right) F - \rho_{max} \frac{R}{qk} H - \mu H \right], \\ \dot{R} &= \frac{1}{s} \left[\alpha R \left(1 - \frac{R}{qC}\right) - \frac{q}{f} \left[\left(\frac{\rho_{max} R}{Y_H k q} + P_H \right) H + \left(\frac{\lambda_{max}}{Y_F} + P_F \right) F \right] \right].\end{aligned}\quad [3]$$

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If we make the natural choice of $s = 1$, $q = 1/C$, and $f = 1/Y_H k$, then we are left with

$$\begin{aligned}\dot{F} &= \lambda F + \xi \rho R H - \sigma (1 - R) F, \\ \dot{H} &= \sigma (1 - R) F - \xi \rho R H - \mu H, \\ \dot{R} &= \alpha R (1 - R) - (\rho R + \delta) H - \beta F\end{aligned}\quad [4]$$

where we have dropped the subscripts on λ_{max} and ρ_{max} for simplicity, and $\xi = C/k$, $\delta = Y_H k P_H / C$, and $\beta = Y_H k \left(\frac{\lambda_{max}}{Y_F} + P_F \right) / C$. The above equations represent the system of equations presented in the main text.

Parameter Values and Estimates

All 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. Below we outline previous measurements and simple estimates of the parameters.

Metabolic rate has been generally reported to follow an exponent close to $\eta = 0.75$ (e.g. (3, 4) and the supplement of (5)). 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 (4), 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 $0.018 \text{ (W g}^{-0.75}\text{)}$ and $0.047 \text{ (W g}^{-0.75}\text{)}$ (3, 5), 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).

An important feature of our is the starting size, m_0 , of a mammal which adjusts the overall timescales for reproduction. This starting size is known to follow an allometric relationship with adult mass of the form ... where estimates for ... range between ... (). We choose ...

The energy to synthesize a unit of biomass, E_m , has been reported to vary between 1800 to 9500 (J g⁻¹) (e.g. (3-5)) in mammals with a mean value across many taxonomic groups of 5,774 (J g⁻¹) (4). The unit energy available during starvation, E' , could range between 7000 (J g⁻¹), the return of the total energy stored during ontogeny (5) to a biochemical upper bound of $E' = 36,000 \text{ (J g}^{-1}\text{)}$ for the energetics of palmitate (5, 8). 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 (5).

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 $0.018 M^{1.25}$ (9), $0.02 M^{1.19}$ (10), and $0.026 M^{1.14}$ (11). We use the values from (10) which falls in the middle of this range. Similarly, the muscle mass follows $M_{\text{muscle}} = u_0 M^\zeta$ with $u_0 = 0.383$ and $\zeta = 1.00$ (11).

We also 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 (12) the total resource use of a population with an individual body size of M is given by $B_{\text{pop}} = 0.00061 x^{-0.03} \text{ (W m}^{-2}\text{)}$. Considering an energy density of 18200 (J g⁻¹) of grass (13) and an NPP between and 1.59×10^{-6} and $7.92 \times 10^{-5} \text{ (g s}^{-1} \text{ m}^{-2}\text{)}$ 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.

Typically the value of $\xi = C/k$ should roughly be 2. The value of ρ , λ , σ , and μ are all simple rates (note that we have not rescaled time in our nondimensionalization) as defined in the maintext. Given that our model considers transitions over entire stages of ontogeny or nutritional states the value of Y must represent yields integrated over entire life stages. Given an energy density of $E_d = 18200 \text{ (J g}^{-1}\text{)}$ for grass (13) the maintenance value is given by $P_F = B_0 M^{3/4} / M E_d$, and the yield for a full organism will be given by $Y_F = M E_d / B_\lambda \text{ (g individual}^{-1} \text{ g grass}^{-1}\text{)}$ where B_λ is the lifetime energy use for reaching maturity given by

$$B_\lambda = \int_0^{t_\lambda} B_0 m(t)^\eta dt. \quad [5]$$

Similarly, the maintenance for hungry individuals $P_H = B_0 (\epsilon_\sigma M)^{3/4} / (\epsilon_\sigma M) E_d$ and the yield for hungry individuals (representing the cost on resources to return to the full state) is given by $Y_H = M E_d / B_\rho$ where

$$B_\rho = \int_{\tau(\epsilon_\sigma \epsilon_\lambda)}^{t_\lambda} B_0 m(t)^\eta dt. \quad [6]$$

which, in combination, allows us to calculate δ and β .

Finally, the value of α can be roughly estimated by the NPP divided by the corresponding biomass densities. This has a range of $Value$ to $Value$ globally. It should be noted that the value of α sets the overall scale of the F^* and H^* steady states along with the B_{tot} for each type, and as such, we use α as our fit parameter such that these steady states match the scale of known data from Damuth (14). We find that the best fit is $\alpha = 9.45 \times 10^{-9} \text{ (s}^{-1}\text{)}$. However, two points are important to note here: first, our overall framework predicts the overall scaling of F^* and H^* independently of α and this correctly matches data, and second, the asymptotic behavior of F^* and H^* is also independent of α , that is, our prediction of the maximum mammal size does not depend on α .

Table 1: Parameter values for mammals

Parameter	Value	References
η	3/4	(e.g. (3-5))
E_m	5774 (J gram ⁻¹)	(3-5)
E'_m	36,000	(5, 8)
B_0	0.047 (W g ^{-0.75})	(5)
γ	1.19	(10)
f_0	0.02	(10)
ζ	1.00	(11)
u_0	0.38	(11)

Rate equations for invaders with modified body mass We allow an invading subset of the resident population with mass M to have an altered mass $M' = M(1 + \chi)$ where χ varies between $\chi_{\min} < 0$ and $\chi_{\max} > 0$, where $\chi < 0$ denotes a leaner invader and $\chi > 0$ denotes an invader with additional endogenous reserves. Importantly, we assume that the invading and resident individuals have the same proportion of non-fat tissues. Thus χ is limited by the proportion of lean mass, such that $\chi_{\min} = -f_0 M^{\gamma-1}$. Similarly, we assume that the invading organisms do not add endogenous reserves above the asymptotic mass of the species M , such that $(1 + \chi)\epsilon_\lambda M < M$, and $\chi_{\max} \approx 0.05$.

Although the starved state of invading organisms remains unchanged, the rate of starvation from the modified full state to the starved state, the rate of recovery from the starved state to

the modified full state, and the maintenance rates of both, will be different, such that $\sigma' = \sigma(M')$, $\rho' = \rho(M')$, $\beta' = \beta(M')$, $\delta' = \delta(M')$. Rates of starvation and recovery for the invading population are easily derived by adjusting the starting or ending state before and after starvation and recovery, leading to the following timescales:

$$t_{\sigma'} = \frac{-M^{1/4}}{B_0/E'_m} \log \left(\frac{\epsilon_\sigma}{\chi + 1} \right), \quad [7]$$

$$t_{\rho'} = \frac{-4M^{1/4}}{B_0/E'_m} \log \left(\frac{1 - (\epsilon_\lambda(\chi + 1))^{1/4}}{1 - (\epsilon_\lambda\epsilon_\sigma)^{1/4}} \right).$$

The maintenance rates for the invading population require more careful consideration. First, we must recalculate the yields Y , as they must now be integrated over life stages that have also been slightly modified by the addition or subtraction of endogenous reserves. Given an energy density of $E_d = 18200$ (J g⁻¹) for grass (13) the maintenance value of the invading population is given by $P_F = B_0(1 + \chi)M^{3/4}/(1 + \chi)ME_d$, and the yield for a full organism will be given by $Y_F = (1 + \chi)ME_d/B'_\lambda$ (g individual · g grass⁻¹) where B'_λ is the lifetime energy use for the invading population reaching maturity given by

$$B'_\lambda = \int_0^{t_{\lambda'}} B_0 m(t)^\eta dt. \quad [8]$$

where

$$t_{\lambda'} = \frac{-4M^{1/4}}{B_0/E_m} \log \left(\frac{1 - (m_0/M)^{1/4}}{(1 - \epsilon_\lambda(1 + \chi))^{1/4}} \right). \quad [9]$$

Note that we do not use this timescale to determine the reproductive rate of the invading consumer—which is assumed to remain the same as the resident population—but only to calculate the lifetime energy use. Similarly, the maintenance for hungry individuals $P'_H = B_0(\epsilon_\sigma(1 + \chi)M)^{3/4}/(\epsilon_\sigma(1 + \chi)ME_d)$ and the yield for hungry individuals (representing the cost on resources to return to the full state) is given by $Y'_H = (1 + \chi)ME_d/B'_\rho$ where

$$B'_\rho = \int_{\tau(\epsilon_\sigma\epsilon_\lambda)}^{t_{\lambda'}} B_0 m(t)^\eta dt. \quad [10]$$

Finally, we can calculate the maintenance of the invaders as

$$\delta' = P'_H Y'_H / \xi \quad [11]$$

$$\beta' = \left(\frac{\lambda_{\max}}{Y'_F} + P'_F \right) Y'_H / \xi$$

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