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 for the steady-state resource abundance in communities of cells (2). Here we leverage these mechanisms, combined with several additional concepts, to define our Nutritional State Model (NSM).

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

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

[1]

where each term has a mechanistic meaning that we detail below (we will denote the dimensional equations with $_d$ before introducing the non-dimensional form that is presented in the main text). In this set of equations $\lambda\left(R_d\right)$ and $\rho\left(R_d\right)$ are the growth and recovery rates as functions of the current resource availability. Typically these can be written as $\lambda\left(R_d\right) = \lambda_{max}S\left(R_d\right)$ or $\lambda\left(R_d\right) = \lambda_{max}S\left(R_d\right)$ where λ_{max} and ρ_{max} are the maximum growth and recovery rates respectively, which scale with body size as discussed later, and $S\left(R_d\right)$ is a saturating function of resources. The saturating function could, for example, be 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 the above equations Y represents the yield coefficient (e.g., Refs. 6, 7) which is the quantity of resources required to build a unit of organism (gram of mammal produced per gram of resource consumed) and P is the specific maintenance rate of resource consumption (g resource · s^{-1} · g organism). If we pick F_d and H_d to have units of (g organisms · 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 · m^{-2} · 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 · 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 non-dimensionalization of the system of equations, it is important to consider the resource regimes associated with the above equations which lead to a simplification. As discussed above, the resource saturation function should be defined by a linear regime proportional to R_d when $R_d << k$, and a constant value for $R_d >> k$. Thus for hungry individuals, H_d, where $R_d << k$, we have that $\rho\left(R_d\right) \approx \rho_{max}R_d/k$, and for the full class, F_d, of organisms $\lambda\left(R_d\right) \approx \lambda_{max}$, such that the above relationships reduce to

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

[2]

We can formally non-dimensionalize this system by choosing the general rescaling of $F = fF_d$, $H = fH_d$, $R = qR_d$, $t = st_d$, in which case our system of equations becomes

$$\dot{F} = \frac{1}{s}\left[\lambda_{max}F + \rho_{max}\frac{R}{qk}H - \sigma\left(1 - \frac{R}{qC}\right)F\right],$$
$$\dot{H} = \frac{1}{s}\left[\sigma\left(1 - \frac{R}{qC}\right)F - \rho_{max}\frac{R}{qk}H - \mu H\right],$$
$$\dot{R} = \frac{1}{s}\left[\alpha R\left(1 - \frac{R}{qC}\right) - \frac{q}{f}\left[\left(\frac{\rho_{max}R}{Y_Hkq} + P_H\right)H + \left(\frac{\lambda_{max}}{Y_F} + P_F\right)F\right]\right].$$

[3]

Reserved for Publication Footnotes

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

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

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., Refs. 3, 4 and the supplement for Ref. 5). We make this assumption in the current paper, although alternate exponents, which are know 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. The exponent 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 (W g$^{-0.75}$) and 0.047 (W g$^{-0.75}$; Refs. 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 framework 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 $m_0 = n_0 M^v$ where estimates for the exponent range between 0.71 and 0.94 (see Ref. 8 for a review). We use $m_0 = 0.097 M^{0.92}$ (9) which encompasses the widest range of body sizes (8).

The energy to synthesize a unit of biomass, E_m, has been reported to vary between 1800 to 9500 (J g^{-1}) (e.g. Refs. 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 $E' = 36,000$ (J g^{-1}) for the energetics of palmitate (5, 10). 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 $M_{fat} = f_0 M^{\gamma}$, with measured relationships following $0.018 M^{1.25}$ (11), $0.02 M^{1.19}$ (12), and $0.026 M^{1.14}$ (13). We use the values from (12) which falls in the middle of this range. Similarly, the muscle mass follows $M_{musc} = u_0 M^{\zeta}$ with $u_0 = 0.383$ and $\zeta = 1.00$ (13).

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 non-dimensionalization) 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 $E_d = 18200$ (J g^{-1}) for grass (14) 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 $Y_F = M E_d/B_\lambda$ (g

individual $\cdot$ g grass $^{-1}$), where B_λ is the lifetime energy use for reaching maturity given by

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

Similarly, the maintenance for hungry individuals is $P_H = B_0(\epsilon_\sigma M)^{3/4}/(\epsilon_\sigma M) E_d$, 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

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

Taken together, these relationships allow us to calculate ρ, δ, and β.

Finally, the value of α can be roughly estimated by the NPP divided by the corresponding biomass densities. From the data in Ref. 15 we estimate the value of α to range between 2.81×10^{-10} (s^{-1}) and 2.19×10^{-8} (s^{-1}) 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 to match these steady states with the data from Damuth (16). We find that the best fit is $\alpha = 9.45 \times 10^{-9}$ (s^{-1}) which compares well with the calculated range above. However, two points are important to note here: first, our framework predicts the overall scaling of F^* and H^* independently of α and this correctly matches data, and second, both the asymptotic behavior and slope of F^* and H^* are independent of α, such that 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	7000	(5, 10)
B_0	0.047 (W g$^{-0.75}$)	(5)
γ	1.19	(12)
f_0	0.02	(12)
ζ	1.00	(13)
u_0	0.38	(13)

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 reserves of body fat. Importantly, we assume that the invading and resident individuals have the same proportion of non-fat tissues. For the allowable values of χ the adjusted mass should exceed the amount of body fat, $1 + \chi > \epsilon_\sigma$, and the adjusted time to reproduce must be positive, which given our solution for $\tau(\epsilon)$ (see main text), implies that $1 - \epsilon_\lambda^{1-\eta} (1 + \chi)^{1-\eta} > 0$. Together these conditions imply that $\chi \in (-f_0 M^{\gamma-1}, 1/\epsilon_\lambda - 1)$ where the upper bound approximately equals 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:

$$t_{\sigma'} = -\frac{M^{1-\eta}}{a'} \ln\left(\frac{\epsilon_\sigma}{\chi + 1}\right), \tag{7}$$

$$t_{\rho'} = \ln\left(\frac{1 - (\epsilon_\lambda \epsilon_\sigma)^{1/4}}{1 - (\epsilon_\lambda(\chi + 1))^{1/4}}\right) \frac{M^{1-\eta}}{a'(1-\eta)}.$$

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 body fat reserves. Given an energy density of $E_d = 18200$ (J g^{-1}) for grass (14) 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 $\cdot$ g grass $^{-1}$) where B'_λ is the lifetime energy use for the invading population reaching maturity given by

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

where

$$t_{\lambda'} = \frac{M^{1-\eta}}{a(1-\eta)} \ln\left(\frac{1 - (m_0/M)^{1-\eta}}{1 - (\epsilon_\lambda(1+\chi))^{1-\eta}}\right). \tag{9}$$

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 calulate the lifetime energy use. Similarly, the maintenance for hungry individuals $P'_H = B_0(\epsilon_\sigma(1+\chi)M)^{3/4}/(\epsilon_\sigma(1+\chi)M)E_d$ and the yield for hungry individuals (representing the cost on resources to return to the full state) is given by $Y'_H = (1+\chi)ME_d/B'_\rho$ where

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

Finally, we can calculate the maintenance of the invaders as

$$\delta' = P'_H Y'_H / \xi \tag{11}$$

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

To determine whether or not the invader or resident population has an advantage, we compute $R^*(M)$ and $R^*(M' = M(1+\chi))$ for values of $\chi \in (-f_0 M^{\gamma-1}, 1/\epsilon_\lambda - 1)$, and the invading population is assumed to have an advantage over the resident population if $R^*(M') < R^*(M)$.

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