

# Supporting Information for “The dynamics of starvation and recovery”

Justin D. Yeakel<sup>\* † ‡ §</sup>, Christopher P. Kempes<sup>† ‡</sup>, and Sidney Redner<sup>† ¶ ‡</sup>

<sup>\*</sup>School of Natural Science, University of California Merced, Merced, CA, <sup>†</sup>The Santa Fe Institute, Santa Fe, NM, <sup>¶</sup>Department of Physics, Boston University, Boston MA, <sup>‡</sup>Contributed equally, and <sup>§</sup>To whom correspondence should be addressed: jdyeakel@gmail.com

Submitted to Proceedings of the National Academy of Sciences of the United States of America

## 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

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

where each term has a mechanistic meaning that we detail below (we will denote the dimensional equations with <sub>d</sub> before introducing the non-dimensional form that is presented in the main text). 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<sup>-1</sup> · g organism). If we pick  $F_d$  and  $H_d$  to have units of (g organisms · m<sup>-2</sup>), then all of the terms of  $\dot{R}_d$ , such as  $\frac{\rho(R_d)}{Y} H_d$ , have units of (g resource · m<sup>-2</sup> · s<sup>-1</sup>) 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<sup>-2</sup>) which is also a natural unit and is simply the biomass density. In this system of units  $\alpha$  (s<sup>-1</sup>) is the specific growth rate of  $R_d$ , and  $C$  is the carrying capacity, or maximum density, of  $R_d$  in a particular environment, and  $k$  is the half-saturation constant (half the density of resources that would lead to maximum growth).

We can formally non-dimensionalize 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

$$\begin{aligned}\dot{F} &= \frac{1}{s} \left[ \lambda_{max} F + \rho_{max} \frac{R}{qk} H - \sigma \left(1 - \frac{R}{qC}\right) F \right], \\ \dot{H} &= \frac{1}{s} \left[ \sigma \left(1 - \frac{R}{qC}\right) F - \rho_{max} \frac{R}{qk} H - \mu H \right], \\ \dot{R} &= \frac{1}{s} \left[ \alpha R \left(1 - \frac{R}{qC}\right) - \frac{q}{f} \left[ \left(\frac{\rho_{max} R}{Y_H k q} + P_H\right) H + \left(\frac{\lambda_{max}}{Y_F} + P_F\right) F \right] \right].\end{aligned}\quad [2]$$

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

$$\begin{aligned}\dot{F} &= \lambda F + \xi \rho R H - \sigma (1 - R) F, \\ \dot{H} &= \sigma (1 - R) F - \xi \rho R H - \mu H, \\ \dot{R} &= \alpha R (1 - R) - (\rho R + \delta) H - \beta F\end{aligned}\quad [3]$$

where we have dropped the subscripts on  $\lambda_{max}$  and  $\rho_{max}$  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 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. 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<sup>-0.75</sup>) and 0.047 (W g<sup>-0.75</sup>; Refs. 3, 5, where the former value represents basal metabolic rate and the latter represents

## Reserved for Publication Footnotes

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<sup>-1</sup>) (e.g. Refs. 3–5) in mammals with a mean value across many taxonomic groups of 5,774 (J g<sup>-1</sup>) (4). The unit energy available during starvation,  $E'$ , could range between 7000 (J g<sup>-1</sup>), the return of the total energy stored during ontogeny (5) to a biochemical upper bound of  $E' = 36,000$  (J g<sup>-1</sup>) 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  $M_{\text{fat}} = f_0 M^\gamma$ , 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  $M_{\text{muscle}} = u_0 M^\zeta$  with  $u_0 = 0.383$  and  $\zeta = 1.00$  (13).

Typically the value of  $\xi = C/k$  should roughly be 2. The value of  $\rho$ ,  $\lambda$ ,  $\sigma$ , and  $\mu$  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<sup>-1</sup>) 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 · g grass<sup>-1</sup>), where  $B_\lambda$  is the lifetime energy use for reaching maturity given by

$$B_\lambda = \int_0^{t_\lambda} B_0 m(t)^\eta dt. \quad [4]$$

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

$$B_\rho = \int_{\tau(\epsilon_\sigma \epsilon_\lambda)}^{t_\lambda} B_0 m(t)^\eta dt. \quad [5]$$

Taken together, these relationships allow us to calculate  $\rho$ ,  $\delta$ , and  $\beta$ .

Finally, the value of  $\alpha$  can be roughly estimated by the NPP divided by the corresponding biomass densities. From the data in Ref. 15 we estimate the value of  $\alpha$  to range between  $2.81 \times 10^{-10}$  (s<sup>-1</sup>) and  $2.19 \times 10^{-8}$  (s<sup>-1</sup>) globally. It should be noted that the value of  $\alpha$  sets the overall scale of the  $F^*$  and  $H^*$  steady states along with the  $B_{\text{tot}}$  for each type, and as such, we use  $\alpha$  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<sup>-1</sup>) 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  $\alpha$  and this correctly matches data, and second, both the asymptotic behavior and slope of  $F^*$  and  $H^*$

Table 1: Parameter values for mammals

Parameter	Value	References
$\eta$	3/4	(e.g. (3–5))
$E_m$	5774 (J gram <sup>-1</sup> )	(3–5)
$E'_m$	7000	(5, 10)
$B_0$	0.047 (W g <sup>-0.75</sup> )	(5)
$\gamma$	1.19	(12)
$f_0$	0.02	(12)
$\zeta$	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  $\chi$  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  $\chi$  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:

$$t_{\sigma'} = -\frac{M^{1-\eta}}{a'} \ln \left( \frac{\epsilon_\sigma}{\chi + 1} \right), \quad [6]$$

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

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<sup>-1</sup>) for grass (14) the maintenance value of the invading population is given by  $P_F = B_0 (1 + \chi) M^{3/4} / (1 + \chi) M E_d$ , and the yield for a full organism will be given by  $Y_F = (1 + \chi) M E_d / B'_\lambda$  (g individual · g grass<sup>-1</sup>) where  $B'_\lambda$  is the lifetime energy use for the invading population reaching maturity given by

$$B'_\lambda = \int_0^{t_{\lambda'}} B_0 m(t)^\eta dt. \quad [7]$$

where

$$t_{\lambda'} = \frac{M^{1-\eta}}{a(1 - \eta)} \ln \left( \frac{1 - (m_0/M)^{1-\eta}}{1 - (\epsilon_\lambda (1 + \chi))^{1-\eta}} \right). \quad [8]$$

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

161 individuals  $P'_H = B_0(\epsilon_\sigma(1+\chi)M)^{3/4}/(\epsilon_\sigma(1+\chi)M)E_d$  and the  
 162 yield for hungry individuals (representing the cost on resources  
 163 to return to the full state) is given by  $Y'_H = (1+\chi)ME_d/B'_\rho$   
 164 where

$$B'_\rho = \int_{\tau(\epsilon_\sigma\epsilon_\lambda)}^{t_{\lambda'}} B_0 m(t)^\eta dt. \quad [9]$$

165 Finally, we can calculate the maintenance of the invaders as

$$\begin{aligned} \delta' &= P'_H Y'_H / \xi \\ \beta' &= \left( \frac{\lambda_{\max}}{Y'_F} + P'_F \right) Y'_H / \xi. \end{aligned} \quad [10]$$

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

## 171 References

- 172 1. Kempes CP, Dutkiewicz S, Follows MJ (2012) Growth,  
 173 metabolic partitioning, and the size of microorganisms.  
 174 *PNAS* 109:495–500.
- 175 2. Kempes CP, Okegbe C, Mears-Clarke Z, Follows MJ, Di-  
 176 etrich LE (2014) Morphological optimization for access  
 177 to dual oxidants in biofilms. *Proceedings of the National*  
 178 *Academy of Sciences* 111:208–213.
- 179 3. West GB, Brown JH, Enquist BJ (2001) A general model  
 180 for ontogenetic growth. *Nature* 413:628–631.
- 181 4. Moses ME, et al. (2008) Revisiting a model of ontogenetic  
 182 growth: Estimating model parameters from theory and  
 183 data. <http://dx.doi.org.proxy.lib.sfu.ca/10.1086/679735>  
 184 171:632–645.
- 185 5. Hou C, et al. (2008) Energy uptake and allocation during  
 186 ontogeny. *Science* 322:736–739.
- 187 6. Pirt S (1965) The maintenance energy of bacteria in grow-  
 188 ing cultures. *Proceedings of the Royal Society of London B:*  
 189 *Biological Sciences* 163:224–231.
- 190 7. Heijnen J, Roels J (1981) A macroscopic model describing  
 191 yield and maintenance relationships in aerobic fermentation  
 192 processes. *Biotechnology and Bioengineering* 23:739–763.
- 193 8. Peters RH (1986) *The Ecological Implications of Body Size*  
 194 (Cambridge University Press, Cambridge) Vol. 2.
- 195 9. Blueweiss L, et al. (1978) Relationships between body size  
 196 and some life history parameters. *Oecologia* 37:257–272.
- 197 10. Stryer L (1995) *Biochemistry, Fourth Edition* (W.H. Free-  
 198 man and Company, New York), pp 608–611.
- 199 11. Dunbrack RL, Ramsay MA (1993) The Allometry of Mam-  
 200 malian Adaptations to Seasonal Environments: A Critique  
 201 of the Fasting Endurance Hypothesis. *Oikos* 66:336–342.
- 202 12. Lindstedt SL, Boyce MS (1985) Seasonality, Fasting En-  
 203 durance, and Body Size in Mammals. *Am. Nat.* 125:873–  
 204 878.
- 205 13. Lindstedt SL, Schaeffer PJ (2002) Use of allometry in pre-  
 206 dicting anatomical and physiological parameters of mam-  
 207 mals. *Lab. Anim.* 36:1–19.
- 208 14. Estermann BL, Wettstein HR, Sutter F, Kreuzer M (2001)  
 209 Nutrient and energy conversion of grass-fed dairy and suck-  
 210 ler beef cattle kept indoors and on high altitude pasture.  
 211 *Animal Research* 50:477–493.
- 212 15. Michaletz ST, Cheng D, Kerkhoff AJ, Enquist BJ (2014)  
 213 Convergence of terrestrial plant production across global  
 214 climate gradients. *Nature* 512:39–43.
- 215 16. Damuth J (1987) Interspecific allometry of population den-  
 216 sity in mammals and other animals: the independence of  
 217 body mass and population energy-use. *Biological Journal*  
 218 *of the Linnean Society* 31:193–246.