

Supporting Information for “The dynamics of starvation and recovery”

Justin D. Yeakel,^{1,2,3,4} Christopher P. Kempes,^{2,3,4} and Sidney Redner^{2,3,4}

¹*School of Natural Sciences, University of California, Merced, Merced, CA 95340, USA*

²*The Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA*

³*Contributed equally*

⁴*Corresponding author*

Mechanisms of Starvation and Recovery To understand the dynamics of starvation, recovery, reproduction, and resource competition, our framework partitions consumers into two classes: (a) a full class that is able to reproduce and, (b) 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 cells². 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 the subscript d 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 \cdot s⁻¹ \cdot g organism⁻¹). 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 these units α (s⁻¹) is the specific growth

rate of R_d , 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 the 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 λ_{\max} and ρ_{\max} for simplicity, and $\xi \equiv C/k$, $\delta \equiv Y_H k P_H / C$, and $\beta \equiv Y_H k \left(\frac{\lambda_{\max}}{Y_F} + P_F \right) / C$. 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 species⁴, 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 $m_0 = n_0 M^\nu$ where estimates for the exponent range between 0.71 and 0.94 (see Ref.⁸ for a review). We use $m_0 = 0.097 M^{0.929}$ which encompasses the widest range of body sizes⁸.

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 ontogeny⁵ 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 starvation⁵.

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 from¹² 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 $\zeta = 1.00$ 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 grass¹⁴ 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⁻¹), where B_λ is the lifetime energy use for reaching maturity given by

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

Similarly, the maintenance resource consumption rate 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 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 B_{tot} for each type. As such, we use α as our fit parameter to match these steady states with the data from Damuth¹⁶. 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 I: Parameter values for mammals

Definition	Parameter	Value	References
Asymptotic adult mass	M	(g)	
Initial mass of an organism	m_0	(g)	
Metabolic rate scaling exponent	η	3/4	(e.g. ³⁻⁵)
Metabolic Normalization Constant	B_0	0.047 (W g ^{-0.75})	⁵
Initial mass scaling exponent	ν	0.92	^{8,9}
Initial mass scaling normalization constant	n_0	0.097 (g ^{1-ν)}	^{8,9}
Fat mass scaling exponent	γ	1.19	¹²
Fat scaling normalization constant	f_0	0.02 (g ^{1-γ)}	¹²
Muscle mass scaling exponent	ζ	1.00	¹³
Muscle scaling normalization constant	u_0	0.38 (g ^{1-ζ)}	¹³
Energy to synthesis a unit of mass	E_m	5774 (J gram ⁻¹)	³⁻⁵
Energy to synthesis a unit of mass during recovery	E'_m	7000 (J gram ⁻¹)	^{5,10}
Specific resource growth rate	α	9.45×10^{-9} (s ⁻¹)	see text
Fraction of asymptotic mass representing full state	ϵ_λ	0.95	³
Fraction of asymptotic mass representing starving state	ϵ_σ	$1 - f_0 M^{\gamma-1}$	see text
Fraction of asymptotic mass representing death	ϵ_μ	$1 - \frac{f_0 M^\gamma + u_0 M^\zeta}{M}$	see text
Carrying capacity (maximum density) of resources	C	(g m ⁻²)	
Half Saturation Constant	k	(g m ⁻²)	
Normalized carrying capacity	ξ	$C/k \approx 2$	
Reproductive fecundity	ν	2	

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. Impor-

tantly, 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:

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

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

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⁻¹) for grass¹⁴ 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

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

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 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

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

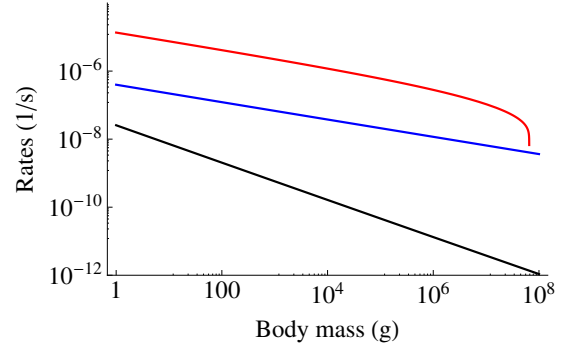


Figure S 1: The rates of reproduction λ (blue), starvation-based mortality μ (red), and survivorship-based death \bar{d} (black) as a function of adult mass.

Finally, we can calculate the maintenance of the invaders as

$$\delta' = P'_H Y'_H / \xi \quad (10)$$

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

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 $R^*(M') < R^*(M)$.

Sensitivity to additional death terms

It should be noted that our set of dynamics (Equations 1 and 3) could include a constant death term of the form $-d_F F$ and $-d_H H$ to represent death not directly linked to starvation. Adding terms of this form to our model would simply adjust the effective value of λ and μ , and we could rewrite Equation 3 with $\lambda' = \lambda - d$ and $\mu' = \mu - d$. These substitutions would not alter the functional form of our model nor the steady-states and qualitative results, however the quantitative values could shift based on the size of d relative to λ and μ .

Survivorship has a well-known functional form which changes systematically with size (e.g.¹⁷). Typically survivorship is defined using the Gompertz curve

$$F = F_0 e^{(c_0/c_1)(1 - e^{c_1 t})} \quad (11)$$

where the parameters have the following allometric dependencies on adult mass $c_0 = a_0 M^{b_0}$ and $c_1 = a_1 M^{b_1}$, with $a_0 = 1.88 \times 10^{-8}$ (s g^{-b₀}), $b_0 = -0.56$, $a_1 = 1.45 \times 10^{-7}$ (s g^{-b₁}), and $b_1 = -0.27$ (see¹⁷ for a review).

We are interested in the specific death rate of the form $\dot{F} = -dF$, and using the derivative of Equation 11 we find that $d = c_0 e^{c_1 t}$. Our model considers the average age rates over a population and lifecycle and the average

death rate is given by

$$\bar{d} = \frac{1}{t_{\text{exp}}} \int_0^{t_{\text{exp}}} c_0 e^{c_1 t} dt \quad (12)$$

$$= \frac{c_0 (e^{c_1 t_{\text{exp}}} - 1)}{c_1 t_{\text{exp}}} \quad (13)$$

where t_{exp} is the expected lifespan following the allometry of $t_{\text{exp}} = a_2 M^{b_2}$ with $a_2 = 4.04 \times 10^6$ (s g^{-b_2}) and $b_2 = 0.30$ ^{17,18}. Given the allometries above we have that

$$\bar{d} = \frac{a_0 \left(e^{a_1 a_2 M^{b_1+b_2}} - 1 \right) M^{b_0-b_1-b_2}}{a_1 a_2} \quad (14)$$

which scales roughly like M^{b_0} because b_1 and b_2 are close in value but opposite in sign. In Figure S1 we compare the value of \bar{d} to the reproductive, λ , and starvation-based mortality, μ , rates. The values of \bar{d} are orders of magnitude smaller than these rates for all mammalian masses, and thus, adding this non-starvation based death rate to our model does not shift our results within numerical confidence.

NSM and the energy equivalence hypothesis

The energy equivalence hypothesis is based on the observation that if one assumes that the total metabolism of an ecosystem B_{tot} is equally partitioned between all species (B_i , the total metabolism of one species, is a constant), then the abundances should follow $N(M) B(M) = B_i$ implying that $N(M) \propto M^{-\eta}$, where η is the metabolic scaling exponent^{19,20}. As $\eta \approx 3/4$ this hypothesis is consistent with Damuth's law¹⁹. However, the actual equivalence of energy usage of diverse species has not been measured at the population level

for a variety of whole populations. Figure S2 recasts the results of the NSM in terms of this hypothesis and shows that $F^* B$ is nearly constant over the same range of mammalian sizes up to the asymptotic behavior for the largest terrestrial mammals.

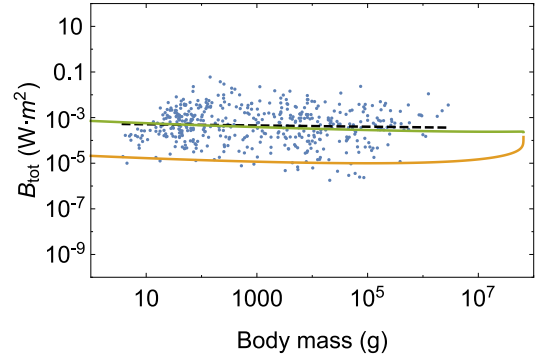


Figure S2: Total energetic use B_{tot} of consumer populations at the steady state as a function of body mass (F^* is shown in green and H^* in orange). The data are from Damuth²¹ and have been converted to total population metabolism using the allometric relationships for metabolic rate (e.g. Refs.³⁻⁵).

Application of NSM limits to aquatic mammals

A theoretical upper bound on mammalian body size is given by $\epsilon_\sigma = 0$, where mammals are entirely composed of metabolic reserves, and this occurs at $M = 8.3 \times 10^8$ (g), or 120 times the mass of a male African elephant. We note this particular limit as it may have future relevance to considerations of the ultimate constraints on aquatic mammals.

- [1] Kempes, C. P., Dutkiewicz, S. & Follows, M. J. Growth, metabolic partitioning, and the size of microorganisms. *PNAS* **109**, 495–500 (2012).
- [2] Kempes, C. P., Okegbe, C., Mears-Clarke, Z., Follows, M. J. & Dietrich, L. E. Morphological optimization for access to dual oxidants in biofilms. *Proceedings of the National Academy of Sciences* **111**, 208–213 (2014).
- [3] West, G. B., Brown, J. H. & Enquist, B. J. A general model for ontogenetic growth. *Nature* **413**, 628–631 (2001).
- [4] Moses, M. E. *et al.* Revisiting a model of ontogenetic growth: Estimating model parameters from theory and data. <http://dx.doi.org.proxy.lib.sfu.ca/10.1086/679735> **171**, 632–645 (2008).
- [5] Hou, C. *et al.* Energy uptake and allocation during ontogeny. *Science* **322**, 736–739 (2008).
- [6] Pirt, S. The maintenance energy of bacteria in growing cultures. *Proceedings of the Royal Society of London B: Biological Sciences* **163**, 224–231 (1965).
- [7] Heijnen, J. & Roels, J. A macroscopic model describing yield and maintenance relationships in aerobic fermentation processes. *Biotechnology and Bioengineering* **23**, 739–763 (1981).
- [8] Peters, R. H. *The Ecological Implications of Body Size*, vol. 2 (Cambridge University Press, Cambridge, 1986).
- [9] Blueweiss, L. *et al.* Relationships between body size and some life history parameters. *Oecologia* **37**, 257–272 (1978).
- [10] Stryer, L. *Biochemistry, Fourth Edition* (W.H. Freeman and Company, New York, 1995).
- [11] Dunbrack, R. L. & Ramsay, M. A. The Allometry of Mammalian Adaptations to Seasonal Environments: A Critique of the Fasting Endurance Hypothesis. *Oikos* **66**, 336–342 (1993).
- [12] Lindstedt, S. L. & Boyce, M. S. Seasonality, Fasting Endurance, and Body Size in Mammals. *Am. Nat.* **125**, 873–878 (1985).
- [13] Lindstedt, S. L. & Schaeffer, P. J. Use of allometry in predicting anatomical and physiological parameters of mammals. *Lab. Anim.* **36**, 1–19 (2002).
- [14] Estermann, B. L., Wettstein, H.-R., Sutter, F. & Kreuzer, M. Nutrient and energy conversion of grass-fed dairy and suckler beef cattle kept indoors and on high altitude pasture. *Animal Research* **50**, 477–493 (2001).
- [15] Michaletz, S. T., Cheng, D., Kerkhoff, A. J. & Enquist, B. J. Convergence of terrestrial plant production across global climate gradients. *Nature* **512**, 39–43 (2014).
- [16] Damuth, J. Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. *Biological Journal of the Linnean Society* **31**, 193–246 (1987).
- [17] Calder, W. A. *Size, function, and life history* (Harvard University Press, 1984).
- [18] Damuth, J. Analysis of the preservation of community struc-

- ture in assemblages of fossil mammals. *Paleobiology* **8**, 434–446 (1982).
- [19] Allen, A. P., Brown, J. H. & Gillooly, J. F. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* **297**, 1545–1548 (2002).
- [20] Enquist, B. J., Brown, J. H. & West, G. B. Allometric scaling of plant energetics and population density. *Nature* **395**, 163–165 (1998).
- [21] Damuth, J. Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. *Biol. J. Linn. Soc.* **31**, 193–246 (1987).