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

$$\dot{F}_d = \lambda_{max} F_d + \rho_{max} R_d H_d / k - \sigma \left(1 - \frac{R_d}{C} \right) F_d,$$

$$\dot{H}_d = \sigma \left(1 - \frac{R_d}{C} \right) F_d - \rho_{max} R_d H_d / k - \mu H_d,$$

$$\dot{R}_d = \alpha R_d \left(1 - \frac{R_d}{C} \right) -$$
$$\left[\left(\frac{\rho_{max} R_d}{Y_H k} + P_H \right) H_d + \left(\frac{\lambda_{max}}{Y_F} + P_F \right) F_d \right]. \quad (1)$$

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 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). 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, 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

$$\dot{F} = \frac{1}{s} \left[\lambda_{max} F + \rho_{max} \frac{R}{qk} H - \sigma \left(1 - \frac{R}{qC} \right) F \right],$$

$$\dot{H} = \frac{1}{s} \left[\sigma \left(1 - \frac{R}{qC} \right) F - \rho_{max} \frac{R}{qk} H - \mu H \right],$$

$$\dot{R} = \frac{1}{s} \left[\alpha R \left(1 - \frac{R}{qC} \right) - \frac{q}{f} \left[\left(\frac{\rho_{max} R}{Y_H kq} + P_H \right) H + \left(\frac{\lambda_{max}}{Y_F} + P_F \right) F \right] \right] \quad (2)$$

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

$$\dot{F} = \lambda F + \xi \rho R H - \sigma \left(1 - R \right) F,$$

$$\dot{H} = \sigma \left(1 - R \right) F - \xi \rho R H - \mu H, \quad (3)$$

$$\dot{R} = \alpha R \left(1 - R \right) - \left(\rho R + \delta \right) H - \beta F$$

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 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$^{-0.75}$) 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 $m_0 = 0.097 M^{0.929}$ 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 $M_{\text{fat}} = f_0 M^\gamma$, 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 $M_{\text{musc}} = u_0 M^\zeta$ 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

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

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

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

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 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 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	v	0.92	8,9
Initial mass scaling normalization constant	n_0	0.097 (g^{1-v})	8,9
Fat mass scaling exponent	γ	1.19	12
Fat scaling normalization constant	f_0	0.02 (g$^{1-\eta}$)	12
Muscle mass scaling exponent	ζ	1.00	13
Muscle scaling normalization constant	u_0	0.38 (g$^{1-\zeta}$)	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:

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

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

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 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

$$B_\lambda' = \int_0^{t_{\lambda'}} B_0 m(t)^\eta \, dt. \tag{7}$$

where

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

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 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

$$B_\rho' = \int_{\tau(\epsilon_\sigma\epsilon_\lambda)}^{t_{\lambda'}} B_0 m(t)^\eta \, dt. \tag{9}$$

Finally, we can calculate the maintenance of the invaders as

$$\delta' = P_H' Y_H'/\xi \tag{10}$$

$$\beta' = \left(\frac{\lambda_{\max}}{Y_F'} + P_F'\right) Y_H'/\xi.$$

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

I. 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 quantitive 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. Typically survivorship is defined using the Gompertz curve

$$F = F_0 e^{(q_0/c)\left(1-e^{ct}\right)} \tag{11}$$

where the parameters have the following allometric dependencies on adult mass.

We are interested in the specific death rate of the form $\cdot F = -dF$, and using the derivative of Equation 11 we find that $d = e^{ct}q_0$. Our model considers the average rates over a population and lifecycle and the average death rate is given by

$$\bar{d} = \frac{1}{t_{exp}} \int_0^{t_{exp}} e^{ct}q_0 dt \tag{12}$$

$$= \frac{q_0(e^{ct_{exp}} - 1)}{ct_{exp}} \tag{13}$$

where t_{exp} is the expected lifespan following the allometry of $t_{exp} =$. Given the allometries above we have that

$$d = \tag{14}$$

which scales roughly like $SCALING$. In figure ?? we compare the value of d to the reproductive and starvation mortality rates . The values of d are orders of magnitude smaller than these rates at all scales, and adding this non-starvation based death rate to our model does not shift our results within numerical confidence.
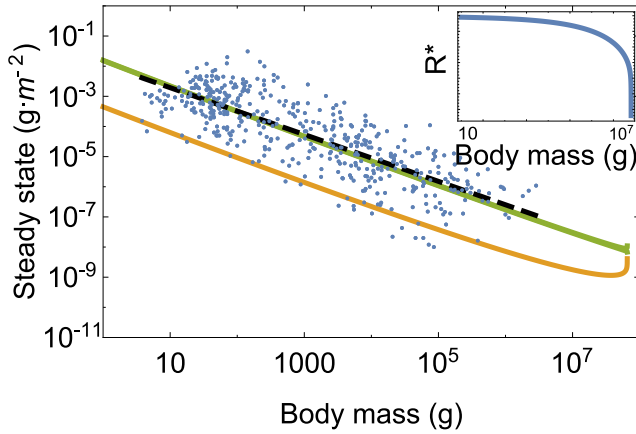
Figure 1: Total energetic use B_{tot} of consumer populations at the steady state as a function of body mass. The data are from Damuth[?] and have been converted to total population metabolism using the allometric relationships for metabolic rate (e.g. Refs.[3–5]).

II. 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[?][?]. As $\eta \approx 3/4$ this hypothesis is consistent with Damuth's law[?], however the actually equivalence of energy usage of diverse species has not been measured at the population level for a variety of whole populations. Figure 2 shows that F^*B is nearly constant over this same range.
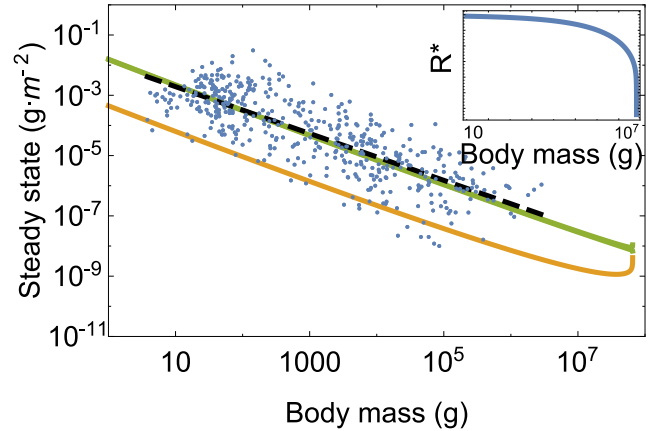

Figure 2: Total energetic use B_{tot} of consumer populations at the steady state as a function of body mass. The data are from Damuth[?] and have been converted to total population metabolism using the allometric relationships for metabolic rate (e.g. Refs.[3–5]).

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