

# The effect of starvation on the dynamics of consumer populations

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## 1 Introduction

The behavioral ecology of most, if not all, organisms is influenced by the energetic state of individuals. An individual's energetic state directly influences how it invests its stores in an uncertain environment. Such behaviors are generally manifested as trade-offs, which often concern investing in individual maintenance and growth or allocating energy towards reproduction (1, 2). The timing of these behaviors is often important and is under strong selective pressure, as they tend to have large effects on the future fitness of the organism (? ). To what extent, and when, organisms invest in these two necessary biological functions – growth and maintenance vs. reproduction – may be driven by habitat, seasonality, evolutionary history, inter- or intra-specific interactions, as well as resource limitation. Importantly, the influence of resource limitation on an organism's ability to maintain its nutritional stores may lead to repeated delays or shifts in reproduction over the course of an organism's life.

Maximizing fitness between growth and maintenance activities vs. reproductive behaviors

in large part structures the life-history of species, and this can be achieved by a variety of potential mechanisms, all of which, to some extent, depend on resource availability. [In extreme case of unicellular organisms, nutrition is unavoidably linked to reproduction because the nutritional state of the individual regulates all aspects of the cell cycle.] Behavioral: The investment of time and energy towards reproductive and parental behaviors depends on resource availability (3). For example, reindeer invest less in calves born after harsh winters (when the mother's energetic state is poor) than in calves born after moderate winters (4), whereas many bird species invest differently in broods during periods of resource scarcity (5, 6), sometimes delaying or foregoing reproduction for a breeding season (7). Freshwater and marine zooplankton have been observed to avoid reproduction under nutritional stress (8), with those that do reproduce evincing lower survival rates (1), while artificially induced stress has been observed to decrease reproductive success in Atlantic cod (9). Physiological: Diverse mammals (47 species in 10 families) exhibit delayed implantation whereby females postpone fetal development (blastocyst implantation) to time with accumulation of nutritional reserves (10, 11). Furthermore, many mammals (including humans) suffer irregular menstrual cycling and higher rates of spontaneous abortion during periods of nutritional stress (12, 13). Spatio-temporal: Organisms may also separate maintenance/growth from reproduction over space and time. For example, many salmonids, birds, and some mammals return to migratory breeding sites to reproduce after one or multiple seasons in alternative environments spent accumulating body mass and nutritional reserves (14, 15). The existence of so many independently evolved mechanisms across such a diverse suite of organisms points to the importance and universality of the fundamental tradeoff between energetic expenditures on the growth and maintenance of tissues vs. reproductive behaviors.

The different strategies employed to avoid reproduction during times of nutritional stress,

and how this is achieved among different organisms, has received tremendous empirical and theoretical attention owing to the importance of these activities in shaping life-history [REF]. Less well understood is how resource limitation and these behavioral/physiological tradeoffs affect dynamics at the level of the population. Traditional Lotka-Volterra models assume a dependence of consumer population growth rates on resource density, thus *implicitly* incorporating the requirement of resource availability for reproduction. Although this implicit dependence connects resource limitation to lower consumer growth rates, the following biological realities are not taken into account:

- some individuals experience nutritional stress at a given time and under a given set of external conditions, while others do not; those that do have multiple pathways enabling reproductive cessation,
- the portion of the population that is not nutritionally stressed is expected to reproduce at a near-constant rate, and
- the rates at which individuals transition from nutritionally poor to replete states and back are governed by the organism's metabolic capabilities of growing and maintaining tissue, which is allometrically constrained (2).

[The neglect of these features has important dynamic shortcomings:] [Here we use body size and allometries to capture a wide variety of taxonomic diversity] [There isn't a deep understanding with how models vary across different life histories, traits, etc... how do equations change with allometric constraints for different class of organisms? i.e. Use body size as a generating parameter to capture a wide variety of diversity.]

To incorporate these elements, resource limitation and the subsequent effects of starvation may be accounted for *explicitly*, such that reproductive growth of a population is permitted

only for individuals with sufficient energetic reserves. Incorporating energetic dynamics that occur at an individual level (16) into a population-based framework (16, 17), though straightforward conceptually, quickly runs into mathematical obstacles (18). [An alternative approach is to start with the macroscale patterns in order to understand certain tradeoffs etc] The complexities associated with scaling individual-level energetics to that of a population has thus limited the development of theoretical models that may aid our understanding of the effects of such tradeoffs on population dynamics.

Here we explore how the energetic tradeoff between maintaining and building tissue and reproduction, which occurs at the level of the individual, may influence the dynamics of a population. We first establish a simple nutritional state-structured population model that captures the essential dynamics of energetic reproductive tradeoffs, and explore the impact of different fluxes on system-level stability. By relating different rate constants to allometric constraints, we uncover important relationships between the timescales of physiological and reproductive processes, and show how organisms of different body sizes and taxonomic affinities are expected may be prone to different dynamics. The general rate laws that control both reproductive and energetic processes of the population, we show that

We show [WHAT]?

## 2 Methods

### 2.1 Model description

We first integrate energetics into the dynamics of a consumer-resource system by assuming that the consumer population can be divided into discrete energetic states, the occupation of each being contingent on the consumption of a single resource  $R$ . In the simplest case, there

are only two energetic states for the consumer population: *i*) an energetically replete (full) state  $F$ , where the consumer reproduces at rate  $\lambda$ , and *ii*) an energetically deficient (hungry) state  $H$ , where reproduction is suppressed, and mortality occurs at rate  $\mu$ . Consumers transition from state  $F$  to state  $H$  by starvation at rate  $\sigma$  and in proportion to the lack of food  $(1 - R)$ . Conversely, consumers recover from state  $H$  to the full state  $F$  at rate  $\rho$  and in proportion to the density of resources consumed  $R$ . The resource has logistic growth with a linear growth rate  $a$  and a carrying capacity of unity. Resources are eliminated by the consumer in both states: by energetically deficient consumers at rate  $\rho$ , and by energetically replete consumers at rate  $b$ . Accordingly, the system of equations is written

$$\begin{aligned}\frac{d}{dt}F &= \lambda F + \rho R H - \sigma(1 - R)F, \\ \frac{d}{dt}H &= \sigma(1 - R)F - \rho R H - \mu H, \\ \frac{d}{dt}R &= \alpha R(1 - R) - R(\rho H + \beta F).\end{aligned}\tag{1}$$

There are three steady states for the 2-stage consumer-resource system: two trivial steady states at  $(R^* = 0, H^* = 0, F^* = 0)$  and  $(R^* = 1, H^* = 0, F^* = 0)$ , and one non-trivial internal steady state where  $(R^* > 0, H^* > 0, F^* > 0)$ . The latter steady state is the one of chief ecological interest, where

$$\begin{aligned}F^* &= \frac{a\lambda\mu(\mu + \rho)}{(\lambda\rho + \mu\sigma)(\lambda\rho + \mu m)}, \\ H^* &= \frac{a\lambda^2(\mu + \rho)}{(\lambda\rho + \mu\sigma)(\lambda\rho + \mu m)}, \\ R^* &= \frac{\mu(\sigma - \lambda)}{\lambda\rho + \mu\sigma}.\end{aligned}\tag{2}$$

Because there is only one internal steady state, as long as it is stable the population trajectories will be globally attracted to it for any set of initial conditions greater than zero.

Analysis of the stability of the consumer-resource system is explored with respect to the local stability of the internal steady state, which is the only feasible steady state as long as both the consumer and resource have non-zero, positive, values. In a multidimensional system, linear stability is determined with respect to the Jacobian Matrix  $\mathbf{J}$ , which is a matrix where each element is defined by the partial derivative of each equation with respect to each variable. In the case of the 2-stage consumer model, the Jacobian evaluated at the internal steady state (denoted by  $|_*$ ) is written

$$\mathbf{J}|_* = \begin{pmatrix} -\frac{\lambda\rho(\sigma-\lambda)}{\lambda\rho+\mu\sigma} & \frac{\mu\rho(\sigma-\lambda)}{\lambda\rho+\mu\sigma} & \frac{\alpha\lambda(\mu+\rho)}{m\mu+\lambda\rho} \\ \frac{\lambda(\mu+\rho)\sigma}{\lambda\rho+\mu\sigma} & -\frac{\mu(\mu+\rho)\sigma}{\lambda\rho+\mu\sigma} & -\frac{\alpha\lambda(\mu+\rho)}{m\mu+\lambda\rho} \\ -\frac{m\mu(\sigma-\lambda)}{\lambda\rho+\mu\sigma} & -\frac{\mu\rho(\sigma-\lambda)}{\lambda\rho+\mu\sigma} & -\frac{\alpha\mu(\sigma-\lambda)}{\lambda\rho+\mu\sigma} \end{pmatrix}. \quad (3)$$

If the parameters of the Jacobian matrix at the internal steady state are such that its leading eigenvalue is  $< 0$ , then the system is stable to small pulse perturbations, conditioned on the value of the starvation rate  $\sigma$  relative to the value of the consumer reproduction rate  $\lambda$ . As  $\sigma$  nears and becomes lower than a given  $\lambda$ , the resource steady state  $R^*$  crosses the origin and exchanges stability to become unstable. As such, a transcritical bifurcation exists at  $\lambda = \sigma$ , such that the existence of an internal stable fixed point is dependent on the condition that  $\sigma > \lambda$ . Biologically, this means that the rate of starvation is greater (operating on a smaller timescale) than the rate of consumer reproduction (operating on a relatively longer timescale). As will be shown in Section XX, this general expectation will hold for most classes of organisms, while the exact difference in timescales between reproduction and starvation can be derived using allometric scaling relationships.

Oscillating, or cyclic, dynamics present additional risks to populations. If cycles are large, stochastic effects may result in extinction. In continuous-time systems, cycles arise when a pair of complex conjugate eigenvalues cross the imaginary axis and attain positive real parts. This condition is called a Hopf bifurcation, and is defined by  $\text{Det}(\mathbf{S}) = 0$ , where  $\mathbf{S}$  is the Sylvester matrix, which is composed of the coefficients of the characteristic polynomial describing the Jacobian matrix. Although the Hopf condition for the specific 2-stage model cannot be easily written, the analytical solution can be explored using a symbolic computational language such as *Mathematica*.

## 2.2 Analysis of a generalized model

We may gain additional insight by that we do not know the specific rate functions from our 2-stage consumer resource model presented in Eq. 1. For example, we assume a linear mortality term for hungry foragers  $\mu H$ , though we may wish to assert that our knowledge of consumer mortality involves those that are energetically deficient, but nothing else. In this case, we would assume only that the rate of mortality is governed by the function  $M(H)$ . Substituting general functions for all rate laws from Eq. 1, we obtain the generalized ODE system

$$\begin{aligned}\frac{d}{dt}F &= G(F) + S(R, H) - K(R, F), \\ \frac{d}{dt}H &= K(R, F) - S(R, H) - M(H), \\ \frac{d}{dt}R &= P(R) - L(R, H, F).\end{aligned}\tag{4}$$

where  $G(F)$  determines consumer growth,  $S(R, H)$  and  $K(R, F)$  are the recovery and starva-

133 tion functions, respectively,  $M(H)$  determines consumer mortality, and  $P(R)$  and  $L(R, H, F)$   
 134 are functions describing the growth and consumption-loss of resources, respectively.  
 135 If the system is written in this generalized manner, we cannot solve for the steady state  
 136 solution  $(F^*, H^*, R^*)$ , however we can normalize the system to the unknown steady states.  
 137 We denote normalized variables and functions in lowercase, such that  $f = F/F^*$ ,  $h = H/H^*$ ,  
 138  $r = R/R^*$ , and for example the normalized mortality function  $m(h) = M(H)/M^*$ , where  $M^*$   
 139 is shorthand for  $M(H^*)$ . Additional rearrangements of terms under equilibrium conditions  
 140 allows us to define two additional sets of scaling parameters with intuitive biological proper-  
 141 ties: the turnover rates of full foragers, hungry foragers, and the resource  $(\alpha_f, \alpha_h, \alpha_r)$ , and  
 142 the proportional branching biomass through different compartments of the model, generally  
 143 designated by the parameter  $\beta$ . For instance,  $\beta_f$  is the proportion of full consumer growth  
 144 due to reproduction, whereas  $(1 - \beta_f)$  is the proportion of full consumer growth due to re-  
 145 cruitment *from* the hungry forager class. Similarly,  $\beta_h$  is the proportion of hungry consumer  
 146 loss due to mortality, whereas  $(1 - \beta_h)$  is the proportion of hungry consumer loss due to  
 147 recruitment *into* the full consumer class (see SUPP for a detailed derivation). Substituting  
 148 the normalized variables and functions into Eq. 5, we obtain

$$\begin{aligned}
 \dot{f} &= \alpha_f [\beta_f g(f) + (1 - \beta_f) s(r, h) - k(r, f)], \\
 \dot{h} &= \alpha_h [k(r, f) - (1 - \beta_h) s(r, h) - \beta_h m(h)], \\
 \dot{r} &= \alpha_r [p(r) - l(r, h, f)],
 \end{aligned} \tag{5}$$

149 and linearization of this normalized, general ODE system yields the Jacobian matrix



$$\mathbf{J}_{\text{gen}}|_* = \begin{pmatrix} \alpha_f \left( \beta_f \frac{\partial g}{\partial f} - \frac{\partial k}{\partial f} \right) & \alpha_f (1 - \beta_f) \frac{\partial s}{\partial h} & \alpha_f \left( (1 - \beta_f) \frac{\partial s}{\partial r} - \frac{\partial k}{\partial r} \right) \\ \alpha_h \frac{\partial k}{\partial f} & -\alpha_h \left( \beta_h \frac{\partial m}{\partial h} + (1 - \beta_h) \frac{\partial s}{\partial h} \right) & \alpha_h \left( \frac{\partial k}{\partial r} - (1 - \beta_h) \frac{\partial s}{\partial r} \right) \\ -\alpha_r \frac{\partial l}{\partial f} & -\alpha_r \frac{\partial l}{\partial h} & \alpha_r \left( \frac{\partial p}{\partial r} - \frac{\partial l}{\partial r} \right) \end{pmatrix}. \quad (6)$$

Due to the normalization procedure, the partial derivatives in Eq. 8 have tangible biological meaning. Because, for example, the partial derivative (containing functions and variables normalized to the unknown steady states)  $\partial g / \partial f = \partial \log G / \partial \log F$ , it scales in such a way that it represents the percent change in consumer growth (governed by  $G(F)$ ) relative to a percent change in the density of full consumers  $F$ , more commonly known as a functional elasticity. For example, if growth is a linear function (e.g.  $G(F) = \lambda F$ ),  $\partial g / \partial f = 1$ ; if growth is a quadratic function (e.g.  $G(F) = \lambda F^2$ ),  $\partial g / \partial f = 2$ , while more complex functions may depend on the value of the steady state. For example, if consumer growth is modeled as Holling Type II growth, such that  $G(F) = c_1 F^2 / (c_2 + F^2)$ , where  $c_1$  and  $c_2$  are unknown constants, then its elasticity will vary between 0 and 2, depending on the steady state value  $F^*$ , which is unknown in the generalized system.

Deriving a Jacobian in terms of the normalized ODE system is useful because it allows us to place strict constraints on the values of the unknown variables (the turnover rates, biomass branching parameters, and the functional elasticities), without assuming detailed knowledge of the functions controlling different rates within the system. In addition, we can now insert a number of assumptions that will align our generalized Jacobian more closely with the original 2-stage consumer resource system. We will assume the following: *i*) both the consumer and resource suffers linear mortality, *ii*) resource growth is logistic, *iii*) recovery and starvation are linear with respect to both full and hungry consumer densities, and *iv*)

169 consumers and resources have equivalent turnover rates scaled to unity. These assumptions  
 170 lead to the following simplifications

$$\begin{aligned}
 & i) \quad \frac{\partial m}{\partial h} = 1, \quad \frac{\partial l}{\partial r} = 1, \quad \frac{\partial l}{\partial f} = 1 - \frac{\partial l}{\partial h}, \\
 & ii) \quad \frac{\partial k}{\partial r} = \left(1 - \frac{1}{R^*}\right)^{-1}, \\
 & iii) \quad \frac{\partial s}{\partial r} = \frac{\partial s}{\partial h} = 1, \quad \frac{\partial k}{\partial f} = 1, \\
 & iv) \quad \alpha_f = \alpha_r = 1,
 \end{aligned} \tag{7}$$

171 where  $R^*$  ranges from 0 to 1. The remaining free parameters include the timescale of hungry  
 172 foragers  $\alpha_h$ , the branching parameters  $\beta_f$  and  $\beta_h$ , the elasticity of consumer growth with  
 173 respect to full consumer densities  $\partial g/\partial f$ , the elasticity of resource growth with respect to  
 174 resource density  $\partial p/\partial r$ , the elasticity of resource loss with respect to full consumer density  
 175  $\partial l/\partial f$ , and the elasticity of starvation with respect to resource density  $\partial k/\partial r$ . See Table XX  
 176 for a list of the free parameters in the generalized model, as well as the ranges of potential  
 177 values for each. These substitutions result in the simplified Jacobian matrix

$$\mathbf{J}_{\text{gen}}|_* = \begin{pmatrix} \left(\beta_f \frac{\partial g}{\partial f} - 1\right) & (1 - \beta_f) & \left((1 - \beta_f) \frac{\partial s}{\partial r} - 1\right) \\ \alpha_h & -\alpha_h & -\alpha_h \left(1 - \frac{\partial k}{\partial r} - \beta_h\right) \\ \frac{\partial l}{\partial h} - 1 & -\frac{\partial l}{\partial h} & \left(\frac{\partial p}{\partial r} - 1\right) \end{pmatrix}. \tag{8}$$

178 Because the remaining free parameters have known ranges, but not specific values, we  
 179 wish to assess the correlations of each to system stability. By randomly drawing values from  
 180 uniform distributions bounded by the known ranges of each free parameter, we obtain an

ensemble of potential Jacobian matrices whereupon the stability of each is determined by numerically calculating the real part of the leading eigenvalue. If the real part of the leading eigenvalue is  $< 1 \times 10^{-6}$ , we assumed the system to be stable. Replicating this procedure on the order of  $10^7$  times allowed us to determine the correlation of each free parameter with stability to the extent that variance was negligible.

## 2.3 Allometric scaling relationships

Nearly all of the rates described in the specific model, and later in the generalized model, are to some extent governed by the body size of the consumer. For example, the scaling relationship between an organism's metabolic rate  $B$  and its body size at reproductive maturity  $M$  is well documented ( ) and plays a central role in a variety of scaling relationships. Organismal metabolic rate  $B$  is known to scale as  $B = B_0 M^\eta$ , where  $\eta$  is the scaling exponent, generally assumed to be  $3/4$  for metazoans, and varies in unicellular species between  $\eta \approx 1$  in eukaryotes and  $\eta \approx 1.76$  in bacteria ( ). Several efforts have shown how a partitioning of this metabolic rate between growth and maintenance purposes can be used to derive a general equation for the growth trajectories and growth rates of organisms ranging from bacteria to metazoans ( ). More specifically, the interspecific trends in growth rate can be approximated by  $\lambda = \lambda_0 M^{\eta-1}$ . This relationship is derived from the simple balance

$$B_0 m^\alpha = E_m \frac{dm}{dt} + B_m m \quad (9)$$

where  $E_m$  is the energy needed to synthesize a unit of mass,  $B_m$  is the metabolic rate to support an existing unit of mass, and  $m$  is the mass at any point in development. It is useful to explicitly write this balance because it can also be modified to understand the rates of

201 both starvation and recovery from starvation.

202 For the rate of starvation, we make the simple assumption that an organism must meet  
203 its maintenance requirements using digested mass as the sole energy source. This assumption  
204 implies the simple metabolic balance

$$\frac{dm}{dt} E'_m = -B_m m \quad (10)$$

205 where  $E'_m$  is the amount of energy stored in a unit of existing body mass which may differ  
206 from  $E_m$ , the energy required to synthesis a unit of biomass. Give the adult mass,  $M$ , of an  
207 organism this energy balance prescribes the mass trajectory of a starving organism:

$$m(t) = M e^{-B_m t / E'_m}. \quad (11)$$

208 Considering that only certain tissues can be digested for energy, for example the brain cannot  
209 be degraded to fuel metabolism, we define the rate for starvation and death by the timescales  
210 required to reach specific fractions of normal adult mass. We define  $m_{starve} = \epsilon M$  where it  
211 could be the case that organisms have a systematic size-dependent requirement for essential  
212 tissues, such as the minimal bone or brain mass. For example, considering the observation  
213 that body fat in mammals scales with overall body size according to  $M_f = f_0 M^\gamma$ , and  
214 assuming that once this mass is fully digested the organism begins to starve, would imply  
215 that  $\epsilon = 1 - f_0 M^\gamma / M$ . Taken together the time scale for starvation is given by

$$t_s = -\frac{E_m \log(\epsilon)}{B_m}. \quad (12)$$

216 The starvation rate is  $\sigma = 1/t_s$ , which implies that  $\sigma$  is independent of adult mass if  $\epsilon$  is a

constant, and if  $\epsilon$  does scale with mass, then  $\sigma$  will have a factor of  $1/\log(1 - f_0 M^\gamma/M)$ . In either case  $\sigma$  does not have a simple scaling with  $\lambda$  which is important for the dynamics that we later discuss.

The time to death should follow a similar relationship, but defined by a lower fraction of adult mass,  $m_{death} = \epsilon' M$ . Consider, for example, that an organism dies once it has digested all fat and muscle tissues, and that muscle tissue scales with body mass according to  $M_{mm} = mm_0 M^\zeta$ , then  $\epsilon' = 1 - (f_0 M^\gamma + mm_0 M^\zeta)/M$ . Muscle mass has been shown to be roughly proportional to body mass () in mammals and thus  $\epsilon'$  is effectively  $\epsilon$  minus a constant. Thus

$$t_d = -\frac{E_m \log(\epsilon')}{B_m} \quad (13)$$

and  $\mu = 1/t_d$ .

It should be noted that we have thus far used mammals an example to describe the size-based relationships for growth, starvation, and death. However, our presentation is general, and other functional forms for  $\epsilon$ , for example, could be determined for other classes of organisms. Considering bacteria, we might expect that starvation or death is defined by the complete digestion of proteins, and in Table 1 we provide all parameter values for bacteria which we later use as a comparison in our analysis.

Completing our allometric analysis, for the rate of becoming full, we again use the balance given in Equation 9 to find the timescale to return to the mature mass from a given reduced starvation mass. The general solution to Equation 9 is given by

$$m(t) = \left[ 1 - \left( 1 - \frac{b}{a} m_0^{1-\alpha} \right) e^{-b(1-\alpha)t} \right]^{1/(1-\alpha)} \left( \frac{a}{b} \right)^{1/(1-\alpha)} \quad (14)$$

with  $a = B_0/E_m$  and  $b = B_m/E_m$ . We are then interested in the timescale,  $t_f = t_2 - t_1$ ,

237 which is the time it takes to go from  $m(t_1) = \epsilon M$  to  $m(t_2) = M$ , which has the final form

238 of

$$t_f = \frac{\log \left( 1 - \left( M \left( \frac{a}{b} \right)^{\frac{1}{\alpha-1}} \right)^{1-\alpha} \right) - \log \left( 1 - \left( M\epsilon \left( \frac{a}{b} \right)^{\frac{1}{\alpha-1}} \right)^{1-\alpha} \right)}{(\alpha - 1)b}. \quad (15)$$

Table 1: Parameter Values For Various Classes of Organisms

	<b>Mammals</b>	<b>Unicellular Eukaryotes</b>	<b>Bacteria</b>
$\eta$	3/4		1.70
$E_m$	10695 (J gram <sup>-1</sup> )		10695 (J gram <sup>-1</sup> )
$E'_m$	$\approx E_m$		$\approx E_m$
$B_0$	0.019 (W gram <sup>-<math>\alpha</math></sup> )		$1.96 \times 10^{17}$
$B_m$	0.025 (W gram <sup>-1</sup> )		0.025 (W gram <sup>-1</sup> )
$a$	$1.78 \times 10^{-6}$		$1.83 \times 10^{13}$
$b$	$2.29 \times 10^{-6}$		$2.29 \times 10^{-6}$
$\eta - 1$	-0.21		0.73
$\lambda_0$	$3.39 \times 10^{-7}$ (s <sup>-1</sup> gram <sup>1-<math>\eta</math></sup> )		56493
$\gamma$	1.19		0.68
$f_0$	0.02		$1.30 \times 10^{-5}$
$\zeta$	1.01		
$mm_0$	0.32		

### 239 3 Results

240 Analysis of the 2-stage consumer resource model shows that the equilibrial states of both  
 241 populations are highly sensitive to changes in starvation and recovery rates of the consumer.

242 The consumer and resource population densities vary inversely: when the consumer densities  
 243 are high, resource densities are low, and vice versa. High starvation and low recovery rates  
 244 result in low consumer densities and high resource densities. If starvation rates are low,  
 245 resources have a fixed point near zero for any value of the recovery rate. Full and hungry  
 246 consumer stages tend have fixed points that are tightly correlated, the extent to which is

driven by the similarity of consumer growth and mortality rates; if  $\lambda = \mu$ , then  $F^* = H^*$ .

A transcritical bifurcation exists at  $\lambda = \sigma$ , such that the condition  $\sigma > \lambda$  is required for biologically reasonable dynamics. The TC bifurcation occurs in this model because we have assumed that the portion of the population that is not starved reproduces at a constant rate. Because the process of starvation is incorporated explicitly, the consumer's rate of reproduction is not dependent on the density of resources. In fact, the existence of the TC bifurcation at  $\lambda = \sigma$  reveals an important biological insight. Reproduction requires maintenance and growth of biological tissues, both of which have strong scaling relationships with body size. Recent work by Kempes et al. [REF] derived the timescale of reproduction in terms of allometric considerations, where  $t_\lambda \propto M^{1-\eta}$  (REF). Starvation is the loss of energy required for maintenance, and we have shown it to have a timescale  $t_\sigma \propto \log(M)$ . Accordingly, the timescale of reproduction is always larger than the timescale of starvation, such that  $\lambda$  must be less than  $\sigma$  by definition. A third important parameter in our framework is the rate of recovery. The recovery timescale  $t_\rho$  controls the rate at which individuals move from the hungry class to the full class, and this requires not only tissue maintenance, but growth, such that it is bounded on the short side by  $t_\sigma$ . Moreover, [why is recovery timescale bounded on the high side], such that it is bounded on the long side by  $t_\lambda$ . Thus, incorporating allometric considerations shows us that  $\lambda < \rho < \sigma$  (alternatively  $t_\lambda > t_\rho > t_\sigma$ ).

The 2-stage consumer resource model exhibits two qualitatively different behavioral regimes. Because portions of the consumer population exist in either full or hungry states simultaneously, the internal fixed point can either be a stable equilibrium, or exhibit sustained oscillatory behavior, depending on the rates of starvation  $\sigma$  and recovery  $\rho$ . The transition from stable non-oscillatory dynamics to oscillatory dynamics occurs at the Hopf bifurcation condition where two complex conjugate eigenvalues cross the imaginary axis and

attain positive real parts. Although there is an analytical solution to the Hopf bifurcation condition, it cannot be written efficiently.

When the starvation rate is low, oscillatory dynamics are more likely to occur for a given value of the recovery rate. This can be understood intuitively: for low starvation rates, resources are depressed by an infusion of full consumers, which subsequently starve thereby allowing the resource to recover and continuing the cycle. When the starvation rate is high, the response of consumer growth to resource abundance is muted, such that oscillations tend to decay over time. Thus, higher starvation rates  $\sigma$  desensitizes changes in the consumer population to changes in resource density, and lower rates of recovery  $\rho$  amplifies this effect.

Both full and hungry consumers remove resources at rates  $b$  and  $\rho$ , respectively. As the rate of resource consumption by full consumers increases, the Hopf condition changes from a convex to a concave function over  $\sigma$ , limiting the potential for oscillatory dynamics. These rates are considered separately because full consumers need only to maintain their tissues, whereas hungry consumers require both growth and maintenance, such that  $t_\rho > t_b$ , or  $\rho < b$ . If this constraint is enacted, the likelihood of oscillatory dynamics is reduced for a given

If instead the consumer's growth was proportional to resource abundance, such that the effects of starvation on reproduction were incorporated explicitly (where the 2-stage consumer resource model collapses to the Lotka-Volterra consumer-resource model with logistic growth of the resource), the TC bifurcation exists only for  $\lambda = \mu$ , such that the rate of mortality cannot exceed the intrinsic birth rate.

whereas the traditional Lotka-Volterra dynamic assumes that the reproductive rate of the consumer is scaled to resource density, such that the growth function would be  $G(F, R) = \lambda RF$ . Thus, the Lotka-Volterra dynamic *implicitly* accounts for starvation in reducing the reproductive rate of the consumer. However, our 2-stage model *explicitly* accounts for starva-



tion as well as recovery, such that individuals who are not starved should adopt a reproductive rate independent of resource density.

We have used scaling relationships between tissue turnover and growth to strictly constrain 5/6 population-level parameters in our 2-stage consumer resource model (including the mortality rate  $t_\mu$ , which we have shown is just a xxx of  $t_\sigma$ ). This exercise accomplishes two goals: 1) it allows us to constrain the plausible parameter space of the two-stage model, and 2)

This allows us to derive many aspects of the system in terms of consumer body mass  $M$  and the allometric scaling exponent  $\eta$ .

### 3.1 Generalized analysis

Constraining the model with allometric scaling relationships yields important insights regarding the tradeoff between [fitness and energy]

## 4 Discussion

In our modeling, foragers look for food by wandering in this changing environment. If such a search is successful, the forager is satiated and it can engage in the essential activity of reproduction. However, if the search is unsuccessful for a sufficiently long period, the forager “starves”. Such a forager can do nothing else but forage, until it either finds food and again becomes satiated or it dies when it goes too long without finding nourishment. These rules are reminiscent of the “starving random walk” model, where a single random walk can take  $\mathcal{S}$  steps without encountering food before starving to death. Moreover, the resource does not regenerate, so that the forager ultimately starves to death. For this idealized model, it was

316 found that the average lifetime of the forager scales algebraically with  $\mathcal{S}$  in  $d=1$  and  $d=2$   
317 dimensions, and as  $\exp(-A\mathcal{S}^\omega)$  for  $d > 2$ . Here the exponent  $\omega \approx \frac{1}{2}$  for  $d = 3$ , while  $\omega \rightarrow 1$   
318 only as  $d \rightarrow \infty$ , with the latter behavior corresponding to the mean-field limit. As we will  
319 discuss, regeneration of the resource, together with the behavioral change between starving  
320 and satiated foragers leads to still much richer dynamical behavior.

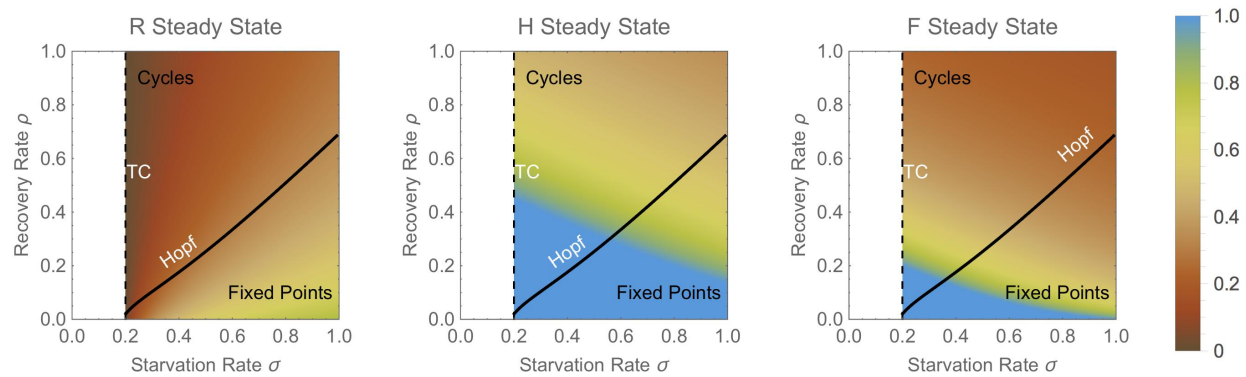


Figure 1

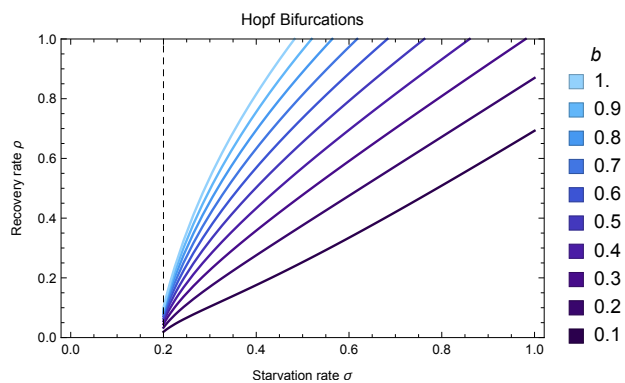


Figure 2

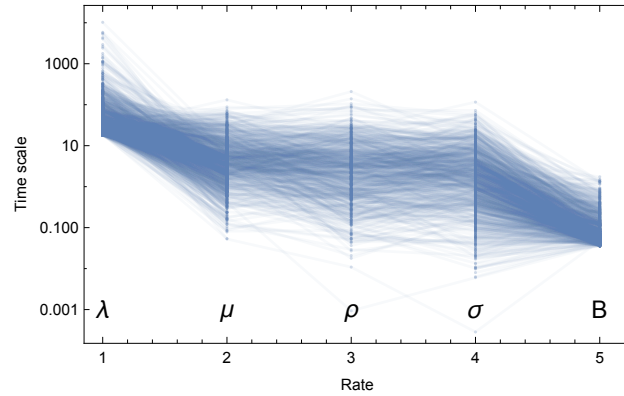


Figure 3

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