The effect of starvation on the dynamics of consumer populations

Yeakel, Kempes, & Redner

July 5, 2016

1 The behavioral ecology of most, if not all, organisms is influenced by the energetic state

2 of individuals. An individual's energetic state directly influences how it invests its stores

3 in an uncertain environment. Such behaviors are generally manifested as trade-offs, which

4 often concern investing in individual maintenance and growth or allocating energy towards

5 reproduction (Kirk, 1997; Kempes et al., 2012). The timing of these behaviors is often

6 important and is under strong selective pressure, as they tend to have large effects on the

7 future fitness of the organism (?). To what extent, and when, organisms invest in these two

8 necessary biological functions – growth and maintenance vs. reproduction – may be driven

9 by habitat, seasonality, evolutionary history, inter- or intra-specific interactions, as well as

10 resource limitation. Importantly, the influence of resource limitation on an organism's ability

11 to maintain its nutritional stores may lead to repeated delays or shifts in reproduction over

12 the course of an organism's life.

13 Maximizing fitness between growth and maintenance activities vs. reproductive behav-

14 iors 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 (Morris, 1987). 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 (Tveraa et al., 2003), whereas many bird species invest differently in broods during periods of resource scarcity (Daan et al., 1988; Jacot et al., 2009), sometimes delaying or foregoing reproduction for a breeding season (Barboza and Jorde, 2002). Freshwater and marine zooplankton have been observed to avoid reproduction under nutritional stress (Threlkeld, 1976), with those that do reproduce evincing lower survival rates (Kirk, 1997), while artificially induced stress has been observed to decrease reproductive success in Atlantic cod (Morgan et al., 1999). 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 (Mead, 1989; Sandell, 1990). Furthermore, many mammals (including humans) suffer irregular menstrual cycling and higher rates of spontaneous abortion during periods of nutritional stress (Bulik et al., 1999; Trites and Donnelly, 2003). 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 (Weber et al., 1998; ?; Moore et al., 2014). 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: *i*) 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; *ii* the portion of the population that is not nutritionally stressed is expected to reproduce at a near-constant rate and this is – on average – determined by body size; *iii* the rates at which individuals transition from nutritionally poor to replete states and back are governed by metabolic constraints (Kempes et al., 2012). Importantly, the neglect of additional constraints may have important dynamic shortcomings, masking the effects of resource limitation on consumer population dynamics.

Resource limitation and the subsequent effects of starvation may be alternatively accounted for *explicitly*, such that reproduction is permitted only for individuals with sufficient energetic reserves. Incorporating energetic dynamics that occur at an individual level (Kooijman, 2000) into a population-based framework (Kooijman, 2000; Sousa et al., 2010), though straightforward conceptually, quickly runs into mathematical obstacles (Diekmann and Metz, 2010), and suffers from over-parameterization. The complexities associated with scaling individual-level energetics to that of a population has thus limited the development of

3

theoretical models that may aid our understanding of the effects of such tradeoffs on population dynamics. An alternative approach to individual-based frameworks is to concentrate on the macroscale relationships to examine the primary effects of reproductive vs. maintenance tradeoffs on populations.

Here we explore how the energetic tradeoff between maintaining and building tissue vs. reproduction can influence the dynamics of populations, and how these dynamics may be constrained by allometric relationships. We begin by establishing a simple nutritional state-structured population model, where consumer starvation, and cessation of reproduction, is the consequence of resource limitation. Similarly, recovery from the starved state – and resumption of reproduction – increases with resource density. Importantly, the rate at which consumers starve and recover from a starved state is wholly constrained by metabolism, which in turn is largely determined by body size, or allometry. 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 may be prone to alternative dynamics.

We show that rates of starvation and recovery (parameterized for endothermic organisms) always result in systems with stable, non-cyclic fixed points. Moreover, larger consumer body size results in rates that are less prone to cyclic dynamics than are rates for smaller organisms, pointing to potential empirical verification of the starvation dynamics framework. Finally, we show that rates of starvation and recovery appear to be constrained to a parameter range where both transient and equilibrial population dynamics result in the lowest risk of extinction for the consumer. This surprising result suggests that the risks associated with different fluxes of consumers in and out of a starved (non-reproductive) state may serve as an important selective driver over evolutionary time.

4

Starvation dynamics

We 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 Nutritional State Model (NSM) there are only two energetic states for the consumer population: i) an energetically replete (full) state F, where the consumer reproduces at a constant rate λ, and ii) an energetically deficient (hungry) state H, where reproduction is suppressed, and mortality occurs at rate μ. Consumers transition from state F to state H by starvation at rate σ and in proportion to the lack of food $(1 - R)$. Conversely, consumers recover from state H to the full state F at rate ρ and in proportion to the density of resources consumed R. The resource has logistic growth with a linear growth rate α and a carrying capacity of unity. Resources are eliminated by the consumer in both states: by energetically deficient consumers at rate ρ, and by energetically replete consumers at rate β. Accordingly, the system of equations is written

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

There are three steady states for the NSM: 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

$$F^* = \frac{a\lambda\mu(\mu+\rho)}{(\lambda\rho+\mu\sigma)(\lambda\rho+\mu m)},$$

$$H^* = \frac{a\lambda^2(\mu+\rho)}{(\lambda\rho+\mu\sigma)(\lambda\rho+\mu m)},$$

$$R^* = \frac{\mu(\sigma-\lambda)}{\lambda\rho+\mu\sigma}.$$

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 NSM 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.

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 σ relative to the value of the consumer reproduction rate λ. As σ becomes less than λ, the resource steady state R^* crosses the origin and becomes unstable. The condition $\sigma = \lambda$ marks a transcritical bifurcation, such that if a consumer's starvation rate is lower than it's reproductive rate, the consumer population's growth becomes exponential and unphysical. Thus, the timescale of starvation must be less than the timescale of reproduction, an expectation that will hold for most classes of organisms, which we will show by deriving allometric scaling relationship that serve to constrain the covariation of parameter values.

[In addition to the hard bound defined by the TC bifurcation, oscillating or cyclic dy-

6

namics represent an implicit constraint by putting populations at risk... also present certain constraints to the feasibility of 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.

Allometric constraints

[Link Allometry stuff to our model - what does it provide to the story] [Introduce biological and linked constraints] [Allometries capture vast amounts of diversity via a single parameter — body size] [Allometries have captured int terest etc across multiple scales and biological classes of organisms]

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 η 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

$$B_0 m^\alpha = E_m \frac{dm}{dt} + B_m m \tag{-1}$$

145 [a and b notation — these parameters are easily measured bioenergetic parameters which
146 are often approximately invariant across organisms of vastly different size. Our notation
147 seeks to illustrate that the allometric model fundamentally depends on a small number of
148 free parameters.] where E_m is the energy needed to synthesize a unit of mass, B_m is the
149 metabolic rate to support an existing unit of mass, and m is the mass at any point in
150 development. It is useful to explicitly write this balance because it can also be modified
151 to understand the rates of both starvation and recovery from starvation. [Spell out the
152 connection to nutritional state more explicitly] [As we will see it is possible to derive both
153 sigma and rho from this balance]

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

$$\frac{dm}{dt}E'_m = -B_m m \tag{-1}$$

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

$$m(t) = Me^{-B_m t/E'_m}. \tag{-1}$$

160 Considering that only certain tissues can be digested for energy, for example the brain cannot
161 be degraded to fuel metabolism, we define the rate for starvation and death by the timescales
162 required to reach specific fractions of normal adult mass. We define $m_{starve} = \epsilon M$ where it

8

could be the case that organisms have a systematic size-dependent requirement for essential tissues, such as the minimal bone or brain mass. For example, considering the observation that body fat in mammals scales with overall body size according to $M_f = f_0 M^\gamma$, and assuming that once this mass is fully digested the organism begins to starve, would imply that $\epsilon = 1 - f_0 M^\gamma / M$. Taken together the time scale for starvation is given by

$$t_\sigma = -\frac{E_m \log\left(\epsilon\right)}{B_m}. \tag{-1}$$

The starvation rate is $\sigma = 1/t_s$, which implies that σ is independent of adult mass if ϵ is a constant, and if ϵ does scale with mass, then σ will have a factor of $1/\log\left(1 - f_0 M^\gamma / M\right)$. In either case σ does not have a simple scaling with λ 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 $\epsilon' = 1 - \left(f_0 M^\gamma + mm_0 M^\zeta\right)/M$. Muscle mass has been shown to be roughly proportional to body mass in mammals and thus ϵ' is effectively ϵ minus a constant. Thus

$$t_d = -\frac{E_m \log\left(\epsilon'\right)}{B_m} \tag{-1}$$

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 ϵ, for example, could be determined for other classes of organisms. Considering bacteria, we might expect that starvation or death is defined

9

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 to find the timescale to return to the mature mass from a given reduced starvation mass. The general solution to Equation is given by

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

with $a = B_0/E_m$ and $b = B_m/E_m$. We are then interested in the timescale, $t_f = t_2 - t_1$, which is the time it takes to go from $m\left(t_1\right) = \epsilon M$ to $m\left(t_2\right) = M$, which has the final form of

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

Table 1: Parameter Values For Various Classes of Organisms

	Mammals	Unicellular Eukaryotes	Bacteria
η	3/4		1.70
E_m	10695 (J gram^{-1})		10695 (J gram^{-1})
E_m'	$\approx E_m$		$\approx E_m$
B_0	0.019 (W gram$^{-\alpha}$)		1.96×10^{17}
B_m	0.025 (W gram^{-1})		0.025 (W gram^{-1})
a	1.78×10^{-6}		1.83×10^{13}
b	2.29×10^{-6}		2.29×10^{-6}
$\eta - 1$	-0.21		0.73
λ_0	3.39×10^{-7} (s^{-1} gram$^{1-\eta}$)		56493
γ	1.19		0.68
f_0	0.02		1.30×10^{-5}
ζ	1.01		
mm_0	0.32		

Allometry leads to stability

Analysis of the 2-stage consumer resource model shows that the equilibrial states of both populations are highly sensitive to changes in starvation and recovery rates of the consumer. The consumer and resource population densities vary inversely: when the consumer densities are high, resource densities are low, and vice versa. High starvation and low recovery rates result in low consumer densities and high resource densities. If starvation rates are low, resources have a fixed point near zero for any value of the recovery rate. Full and hungry 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 λ must be less than σ by definition. A third important parameter in our framework is the rate of recovery. The recovery timescale t_ρ 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_σ. Moreover, [why is recovery timescale bounded on the high side], such that it is bounded on the long side by t_λ. Thus, incorporating

11

216 allometric considerations shows us that $\lambda < \rho < \sigma$ (alternatively $t_\lambda > t_\rho > t_\sigma$).

217 The 2-stage consumer resource model exhibits two qualitatively different behavioral

218 regimes. Because portions of the consumer population exist in either full or hungry states

219 simultaneously, the internal fixed point can either be a stable equilibrium, or exhibit sus-

220 tained oscillatory behavior, depending on the rates of starvation σ and recovery ρ. The

221 transition from stable non-oscillatory dynamics to oscillatory dynamics occurs at the Hopf

222 bifurcation condition where two complex conjugate eigenvalues cross the imaginary axis and

223 attain positive real parts. Although there is an analytical solution to the Hopf bifurcation

224 condition, it cannot be written efficiently.

225 When the starvation rate is low, oscillatory dynamics are more likely to occur for a given

226 value of the recovery rate. This can be understood intuitively: for low starvation rates,

227 resources are depressed by an infusion of full consumers, which subsequently starve thereby

228 allowing the resource to recover and continuing the cycle. When the starvation rate is high,

229 the response of consumer growth to resource abundance is muted, such that oscillations tend

230 to decay over time. Thus, higher starvation rates σ desensitizes changes in the consumer

231 population to changes in resource density, and lower rates of recovery ρ amplifies this effect.

232 Both full and hungry consumers remove resources at rates b and ρ, respectively. As the

233 rate of resource consumption by full consumers increases, the Hopf condition changes from

234 a convex to a concave function over σ, limiting the potential for oscillatory dynamics. These

235 rates are considered separately because full consumers need only to maintain their tissues,

236 whereas hungry consumers require both growth and maintenance, such that $t_\rho > t_b$, or $\rho < b$.

237 If this constraint is enacted, the likelihood of oscillatory dynamics is reduced for a given

238 If instead the consumer's growth was proportional to resource abundance, such that the

239 effects of starvation on reproduction were incorporated explicitly (where the 2-stage consumer

12

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 starvation 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_μ, which we have shown is just a xxx of t_σ). 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 η.
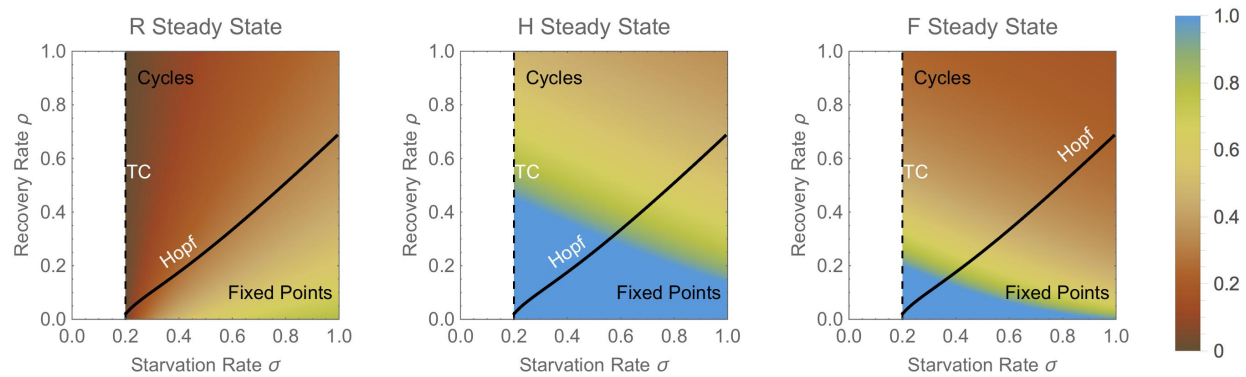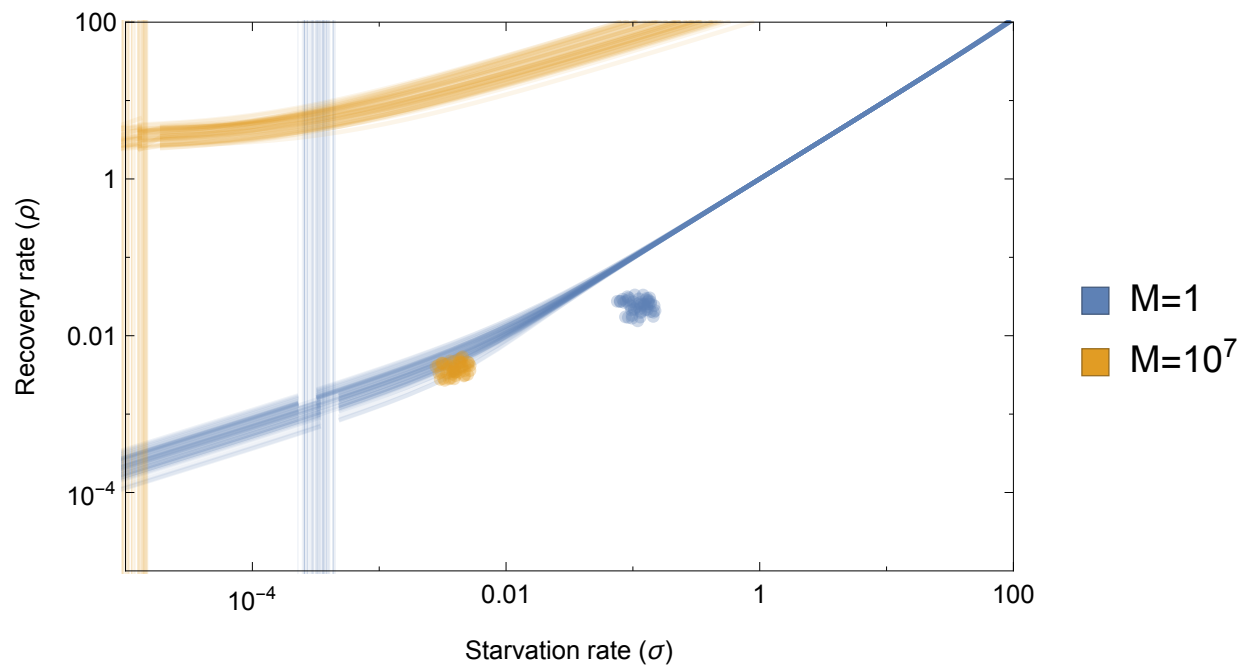
Minimizing extinction risk

Figure 1

Figure 2
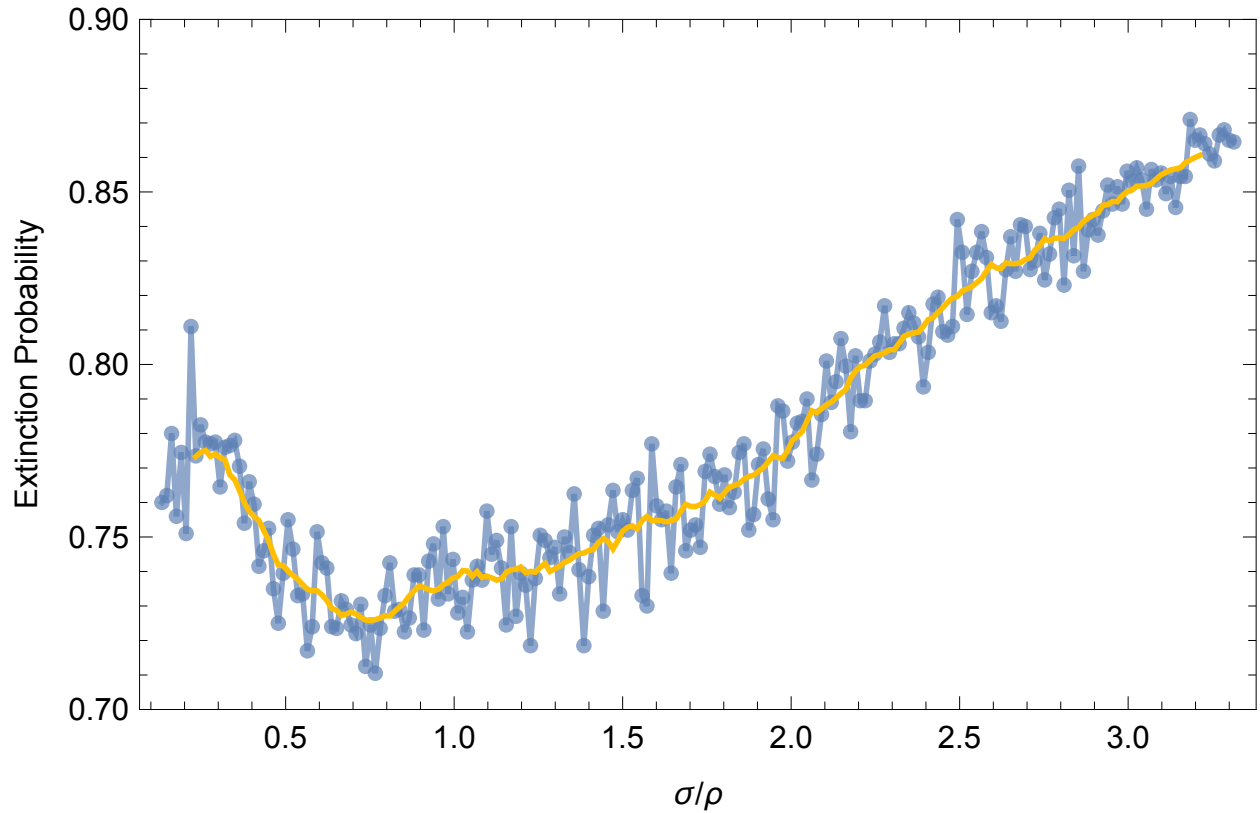
Figure 3

References

Barboza, P. and Jorde, D. (2002). Intermittent fasting during winter and spring affects body composition and reproduction of a migratory duck. *J Comp Physiol B*, 172(5):419–434.

Bulik, C. M., Sullivan, P. F., Fear, J. L., Pickering, A., Dawn, A., and McCullin, M. (1999). Fertility and Reproduction in Women With Anorexia Nervosa. *J. Clin. Psychiatry*, 60(2):130–135.

Daan, S., Dijkstra, C., Drent, R., and Meijer, T. (1988). Food supply and the annual timing of avian reproduction. In *Proceedings of the International . . . .*

15

Diekmann, O. and Metz, J. A. J. (2010). How to lift a model for individual behaviour to the population level? *Philos. T. Roy. Soc. B*, 365(1557):3523–3530.

Jacot, A., Valcu, M., van Oers, K., and Kempenaers, B. (2009). Experimental nest site limitation affects reproductive strategies and parental investment in a hole-nesting passerine. *Animal Behaviour*, 77(5):1075–1083.

Kempes, C. P., Dutkiewicz, S., and Follows, M. J. (2012). Growth, metabolic partitioning, and the size of microorganisms. *PNAS*, 109(2):495–500.

Kirk, K. L. (1997). Life-History Responses to Variable Environments: Starvation and Reproduction in Planktonic Rotifers. *Ecology*, 78(2):434–441.

Kooijman, S. A. L. M. (2000). *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge.

Mead, R. A. (1989). The Physiology and Evolution of Delayed Implantation in Carnivores. In *Carnivore Behavior, Ecology, and Evolution*, pages 437–464. Springer US, Boston, MA.

Moore, J. W., Yeakel, J. D., Peard, D., Lough, J., and Beere, M. (2014). Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. *J. Anim. Ecol.*

Morgan, M. J., Wilson, C. E., and Crim, L. W. (1999). The effect of stress on reproduction in Atlantic cod. *Journal of Fish Biology*, 54(3):477–488.

Morris, D. W. (1987). Optimal Allocation of Parental Investment. *Oikos*, 49(3):332.

Sandell, M. (1990). The Evolution of Seasonal Delayed Implantation. *The Quarterly Review of Biology*, 65(1):23–42.

288 Sousa, T., Domingos, T., Poggiale, J. C., and Kooijman, S. A. L. M. (2010). Dynamic energy
289   budget theory restores coherence in biology. *Philos. T. Roy. Soc. B*, 365(1557):3413–3428.

290 Threlkeld, S. T. (1976). Starvation and the size structure of zooplankton communities.
291   *Freshwater Biol.*, 6(6):489–496.

292 Trites, A. W. and Donnelly, C. P. (2003). The decline of Steller sea lions Eumetopias jubatus
293   in Alaska: a review of the nutritional stress hypothesis. *Mammal Review*, 33(1):3–28.

294 Tveraa, T., Fauchald, P., Henaug, C., and Yoccoz, N. G. (2003). An examination of a com-
295   pensatory relationship between food limitation and predation in semi-domestic reindeer.
296   *Oecologia*, 137(3):370–376.

297 Weber, T. P., Ens, B. J., and Houston, A. I. (1998). Optimal avian migration: A dynamic
298   model of fuel stores and site use. *Evolutionary Ecology*, 12(4):377–401.