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 vs. producing offspring [Mangel], among a host of other behavioral duties [REFS]. 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 [Mangel]. 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, or even resource limitation. The influence of resource limitation on an organism's ability to maintain its nutritional stores may lead to delays or shifts in reproduction.

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. Behavioral: The investment of time and energy towards reproductive and parental behaviors depends on resource availability (1). 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 (2), whereas many bird species invest differently in broods during periods of resource scarcity (3, 4), sometimes delaying or foregoing reproduction for a breeding season (5). Resource limitation can also alter the behaviors of species in well-mixed environments: freshwater and marine zooplankton have been observed to avoid reproduction under nutritional stress (6), while those that do reproduce evince lower survival rates (7). Similarly, artificially induced stress has been observed to decrease reproductive success in Atlantic cod (8). Physiological: Diverse mammals (47 species in 10 families) exhibit delayed implantation whereby females postpone fetal development (blastocyst implantation), often timing with accumulation of nutritional reserves (9, 10). Furthermore, many mammals (including humans) suffer irregular menstrual cycling and higher rates of spontaneous abortion during periods of nutritional stress (11, 12). 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 (13**?** , 14). 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 spending energy on tissues vs. spending energy on passing down genetic material.

Organisms employ different strategies to avoid reproduction during times of nutritional stress, and how this is achieved 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

reproduces at a near-constant rate, constrained by allometric relationships, and iii) the rate

at which individuals transition from nutritionally poor to replete states (and vice versa) are

governed by the organism's metabolism, which is also strongly constrained by allometry.

To incorporate these important elements, resource limitation and the subsequent effects of

starvation can be accounted for *explicitly*, such that reproductive growth of a population

is only allowed to occur for individuals with sufficient energetic reserves. Incorporating

energetic dynamics that occur at an individual level [REF] into a population-based framework

(15, 16), though straightforward conceptually, has many challenges that arise mathematically

(17), and this has limited simple theoretical models aiding our understanding of larger-scale

dynamics.

Here we explore how reproductive trade-offs, which occur at the level of the individual,

may influence the dynamics of a population. We first establish a simple stage-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 relationships, we uncover important constraints in the timescales of

3

different physiological processes that determine dynamics and investigate how organisms of alternative body sizes and taxonomic affinities are expected to evince contrasting population-level dynamics. We then develop a more general dynamic model in order to understand if there are common attributes of these energetically-constrained systems that have implications beyond assumptions inherent to the specific model. 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 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 a 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 b. Accordingly, the system of equations is written

$$\frac{\mathrm{d}}{\mathrm{dt}}F = \lambda F + \rho H R - \sigma(1 - R)F,$$

$$\frac{\mathrm{d}}{\mathrm{dt}}H = \sigma(1 - R)F - \rho R H - \mu H,$$

$$\frac{\mathrm{d}}{\mathrm{dt}}R = aR(1 - R) - R(\rho H + bF). \tag{1}$$

81   There are three steady states for the 2-stage consumer-resource system: two trivial steady

82 states at $(R^* = 0, H^* = 0, F^* = 0)$ and $(R^* = 1, H^* = 0, F^* = 0)$, and one non-trivial internal

83 steady state where $(R^* > 0, H^* > 0, F^* > 0)$. The latter steady state is the one of chief

84 ecological interest, where

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

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

$$R^* = \frac{\mu(\sigma - \lambda)}{\lambda\rho + \mu\sigma}. \tag{2}$$

85 Because there is only one internal steady state, as long as it is stable the population trajec-

86 tories will be globally attracted to it for any set of initial conditions greater than zero.

87   Analysis of the stability of the consumer-resource system is explored with respect to the

88 local stability of the internal steady state, which is the only feasible steady state as long

89 as both the consumer and resource have non-zero, positive, values. In a multidimensional

90 system, linear stability is determined with respect to the Jacobian Matrix $\mathbf{J}$, which is a

91 matrix where each element is defined by the partial derivative of each equation with respect

92 to each variable. In the case of the 2-stage consumer model, the Jacobian evaluated at the

⁹³ internal steady state (denoted by $|_*$) is written

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

⁹⁴ If the parameters of the Jacobian matrix at the internal steady state are such that its

⁹⁵ leading eigenvalue is < 0, then the system is stable to small pulse perturbations, conditioned

⁹⁶ on the value of the starvation rate σ relative to the value of the consumer reproduction

⁹⁷ rate λ. As σ nears and becomes lower than a given λ, the resource steady state R^* crosses

⁹⁸ the origin and exchanges stability to become unstable. As such, a transcritical bifurcation

⁹⁹ exists at $\lambda = \sigma$, such that the existence of an internal stable fixed point is dependent on the

¹⁰⁰ condition that $\sigma > \lambda$. Biologically, this means that the rate of starvation is greater (operating

¹⁰¹ on a smaller timescale) than the rate of consumer reproduction (operating on a relatively

¹⁰² longer timescale). As will be shown in Section XX, this general expectation will hold for

¹⁰³ most classes of organisms, while the exact difference in timescales between reproduction and

¹⁰⁴ starvation can be derived using allometric scaling relationships.

¹⁰⁵ Oscillating, or cyclic, dynamics present additional risks to populations. If cycles are

¹⁰⁶ large, stochastic effects may result in extinction. In continuous-time systems, cycles arise

¹⁰⁷ when a pair of complex conjugate eigenvalues cross the imaginary axis and attain positive

¹⁰⁸ real parts. This condition is called a Hopf bifurcation, and is defined by $\mathrm{Det}(\mathbf{S}) = 0$,

¹⁰⁹ where $\mathbf{S}$ is the Sylvester matrix, which is composed of the coefficients of the characteristic

¹¹⁰ polynomial describing the Jacobian matrix. Although the Hopf condition for the specific 2-

¹¹¹ stage model cannot be easily written, the analytical solution can be explored using a symbolic

¹¹² 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 μH, 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

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

where $G(F)$ determines consumer growth, $S(R, H)$ and $K(R, F)$ are the recovery and starvation functions, respectively, $M(H)$ determines consumer mortality, and $P(R)$ and $L(R, H, F)$ are functions describing the growth and consumption-loss of resources, respectively.

If the system is written in this generalized manner, we cannot solve for the steady state solution $(F^*,\ H^*,\ R^*)$, however we can normalize the system to the unknown steady states. We denote normalized variables and functions in lowercase, such that $f = F/F^*$, $h = H/H^*$, $r = R/R^*$, and for example the normalized mortality function $m(h) = M(H)/M^*$, where M^* is shorthand for $M(H^*)$. Additional rearrangements of terms under equilibrium conditions allows us to define two additional sets of scaling parameters with intuitive biological properties: the turnover rates of full foragers, hungry foragers, and the resource $(\alpha_f,\ \alpha_h,\ \alpha_r)$, and

the proportional branching biomass through different compartments of the model, generally designated by the parameter β. For instance, β_f is the proportion of full consumer growth due to reproduction, whereas $(1 - \beta_f)$ is the proportion of full consumer growth due to recruitment *from* the hungry forager class. Similarly, β_h is the proportion of hungry consumer loss due to mortality, whereas $(1 - \beta_h)$ is the proportion of hungry consumer loss due to recruitment *into* the full consumer class (see SUPP for a detailed derivation). Substituting the normalized variables and functions into Eq. 5, we obtain

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

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

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

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)

consumers and resources have equivalent turnover rates scaled to unity. These assumptions

lead to the following simplifications

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

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

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

Because the remaining free parameters have known ranges, but not specific values, we wish to assess the correlations of each to system stability. By randomly drawing values from 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 generalized upon in the generalized model, are to some extent governed by the body size of the consumer. The scaling relationship between an organism's metabolic rate B and its body size at reproductive ma-

10

$_{179}$ turity M plays a central role in other scaling relationships. Organismal metabolic rate B is

$_{180}$ known to scale as $B = B_0 M^\eta$, where η is the scaling exponent, generally assumed to be $3/4$

$_{181}$ for metazoans, etc. Kempes et al. [REF] show how the population-level growth rate also

$_{182}$ can be related to body size as $\lambda = \lambda_0 M^{\eta-1}$.

$_{183}$ Population growth requires that individuals

3 Results

$_{184}$

$_{185}$ Analysis of the 2-stage consumer resource model shows that the equilibrial states of both

$_{186}$ populations are highly sensitive to changes in starvation and recovery rates of the consumer.

$_{187}$ The consumer and resource population densities vary inversely: when the consumer densities

$_{188}$ are high, resource densities are low, and vice versa. High starvation and low recovery rates

$_{189}$ result in low consumer densities and high resource densities. If starvation rates are low,

$_{190}$ resources have a fixed point near zero for any value of the recovery rate. Full and hungry

$_{191}$ consumer stages tend have fixed points that are tightly correlated, the extent to which is

$_{192}$ driven by the similarity of consumer growth and mortality rates; if $\lambda = \mu$, then $F^* = H^*$.

$_{193}$ A transcritical bifurcation exists at $\lambda = \sigma$, such that the condition $\sigma > \lambda$ is required

$_{194}$ for biologically reasonable dynamics. The TC bifurcation occurs in this model because

$_{195}$ we have assumed that the portion of the population that is not starved reproduces at a

$_{196}$ constant rate. Because the process of starvation is incorporated explicitly, the consumer's

$_{197}$ rate of reproduction is not dependent on the density of resources. In fact, the existence of

$_{198}$ the TC bifurcation at $\lambda = \sigma$ reveals an important biological insight. Reproduction requires

$_{199}$ maintenance and growth of biological tissues, both of which have strong scaling relationships

$_{200}$ 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 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 σ and recovery ρ. 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 σ desensitizes changes in the consumer population to changes in resource density, and lower rates of recovery ρ amplifies this effect.

²²⁵ Both full and hungry consumers remove resources at rates b and ρ, respectively. As the

²²⁶ rate of resource consumption by full consumers increases, the Hopf condition changes from

²²⁷ a convex to a concave function over σ, limiting the potential for oscillatory dynamics. These

²²⁸ rates are considered separately because full consumers need only to maintain their tissues,

²²⁹ whereas hungry consumers require both growth and maintenance, such that $t_\rho > t_b$, or $\rho < b$.

²³⁰ If this constraint is enacted, the likelihood of oscillatory dynamics is reduced for a given

²³¹ If instead the consumer's growth was proportional to resource abundance, such that the

²³² effects of starvation on reproduction were incorporated explicitly (where the 2-stage consumer

²³³ resource model collapses to the Lotka-Volterra consumer-resource model with logistic growth

²³⁴ of the resource), the TC bifurcation exists only for $\lambda = \mu$, such that the rate of mortality

²³⁵ cannot exceed the intrinsic birth rate.

²³⁶ whereas the traditional Lotka-Volterra dynamic assumes that the reproductive rate of the

²³⁷ consumer is scaled to resource density, such that the growth function would be $G(F, R) =$

²³⁸ λRF. Thus, the Lotka-Volterra dynamic *implicitly* accounts for starvation in reducing the

²³⁹ reproductive rate of the consumer. However, our 2-stage model *explicitly* accounts for starva-

²⁴⁰ tion as well as recovery, such that individuals who are not starved should adopt a reproductive

²⁴¹ rate independent of resource density.

²⁴² We have used scaling relationships between tissue turnover and growth to strictly con-

²⁴³ strain 5/6 population-level parameters in our 2-stage consumer resource model (including

²⁴⁴ the mortality rate t_μ, which we have shown is just a xxx of t_σ). This exercise accomplishes

²⁴⁵ two goals: 1) it allows us to constrain the plausible parameter space of the two-stage model,

²⁴⁶ and 2)

²⁴⁷ This allows us to derive many aspects of the system in terms of consumer body mass M

²⁴⁸ and the allometric scaling exponent η.

13

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

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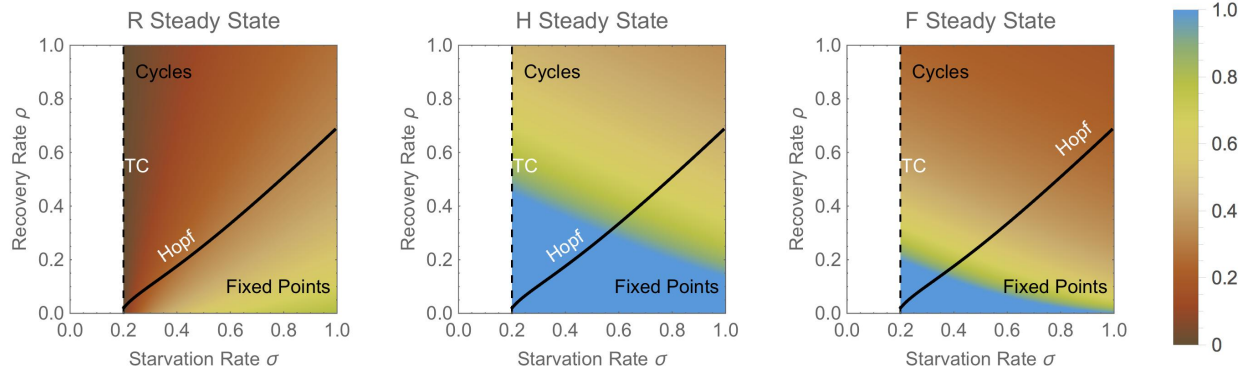[2] T. Tveraa, P. Fauchald, C. Henaug, and N. G. Yoccoz, "An examination of a compen-
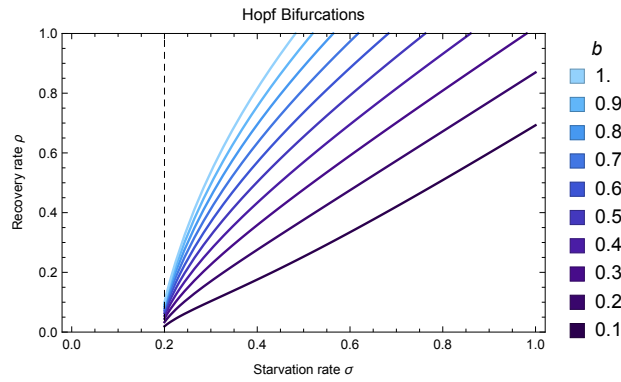
Figure 1

Figure 2

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