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Abstract

We introduce a minimal model of foraging in which the interplay between reproduction and starvation of the foragers, and the regeneration of resources, controls the dynamics. The system consists of a resource that renews by logistic growth, as well as two classes of foragers—satiated and starving. Satiated foragers reproduce at a fixed rate and are not vulnerable to mortality. However, a satiated forager can starve when resources are scarce; conversely, a starving forager can become satiated when the resource is abundant. Starving foragers do not reproduce and they die at a rate μ. We investigate the dynamics of this system, both in the well-mixed (mean-field) limit and by stochastic simulations in two dimensions. For parameters that correspond to a benign environment, the system settles into a fixed point. However, the forager populations oscillate in time with an increasing amplitude as the environment becomes more harsh. **needs closing sentence(s).**

1 Introduction

Foraging for food (resources) is an essential task of many living organisms [?, ?, ?, ?, ?, ?, ?, ?, ?]. Our focus here is on foraging in an environment where the consumed resource can regenerate, and with the new feature that the energetic state of the foragers affects their behavior. This state—either starving (energetically deficient) or satiated (energetically replete)—determines how the forager behaves in this time-dependent environment. We will specifically investigate the influence of a forager's energetic state and its reproductive behavior on the long-time dynamics of the population. As has been shown in [examples], individuals that are energetically deficient are unlikely to engage is reproduction. Even when such individuals do reproduce, the offspring are often naturally aborted if there is insufficient caloric resources available to the parent. On the other hand, satiated foragers do reproduce, which thereby exerts increased pressure on resources. In turn, this can lead to a population collapse when the resources are subsequently depleted by the earlier growing population. Our goal is to understand this interplay between the foragers' energetic state and environmental resources on the population dynamics.

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.

We will begin by defining our stage-structured population model that encapsulates the trade-off between regeneration, reproduction, and starvation. We will first explore how the rates of these processes impact the population dynamics in the mean-field limit, where resources and foragers are always perfectly mixed. Under this perfect mixing condition, the species densities can be described by rate equations, and we will investigate the dynamical behaviors that arise from these equations. We will also compare this continuous rate-equation approach with stochastic simulations that account for discreteness effects due to the finiteness of the population. Next, we will extend these stochastic simulations to the physical situation where the foragers perform random walks in two dimensions. Intriguing spatial organization effects arise, in which waves of satiated foragers reproduce and deplete the environment, followed by satiated foragers subsequently become starving foragers, many of whom eventually die. This allows for a later recovery of the environment and ultimately to repeated cycles of boom and bust. As we shall discuss, this quasi-cyclic behavior arises when the environment is "stressed", because the consumption and reproduction rates are high. Conversely, for smaller environmental stress, the system converges to a fixed point.

Finally, we will develop a more general model to understand if there are common attributes of the dynamics outlined above that have implications beyond our simple stage-structured model.

2 The Model

We incorporate energetics into the model dynamics by assuming that the foragers can exist in two discrete energetic states—satiated and starving. Satiated (or full) foragers F are those that have just encountered and consumed a unit of resource R. On the other hand, a satiated forager that does not encounter a resource as it wanders is converted to a starving forager S with rate σ. Whenever a forager, either satiating or starving, encounters resources, one unit of the resource is consumed. If the forager was starving, it is recruited into the satiated population with rate ρ. During the time that a forager is starving, it dies with a fixed mortality rate μ, while satiated foragers do not experience mortality risk. Furthermore, satiated foragers reproduce with rate λ. Finally, we assume that, in the absence of foragers, the underlying resource undergoes logistic growth, with growth rate α and carrying capacity equal to one.

According to these processes and also under the assumption that the densities of satiated foragers, starving foragers, and resources (also denoted by F, S, and R, respectively) are perfectly mixed, they evolve according to the rate equations:

$$
\begin{aligned}
\dot{F} &= \lambda F + \rho R S - \sigma(1-R)F \,, \\
\dot{S} &= \sigma(1-R)F - \rho R S - \mu S \,, \\
\dot{R} &= \alpha R(1-R) - R(F+S),
\end{aligned}
\tag{1}
$$

where the overdot denotes time derivative.

This system of equations admits three fixed points. Two of them, at $(F^* = 0, S^* = 0, R^* = 0)$ and $(F^* = 0, S^* = 0, R^* = 1)$ correspond to an environment without foragers. In this case, the latter fixed point is stable. There is also a non-trivial fixed point in which all populations are represented, $(F^*, S^*, R^* > 0)$, corresponding to an ecologically active fixed point at

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

If this unique fixed point is stable, the species populations will be globally attracted to it for any set of initial conditions with values greater than zero.

To determine the stability of the non-trivial fixed point, we compute the Jacobian Matrix $\mathbf{J}$, whose elements are given by $J_{ij} = \partial X_i / \partial X_j$, where X_i, with $i = 1, 2, 3$, refers to the densities F, S, R, respectively. At the non-trivial fixed point, the Jacobian matrix is

$$\mathbf{J}|_* = \begin{pmatrix} \lambda - \sigma(1 - R^*) & \rho R^* & \sigma(S^* + F^*) \\ \sigma(1 - R^*) & -\rho R^* - \mu & -\rho(S^* + F^*) \\ -R^* & -R^* & \alpha(1 - 2R^*) - (S^* + F^*) \end{pmatrix}. \quad (3)$$

Whether the internal fixed point is attracting or repelling is conditioned on the values of the parameters in the system. If the parameters of the Jacobian matrix (at the internal fixed point) are such that its eigenvalues have negative real values, then it is stable. The stability of the system changes if a Saddle-Node bifurcation is crossed, such that a single eigenvalue obtains a positive real part, defined by the condition $\text{Det}(\mathbf{J}) = 0$. A single Transcritical bifurcation exists at $\lambda = \sigma$, such that the condition $\sigma < \lambda$ is required for stability of the internal fixed point.

In traditional consumer-resource models, the growth of the consumer scales to both itself as well as the resource. The reasoning behind this is sound: as the resource density declines, the growth of the consumer is likewise expected to decline. This dynamic implicitly incorporates the idea that resource depletion lowers consumer growth rates. However, because we model the effects of starvation by the explicit inclusion of a starving consumer class, we assume that the satiated component of the consumer population has a fixed reproductive rate, which is not dependent on resource density. Thus, as resource density declines, the recruitment of satiated consumers into the starving class increases, serving to lower consumer growth mechanistically.

Introducing mechanistic starvation imposes an added requirement for the internal fixed point to be stable: the rate of starvation must be greater than the rate of consumer reproduction. If this is violated, the consumer class reproduces faster than it starves, irrespective of resource density, increasing exponentially. We suggest that the criterion $\sigma < \lambda$ is in fact biologically reasonable because starvation occurs on a much shorter timescale than reproduction.

Of additional interest is the existence of parameter regions that permit the existence of cyclic behavior. 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 **S** is the Sylvester matrix, which is composed of the coefficients of the characteristic polynomial describing the Jacobian matrix. Although the Hopf condition cannot be solved analytically for the specific 2-stage model, it can be explored numerically.

3 Results

To determine how the consumer-resource system impacted by different rates of starvation, we analyze the systems with respect to p.

4 Discussion

4.1 Generalized starvation model

Our conclusions of the mean-field limit starvation model are of course contingent on the functional forms chosen for the birth, death, starvation, and recovery functions. To expand understanding of the starvation/reproduction tradeoff on stability, we examine a generalization of our model.

To generalize the starvation model, we define the functions controlling reproduction, mortality, and starvation for the original rate equations, such that

$$
\begin{aligned}
\dot{F} &= \lambda F + \rho RS - \sigma(1 - R)F = G(F) + H(R, S) - K(R, F)\,, \\
\dot{S} &= \sigma(1 - R)F - \rho RS - \mu S = K(R, F) - H(R, S) - M(S)\,, \qquad (4) \\
\dot{R} &= \alpha R(1 - R) - R(F + S) = P(R) - L(R, S, F).
\end{aligned}
$$

Although we cannot solve for the fixed points of the generalized model, we can define them as R^*, S^*, and F^* for the resource, starving consumer class, and satiated consumer class, respectively. We then define the variables normalized to the fixed point, where

$$
r = \frac{R}{R^*}, \quad s = \frac{S}{S^*}, \quad \text{and } f = \frac{F}{F^*}. \qquad (5)
$$

By substitution, we can rewrite the general model in terms of normalized variables and functions

$$\dot{f} = \frac{G^*}{F^*}g(f) + \frac{H^*}{F^*}h(r,s) - \frac{K^*}{F^*}k(r,f)\,,$$
$$\dot{s} = \frac{K^*}{S^*}k(r,f) - \frac{H^*}{S^*}h(r,s) - \frac{M^*}{S^*}m(s)\,, \qquad (6)$$
$$\dot{r} = \frac{P^*}{R^*}p(r) - \frac{L^*}{R^*}l(r,s,f)\,.$$

where, for example, we use the shorthand $G^* = G(F^*)$. The normalized general model has the important property that at the fixed point $\dot{f} = \dot{s} = \dot{r} = 0$, then $g(f) = h(r,s) = k(r,f) = m(s) = p(r) = l(r,s,f) = 1$. This allows us to define the following *scale parameters*. These include those associated with the timescales of the system: $a_f = G^*/F^* + H^*/F^* = K^*/F^*$, $a_s = K^*/S^* = H^*/S^* + M^*/S^*$, and $a_r = P^*/R^* = L^*/R^*$, respectively denoting the turnover time for satiated consumers, starving consumers, and resources. We also define those scale parameters associated with the branching of biomass through the system, where $\beta_f = a_f^{-1}G^*/F^*$, which denotes the proportion of gain to the satiated consumer class due to growth (and $1 - \beta_f$ is the proportion of gain due to recovery from starvation), and $beta_s = a_s^{-1}M^*/S^*$, which denotes the proportion of loss to the starving consumer class due to natural mortality (and $1 - \beta_s$ is the proportion of loss due to recovery).

The normalized general model can then be written

$$\dot{f} = a_f \left[\beta_f g(f) + (1 - \beta_f)h(r,s) - k(r,f)\right]\,,$$
$$\dot{s} = a_s \left[k(r,f) - (1 - \beta_s)h(r,s) - \beta_s m(s)\right]\,, \qquad (7)$$
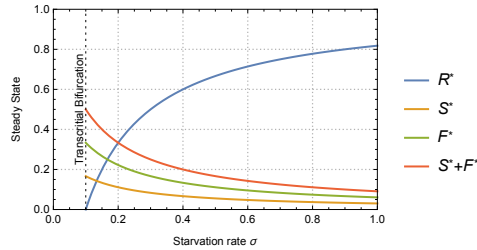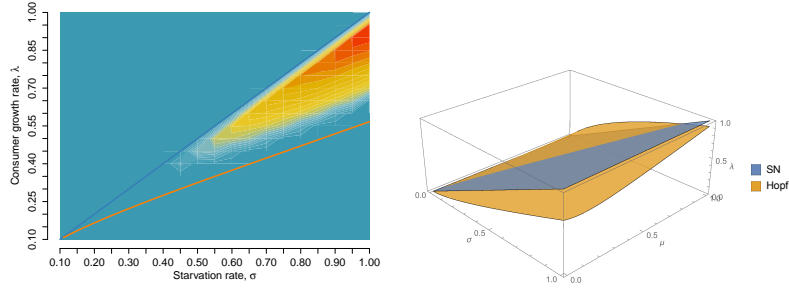$$\dot{r} = a_r \left[p(r) - l(r,s,f)\right]\,.$$

Figure 1: Fixed points.

Figure 2: Hopf bifurcation
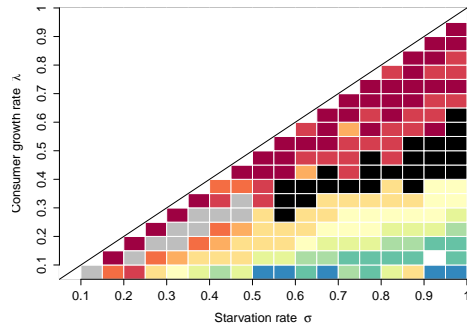
Figure 3: Time series frequencies for spatial simulation model

Figure 4: Generalized modeling results
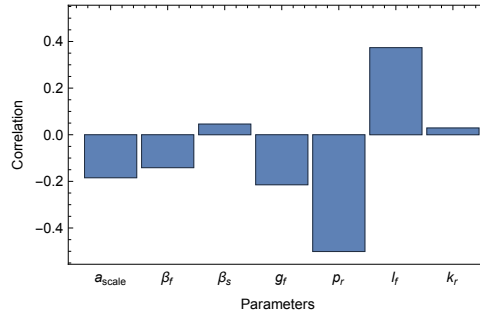
7

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