Event-Driven Simulation of Foraging Dynamics

Abstract.

We outline an event-driven simulation for the foraging model, which involves a resource that renews by logistic growth, as well as two classes of foragers—full and hungry. Full foragers reproduce at a fixed rate and are not vulnerable to mortality. However, a full forager can become hungry when resources are scarce; conversely, a hungry forager can become full when the resource is abundant. Hungry foragers do not reproduce and die at a fixed rate.

1. The Model

We assume that foragers can exist in two discrete states—full and hungry. Full foragers F are those that have just encountered and consumed a unit of resource R. On the other hand, a full forager that does not encounter a resource as it wanders converts to a hungry forager H with rate equal to the product of a parameter σ and the density of non-resources. Whenever a forager, either full or hungry, encounters a resource, one unit of the resource is consumed. If the forager was hungry, it turns into a full forager with rate ρ. During the time that a forager is hungry, it dies with mortality rate μ, while full foragers do not experience mortality risk. Furthermore, full 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 full foragers, hungry foragers, and resources (also denoted by F, H, and R, respectively) are perfectly mixed, they evolve according to the rate equations:

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

where the overdot denotes time derivative. An important feature is the assumption that the carrying capacity is set equal to 1. This means that when the system is completely occupied by resources there can be no further generation of the resource. The approach described below can be generalized to carrying capacity less than 1, but one can take the carrying capacity equal to 1 without loss of generality.

We now outline an event-driven algorithm that mimic these rate equations. Suppose that the system at a given time consists of N_F full foragers, N_H hungry foragers, and N_R individual resources. The total number of particles $N = N_F + N_H + N_R$. There are six basic processes embodied by the rate equations (1):

(i) Reproduction: $F \to F + 1$

(ii) Starvation: $F \to H$

(iii) Recruitment: $H \to F$

(iv) Death: $H \to H - 1$

(v) Resource growth: $R \to R + 1$

(vi) Resource consumption: $R \to R - 1$

In an event-driven simulation, one of the above events is picked with the appropriate probability (to be defined below), the selected event is implemented, and then the time is updated accordingly. The total rate for any event is proportional to

$$\mathcal{R} = F\big[\lambda + \sigma(1 - R)\big] + H\big[\rho R + \mu\big] + R\big[\alpha(1 - R) + (F + H)\big]\,. \tag{2}$$

Here $F = N_F/V$, $H = N_H/V$, and $R = N_R/V$, where N_i is the total number of particle of type i and V is the total number of lattice sites. Thus F, H, and R are the densities of each type of entity in the system. The total rate is define only up to an overall constant, but this constant is immaterial because the time step is also proportional to this same constant.

Now we define the steps of an event-driven simulation.

(i) With probability $\lambda F/\mathcal{R}$ implement the reproduction step. This step consists of picking one of the full foragers and allowing it to reproduce.

(ii) With probability $\sigma(1 - R)F/\mathcal{R}$ implement the starvation step; a full forager is picked and it changes to a hungry forager.

(iii) With probaibility $\rho HR/\mathcal{R}$ implement the recruitment step; a hungry forager is picked and becomes full.

(iv) With probability $\mu H/\mathcal{R}$ implement the death step; a hungry forager is picked and is removed.

(v) With probability $\alpha R(1 - R)/\mathcal{R}$ implement the growth step; a unit of resource is created.

(vi) With probability $(F + H)R/\mathcal{R}$ implement the consumption step; a unit of resource is removed.

By explicit construction, the probabilities for the above events sum to 1.

We now determine the change in the expected number of individuals of each type in a single event. For full foragers, the change in its number N_F is

$$\Delta N_F = \Big[F\big(\lambda - \sigma(1 - R)\big) + \rho HR\Big]\,/\mathcal{R}\,. \tag{3a}$$

The term proportional to F comes from processes in which a full forager is picked, while the term proportional to N_H comes from processes in which a hungry forager is picked and converted to a full forager. Thus the change in the density of full foragers is

$$\Delta F = \frac{\Delta N_F}{V} = \Big[F\big(\lambda - \sigma(1 - R)\big) + H\rho R\Big]\,/V\mathcal{R}\,. \tag{3b}$$

Thus if we take the time step for each event to be $\Delta t = (V\mathcal{R})^{-1}$, the above reduces to the rate equation (1) for F. Thus in each microscopic event of the model, the time should be advanced by $\Delta t = (V\mathcal{R})^{-1}$.

In a similar fashion, the change in the expected number of hungry foragers in a single event is given by

$$\Delta N_H = \left[-H(\rho R + \mu) + F\sigma(1-R)\right]/\mathcal{R}\,, \tag{4a}$$

so that the change in the density of hungry foragers simply is

$$\Delta H = \left[-H(\rho R + \mu) + F\sigma(1-R)\right]/V\mathcal{R}\,. \tag{4b}$$

Finally, the change in the expected number of individual resources in a single event is given by

$$\Delta N_R = \Big[R\big(\alpha(1-R)\big) - (F+H)\Big]/\mathcal{R}\,, \tag{5a}$$

so that the change in the resource density is

$$\Delta R = \Big[R\big(\alpha(1-R)\big) - (F+H)\Big]/V\mathcal{R}\,. \tag{5b}$$

The equations for ΔF, ΔH, and ΔR would then reproduce the original rate equations (1) when the time step for an elemental event is taken to be $\Delta t = (V\mathcal{R})^{-1}$. To summarize, pick an event according to the probabilities enumerated above and update the densities according (3b), (4b), and (5b), and then increment the time by $(N\mathcal{R})^{-1}$ after each event.

There are several details of the simulation that need to be specified. First, there is no constraint on the number of foragers on any site, but given that we are describing a harsh environment, the parameters should be chosen so that this number is not large. The carrying capacity of the resource has been set to 1, so that the number of individual resources at any site should be either 0 or 1. Finally, when a full forager reproduces, its offspring should be placed anywhere. With these details, a simulation that is based on the above sprocedure should reproduce the predictions of the rate equations (1).

We now generalize the above approach to the situation where the foragers are diffusing on a lattice. Suppose that the full and hungry foragers diffuse with respective diffusion coefficients D_F and D_H. In this case, the rate equations (1) generalize to the set of partial differential equations

$$\begin{aligned}
\frac{\partial F}{\partial t} &= \lambda F + \rho R H - \sigma(1-R)F + D_F\nabla^2 F\,,\\
\frac{\partial H}{\partial t} &= \sigma(1-R)F - \rho R H - \mu H + D_H\nabla^2 H\,,\\
\frac{\partial R}{\partial t} &= \alpha R(1-R) - R(F+H).
\end{aligned} \tag{6}$$

Here the densities F, H, R are now functions of space and time, $F = F(\mathbf{r}, t)$ and similarly for H and R.

To construct an event-driven simulation that mimic these rate equations, we have to include two additional processes:

vii Full forager diffusion

viii Hungry forager diffusion

In an event-driven simulation, one of the eight possible events is picked with the appropriate probability (see below), the selected event is implemented, and the time is updated accordingly.

The total rate for any event is

$$\mathcal{R} = F\big[\lambda + \sigma(1-R) + D_F\big] + H\big[\rho R + \mu + D_H\big] + R\big[\alpha(1-R) + (F+H)\big]\,. \qquad (7)$$

Now we define the steps of an event-driven simulation.

(i) With probability $\lambda F/\mathcal{R}$ implement the reproduction step. This step consists of picking one of the full foragers and allowing it to reproduce.

(ii) With probability $\sigma(1-R)F/\mathcal{R}$ implement the starvation step; a full forager is picked and it changes to a hungry forager.

(iii) With probaibility $\rho HR/\mathcal{R}$ implement the recruitment step; a hungry forager is picked and becomes full.

(iv) With probability $\mu H/\mathcal{R}$ implement the death step; a hungry forager is picked and is removed.

(v) With probability $\alpha R(1-R)/\mathcal{R}$ implement the growth step; a unit of resource is created.

(vi) With probability $(F+H)R/\mathcal{R}$ implement the consumption step; a unit of resource is removed.

(vii) With probability $D_F F/\mathcal{R}$, a full forager moves; pick one such forager at random and move it.

(viii) With probability $D_H H/\mathcal{R}$, a full forager moves; pick one such forager at random and move it.

By explicit construction, the probabilities for the above events sum to 1.

We now determine the change in the expected number of individuals of each type at a given site $\mathbf{R}$ in a single event. For full foragers, the change in its number $N_F(\mathbf{R})$ at site $\mathbf{R}$ is

$$\Delta N_F(\mathbf{R}) = \big[F(\mathbf{R})\big(\lambda - \sigma(1-R(\mathbf{R}))\big) + \rho HR\big]\,/\mathcal{R}\,. \qquad (8a)$$

The term proportional to F comes from processes in which a full forager is picked, while the term proportional to N_H comes from processes in which a hungry forager is picked and converted to a full forager. Thus the change in the density of full foragers is

$$\Delta F = \frac{\Delta N_F}{V} = \big[F\big(\lambda - \sigma(1-R)\big) + H\rho R\big]\,/V\mathcal{R}\,. \qquad (8b)$$

Thus if we take the time step for each event to be $\Delta t = (V\mathcal{R})^{-1}$, the above reduces to the rate equation (1) for F. Thus in each microscopic event of the model, the time should be advanced by $\Delta t = (V\mathcal{R})^{-1}$.

In a similar fashion, the change in the expected number of hungry foragers in a single event is given by

$$\Delta N_H = \left[-H(\rho R + \mu) + F\sigma(1-R)\right]/\mathcal{R}\,, \tag{9a}$$

so that the change in the density of hungry foragers simply is

$$\Delta H = \left[-H(\rho R + \mu) + F\sigma(1-R)\right]/V\mathcal{R}\,. \tag{9b}$$

Finally, the change in the expected number of individual resources in a single event is given by

$$\Delta N_R = \big[R\big(\alpha(1-R)\big) - (F+H)\big]/\mathcal{R}\,, \tag{10a}$$

so that the change in the resource density is

$$\Delta R = \big[R\big(\alpha(1-R)\big) - (F+H)\big]/V\mathcal{R}\,. \tag{10b}$$

The equations for ΔF, ΔH, and ΔR would then reproduce the original rate equations (1) when the time step for an elemental event is taken to be $\Delta t = (V\mathcal{R})^{-1}$. To summarize, pick an event according to the probabilities enumerated above and update the densities according (3b), (4b), and (5b), and then increment the time by $(N\mathcal{R})^{-1}$ after each event.

There are several details of the simulation that need to be specified. First, there is no constraint on the number of foragers on any site, but given that we are describing a harsh environment, the parameters should be chosen so that this number is not large. The carrying capacity of the resource has been set to 1, so that the number of individual resources at any site should be either 0 or 1. Finally, when a full forager reproduces, its offspring should be placed anywhere. With these details, a simulation that is based on the above sprocedure should reproduce the predictions of the rate equations (1).