

# 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  $\sigma$  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  $\rho$ . During the time that a forager is hungry, it dies with mortality rate  $\mu$ , while full foragers do not experience mortality risk. Furthermore, full foragers reproduce with rate  $\lambda$ . Finally, we assume that, in the absence of foragers, the underlying resource undergoes logistic growth, with growth rate  $\alpha$  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. This algorithm is based on picking *sites* at random, rather than *particles* at random. However, we show how to recast this site-based simulation into a particle-based simulation with an concomitant increase in efficiency. We will also generalize to the

situation where the full and hungry foragers undergo diffusion with possibly different diffusion coefficients on a finite-dimensional lattice.

Suppose that the system at some time consists of  $N_F$  full foragers,  $N_H$  hungry foragers, and  $N_R$  individual resources. The total number of particles  $N = N_F + N_H + N_R$ . In each elemental event a lattice site is picked: on average, it is occupied by a full forager with probability  $N_F/V$ , a hungry forager with probability  $N_H/V$ , a resource with probability  $N_R/V$ , or, on average, the site may be empty with probability  $1 - \rho$ , where  $\rho = (N_F + N_H + N_R)/V$  is the total density of particles, on average and  $V$  is the total number of lattice sites.. I use the term “on average” because it is possible to have rare realizations where all particles are concentrated on just a few sites. However, for large systems, the actually number of particles at a given site will not significantly deviate from the average number.

If a site that is occupied by an  $F$  is picked, it reproduces at rate  $\lambda$  and becomes hungry with rate  $\sigma(1 - R)$ . If a site that is occupied by an  $H$  is picked, it becomes full with rate  $\rho R$  and dies with rate  $\mu$ . Finally, if a site that is occupied by an  $R$  is picked, it grows with rate  $\alpha(1 - R)$  and is eaten with rate  $(F + H)$ . Thus the total rate for each elemental event is

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

Now let's look at how the system evolves according to its constituent processes. If an  $F$  is picked, then it may either reproduce or go hungry according to the steps outlined above. That is:

$$\begin{array}{ll} \text{growth, prob. } \lambda/\mathcal{R} & N_F \rightarrow N_F + 1, \\ \text{starve, prob. } \sigma(1 - R)/\mathcal{R} & N_F \rightarrow N_F - 1, N_H \rightarrow N_H + 1. \end{array}$$

Similarly, if an  $H$  is picked, it may either become full or die following the processes given above. That is:

$$\begin{array}{ll} \text{become full, prob. } \rho R/\mathcal{R} & N_H \rightarrow N_H - 1, N_F \rightarrow N_F + 1, \\ \text{die, prob. } \mu/\mathcal{R} & N_H \rightarrow N_H - 1. \end{array}$$

Finally, if an  $R$  is picked, it may either grow or be eaten following the processes given above. That is:

$$\begin{array}{ll} \text{grow, prob. } \alpha(1 - R)/\mathcal{R} & N_R \rightarrow N_R + 1, \\ \text{eaten, prob. } (F + H)/\mathcal{R} & N_R \rightarrow N_R - 1. \end{array}$$

We now determine the change in the expected number of individuals of each type in a single event that are consistent with the above processes. For full foragers, this change is

$$\Delta N_F = \left[ \frac{N_F}{V} (\lambda - \sigma(1 - R)) + \frac{N_H}{V} \rho R \right] / \mathcal{R}. \quad (3a)$$

The term proportional to  $N_F$  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 it converted to a full forager. Consequently, the change in the density of full foragers simply is

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

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

$$\Delta N_H = \left[ -\frac{N_H}{V}(\rho R + \mu) + \frac{N_F}{V}\sigma(1 - R) \right] / \mathcal{R}, \quad (4a)$$

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

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

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

$$\Delta N_R = \left[ \frac{N_R}{V}(\alpha(1 - R)) - \frac{(N_F + N_H)}{V} \right] / \mathcal{R}, \quad (5a)$$

so that the change in the density of resources is

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

The equations for  $\Delta F$ ,  $\Delta H$ , and  $\Delta R$  would then reproduce the original rate equations (1) when the time step for an elemental event is taken to be  $\Delta t = (V\mathcal{R})^{-1}$ .

However, this approach is inefficient if many of the lattice sites are empty because an empty site is likely to be picked and then nothing happens. Instead, we would rather pick *actual particles* rather than *lattice sites*. If the particle density is  $\rho = N/V$ , then in picking a *particle* at random always leads to a non-trivial update, while picking a *site* at random leads to a non-trivial update with probability  $\rho$ . Thus by picking *particles* at random—an  $F$  with probability  $N_F/N$ , an  $H$  with probability  $N_H/N$ , or an  $R$  with probability  $N_R/N$ —compared to picking *sites* at random, leads to an overall speedup of the simulation by a factor of  $1/\rho$ . Therefore, for the particle-based upate, time increment changes to  $\Delta t = (1/\rho) \times (V\mathcal{R})^{-1} = (N\mathcal{R})^{-1}$ .

To summarize, pick a particle of type  $i$  with  $N_i/N$ , and update the densities  $N_i/V$  according (3b), (4b), and (5b), and then increment the time by  $(N\mathcal{R})^{-1}$  after each event. It is important to appreciate that this approach implicitly assumes that the number of particles on each site is small. This assumption is reasonable if we are describing a harsh environment where a non-negligible fraction of the foragers are either going hungry or starving.

We can straightforwardly 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  $R$ .

We now determine the total rate for an elemental event. If an  $F$  is picked, it reproduces at rate  $\lambda$ , becomes hungry with rate  $\sigma(1 - R)$ , and moves with rate  $D_F$ . If an  $H$  is picked, it becomes full with rate  $\rho R$ , dies with rate  $\mu$ , and moves with rate  $D_H$ . As before, if an  $R$  is picked, it grows with rate  $\alpha(1 - R)$  and is eaten with rate  $(F + H)$ . Thus the total rate for each elemental event is

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

Here the subscript  $d$  indicates that this rate pertains to the foraging model with diffusing foragers on a  $d$ -dimensional lattice.

As before, we determine at how the system evolves according to the various constituent processes. If an  $F$  is picked, it may either reproduce, go hungry, or move. That is:

$$\begin{array}{ll}\text{growth, prob. } \lambda/\mathcal{R}_d & N_F \rightarrow N_F + 1, \\ \text{starve, prob. } \sigma(1 - R)/\mathcal{R}_d & N_F \rightarrow N_F - 1, \\ \text{move, prob. } D_F/\mathcal{R}_d & N_F \rightarrow N_F.\end{array}$$

Similarly, if an  $H$  is picked, it may become full, die, or move following the processes given above. That is:

$$\begin{array}{ll}\text{become full, prob. } \rho R/\mathcal{R}_d & N_H \rightarrow N_H - 1, N_F \rightarrow N_F + 1, \\ \text{die, prob. } \mu/\mathcal{R}_d & N_H \rightarrow N_H - 1, \\ \text{move, prob. } D_H/\mathcal{R}_d & N_H \rightarrow N_H.\end{array}$$

The evolution of the resource is the same as the mean-field case. Following the same logic as in the mean-field case, the evolution of the densities will be described by the evolution equations (6) when the time step of each elemental event is taken to be  $(N\mathcal{R}_d)^{-1}$ .

There are several additional detailed subtleties of the simulation that are worth mentioning. First, it seems that there does not need to be any constraint on the number

of foragers on any site, so I think it's best to let this number be arbitrary. However, 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.

Now let's turn to the mechanics of the various update events. In the mean-field limit, when a full forager reproduces, its offspring should be placed anywhere. For a finite-dimensional lattice, it seems reasonable to place the offspring at the same site as the parent. However, because the implicit assumption of low density, perhaps it would be better to put the newly born forager on the closest lattice site that is not occupied by another forager. Diffusion of a full forager on a lattice can be modeled by allowing it to hop to a nearest neighbor; similarly for the motion of hungry foragers.

The mechanics of the resource evolution is a bit subtle. In the mean-field limit, if an individual resource is picked a new resource is created with probability proportional to  $1 - R$ , where  $R$  is the global density of resource, which is necessarily less than 1. If a new resource is created, it should be placed randomly on any one of the sites that does not contain a resource, but this site could be occupied by a forager. On a lattice, the creation of a new resource should be proportional to a local version of  $1 - R$ . I think it's reasonable to consider the  $z$  nearest-neighbor sites of the current resource and put a new individual resource at one of the vacant nearest neighbors with probability  $1 - n/z$ , where  $n$  is the number of individual resources in the local neighborhood of  $z$  sites. The disappearance of an individual resource by consumption is straightforward.