Answers to Exercise 27

Range Expansion

The overall conclusion is that range expands more or less linearly, and the rate of range expansion depends largely on R_{max} and E_{min}. In a model that treats space and time continuously, rather than discretely as your model does, the radius of the range increases linearly with time (see Case 2000).

1. The total population and the local populations grow logistically. The local population at the center of the range grows faster than any other local population and achieves a higher carrying capacity.

   As we mover farther from the center of the range, and closer to the edge, local population growth rates slow, and carrying capacities decrease.

   Why does this happen? Is it because we seeded the habitat at the center?

   Try starting the model with two individuals in any noncentral cell. The seed population will grow faster at first, but sooner or later the central population will overtake it. At equilibrium, local carrying capacity will be highest at the center of the range and decline toward the edges.

   This pattern emerges because our model has an "absorbing boundary." That is, the local populations at the edge of the suitable habitat (sites A and M) lose members by emigration at the same rate as any other, but they gain immigrants from only one adjacent cell. Therefore they grow more slowly than more central populations, and consequently contribute fewer emigrants to their neighbors. This slows the growth of the adjacent cells toward the center of the range, and the effect ripples inward, attenuated by distance from the edge.

   You can change the model to have a "reflecting boundary." In the *absorbing boundary*, half the emigrants that leave a local population at the edge of the range simply disappear; presumably, they die after moving into unsuitable habitat. In a *reflecting boundary* model, all the emigrants from a local population at the edge of the range move into adjacent suitable habitat.

   Would this change the behavior of the model? We leave this as an exercise for adventurous students.

2. The range expands linearly. Depending on where you place the seed population, and how high you set growth and emigration rates, there may or may not be an initial lag period. Once all cells are occupied, obviously range expansion ceases.

   The stair-step appearance of the graph of range expansion results from our use of discrete cells. If we could model continuous habitat, we would see a smooth line.

3. You can model geometrically growing populations by changing R_{dd} to 0 and R_{max} to 0.2. (If R_{max} is too large, it produces overflow errors in the program.)

   The total and local populations grow geometrically, but the range still expands linearly.

4. In general, changing the emigration parameters does not change the overall behavior of the model. That is, for reasonable values of E_{min} and E_{dd}, local populations grow logistically or geometrically, as determined by R_{max} and R_{dd}, and range expands linearly.

   Obviously, if you set E_{min} and E_{dd} to 0, the range does not expand at all.

   Finally, the model is rather sensitive to the parameter values. That is, is you take any of the parameters very far from the starting values given above, you can see the same kind of chaotic behavior we saw in the simple logistic model. This can produce overflow or underflow errors and negative population sizes.

   The overall conclusion so far is that range expands linearly, regardless of whether the population grows geometrically or logistically, and regardless of the emigration rate (provided that it is greater than zero and not too large).

5. Try changing parameter values in small increments, and observing the effect on the graph of range expansion. Look especially at how long it takes the population to fill the suitable habitat.

   You should see that the rate of range expansion is proportional to R_{max} and E_{min}. It is not much affected by R_{dd} and E_{dd}, although these parameters affect carrying capacities of the local populations.

   In biological terms, the model predicts that range expansion is strongly influenced by the growth and emigration rates of local populations when those populations are small. Whether this is realistic is open to question. You might imagine, for example, that individuals would not emigrate from a population until it reached its carrying capacity. Would that change the way range expands?