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RANGE EXPANSION

Objectives

- Build a spatially explicit model of range expansion by a logistically growing population.
- Model the expansion of a species' range in one and two dimensions.
- Determine how the rate of range expansion relates to population growth and emigration.

Suggested Preliminary Exercise: Logistic Population Models

INTRODUCTION

Species occasionally invade new habitat, often as an intentional or unintentional result of human activities. Invaders usually consist of a few founding individuals, occupying a small area. If the invasion is successful, the invading population grows in numbers and in area occupied—its **range**. Invading species often become pests, displacing or attacking native species, poisoning livestock, or otherwise making nuisances of themselves. It is therefore important to understand how and why a species' range expands. We will focus on two factors that influence range expansion: population growth and emigration rate. You will determine how a population's range expands or contracts, depending on its rates of growth and emigration.

In this exercise, you will treat each cell in the spreadsheet as a patch of habitat, which may house a local population. Each local population may grow or shrink according to its birth and death rates, and it may exchange members with neighboring local populations by emigration and immigration. The number of cells occupied by local populations is the range of the population. The model developed here is loosely based on one in Case (2000).

We begin by assuming that the local population in each cell grows according to a logistic model:

$$N_{t+1} = N_t + (b + b'N_t)N_t - (d + d'N_t)N_t \qquad \text{Equation 1}$$

Here, N_t and N_{t+1} represent the size of the local population at times t and $t + 1$, b represents the per capita birth rate and d the per capita death rate, each when the local population is very small and uncrowded. The symbols b' and d' represent the change in per capita birth and death rates caused by each additional member of the local population. This is the same equation as you used for the logistic model in Exercise 8.

Equation 1 ignores immigration and emigration, which we want to include in our model for this exercise. We could just add terms for immigration and emigration, but the model would rapidly become unwieldy. So let's simplify Equation 1 a bit first. If we multiply out the terms in parentheses, we get

$$N_{t+1} = N_t + bN_t + b'N_t^2 - d\,N_t - d'N_t^2$$

We can rearrange these terms to get

$$N_{t+1} = N_t + bN_t - dN_t + b'N_t^2 - d'N_t^2$$

Factoring gives us

$$N_{t+1} = N_t + (b - d)N_t + (b' - d')N_t^2$$

We can use the symbol R_{max} to represent the population's maximum geometric rate of growth and R_{dd} for the density-dependent reduction in population growth rate—i.e., the amount by which each added member of the population reduces the population's per capita rate of growth. If we define $R_{max} = b - d$ and $R_{dd} = b' - d'$, we can write

$$N_{t+1} = N_t + R_{max}N_t + R_{dd}N_t^2$$

Factoring out N_t once again gives us

$$N_{t+1} = N_t + (R_{max} + R_{dd}N_t)N_t \qquad \text{Equation 2}$$

As the above derivation shows, this model is identical to the logistic model you used in an earlier exercise, but instead of showing per capita birth and death rates and their density-dependent changes explicitly, it combines all that into R_{max} and R_{dd}.

Next, we incorporate emigration out of the cell, symbolized E:

$$N_{t+1} = N_t + (R_{max} + R_{dd}N_t)N_t - (E_{min} + E_{dd}N_t)N_t \qquad \text{Equation 3}$$

Here E_{min} represents the minimum emigration rate and E_{dd} the density-dependent increase in emigration, that is, the amount by which each added member increases the per capita emigration rate from the cell. According to this model, a small proportion of the members of the population emigrate when the population of the cell is small, and the proportion emigrating increases as the population grows (see the exercise, "Metapopulation Dynamics").

These emigrants have to go somewhere, and in this model we will assume they move equally into immediately adjacent cells to the right and left of their natal cell. From the point of view of the population in a cell, new members move in from neighboring cells at rates determined by the sizes of the populations in those neighboring cells, which we simply call Left and Right. We can now write the whole equation for the population of a cell as

$$\begin{aligned} N_{t+1} = N_t &+ (R_{max} + R_{dd}N_t)N_t - (E_{min} + R_{dd}N_t)N_t + \\ &0.5(E_{min} + E_{dd}\text{Left}_t)\text{Left}_t + 0.5(E_{min} + E_{dd}\text{Right}_t)\text{Right}_t \end{aligned} \qquad \text{Equation 4}$$

In words, the population of each cell grows by reproduction of its own members and loses members by emigration. It also receives members from adjacent cells. The factor of one-half in each of these immigration terms comes from the assumption that half of the emigrants from each cell go to the left, and half go to the right.

Although we have written this equation as a logistic model, you can make it into a geometric model by setting R_{dd} to zero. Notice that this makes $(R_{max} + R_{dd}N_t)N_t = (R_{max} + 0N_t)N_t = R_{max}N_t$, which is our old geometric model (with immigration from neighboring cells added).

Likewise, the model assumes that emigration grows in a density-dependent fashion, but you can make emigration a constant proportion of population size by setting E_{dd} to zero. If you set E_{min} to zero, that represents a situation in which no individuals leave

the population when it is very small (when $N_t = 0$, strictly speaking). If you set both E_{min} and E_{dd} to zero, it represents a situation with no emigration at all.

Thus by choosing appropriate values for the model parameters, you can model geometric or logistic population growth, with density-dependent or density-independent emigration, or no emigration at all. You will use the model to find out how a species' range expands under each of these scenarios.

PROCEDURES

First we will model range expansion in one dimension. You might think of one-dimensional habitat as something like a narrow stream, or a narrow riparian zone. Then we will expand the model to two dimensions and see if any of the model predictions change.

As always, save your work frequently to disk.

INSTRUCTIONS	**ANNOTATION**

A. Set up the one-dimensional model.

1. Open a new spreadsheet and set up titles and column headings as shown in Figure 1. Enter the parameter values shown for R_{max}, R_{dd}, E_{min}, and E_{dd}.

These are all literals, so just select the appropriate cells and type them in.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
1	*Range Expansion Across Uniform One-Dimensional Habitat*																	
2																		
3			Parameters															
4			R_{max}	0.6	E_{min}	0.5												
5			R_{dd}	-0.01	E_{dd}	0.001												
6																		
7								Local populations										
8	Time		Site A	Site B	Site C	Site D	Site E	Site F	Site G	Site H	Site I	Site J	Site K	Site L	Site M		Total pop	Range
9	0																	
10	1																	
11	2																	
12	3																	

Figure 1

2. Set up a linear series from 0 to 50 in column A.

In cell A9 enter the value 0.
In cell A10 enter the formula **=A9+1**; copy this formula into cells A11–A59.

3. Enter zeros into cells C9–H9, and cells J9 through O9. Enter the value 2 into cell I9.

These are the initial population sizes in each habitat patch, or site. For now, we model a situation in which the population begins with two individuals at the center of the potential range. We call these the "seed population." You can change the initial conditions later.

4. In cell C10, enter a formula into to calculate the size of the population in that cell at time 1.

Enter the formula **=C9+($D$4+$D$5*C9)*C9-($F$4+$F$5*C9)*C9+0.5*($F$4+$F$5*B9)*B9+0.5*($F$4+$F$5*D9)*D9**.
This corresponds to Equation 4:

$$N_{t+1} = N_t + (R_{max} + R_{dd}N_t)N_t - (E_{min} + R_{dd}N_t)N_t + 0.5(E_{min} +$$
$$E_{dd}\text{Left}_t)\text{Left}_t + 0.5(E_{min} + E_{dd}\text{Right}_t)\text{Right}_t$$

Note that the formula refers to cell B9, which is empty. The spreadsheet treats empty cells as zero values. In effect, we assume that cell B9 is unsuitable habitat, from which no emigrants emerge and within which immigrants die.

5. Copy the formula into cells D10–O10.

Note that the formula in cell O10 refers to cell P9, which is empty. The same interpretation applies here as in the case of cell B9.

6. Copy cells C10–O10 into cells C11–O59.

7. In cell Q9, enter a formula to calculate the total population (in all cells) at time 0. Copy this formula down the column.

Enter the formula **=SUM(C9:P9)**. Copy the formula in cell Q9 and paste it into cells Q10–Q59.

8. In cell R9, enter a formula to calculate the total range of the population at time 0. Copy this formula down the column.

Enter the formula **=COUNTIF(C9:O9,">1")**. Note the quotation marks around >1. Copy this formula into cells R10–R59. This formula tells the spreadsheet to count the number of cells in columns C–O of the current row that contain values greater than one.

We use the cutoff value of 1 rather than 0, because if we use 0 the behavior of the model becomes unrealistic due to the way the spreadsheet handles very small numbers. This cutoff is also more biologically reasonable, because we should not count habitat as occupied until the population there has reached some minimum size. Later, you can try raising the threshold value higher than 1 to see what effect that has.

9. Save your work.

Your one-dimensional model is now complete. You can now use it to graph various aspects of the population's size and range.

B. Graph various aspects of the one-dimensional model.

1. Graph the total population size against time. Edit your graph for readability.

Select cells A8–A59. Hold down the control key (Windows) or the ⌘ key (Macintosh) and select cells Q8–Q59. Make an XY graph. Your graph should resemble Figure 2.

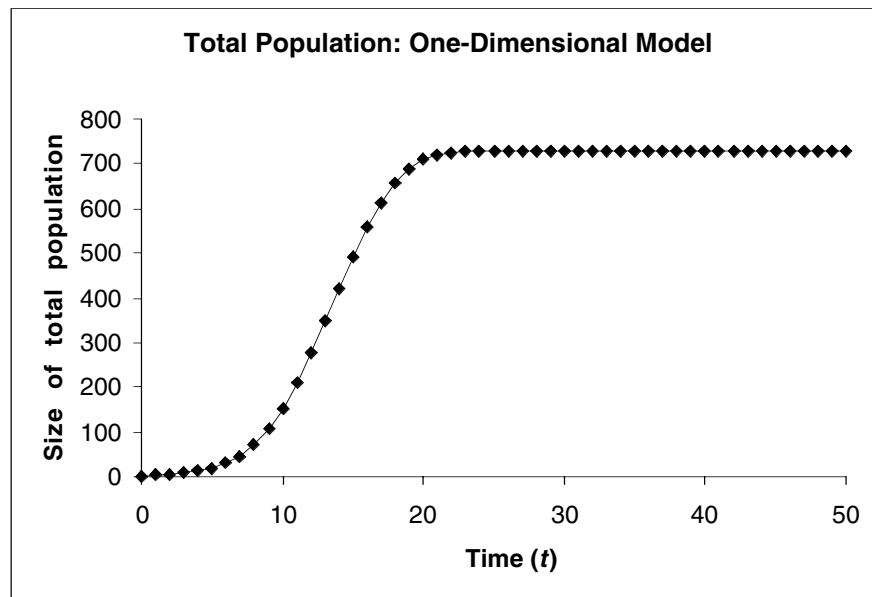**Total Population: One-Dimensional Model**

Figure 2

2. Graph the range of the population (number of occupied cells) against time. Edit your graph for readability.

Select cells A8–A59. Hold down the control key (Windows) or the ⌘ key (Macintosh) and select cells R8–R59. Make an XY graph. Your graph should resemble Figure 3.
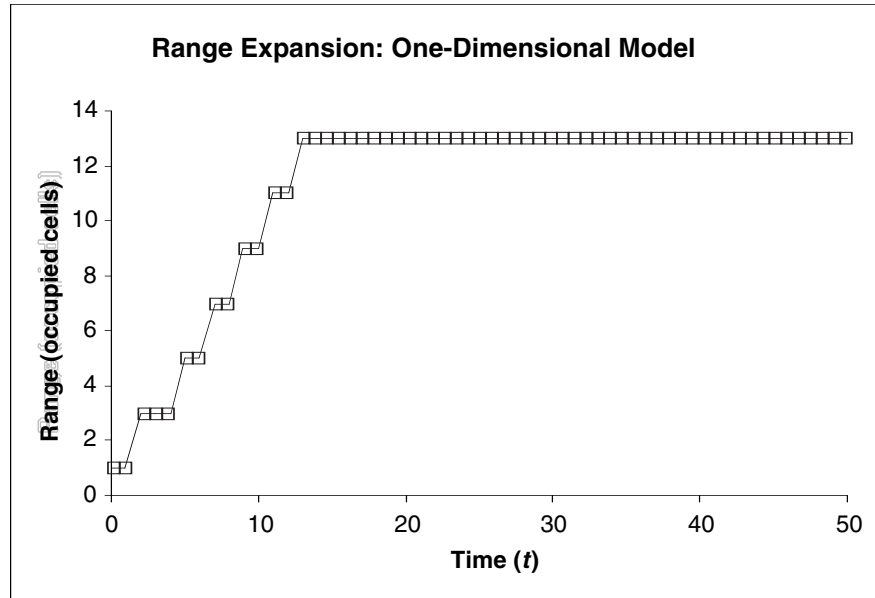
Range Expansion: One-Dimensional Model

Range (occupied cells)

Time (t)

Figure 3

3. Graph the population sizes at three sites: (1) the "seed population" (see Step 3 above); (2) a local population about halfway from the middle to the edge of the range; and (3) a local population at the edge of the range. Edit your graph for readability.

Select cells A8–A59.
Hold down the control key (Windows) or the ⌘ key (Macintosh), and select cells C8–C59.
Hold down the control key (Windows) or the ⌘ key (Macintosh), and select cells F8–F59.
Hold down the control key (Windows) or the ⌘ key (Macintosh), and select cells I8–I59.
Make an XY graph. Your graph should resemble Figure 4.

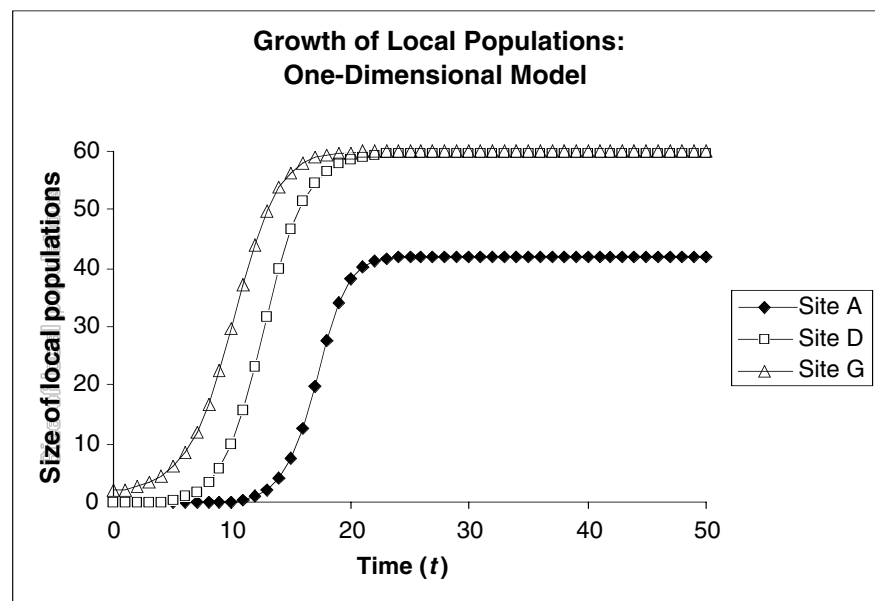**Growth of Local Populations:
One-Dimensional Model**

Size of local populations

Time (t)

Site A
Site D
Site G

Figure 4

Expanding into Two Dimensions

In the next part of the exercise, we examine range expansion in two dimensions. You can visualize this as a homogeneous plain—perhaps a tract of prairie or forest. In the spreadsheet, you will model this with a two-dimensional grid of cells. We can refer to neighboring populations as UpLeft, Up, UpRight, etc. (Figure 5).

In two dimensions, each cell will lose emigrants to, and receive immigrants from, eight neighboring cells instead of two. We can represent this in an equation similar to Equation 4:

$$N_t = N_{t+1} + (R_{max} + R_{dd}N_t)N_t - (E_{min} + E_{dd}N_t)N_t +$$
$$(1/8)(E_{min} + E_{dd}UpLeft_t)UpLeft_t + (1/8)(E_{min} + E_{dd}Up_t)Up_t +$$
$$(1/8)(E_{min} + E_{dd}UpRight_t)UpRight_t + (1/8)(E_{min} + E_{dd}Left_t)Left_t + \qquad \text{Equation 5}$$
$$(1/8)(E_{min} + E_{dd}Right_t)Right_t + (1/8)(E_{min} + E_{dd}DownLeft_t)DownLeft_t +$$
$$(1/8)(E_{min} + E_{dd}Down_t)Down_t + (1/8)(E_{min} + E_{dd}DownRight_t)DownRight_t$$

UpLeft	Up	UpRight
Left	Focal Population	Right
DownLeft	Down	DownRight

Figure 5   Eight neighboring populations around a central, focal population.

INSTRUCTIONS

ANNOTATION

C. Set up the two-dimensional model.

These are all literals, so just select the appropriate cells and type them in.

1. Open a new spreadsheet and set up labels in cells A1–F5 as shown in Figure 6. Enter the labels shown in cells A9, A11, and A13. Enter the parameter values shown for R_{max}, R_{dd}, E_{min}, and E_{dd}.

	A	B	C	D	E	F	G	H	I
1	*Range Expansion Across Uniform Two-Dimensional Habitat*								
2									
3			Parameters						
4			R_{max}	0.75	E_{min}	0.5			
5			R_{dd}	-0.1	E_{dd}	0.001			
6									
7									
8									
9	Time		0.00	0.00	0.00	0.00	0.00	0.00	0.00
10	0		0.00	0.00	0.00	0.00	0.00	0.00	0.00
11	Total pop		0.00	0.00	0.00	0.00	0.00	0.00	0.00
12	2.00		0.00	0.00	0.00	2.00	0.00	0.00	0.00
13	Range		0.00	0.00	0.00	0.00	0.00	0.00	0.00
14	1		0.00	0.00	0.00	0.00	0.00	0.00	0.00
15			0.00	0.00	0.00	0.00	0.00	0.00	0.00
16									

Figure 6

2. Set up a two-dimensional matrix of cells to represent the local populations at time 0.

The matrix of cells C9–I15 represent the area of suitable habitat. At time 0, the habitat is empty except for a small seed population in cell F12.

Enter the values shown for the local populations at time 0. The easiest way to do this is to enter a value of 0 into cell C9, then copy that and paste it into cells C10–C15. Then copy cells C9–C15 and paste into cells D9–I15. Finally, enter a value of 2 into cell F12.

3. Mark this matrix as representing time 0.

In cell A10, enter the value 0.

4. In cell A12, enter a formula to calculate the total population size.

Enter the formula **=SUM(B9:I15)**.

5. In cell A14, enter a formula to calculate the range of the population.

Enter the formula **=COUNTIF(C9:I15,">1")**.

6. Set up a separate matrix of cells to represent the population at time 1.

Copy cells A9–I15 and paste into cells A17–I23. Change the time-value in cell A18 from 0 to **=A10+1**.

7. Enter formulae to calculate the size of each local population at time 1.

Equation 5 above is the basis for this formula. In cell C17, enter the formula **=C9+($D$4+$D$5*C9)*C9-($F$4+$F$5*C9)*C9+(1/8)*($F$4+$F$5*B8)*B8+(1/8)*($F$4+$F$5*C8)*C8+(1/8)*($F$4+$F$5*D8)*D8+(1/8)*($F$4+$F$5*B9)*B9+(1/8)*($F$4+$F$5*D9)*D9+(1/8)*($F$4+$F$5*B10)*B10+(1/8)*($F$4+$F$5*C10)*C10+(1/8)*($F$4+$F$5*D10)*D10.**
Copy this formula into cells C18–C23.
Copy cells C17–C23 and paste into cells D17–I23.

8. Copy the entire matrix of cells for time 1 down the spreadsheet to model the spread of the species through time 15.

Copy cells A17–I23. Paste separately into each of the following cells: A25, A33, A41, A49, A57, A65, A73, A81, A89, A97, A105, A113, A124, and A129.

9. Set up titles and column headings as shown in Figure 7.

These are all literals, so just select the appropriate cells and type them in.

	L	M	N	O	P	Q
8	Time	Total pop	Central pop	Medial pop	Edge pop	Range
9	0					
10	1					
11	2					
12	3					

Figure 7

10. Set up a linear series from 0 to 15 in cells L9–L22.

Enter the value 0 in cell L9.
In cell L10, enter the formula **=L9+1**.
Copy this formula into cells L11–L22.

11. Set up cells M9–M22 to echo the values of total population size at times 0–15.

In cell M9, enter the formula **=A12**.
In cell M10, enter the formula **=A20**.
In cell M11, enter the formula **=A28**.
Continue down the column, incrementing the row address by 8, until you reach cell M22, which should contain the formula **=A132**.

12. Set up cells series in columns N, O, and P to echo the population size of the central population (Central Pop), a local population about halfway to the edge of the suitable habitat (Medial Pop), and a local population at the edge of suitable habitat (Edge Pop).

In cells N9–N22, enter the formulae **=F12** through **=F132**, in steps of 8, as you did for the formula in column M.
Similarly, in cells O9 through O22, enter the formulae **=D10** through **=D130** in steps of 8.
In cells P9 through P22, enter the formulae **=C9** through **= C129** in steps of 8.

13. Set up series in column Q to echo the size of the range at times 0 through 15.

In cells Q9 through Q22, enter the formulae **=A14** through **=A134** in steps of 8.

14. Save your work.

Your spreadsheet is now complete.

D. Graph aspects of the two-dimensional model.

1. Graph total population size against time.

Select cells L9 through M22, and make an XY graph. Edit your graph for readability. It should resemble Figure 8.

Total Population: Two-Dimensional Model

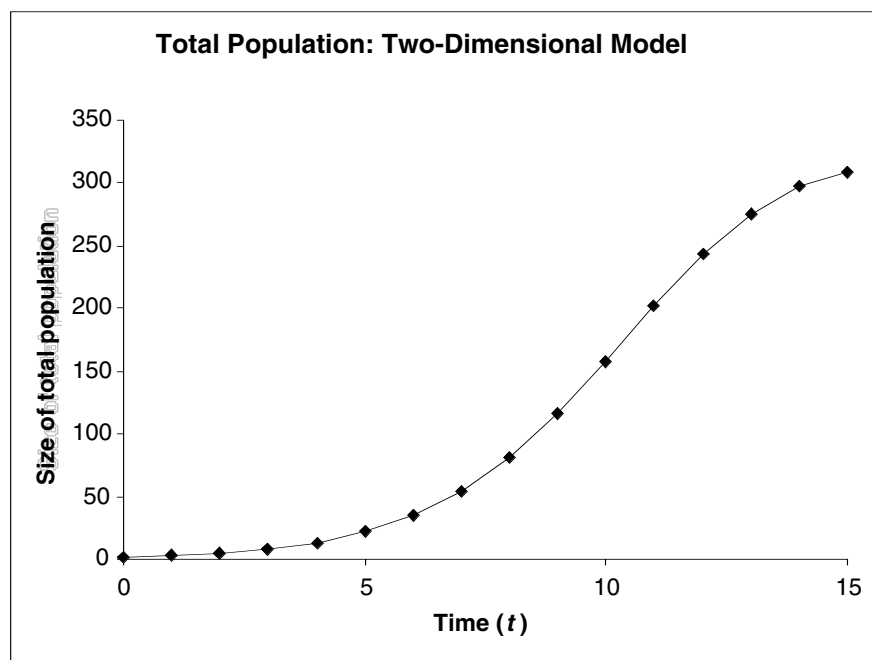Size of total population (n) vs Time (t)

Figure 8

2. Graph the sizes of the central population, medial population, and edge population against time.

Select cells L9 through L22. Hold down the key (Macintosh) or control key (Windows) while selecting cells N9 through P22. Make an XY graph. Edit your graph for readability. It should resemble Figure 9.
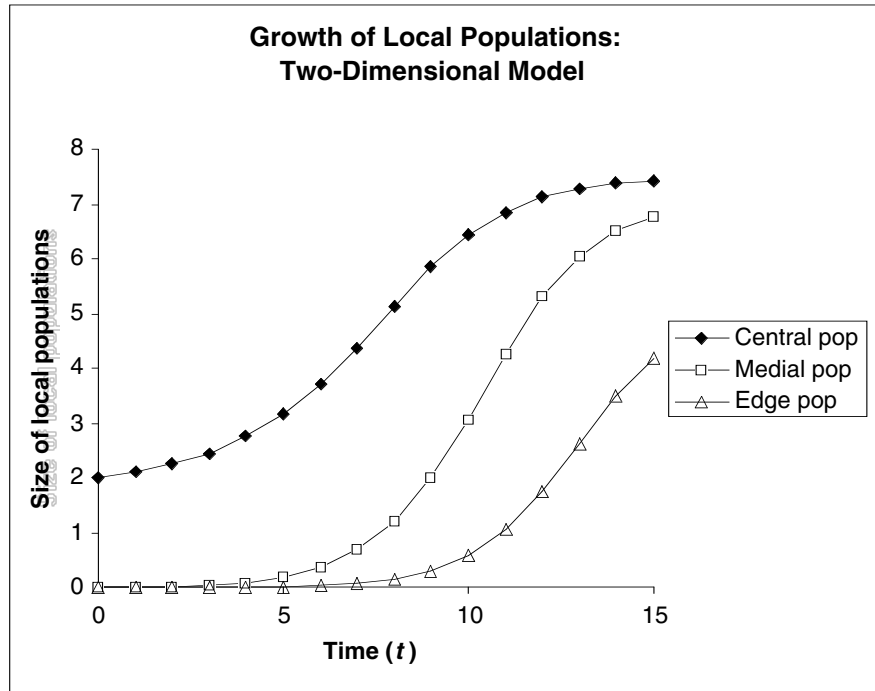
Growth of Local Populations: Two-Dimensional Model

Figure 9

3. Graph the range of the population against time.

Select cells L9 through L22. Hold down the key (Macintosh) or control key (Windows) while selecting cells Q9 through Q22. Make an XY graph. Edit your graph for readability. It should resemble Figure 10.
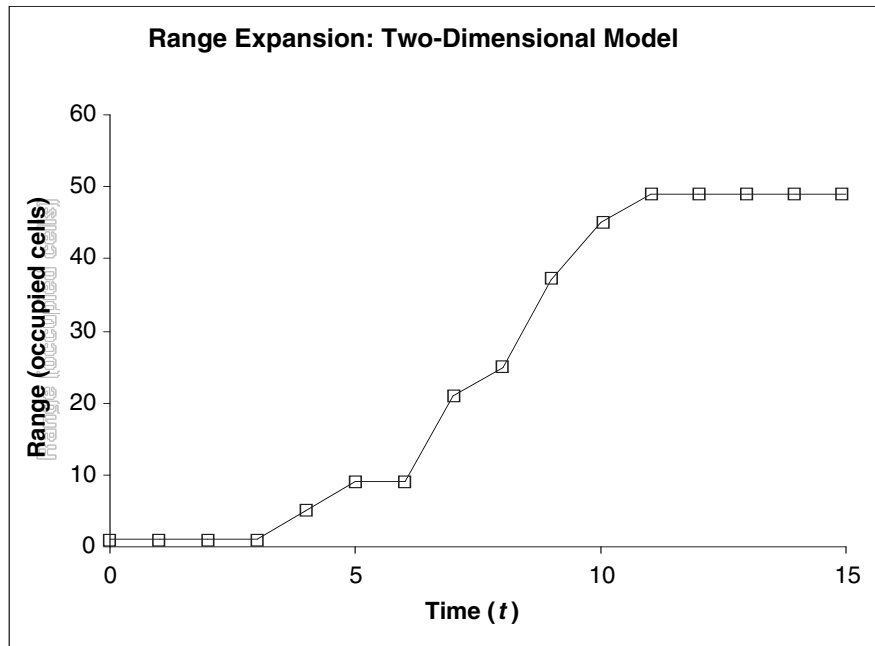
Range Expansion: Two-Dimensional Model

Figure 10

QUESTIONS

Answer questions 1–5 first for the parameters given for the one-dimensional model, and then again using the parameters in the two-dimensional model. (You should find that the two models behave very similarly.)

1. With the parameter values given, how do the local populations and the total population grow?

2. How does the range of this population expand?

3. Can you change parameter values to model geometrically growing local populations?

   Does this affect the predictions of the model?

4. Does changing the emigration parameters change the behavior of the model?

5. How is the rate of range expansion affected by rates of local population growth and emigration?

ADDITIONAL THINGS TO TRY

1. Set R_{max} high enough to produce cyclic or chaotic behavior in the seed population, and graph a few populations (columns) as well as total population. How do the dynamics of these populations compare to dynamics of isolated logistic populations?

2. Start two or more populations at nonzero values (i.e., set up two or more seed populations). Graph each seed population and the total population. What happens when their ranges meet and overlap?

LITERATURE CITED

Case, T. J. 2000. *An Illustrated Guide to Theoretical Ecology.* Oxford University Press, New York.