

2

Spatial, Temporal, and Individual Variation in Birth and Death Rates

As you have seen in Chapter 1, populations have the capacity to either grow explosively or decline to extinction in short order. We know from experience, however, that natural populations are not climbing to infinity or collapsing to zero within the time frames predicted by exponential growth. Nature is more complicated than that. A population grows slower in some years than in others and in some places better than in others. This temporal and spatial variation means that populations are unlikely to grow at a constant rate. In this chapter we meld such variation into our models for population growth. We explore these models with an eye toward seeing if such variability can prevent explosions and/or collapses, or simply delay them.

MOVEMENTS AND POPULATION GROWTH

Real populations occupy physical space and individuals move across this space. If we could visualize the position of each individual—say through a high resolution aerial photography—we would have a snapshot of the population’s distribution at that instant. If this snapshot captured the entire species, it would also depict the **species’ geographic range**. While individuals move many times over their lifetimes, the borders of the geographic range may stay relatively constant, except on a much longer time scale. How might this range expand over time? Consider the simplest case where all space is essentially identical in terms of its ability to support population growth; that is, the space is **uniform** in topography and habitat type. Imagine that we inoculate some part of that space with a few individuals of some focal species; we watch the population size grow and as it grows we watch the individuals move across space. We ultimately want to know how quickly the population spreads. To answer this question we need to back up and first examine the rate of spread of a population where individuals only move, but do not die or give birth. Then we will superimpose the birth and death processes that give rise to exponential growth (from Chapter 1).

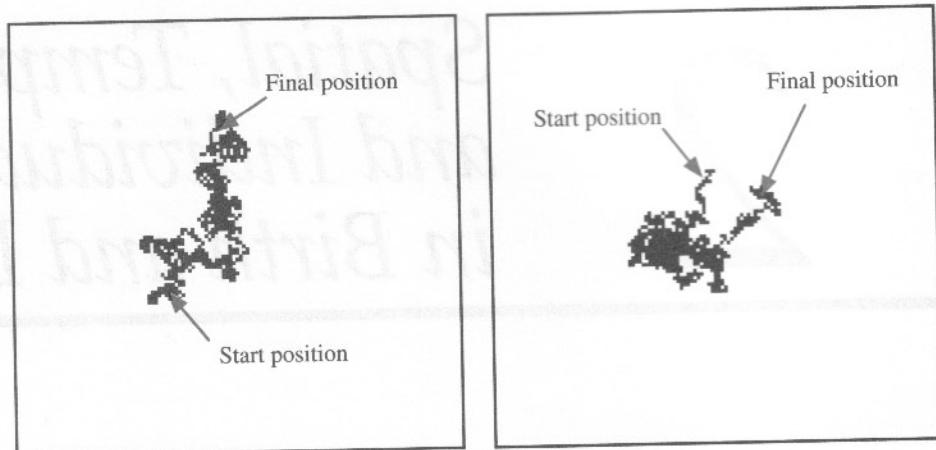
Random Walks and Diffusion

A starting place to think about the small-scale movement of individuals is simply to assume a blind random walk. Figure 2.1 shows the trails of two individuals following such a walk on a plane (i.e., in two dimensions). Each time period, an individual moves to one of the eight neighboring cells at random.

For most animals a random walk will probably be a poor approximation to their actual movements. Real animals will change their rate of movement over time, in different regions of space, or because of different experiences that they have had. Importantly, real organisms certainly do not choose which direction to head just by chance alone. All these complications produce deviations from a random walk model. Nevertheless, a random walk is a good starting place to examine the effect of the simplest kinds of movement on population dynamics.

Figure 2.1

Two examples of a simulated random walk. Each time the individual lands on a new pixel, it is colored black to indicate the path.



The population consequence of many individuals simultaneously undergoing random walks in continuous time and across continuous space is called **diffusion**. Figure 2.2 illustrates this movement.

The exact position of each particle cannot be predicted since their movements are truly random. Nevertheless, it is possible to derive statistical properties of the collection of particles as they move around.

- The center of this circle should, on average, not change over time because movements are equally likely in each direction. Hence the expected value of all the x and y positions of all the particles will not change over time (again assuming a very large number of particles).
- The particles spread out over time. The radius of the circle contains 90% of all the particles in Figure 2.2, but this particular percentage is arbitrary. The radius is proportional to the expected standard deviation of the particles' positions in the x and y directions. Later we examine this rate of spread in more detail.
- Finally, particle density (number of individuals per grid cell) quickly takes on the shape of a sample from a normal distribution in two-dimensional space (Figure 2.3). This is called a **bivariate normal** distribution because it is normal or Gaussian in both variables (x and y).

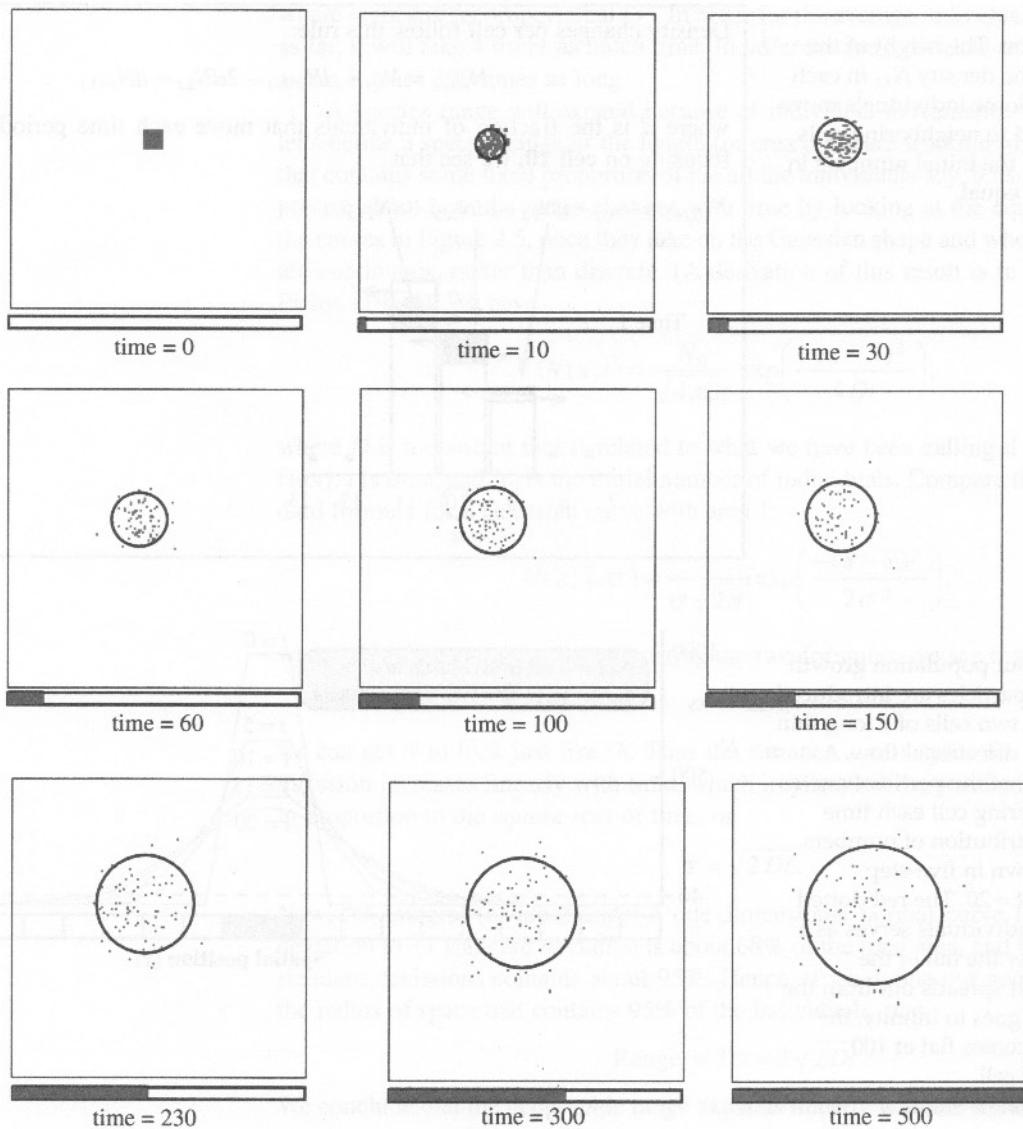
Now we make some of these arguments a bit more quantitative. Imagine that space is simply linear (i.e., one-dimensional) and uniform (i.e., with no spatial heterogeneity). A long linear and stagnant stream provides a convenient analogy. To make the scene more intuitive, you can think of the individuals as N dye particles introduced into the center of the stream. For purposes of simulating this on a computer, we divide this stream into 20 connected grid cells numbered from 1 to 20. Each time period a fraction d of the particles in each cell moves to the left and another fraction d moves to the right (Figure 2.4).

To see the effects of diffusion, imagine that at time 0 all the individuals are confined to the central two cells and that each of these cells has 1000 individuals. All the other cells on either side of the central two cells have zero individuals; thus the total initial population is $N = 2000$. At each time period, one-tenth of the individuals in each cell move to the left and another tenth move to the right ($d = 0.1$). We have in tabular form the following numbers across space for three successive time periods:

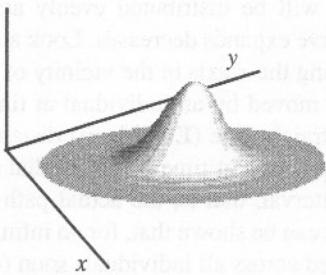
	Time 0:	1000	1000	
	Time 1:	100	900	900
	Time 2:	10	170	820

These numbers show that after two time periods, the individuals have moved out of the central two cells and are distributed across the first four cells. The total population remains constant at 2000, but the distribution is changing.

Exercise 2.1: Write a program to simulate this random walk.

**Figure 2.2**

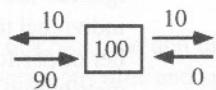
Diffusion: Independent random walks. At time 0, 70 particles clustered in the center of the box, begin individual random walks. As for Figure 2.1, space here is really a very fine grid where each grid cell is a single pixel. The particles occupy a single pixel at any one time and move from one pixel to the next each time step. The direction of movement is random: all eight directions have equal probability. The configuration of the particles in space is shown for several successive time steps up to time 500. Since the time intervals between subfigures are not equal, the bars below provide an index of the elapsed time from the beginning of the simulation. The circle in each subfigure encloses 90% of the particles. The center of this circle is at the mean position (\bar{x} , \bar{y}) of all the particles at time $t = 0$ (i.e., $\bar{x} = \sum x_i/70$ and $\bar{y} = \sum y_i/70$).

**Figure 2.3**

Density. A bivariate (x and y) normal distribution, where x and y are uncorrelated and have equal variance.

Exercise: In the preceding “pyramid” of numbers, where did the number $N_x = 170$ come from at time 2?

Solution: The number in that same cell in the previous time step ($t = 1$) was $N_x = 100$:



$$100 - 20 + 90 = 170.$$

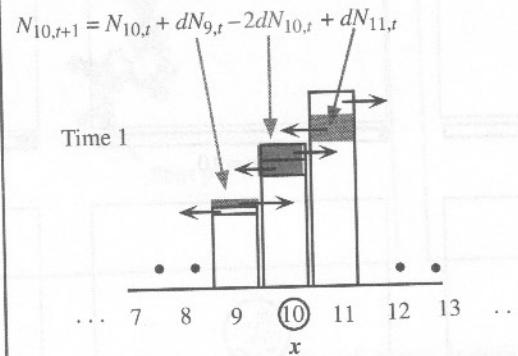
Figure 2.4

Discrete Diffusion. The height of the bars measures the density $N_{x,t}$ in each cell x at time t . Some individuals move each time period to neighboring cells. In this example, the initial numbers in the cells are not equal.

Density changes per cell follow this rule:

$$N_{x,t+1} = N_{x,t} + dN_{x-1,t} - 2dN_{x,t} + dN_{x+1,t} \quad (2.1)$$

where d is the fraction of individuals that move each time period. For example, focusing on **cell 10**, we see that

**Figure 2.5**

Diffusion without population growth. Two thousand particles are introduced into the central two cells of a long thin stream with no directional flow. A fraction, $d = 0.1$, of the particles moves to each neighboring cell each time period. The distribution of numbers per cell are shown in five-step intervals up to $t = 20$. The red dotted line at $N = 40$ individuals serves as a marker to follow the tail of the distribution as it spreads out from the center. As time goes to infinity, the distribution becomes flat at 100 individuals per cell.

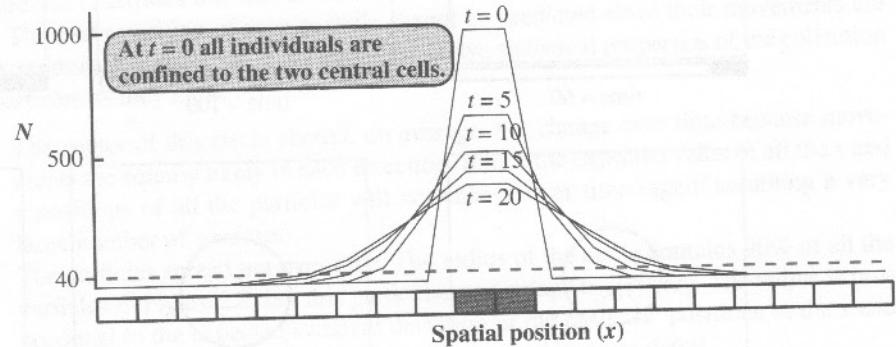


Figure 2.5 shows the continuation of this process. The abundance curve for each time period shows N_t in the center point of each cell. A special rule is invoked at the extreme end positions 1 and 20: simply let dN_1 individuals in cell 1 move to the right and dN_{20} individuals in cell 20 move to the left. This creates a **reflecting boundary** since no individuals fall off the edge.

The $N = 2000$ individuals become redistributed over space; the curve describing their abundance across space becomes normally distributed as time goes on. Every time step, the variance of this distribution curve increases. This “flattening” of the curve is a feature of **diffusion**. The greater the fraction of individuals in each cell that moves every time period, d , the sooner the particles will be distributed evenly across the stream. Also as time goes on, the *rate* that the curve expands decreases. Look at the successive distances from one curve to the next, along the x axis in the vicinity of the tails (the red dotted line). Define the radial distance moved by an individual at time t in a one- or two-dimensional random walk as the straight line (**Euclidean**) distance from that individual’s position at time t to its initial position at time 0. This radial distance ignores the path of movement over this time interval, that is, the actual path that the individual took to arrive at its present position. It can be shown that, for an infinite number of particles, the mean radial distance averaged across all individuals soon (once the distribution curve takes on the bell shape) increases at a rate directly proportional to the **square root** of time. That is,

Radial distance moved by an individual in a random walk $\propto \sqrt{\text{time}}$,

where \propto means “is proportional to”. In order for the average individual to wander twice as far, it will take 4 times as much time. In order for the individual to wander 10 times as far, it takes 100 times as long.

A species range will expand because of individual movements. For the moment, let's define a species range as the length (or area if we are working in two dimensions) that contains some fixed proportion of all the individuals—say, 95%. We can be more precise about how the range changes with time by looking at the equation describing the curves in Figure 2.5, once they take on the Gaussian shape and when space and time are continuous, rather than discrete. (A derivation of this result is in Berg (1983) and Pielou (1969)). We have

$$\mathcal{N}(x, t) = \frac{N_0}{\sqrt{4\pi Dt}} \exp\left(\frac{-(x - \bar{x})^2}{4Dt}\right),$$

where D is a constant that is related to what we have been calling d (more about this later), t is time, and N_0 is the initial number of individuals. Compare this with the standard formula for a Gaussian curve with area 1:

$$N(x; \bar{x}, \sigma) = \frac{1}{\sigma \sqrt{2\pi}} \exp\left(\frac{-(x - \bar{x})^2}{2\sigma^2}\right), \quad (2.2)$$

where σ^2 is the variance. By comparing the two formulas, we see that, if we set

$$\sigma^2 = 2Dt,$$

we can get N to look just like \mathcal{N} . Thus the variance across space for one-dimensional diffusion increases linearly with time, which implies that the standard deviation grows in proportion to the square root of time, or

$$\sigma = \sqrt{2Dt}.$$

Now, the integral (or area) under a one-dimensional normal curve from -1 standard deviation to $+1$ standard deviation is about 68% of the total area, and the area under ± 2 standard deviations contains about 95%. Hence, if we define our geographic range as the radius of space that contains 95% of the individuals, then

$$\text{Range} = 2\sigma = 2\sqrt{2Dt}.$$

We conclude that the geographic range expands linearly with the square root of time. It also increases with the square root of D , not D itself.

A remarkable feature of diffusion is that this same linear relationship between average distance moved and the square root of time does not depend upon the size of space and is true for diffusion in two dimensions, three dimensions, or even higher dimensions. Thus for a group of individuals diffusing in two dimensions, the mean displacement (the radius of the particles' boundary from the center of release) expands across space at a rate proportional to the square root of time. This means that the geographic area occupied by the particles (i.e., the area of the circle that contains a fixed proportion of individuals, as in Figure 2.2) is proportional to the square of the radius and thus increases linearly with time, or

$$\text{Area occupied in two dimensions} \propto \text{radius}^2 \propto \sqrt{\text{time}} \sqrt{\text{time}} = \text{time}.$$

Coming back to the particles enclosed by the circle in Figure 2.2, the radius of the circle increases with the square root of time and thus the area of the circle increases linearly with time.

Fick's Law (Advanced)

We have illustrated diffusion in discrete time and discrete space. **Fick's law** describes the properties of diffusion for continuous time and space (Figure 2.6). The parameter D in Eq. (2.3b) is called the **diffusion coefficient** and has units of distance² per unit time. For a small molecule in water at about room temperature, $D \approx 10^{-5} \text{ cm}^2/\text{sec}$. This molecule would diffuse about 1 cm in 14 hr. One physical interpretation of D is related to

Figure 2.6

Fick's law of diffusive movements.

For discrete space and discrete time, the iteration equation for density change in one dimension is

$$\Delta N_x = N_{x,t+1} - N_{x,t} = -2dN_{x,t} + dN_{x-1,t} + dN_{x+1,t}. \quad (2.3a)$$

We express this change on the right in order of the cells from left to right as

$$= d[(N_{x-1,t} - N_{x,t}) - (N_{x,t} - N_{x+1,t})]$$

= (the difference from $x - 1$ to x) - (the difference from x to $x + 1$).

Note that ΔN_x is then a difference between two differences or, in other words, the *change of a change*.

As both time and space become continuous, this formula becomes:

$$\frac{dN(x,t)}{dt} = D \frac{\partial^2 N(x,t)}{\partial^2 x}. \quad (2.3b)$$

The rate that the density at spatial position x is changing at time t

D is the diffusion parameter.

. . . is proportional to the second derivative of the change in density across space at point x and at time t .

A solution to Eq. (2.3b) for N_0 individuals released at point \bar{x} is the normal distribution of Eq. (2.2):

$$N(x,t) = \frac{N_0}{\sqrt{4\pi Dt}} \exp\left(\frac{-(x-\bar{x})^2}{4Dt}\right)$$

For two-dimensional space (spatial dimensions x and y), Eq. (2.3b) becomes

$$\frac{dN(x,y,t)}{dt} = D \left[\frac{\partial^2 N(x,y,t)}{\partial^2 x} + \frac{\partial^2 N(x,y,t)}{\partial^2 y} \right],$$

with a solution for the radius r from the point of release (\bar{x}, \bar{y}) of

$$N(r,t) = \frac{N_0}{4\pi Dt} \exp\left(\frac{-r^2}{4Dt}\right).$$

the mean squared displacement (i.e., Euclidean distance) of the particles $\overline{\delta^2}$ per unit time, or

$$D = \frac{\overline{\delta^2}}{4t} \quad (\text{in two dimensions}) \quad (2.4a)$$

$$D = \frac{\overline{\delta^2}}{2t} \quad (\text{in one dimension}) \quad (2.4b)$$

That is, the recipe for D is: take the Euclidean distance of each individual from its position at an earlier time, δ_i , square each of these distances, δ_i^2 , take the average of these squares, and then divide by either $4t$ or $2t$.

There is one last important connection we can make involving D . We have discussed the bivariate normal distribution of particles over space, which is a solution to the diffusion equation. The variance of any random variable δ is defined as variance = $E(\delta^2) - (E(\delta))^2$, where $E()$ means the expected value, the mean. Since we are assuming that movements in each direction are equally likely, $E(\delta) = 0$ because movements to the left, on average, cancel out movements to the right. Thus the variance is just $E(\delta^2)$, which is the mean squared displacement, that is, $\overline{\delta^2}$. We can also connect $\overline{\delta^2}$ with the variance equation, Eq. (2.2); namely, $\overline{\delta^2} = \sigma^2$. The reason for the difference in the constant (2 versus 4) in Eqs. (2.4a) and (2.4b) is that in two dimensions the distance moved has both a Δx and a Δy component. Thus the square of the Euclidean distance $\delta_{x,y}$ is

$$\delta_{x,y}^2 = (\Delta x)^2 + (\Delta y)^2.$$

Considerations of symmetry show that $(\Delta x)^2 = (\Delta y)^2$. Consequently, if the variance (after one time step) in one dimension is defined to be $2D$, then the variance in two dimensions is twice that, or $4D$, since the variance of a sum of independent variables is the sum of the individual variances.

Since D is a kind of variance, we now understand why its units are distance² per time unit. We can also derive a rough approximation of the diffusion coefficient D for continuous time and space from the fraction dispersing each time step in discrete space and time, which we have been calling d . Consider the following table that calculates the mean squared displacement along one dimension for individuals moving out of cell 0 to cells -1 and $+1$ in a single time step.

Distance moved, δ	Distance squared, δ^2	Probability	Probability times distance squared
-1	1	d	d
0	0	$1 - 2d$	0
1	1	d	d

Thus the mean squared displacement is the sum of the terms in the last column which is $\delta^2 = 2d$ and substituting this into Eq. (2.4b), we find that $D = d$. This is not a mathematically rigorous derivation because it glosses over the complications that arise from going to continuous space and time, but it does illustrate the point that D and d are closely related. More formally, for one-dimensional space, D is,

$$D \equiv d \frac{\Delta x^2}{\Delta t}$$

And D goes to d as long as Δx^2 and Δt decrease at about the same rate as they both go to zero.

For most students, the fact that Fick's law says that the growth rate dN/dt at each position is proportional to the second derivative in Eq. (2.3b) seems strange, but a little thought shows that this relationship has to be the case. It is clear from Eq. (2.3a) that the net change in density at position x at time t is 0 unless there is some differential in density between that point and its neighbors. If $N_{x,t} = N_{x-1,t} = N_{x+1,t}$, then $N_{x,t+1} = N_{x,t}$. However, a differential in density can still give zero net change if it is linear across space. Berg (1983) provides a delightful proof of this relationship. We illustrate it with an example based on applying the discrete space random walk of Eq. (2.3a), as illustrated in Figure 2.7.

Movements Plus Geometric Growth

With the understanding of simple diffusion given by Figures 2.6 and 2.7, we can return to the simple case of one-dimensional space and now add geometric population growth with discrete rate λ in each cell. The complete dynamics may be modeled as a difference equation for each cell x :

$$N_{x,t+1} = \lambda N_{x,t} - 2dN_{x,t} + dN_{x-1,t} + dN_{x+1,t}.$$

Figure 2.8 shows the result of a simulation in which the dispersal fraction d is again 0.1 and $\lambda = 1.1$ /time step in each of the 20 cells. Thus, if each cell was a closed population, the cell's population would increase by 10% each time step.

The two shaded cells in the center receive 100 individuals each at $t = 0$; all the other cells have zero individuals. The population changes in each cell are due to both population growth and movements to and from immediate neighbors. The result is displayed each 5 time steps. The average individual's displacement from its initial position still increases with the square root of time, but now individuals give birth while they are wandering across space. Each of their offspring then begins a new random walk from its birthplace. The population of individuals in each cell is shown as the successive curves for different elapsed times; these curves do not flatten out, as they do for pure diffusion without population growth, but instead become amplified as time advances.

so the total abundance of individuals in each cell is constant over time. This is called **pure diffusion**. It is a very common process in nature.

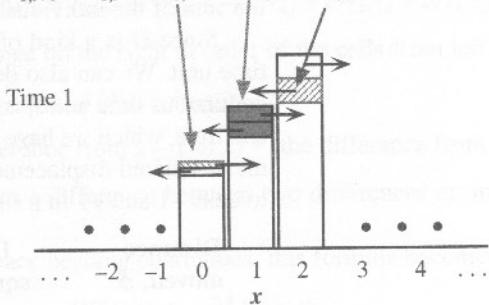
Suppose now that some of the individuals in each cell move out to other cells. This is called **emigration**. If individuals can move out of their cell, then the density in that cell will decrease. If individuals can move into a cell, then the density in that cell will increase. This is called **immigration**.

What happens if there is no net movement?

Imagine that the total number of individuals in each cell is constant over time. This is called **constant density**. If the density in each cell is constant over time, then the slope of density across space is zero. In other words, the slope of density is zero at all times.

Focus on the cell $x = 1$. Its change in density over time is described by

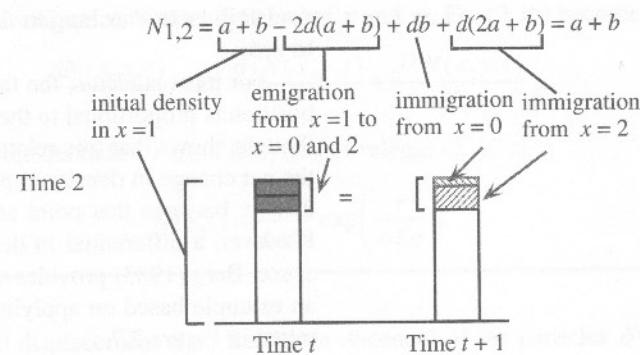
$$N_{1,t+1} = N_{1,t} + dN_{0,t} - 2dN_{1,t} + dN_{2,t}$$



If the slope in density is constant over space, then $N_{x,t}$ can be described by applying the formula for a straight line with slope a and y intercept b , $N_{x,t} = ax + b$. The cell densities at time 1 are:

x	$N_{x,1}$
0	b
1	$a + b$
2	$2a + b$

So cell 1, at time $t = 1$ contains $N_{1,1} = a + b$ individuals. But at time 2, cell 1 will also contain $a + b$:



Conclusion: No net change in local density occurs if the slope of density is constant across space. Net density changes per cell require that the slope vary across space. Since the slope itself is the first derivative, dN_x/dx , its rate of change over space is the second derivative, d^2N_x/d^2x .

Figure 2.7

Density changes over time for diffusion are given by the second derivative of density over space.

Consequently, as shown by the dashed line across Figure 2.8 at the initial number $N_0 = 100$, successively more peripheral cells reach this threshold abundance as time goes on. Moreover, if you look carefully at these intersection points from left to right, you see that, unlike the case for pure diffusion, they are regularly spaced (except for the first two time periods). That is, the **wave front of population advance moving across this space quickly reaches a constant velocity**. This constancy is very different from the dynamics when only diffusion occurs (Figure 2.5).

Figure 2.9 plots the number of cells in Figure 2.8 that reached more than 40 individuals as time goes on. This is repeated for a greater movement rate, $d = 0.2$.

These lines have steps because even though the distribution curve spreads out smoothly over time, the number of individuals in a cell has to exceed the threshold level

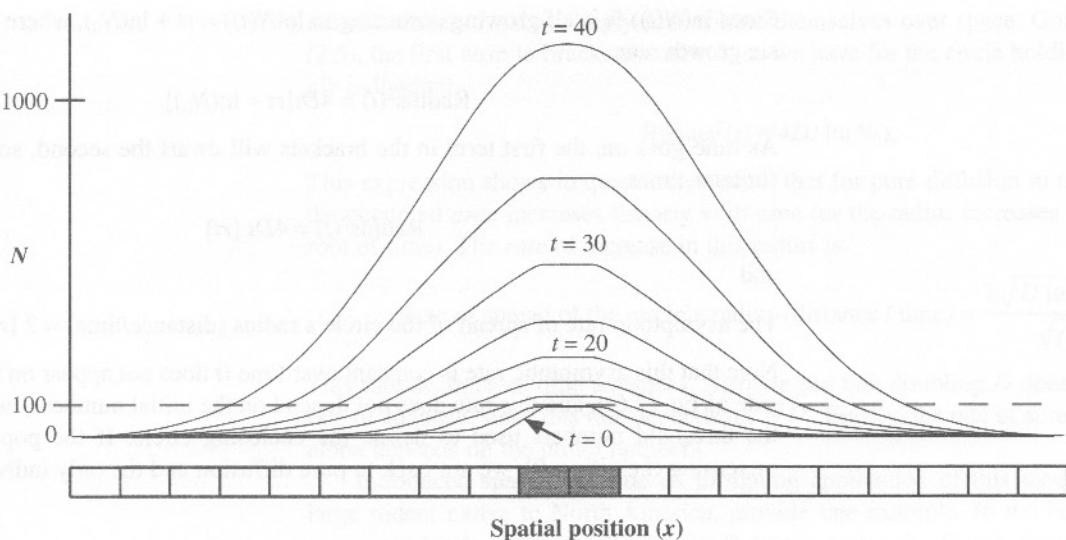
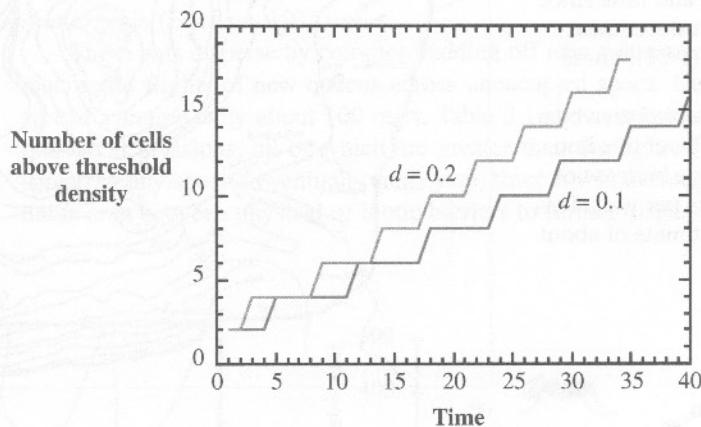


Figure 2.8

Diffusion with geometric growth. At $t = 0$, 100 particles are introduced into each of the two central cells. For all cells, $\lambda = 1.1$ and $d = 0.1$. The red dotted line at $N = 100$ serves as a marker to follow the population wave as it moves outward from the center. For purposes of simulation, the population in each cell first changes through its λ , then movements occur, and so on, for each time step.

Figure 2.9

The one-dimensional spread of a diffusing and geometrically growing population ($\lambda = 1.1$, so $r = 0.095$) for two different movement rates, d . The length of the occupied region ($N(x) > 40$) grows approximately linearly with time. Since the process is symmetrical in space, the occupied length advances in steps of 2 cells, one on each side. Note that doubling d did not double the slope, but increased it by a factor of $\sqrt{2}$.



(set at 40 per cell) for that cell to be counted in the range. Since we have only 20 cells, this produces the steps. If we draw a line connecting the step centers, we see that the advance of the population is roughly linear with time in both cases. This result is also true for two dimensions. That is, assuming that each spatial location is identical in terms of the λ that it supports, **the radius of the population's occupied area eventually grows linearly with time**. Thus the area occupied grows at a rate proportional to the *square* of time. In order for the occupied area to grow 4 times as large, it takes only twice as much time. In order for the area to grow 9 times as large, it takes 3 times as long.

Intuition suggests that the area occupied by the population will grow at a faster rate if a greater fraction of individuals move each time step and if local populations have a higher growth rate λ . Intuition is correct; diffusive movements on the plane in combination with exponential growth yields the result that the area of the circle that is expected to contain all but a single individual has a radius² given by (Pielou 1969)

$$\text{Radius}^2(t) = 4Dt \ln(N(t)).$$

Since $\ln(N(t))$ is itself growing according to $\ln(N(t)) = rt + \ln(N_0)$, where r is the intrinsic growth rate,

$$\text{Radius}^2(t) = 4Dt[rt + \ln(N_0)]. \quad (2.5)$$

As time goes on, the first term in the brackets will dwarf the second, so we can write for later times

$$\text{Radius}^2(t) = 4Dt [rt]$$

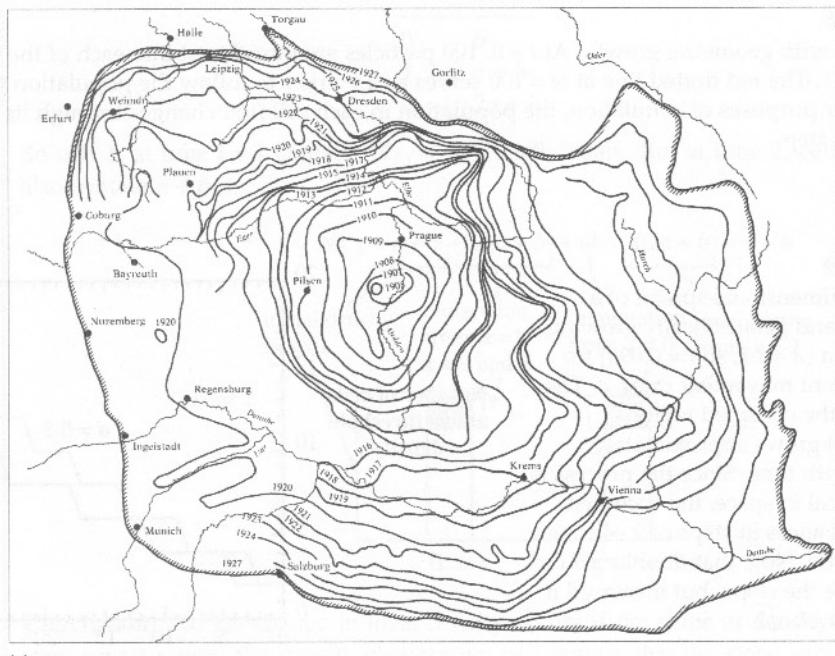
and

$$\text{The asymptotic rate of spread of the circle's radius (distance/time)} = 2 [rD]^{0.5}. \quad (2.6)$$

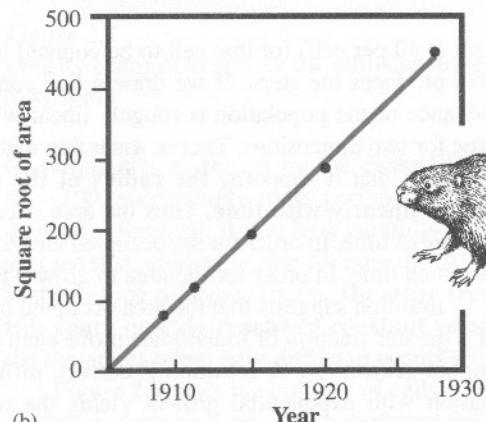
Note that this asymptotic rate is constant over time (t does not appear on the right-hand side of Eq. (2.6)), and this rate does not depend on the initial numbers, nor the value of the threshold numbers used to define the enclosing circle. If the population is not increasing (i.e., if $r = 0$), we are back to pure diffusion and the only individuals are the

Figure 2.10

Five muskrats were introduced into Bohemia near Prague in 1905. (a) Contour lines for the spread of the muskrat (*Ondatra zibethica*) 1905–1927. After Elton (1958). (b) The total area occupied plotted by year. Note the straight-line relationship between the square root of the area and time since the muskrats were introduced near Prague. After Skellam (1951). These values were obtained by approximating the occupied area by a circle. Dividing the slope of this line by $\sqrt{\pi}$ gives the average increase of the radius in kilometers per year. This procedure yields an estimate of about 11.8 km/yr.



(a)



(b)

initial numbers N_0 that simply redistribute themselves over space. Going back to Eq. (2.5), the first term in brackets is now 0, so we have for the circle holding all but a single individual

$$\text{Radius}^2(t) = 4Dt \ln(N_0).$$

This expression shows in quantitative detail that for pure diffusion in two dimensions, the occupied *area* increases linearly with time (or the radius increases with the square root of time). The *rate* of increase in this radius is

$$\text{Rate of spread of the circle's radius (distance / time)} = \frac{2\sqrt{D \ln(N_0)}}{\sqrt{t}}.$$

This rate declines as time advances. Also we see that doubling D does not double the rate of advance, since this rate depends on \sqrt{D} . Finally, the rate of spread for diffusion alone depends on the initial numbers.

Introduced species provide an intriguing application of this model. Muskrats, a large rodent native to North America, provide one example. In the beginning of this century a landowner near Prague in Bohemia (now the Czech Republic) imported muskrats from North America to raise the animals for their pelts. Unfortunately, five animals escaped in 1905. As the population grew and individuals dispersed, the boundaries of the muskrat population increased over time (Figure 2.10). As predicted by the model, the occupied radius grew at roughly a constant rate (about 12 km/yr, averaged over all the compass directions). The student interested in this invasion will enjoy the more detailed analysis provided by Andow et al. (1990).

The spread of exotic Argentine ants (*Linepithema humilis*) in an old field near San Diego, California (Figure 2.11), provides another example—this time on a much finer spatial scale (Erickson 1971).

These ants disperse by colonies budding off new colonies adjacent to them, rather than aerial flights of new queens across unoccupied space. Consequently, the rate of spread averages only about 100 m/yr. Table 2.1 shows some other rates of spread for biological invasions, all of which are greater than the figure for Argentine ants. The spread of any species eventually must stop, since it will eventually occupy all the habitable area between physical or biotic barriers to further dispersal.

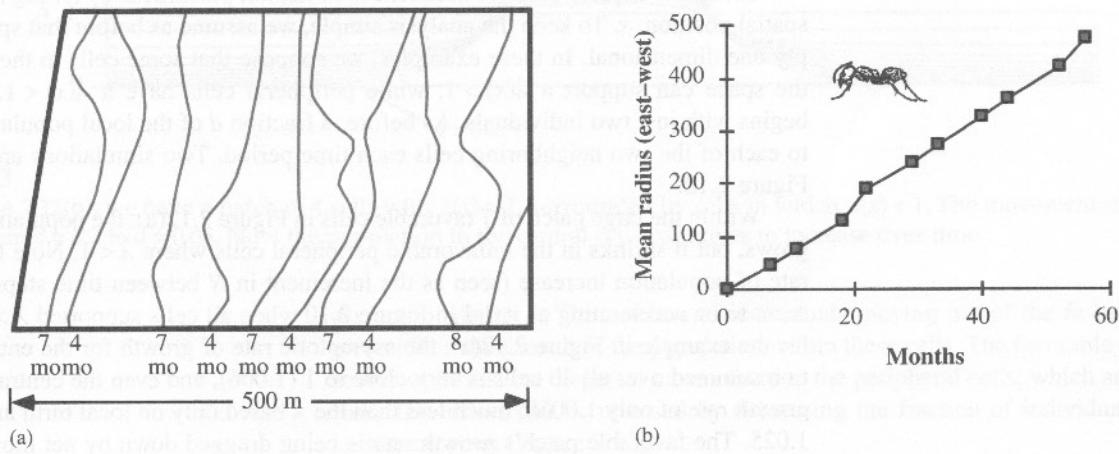


Figure 2.11
(a) The spread of Argentine ants across an old field. Each contour gives the approximate limit of the ants at various times. Time is expressed in months since the last census. (b) The positions in the east–west direction are averaged (across the north–south direction), and these averages are plotted as a function of elapsed time in months. Again we see an approximate linear increase in the occupied radius over time. Modified from Erickson (1971).

Table 2.1. The Observed Rates of Range Expansion for Some Biological Invasions, from Grosholz (1996).

Species	Latin name	Observed velocity of spread (km/yr)
Terrestrial species		
Weedy plant	<i>Impatiens glandulifera</i>	9.4–32.9
Gypsy moth	<i>Lymantria dispar</i>	9.6
Cabbage butterfly	<i>Pieris rapae</i>	14.7–170
Cereal leaf beetle	<i>Oulema melanopus</i>	26.5–89.5
Muskrat	<i>Ondatra zibethica</i>	0.9–25.4
Grey squirrel	<i>Sciurus carolinensis</i>	7.66
Collared dove	<i>Streptopelia decaocto</i>	43.7
European starling	<i>Sturnus vulgaris</i>	200
Plague bacterium (in human host)	<i>Yersinia pestis</i>	400
Marine Species		
Tunicate	<i>Botrylloides leachi</i>	16
Bryozoan	<i>Membranipora membranacea</i>	20
Crab	<i>Carcinus maenas</i>	55
Crab	<i>Hemigrapsus sanguineus</i>	12
Barnacle	<i>Elminius modestus</i>	30
Snail	<i>Littorina littorea</i>	34
Mussel	<i>Mytilus galloprovincialis</i>	115
Mussel	<i>Perna perna</i>	95

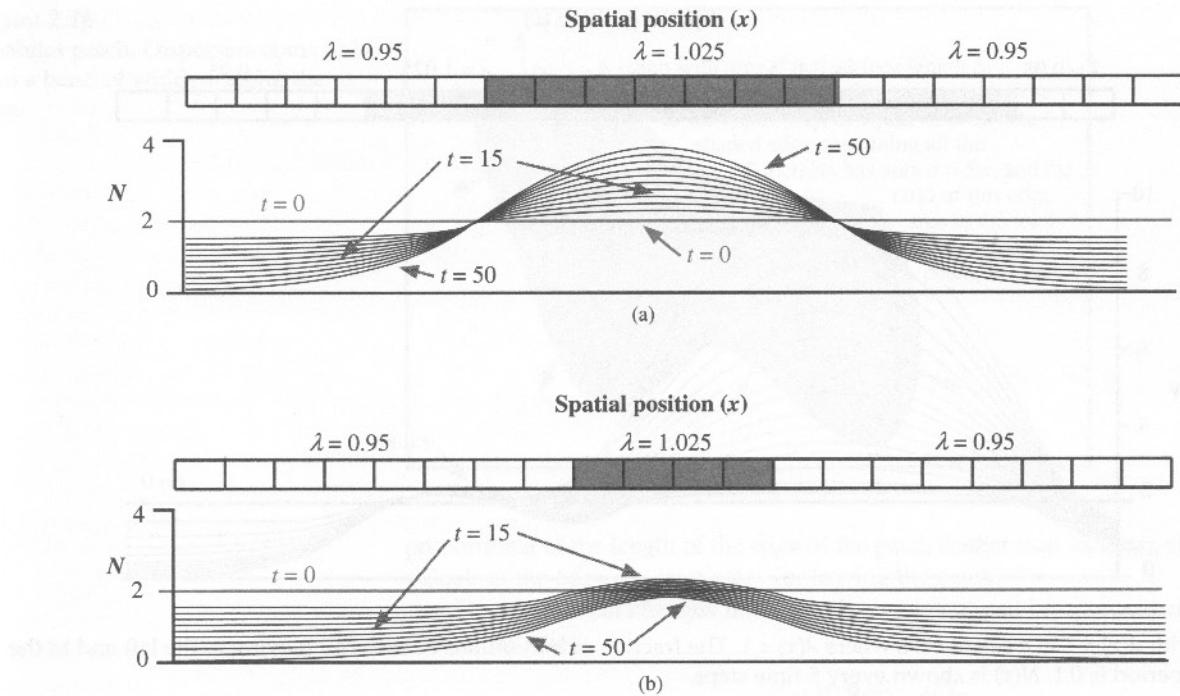
SPATIAL VARIATION

In the models we have developed so far, each point in space is treated as ecologically equivalent, yet in reality different positions on the earth's surface have different physical features, different weather, and different biotic conditions. A population's growth rate is likely to vary from one place to another. The regions of space where populations increase and areas where $\lambda < 1$ may form a patchwork quilt. Fragmentation of an animal's natural habitat by human activities such as deforestation and urban development creates a mosaic of small islandlike favorable patches of natural habitat isolated from one another by agricultural lands or urban/suburban regions.

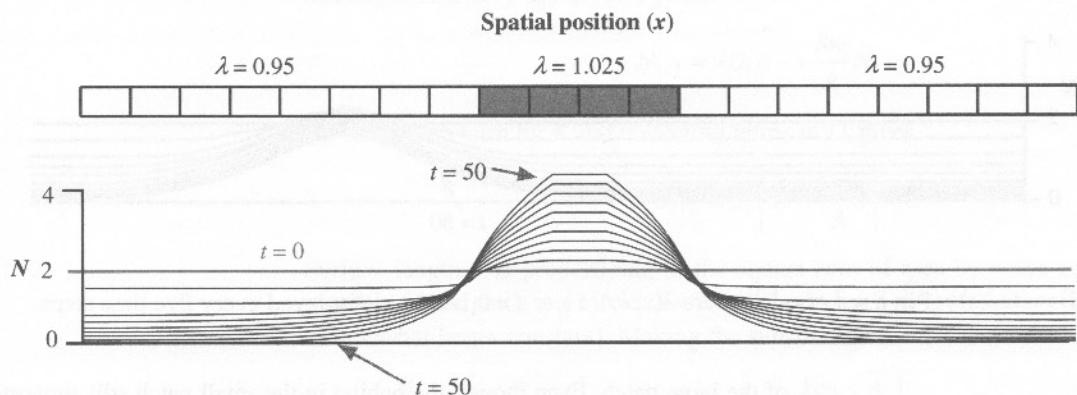
Let's now explore some consequences of habitat patchiness by letting λ vary with spatial position, x . To keep the analysis simple, we assume as before that space is simply one dimensional. In these examples, we suppose that some cells in the interior of the space can support a $\lambda(x) > 1$, while peripheral cells have a $\lambda(x) < 1$. Each cell begins with just two individuals. As before, a fraction d of the local population moves to each of the two neighboring cells each time period. Two simulations are shown in Figure 2.12.

Within the large patch of 7 favorable cells in Figure 2.12(a), the population steadily grows, but it shrinks in the unfavorable peripheral cells where $\lambda < 1$. Note too that the rate of population increase (seen as the increment in N between time steps) does not seem to be accelerating as it did in Figure 2.10 when all cells supported $\lambda > 1$. In fact, for the example in Figure 2.12(a), the asymptotic rate of growth for the entire population summed over all 20 cells is very close to 1 (1.006), and even the central cell has a growth rate of only 1.0068, much less than the λ based only on local birth and death of 1.025. The favorable patch's growth rate is being dragged down by net movements of individuals into the unfavorable peripheral sites. We can think of the interior patch as a **source** population "discharging" a net flow of individuals out. The peripheral cells represent a **sink** population that receives a net flow of individuals. In this way sink populations are being subsidized by the large interior patch.

For the small favorable patch size of 4 cells in Figure 2.12(b), the population first increases for about the first 15 time periods, but then begins to shrink. As time goes on, the populations in both the favorable patch and the peripheral unfavorable cells decline

**Figure 2.12**

The intrinsic growth rate, $\lambda(x)$, varies across space, x . In the red region $\lambda > 1$, and in the white region $\lambda < 1$. Each cell begins with two individuals at $t = 0$ (the red horizontal line). In both cases $d = 0.2$; the only difference is the size of the region with $\lambda > 1$. The population density across space is drawn every 5 time steps.

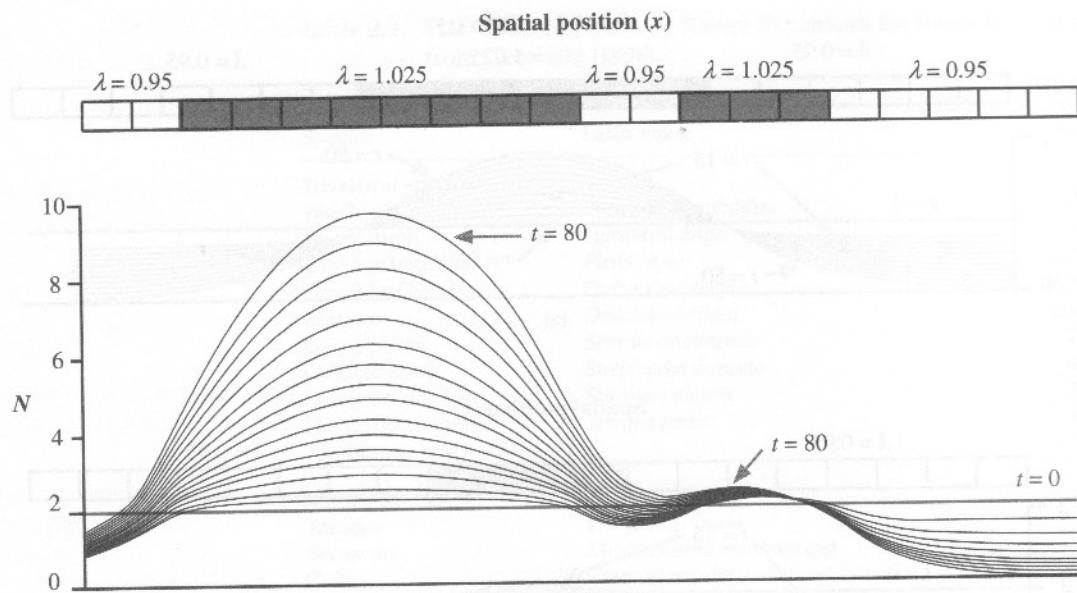
**Figure 2.13**

As in Figure 2.12(b), we have a patch of 4 cells with $\lambda(x) > 1$, surrounded by cells in which $\lambda(x) < 1$. The movement rate is reduced from $d = 0.2$ to $d = 0.05$. Now the population in the central cells continues to increase over time.

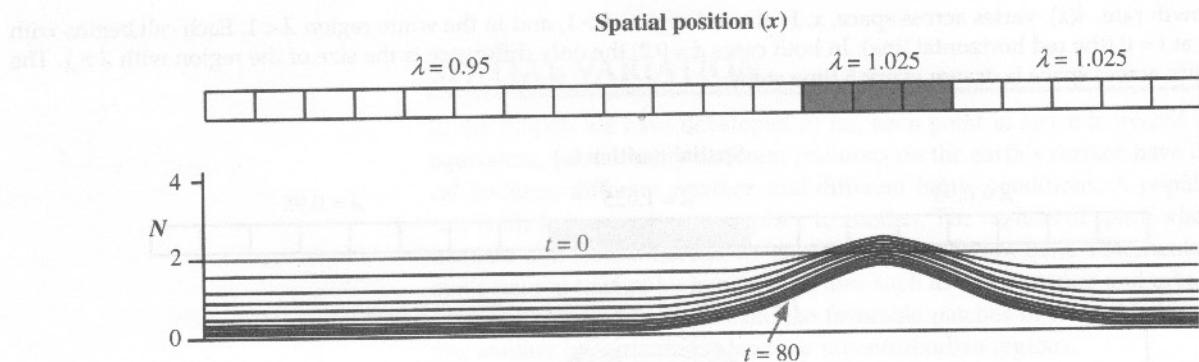
Asymptotically to 0. The net loss of individuals moving out of the favorable patch is greater than the growth of the population within these cells. The favorable patch is a net source of births, but dispersal moves them to the peripheral cells, which are a dead-end sink. This effect can be reversed by decreasing the fraction of individuals that move each generation (Figure 2.13).

Figure 2.14 presents two favorable patches, both with $\lambda(x) > 1$. They are separated by a region of space where $\lambda(x) < 1$. The simulation shows that the population in each patch continues to increase over time, although this rate of increase is much less in the small patch than the large one.

Now imagine that the large patch in Figure 2.14 is destroyed. We do this by decreasing the $\lambda(x)$ for these 8 cells to the background level of 0.95. The small patch is left unharmed, but a large source of immigrants to it has been eliminated by the destruction

**Figure 2.14**

Two patches with $\lambda(x) > 1$ in a sea of cells where $\lambda(x) < 1$. The fraction of individuals in each cell moving to the left and to the right per time period is 0.1. $N(x)$ is shown every 5 time steps.

**Figure 2.15**

One small patch with $\lambda(x) > 1$ in a sea of cells where $\lambda(x) < 1$. Here $d = 0.1$. $N(x)$ is displayed every five time steps.

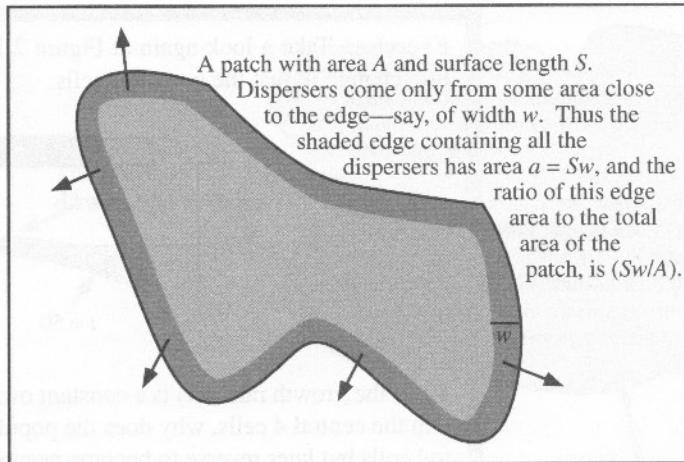
of the large patch. Even though the habitat in the small patch still supports a $\lambda > 1$, the population in the small patch, after an initial spurt of positive growth, declines asymptotically to 0 once its larger neighbor is destroyed (see Figure 2.15).

Thus a population occupying a habitat patch is prone to extinction from a combination of low growth rate, high dispersal rate, small patch size, and isolation from neighboring patches. The loss of individuals dispersing out of the patch can then be greater than the population growth rate per time period within the patch. **One important conclusion is that it might be difficult to preserve highly motile species with small conservation parks.**

This interaction between patch size and dispersal rate can also be developed using a simple analytical argument. Imagine a two-dimensional habitat patch within a defined region (Figure 2.16). The number of organisms inside the patch at time t is N_t , and the density (D_t) is the number per unit area, or N_t/A . Birth and death of individuals within the patch create a local growth rate of λ . To consider the total change in numbers, however, we must also include the movement of individuals out of the patch. Once individuals leave, they die. We assume that the patch is so isolated by regions with $\lambda < 1$ that the immigration of individuals into the patch is negligible. The total emigration rate is

Figure 2.16

A habitat patch. Dispersers come only from a band of width w along the edge.



proportional to the length of the edge of the patch (rather than its area), since only individuals at the edge are candidates for leaving the patch.

Thus numerical changes in the patch population can be approximated by the difference equation:

$$N_{t+1} = \lambda D_t A - e f N_t, \quad (2.7)$$

where e describes the emigration rate for individuals in the edge area and f is the fraction of the edge area compared to the total patch area. We assume that the population density in the edge is equivalent to the density in the core area. As shown in Figure 2.16, this fraction f is given by Sw/A , where S is the surface length of the patch. Substituting this expression for f in Eq. (2.7) yields

$$N_{t+1} = \lambda D_t A - e \frac{Sw}{A} N_t.$$

Dividing each term by A and collecting terms in D_t gives

$$D_{t+1} = D_t \left[\lambda - \frac{Sew}{A} \right].$$

Surface length S is proportional to the square root of area by some constant k . (For example, if the patch is a circle, $S = 2(\pi A)^{0.5}$ and $k = 2\sqrt{\pi}$; for other shapes, k will be a somewhat larger constant). Making the substitution $S = k\sqrt{A}$ yields

$$D_{t+1} = D_t \left[\lambda - \frac{kew\sqrt{A}}{A} \right]$$

and thus

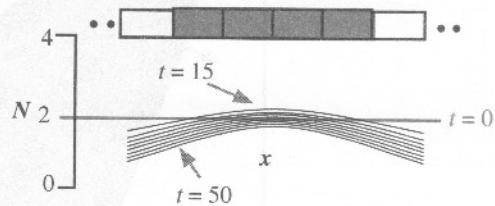
$$D_{t+1} = D_t \left[\lambda - \frac{kew}{\sqrt{A}} \right].$$

If the population in the patch is to increase, $D_{t+1} > D_t$, which implies that the term in brackets must be greater than 1, which in turn implies that the following inequality be satisfied:

$$\lambda > \frac{kew}{\sqrt{A}} + 1.$$

This inequality is easier to fulfill as area increases, as the emigration rate e decreases and as λ increases. Note also that it is no longer sufficient for λ to simply exceed 1 if the patch's population is to increase (an observation we witnessed earlier in the simulations of Figure 2.12b).

Exercise: Take a look again at Figure 2.12(b). Here's a blow-up of the population change in just the 6 central cells:



Since the growth rate $\lambda(x)$ is a constant over time in each cell x and is greater than 0 in the central 4 cells, why does the population size N first increase in these central cells but later reverse to become negative after $t = 15$? What happens to cause this reversal?

INDIVIDUAL VARIATION AND TEMPORAL VARIATION

A population's per capita growth rate, λ , incorporates each individual's probability of reproducing or dying per unit time. An organism's physiology, age, body size, behavior, prior experience, anatomy, and location all influence its probability of giving birth and of dying. Since these factors can vary over time and across individuals, the population growth rate for collections of individuals should, in fact, be a variable, not a constant as we have been assuming so far. The fate of a finite population, particularly a small population, is influenced by these factors, which contain chance elements. It is sometimes useful to distinguish **temporal** (or **environmental**) **variation** in the favorableness of the environment and **between-individual variation** (also called **demographic variability**) at the same moment of time.

Even without a complete understanding of the actual cause of this variability, we can still describe statistical properties of collections of individuals and predict, for example, the expected size of a population, whether the population might ultimately decline to extinction, and, if so, in what time frame. Shortly, we make a stab at some of these predictions. Some students may want to refer to Appendix 6 for definitions of the terms **expected value**, **mean**, and **variance**. Figure 2.17 introduces the logic and notation that we will follow.

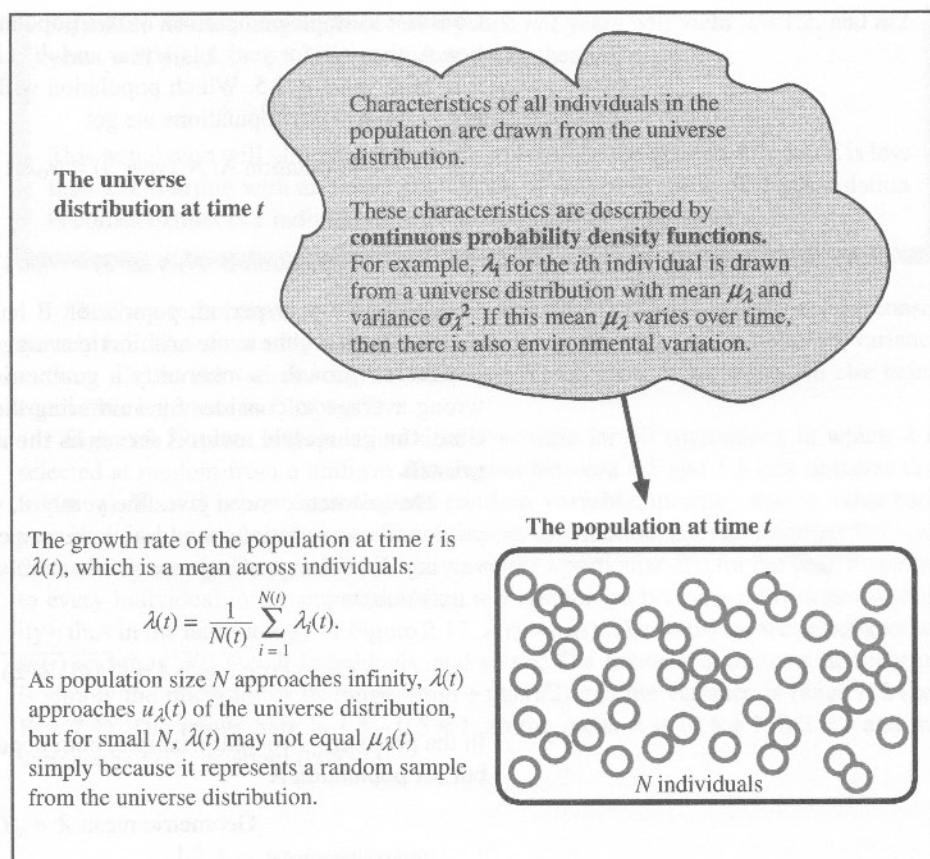
For a population of N individuals, we figuratively draw λ_i out of a hat (the universe distribution) for each of the $i = 1$ to N individuals at each time period. For example, if individual i has a λ_i of 1.5, it will be replaced by 1.5 individuals in the next year. This could be accomplished by it surviving over the year plus having a 50% chance of giving birth to a single offspring, or it might die but have a 50% chance of giving birth to three offspring. We will not concern ourselves with these individual details, since we want to focus here on the populational consequences of variation in λ_i . The realized population growth rate in year t , $\lambda(t)$, is the arithmetic average of these λ_i values over the N individuals. To get the individual λ_i we must specify the distribution from which they are chosen. This is the **universe distribution**, shown as a cloud in Figure 2.17. Its shape (normal or uniform, etc.) and its mean and variance need to be specified.

We explore the case of pure temporal variability later by letting the universe distribution collapse to a single number (without any variance) each year, applied to all individuals, but this number varies from one year to the next, as specified by still another random distribution. We explore the case of pure between-individual variation by assuming that the universe distribution has some variance within a single year as shown in Figure 2.17, but the mean and variance remain constant over time.

When there is some between-individual variation, the "realized mean" λ for a finite population of N individuals will usually, by chance, not equal the mean of the universe distribution, μ_λ . For example, let's choose λ_i for each individual i by a toss of a coin for

Figure 2.17

To model individual variation requires that we find a plausible way to assign different values to different members of a population. Selecting these values from some continuous random variate is a reasonable approach. Here this random variate is called the universe distribution and is represented by a cloud, since it is never depleted by sampling and because its parameters may shift over time. Two types of variation affect $\lambda(t)$ and thus N_{t+1} : possible temporal variation in the universe distribution (i.e., if μ_λ varies over time) and the chance sampling of individuals that goes into determining the realized values for λ_i that contribute to the mean, $\lambda(t)$, for the population at each time step.



a very small population of $N = 2$ individuals. The universe distribution λ_i is either 0 (for tails) or 1 (for heads) with probability 0.5 for each outcome. The mean of this random distribution, μ_λ , is 0.5, and the variance is $(0.5)^2 = 0.25$. With only two individuals, by chance, both might have $\lambda = 1$, and this event has the substantial probability of $(0.5)(0.5) = 0.25$. This particular sample of $N = 2$ has a realized mean λ of 1 even though the universe distribution has a mean of 0.5. This discrepancy arises because of sampling error: **simply by chance you are not likely to duplicate the true mean and variance in a sample**. As population size, N , increases, large divergences between the realized mean for a sample, λ , and the universe mean, μ_λ , become increasingly unlikely. For example, the probability of drawing a population of $N = 100$ with a realized sample mean of $\lambda = 1$, using the same coin toss, is extremely remote: 0.5^{100} .

To summarize, first we imagine an underlying universe distribution from which the probabilities for individuals are assigned. Second, we have for a finite number of individuals a sample realization of those probabilities, which forms the between-individual variation. Finally, we wish to combine these processes to explore the population consequences of those realizations. Both shifts in the universe distribution over time and different possible realizations for samples drawn from the same universe distribution produce population variation. We first consider the consequences of temporal variability alone, then between-individual variability alone, and finally put the two together.

Temporal Variability Alone

Here we assume that the variance in the universe distribution, σ_λ^2 , is 0, so sampling error for between-individual differences can be ignored as a determinant of variability in λ . All individuals in the population behave identically, and the population mean $\lambda(t)$ at time t exactly equals the universe mean $\mu(t)$ at each time step, since the universe distribution is simply a point. Yet, as the notation suggests, this point varies over time.

Consider a simple comparison of two populations with the same initial size: in population A, the $\lambda(1)$ for year 1 is 1/year and $\lambda(2)$ is 2/year. In the second population, B, the λ in both years is 1.5. Which population will be the largest after two years? Applying Eq. (1.3a) to both populations we get

$$\text{Population A: } N_2(\text{year 3}) = N_0\lambda(1)\lambda(2) = N_0(1)(2) = 2N_0$$

and

$$\text{Population B: } N_2(\text{year 3}) = N_0\lambda(1)\lambda(2) = N_0(1.5)(1.5) = 2.25N_0.$$

Over this two year period, population B has grown more than A even though both populations have the same arithmetic average population growth rate of 1.5. Because population growth is inherently a geometric process, the arithmetic mean λ is the wrong average to consider for answering the question. Instead, **when λ 's vary over time, the geometric mean λ serves as the appropriate measure of net population growth.**

The geometric mean gives the yearly λ , which, if reproduced year after year for n years without variation, would give the same final population size as does a series of varying $\lambda(t)$. The geometric mean of n numbers is the n th root of the product of those n numbers, or

$$\text{Geometric mean } \lambda = \sqrt[n]{\lambda(1)\lambda(2)\lambda(3)\cdots\lambda(n)} = \left[\prod_{i=1}^n \lambda(i) \right]^{1/n}. \quad (2.8)$$

In the preceding two-year example, both populations have an arithmetic mean λ of 1.5, but for population A

$$\text{Geometric mean } \lambda = \sqrt{(1)(2)} = \sqrt{2} = 1.414$$

and for population B

$$\text{Geometric mean } \lambda = \sqrt{(1.5)^2} = 1.5.$$

In fact, the arithmetic mean is *always* greater than or equal to the geometric mean. To understand why this is the case, note that taking the natural log of Eq. (2.8) yields

$$\begin{aligned} \ln \text{of the geometric mean} &= \ln \left[\prod_{i=1}^n \lambda(i) \right]^{1/n} \\ &= (1/n) \ln(\lambda(1)\lambda(2)\lambda(3)\cdots\lambda(n)) \\ &= (1/n) [\ln(\lambda(1)) + \ln(\lambda(2)) + \ln(\lambda(3)) + \cdots + \ln(\lambda(n))] \\ &= (1/n)(n) (\text{arithmetic mean of } \ln(\lambda)) \\ &= \text{arithmetic mean of } \ln(\lambda). \end{aligned} \quad (2.9)$$

Now let's look at what the \ln function does graphically, as illustrated in Figure 2.18. Note how equal intervals on the x axis in Figure 2.18 get "translated" into nonequal intervals on the y axis plotting $\ln\lambda$. In this way, higher values of λ are discounted in the mean for $\ln\lambda$ compared to the mean of λ . Consequently, the arithmetic mean λ (the mean of the values on the x axis) will be greater than the geometric mean λ . The geometric mean equals the arithmetic mean only when the numbers have no variance, as when the geometric mean, 2, of 2, 2, 2 is identical to the arithmetic mean. The greater the variance among the numbers, the greater is the difference between the arithmetic and geometric means.

Problem: Consider a hypothetical bird population: 50% of the time the population increases by 20% and the other 50% of the time the population decreases by 20%. Assuming that the two kinds of years are independent over time, what will happen to this population?

Solution: Over a long sequence of n years: $n/2$ years will yield $\lambda = 1.2$, and $n/2$ years will yield $\lambda = 0.8$. The geometric mean then is

$$\lambda = (0.8^{n/2} 1.2^{n/2})^{1/n} = \sqrt{(0.8)} \sqrt{(1.2)} = 0.9798.$$

This population will ultimately become extinct since the geometric mean λ is less than 1.0. Starting with an initial abundance of 400 birds, 90% of the population becomes extinct (<1 individual) before 400 years, by simulation.

The long-term behavior of a population, and particularly its persistence, are consequently influenced not only by the mean λ across years but also the temporal variance in these λ 's. As the variance increases, the geometric mean λ decreases, all else being equal (this is proven in Chapter 7).

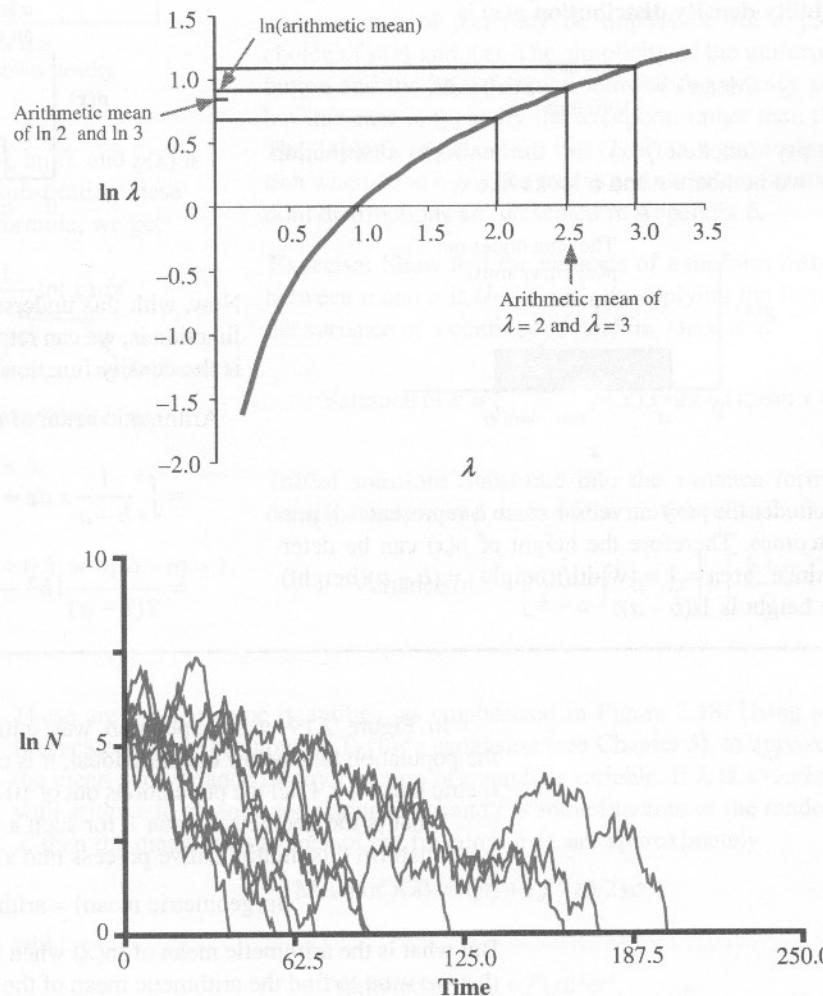
Figure 2.19 plots $\ln(\text{population size})$ over time for 10 simulations in which λ is selected at random from a uniform distribution between 0.5 and 1.5 (the universe distribution). Thus λ is now a **continuous random variable**, meaning that its value each year is chosen at random from some continuous distribution. All real numbers between 0.5 and 1.5, are equally probable. When we select a particular $\lambda(t)$ for the year, it applies to every individual in the population (i.e., we assume no between-individual variability); thus in the terminology of Figure 2.17, $\lambda(t) = u_\lambda(t)$. The next year we select another $u_\lambda(t)$ and thus $\lambda(t)$ for all individuals, and so on. The **mean** of a uniform distribution is simply the midpoint of its range, $(\min + \max)/2$ and the variance is $\text{range}^2/12$ (see Box 2.1). The **range** here is $1.5 - 0.5 = 1$, so the mean λ is $(0.5 + 1.5)/2 = 1$ and the variance is $1/12$, or about 0.08333.

Figure 2.18

The natural logarithm of a number (red curve) versus the number. The vertical lines show two values of λ (2 and 3) and how they map onto the $\ln \lambda$ scale. The arithmetic mean of these two numbers is 2.5, the midpoint between them. The mean of $\ln 2$ and $\ln 3$ is the midpoint between them and is also shown and compared with $\ln 2.5$, the \ln of the arithmetic mean. Because the slope of the \ln function is always positive but declining (i.e., a negative second derivative), the $\ln(\text{arithmetic mean})$ must always lie above the mean of the \ln 's of a series of different numbers.

Figure 2.19

Geometric growth when λ is drawn randomly each time step from the uniform distribution [0.5 to 1.5]. Here the arithmetic mean $\lambda = 1$, but the populations tend to decline to extinction because the geometric mean $\lambda < 1$ (≈ 0.959).



Box 2.1 (Advanced; Requires Calculus). The Mean of a Function of a Continuous Random Variable

For the uniform distribution, it is possible to find an exact solution for the geometric mean to compare to the approximation formula, Eq. (2.12). Most of you are familiar with discrete random events like the flip of a coin or the roll of a die. The formula for the mean, or expected value, of a discrete random variable x is defined as

$$\text{Mean } x = \bar{x} = \sum_{i=\min}^{\max} p_i x_i.$$

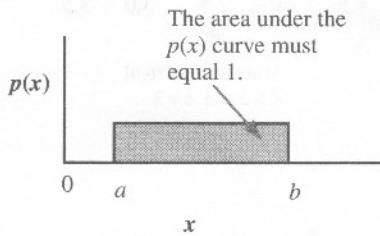
Here p_x is the probability of each possible discrete outcome x . For a roll of a die there are 6 possible outcomes x , the numbers 1 through 6, and each x has equal probability $p_x = 1/6$. Thus the mean outcome is

$$\sum_{i=1}^6 \frac{1}{6} x_i = \frac{1}{6} \sum_{i=1}^6 x_i = \frac{1}{6} [1+2+3+4+5+6] = 3.5.$$

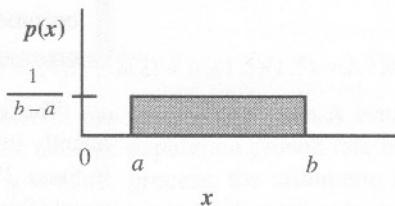
By extension, for a continuous random distribution x , the formula for the mean of a continuous random variable x with a **probability density distribution** $p(x)$ is

$$\text{Mean } x = \int_{\text{lower limit}}^{\text{upper limit}} p(x) x dx.$$

The density function $p(x)$ for the uniform distribution between two numbers a and b looks like



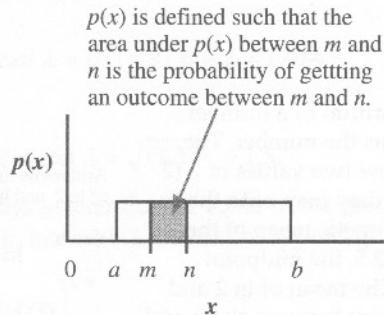
The area under the $p(x)$ curve is 1 since it represents all possible outcomes. Therefore the height of $p(x)$ can be determined since $\text{area} = 1 = (\text{width})(\text{height}) = (b-a)(\text{height})$. Thus the height is $1/(b-a)$.



While the probability of getting any particular exact value of x is infinitesimally small, the density function $p(x)$ is defined such that for any interval of x —say, from m to n —the probability of getting any of the possible outcomes within that interval (m, n) is

$$\int_m^n p(x) dx = \text{probability of outcomes between } m \text{ and } n.$$

In graphical terms:



Now, with this understanding of what a probability density function is, we can return to the formula for the mean. If $p(x)$ is the density function for the uniform distribution, then the

Arithmetic mean of the uniform distribution from a to b

$$\begin{aligned} &= \int_a^b \frac{1}{b-a} x dx = \frac{1}{b-a} \int_a^b x dx = \frac{1}{b-a} \left[\frac{x^2}{2} \right]_a^b \\ &= \frac{1}{2(b-a)} [b^2 - a^2] = \frac{1}{2(b-a)} (b-a)(b+a). \end{aligned}$$

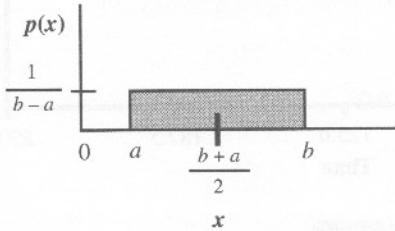
In Figure 2.19 each population was initiated with a population size of 400. If the population falls below one individual, it is considered extinct. Consistent with a geometric mean $\lambda < 1$, all the populations out of 10 simulations went extinct before time 250.

What is the geometric mean λ for such a random process? By taking natural logs we transform this multiplicative process into a simpler additive process (see Eq. (2.9)):

$$\ln(\text{geometric mean}) = \text{arithmetic mean of } \ln \lambda.$$

But what is the arithmetic mean of $\ln(\lambda)$ when λ is a continuous random variable? Note that we want to find the arithmetic mean of the logs, *not* the log of the arithmetic mean.

Mean of a uniform distribution = $(b + a)/2$
= the midpoint between a and b .



For this problem we want to know the mean, not of x , but of a function f of x , $f(x)$. Our particular concern is with $f(x) = \ln x$. Yet, in general, for any $f(x)$, the mean will depend on the probability density function $p(x)$. To convey this dependence we write $f(x)$ as $f(p(x))$. Then

$$\text{Mean of } f(p(x)) = \int_{\text{lower limit}}^{\text{upper limit}} p(x)f(x)dx.$$

The formula for the mean of $f(x)$ when x is a continuous random variable with probability density function $p(x)$

In our case $f(x) = \ln x$, and $p(x)$ is the uniform distribution from a to b . Substituting these expressions for $p(x)$ and $f(x)$ into the formula, we get

$$\text{Mean of } f(x) = \ln x = \int_a^b \frac{1}{b-a} \ln(x) dx$$

the $p(x)$ function the $f(x)$ function

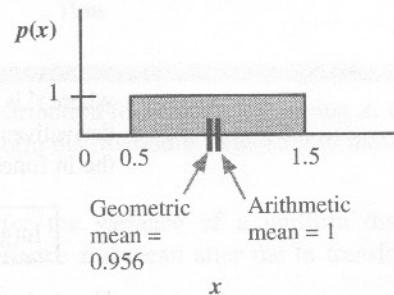
With a trick from calculus, this integral evaluates as

$$\frac{1}{b-a} [x \ln(x) - x] \Big|_{x=a}^{x=b}$$

For the problem at hand, $b = 1.5$ and $a = 0.5$, so $1/(b-a) = 1$, and

$$\begin{aligned} \text{mean of } \ln(x) &= [1.5 \ln(1.5) - 1.5] - [0.5 \ln(0.5) - 0.5] \\ &= -0.892 + 0.847 \\ &= -0.0452. \end{aligned}$$

By this analytical method, we find that the geometric mean = $\exp(\text{mean } \ln(x)) = \exp(-0.0452) = 0.956$, which is very close to the approximate solution, 0.959, that we found earlier.



The advantage of the approximate method is that finding an analytical formula giving the exact solution for the mean and variance of $f(x)$ may be impossible for a particular choice of $p(x)$ and $f(x)$. The simplicity of the uniform distribution and the $\ln(x)$ function allowed for an easy solution, but this ease is typically the exception rather than the rule. The Taylor's expansion in Eq. (2.12) is a good approximation when $\sigma^2 \ll \mu^2$. The means and variances for some random distributions are presented in Appendix 6.

Exercise: Show that the variance of a uniform distribution between a and b is $(b-a)^2/12$, by applying the formula for the variance of a continuous random variable x :

$$\text{Variance of } x = \int_{\text{lower limit}}^{\text{upper limit}} p(x)x^2dx - (\text{mean } x)^2.$$

Initial solution: Substitute into the variance formula the density function and mean of the uniform distribution:

$$\text{Variance of } x = \left[\frac{1}{b-a} \int_a^b x^2 dx \right] - \left[\frac{b+a}{2} \right]^2$$

These are not the same quantities, as emphasized in Figure 2.18. Using some tricks from calculus, we can apply a Taylor's expansion (see Chapter 5), to approximate both the mean and variance of any function of a random variable. If λ is a random variable with arithmetic mean μ and variance σ^2 and f is some function of the random variable λ , then the mean and variance of the function, $f(\lambda)$, are approximately

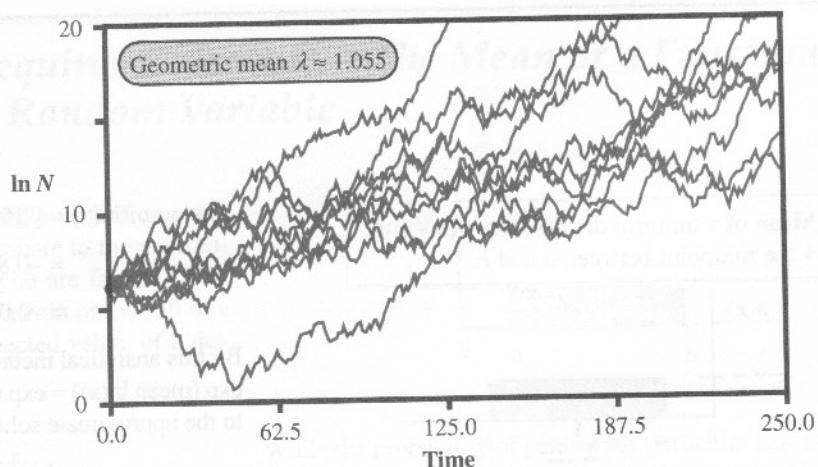
$$\text{Mean of } f(\lambda) \approx f(\mu) + (f''(\mu)/2)\sigma^2 \quad (2.10)$$

and

$$\text{Variance of } f(\lambda) \approx f'(\mu)^2\sigma^2, \quad (2.11)$$

Figure 2.20

Geometric growth when λ is a random variable each time step. In this case, λ is drawn randomly from a uniform distribution [0.55 to 1.65], and the arithmetic mean and the geometric mean λ are both greater than 1. Compare to Figure 2.19.



where f' is the first derivative of f with respect to λ and f'' is the second derivative. These derivatives are evaluated at the mean $\lambda = \mu$. Applying the relationship in Eq. (2.10) to the \ln function, we reach

$$\ln(\text{geometric mean } \lambda) = \text{arithmetic mean of } \ln \lambda \approx \ln(\mu) - (\sigma^2/2\mu^2). \quad (2.12)$$

The derivative $f'(\lambda)$ of $\ln \lambda$ is $1/\lambda$; the second derivative $f''(\lambda)$ is the derivative of $1/\lambda$, which is $-1/\lambda^2$. We evaluate these derivatives at $\lambda = \mu$, substituting μ for λ , to get $-1/\mu^2$.

If we apply Eq. (2.12) to the uniform distribution from 0.5 to 1.5 for λ and substitute in $\mu = 1.0$ and $\sigma^2 = 1/12 = 0.08333$, we calculate $\ln(\text{geometric mean } \lambda) \approx [\ln(1) - (1/12)/(2(1^2))] = [0 - (0.08333/2)] = -0.0417$. Finally, taking antilogs, the geometric mean λ is $\approx e^{-0.0417} \approx 0.959$. This value compares favorably with the exact geometric mean, 0.956, obtained using calculus (Box 2.1).

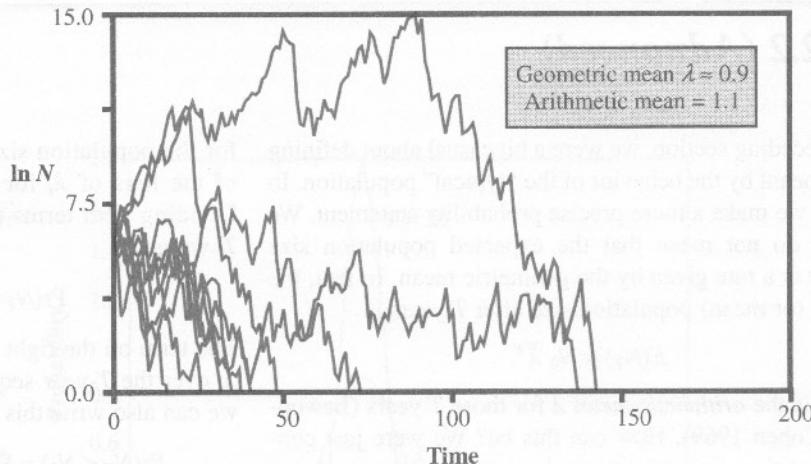
Populations with $\lambda(t)$ drawn randomly between 0.5 and 1.5 each year should usually trend toward 0 because the geometric mean is less than 1. This trend matches the results in Figure 2.19. Figure 2.20 shows the results of simulating 10 populations again beginning each with $N = 400$ individuals) when $\lambda(t)$ is drawn randomly from a uniform distribution with range 0.55 to 1.65. The arithmetic mean λ is now greater than 1, 1.1, but the range is also larger, 1.1. Hence the variance is $(1.1^2/12) = 0.10083$. The \ln of the geometric mean (using Eq. 2.12) is approximately $\ln(1.1) - (0.10083/(2)(1.1)^2) = 0.0536$, and the geometric mean λ is therefore $\approx e^{0.0536} = 1.055$. Since the geometric mean is greater than 1 (in spite of the larger variance), the typical population should trend upward.

Not a single population in Figure 2.20 became extinct after 250 time steps, although one nearly did so before recovering. Having a geometric mean λ greater than 1 does not necessarily mean that each population is immune from extinction. Rather, it means that the average population will increase in size geometrically as time goes on. As the population size continues to increase, it “escapes” from the threat of extinction since it takes an increasingly longer succession of bad years to bring it back down. If there were an upper limit to population size (a subject we explore in depth in Chapter 5), then populations could not as readily escape the threat of extinction. The likelihood of extinction increases as the upper limit of population size decreases (Middletown et al. 1995).

Finally, one more example will illustrate the importance of the difference between geometric mean and arithmetic mean rates of population growth. For this example, the arithmetic mean is greater than 1 but the geometric mean is less than 1 (Figure 2.21). In this simulation not a single population out of 10 survives to time 200.

Figure 2.21

Geometric growth when λ each year is drawn randomly from a uniform distribution [0.1 and 2.1]. Compare to Figures 2.19 and 2.20. These populations tend to decline because the geometric mean λ is less than 1.



Problem: Given a uniform distribution for temporally varying λ , with a mean λ of 1.1, what range of this uniform distribution is necessary to make the geometric mean λ equal to 1.0?

Answer: Apply Eq. (2.11) for the variance of a uniform distribution and Eq. (2.12) to calculate the variance and mean after the ln transformation: The required range ≈ 1.664 .

The initial population size also makes a difference in the average persistence time before a population becomes extinct. For example, if all the populations begin with 800 individuals instead of 400, the average time to extinction is much greater. Conversely, if the populations begin with a very small size (e.g., < 10), many might become extinct even though the geometric mean, λ , might be greater than 1. A complete development of these expected extinction rates is beyond the scope of this primer, but interested students can learn more from Pielou (1969), Nisbet and Gurney (1982), and Box 2.2.

Between-Individual Variability Alone

As we discussed earlier, another source of variability in population growth is due to chance events that affect whether an individual gives birth or dies at any single moment. Even two identical twins will not necessarily produce the same number of offspring. They may both be drawn from the very same universe distribution, but by chance one gets struck by lightning and thus has a low λ , while the other becomes rich and prosperous, leaves many children, and thus has a high λ .

If the initial size of a population is N individuals at time t , then on average at time $t+1$, it will have size

$$\bar{N}_{t+1} = \mu_\lambda N_t, \quad (2.13)$$

where the over bar represents expected values. Again μ_λ is the arithmetic mean of the universe distribution for λ_t and this distribution is not changing over time. For T time units into the future,

$$\bar{N}_{t+T} = \mu_\lambda^T N_t. \quad (2.14)$$

The only factor causing variability in growth rate here is the chance sampling by random draws from the universe distribution for each individual. As you can see for the

Box 2.2 (Advanced)

In the preceding section, we were a bit casual about defining what is meant by the behavior of the “typical” population. In this box, we make a more precise probability statement. We certainly do not mean that the expected population size increases at a rate given by the geometric mean. In fact, the expected (or mean) population size after T years is

$$E(N_T) = N_0 \bar{\lambda}^T,$$

where $\bar{\lambda}$ is the *arithmetic mean* λ for those T years (Lewontin and Cohen 1969). How can this be? We were just convinced that the geometric mean λ —not the arithmetic average—tells us whether the population is likely to increase or decrease. That too is correct. The discrepancy arises because, while the average population size is growing toward infinity as long as $\bar{\lambda} > 1$, the probability of the population becoming extinct after T years is governed by the geometric mean. How can the expected population size increase at the same time that the probability of extinction increases? This can happen because the probability distribution for population size at time T becomes increasingly skewed as time goes on—it becomes increasingly L-shaped. While most populations are close to zero, a thin tail of the probability distribution contains a tiny fraction of populations that are huge in size. Thus the mean population size $E(N_T)$ increases geometrically with time, despite the fact that nearly all populations are below this mean population size and, in fact, are growing smaller!

It is too difficult for us to calculate this highly skewed probability distribution for N at time T , but without too much effort we can calculate precisely the probability that after T years a population will be below its initial number, N_0 . Such a population is on its way to extinction. We can show that this probability is given directly by the geometric mean λ and the elapsed time T . Let’s write this probability as

$$\Pr(N_T < N_0).$$

Since the logarithm of a number is a smoothly increasing function of that number, we may also write

$$\Pr(N_T < N_0) = \Pr(\ln N_T < \ln N_0).$$

And since

$$\Pr(N_T < N_0) = \Pr\left(\sum_{i=1}^T \ln \lambda_i < 0\right)$$

for the population size at time T to be below N_0 , the sum of the logs of λ_i for those T years must be less than 0. Dividing both terms in the last inequality on the right by T , we get

$$\Pr(N_T < N_0) = \Pr(\overline{\ln \lambda}_T < 0).$$

The term on the right is the probability that the mean of $\ln \lambda_i$ over the T -year sequence is less than 0. From Eq. (2.9), we can also write this probability as

$$\Pr(N_T < N_0) = \Pr(\ln(\text{geometric mean } \lambda)_T < 0).$$

We assume that $\ln \lambda_i$ from one year to the next are independently drawn from the same universe distribution with mean u_G and standard deviation σ_G . For any given string of T years, the realized $(\overline{\ln \lambda})_T$ for those years is a sample mean from this universe distribution. From the Central Limit Theorem, this sample mean will be approximately normally distributed and have mean u_G and variance σ_G^2/T . We are interested in the probability of $(\overline{\ln \lambda})_T$ being less than 0; this corresponds to a population that has decreased by year T . This probability is given by the integral of the normal distribution (N) (with mean u_{ln} and variance σ_G^2/T) from $-\infty$ to 0:

$$\Pr(N_T < N_0) = \int_{-\infty}^0 N(x; u_G, \sigma_G / \sqrt{T}) dx.$$

If the geometric mean λ is less than 1, then u_G , which is the log transform, is less than 0. As time T goes on, the sample standard deviation decreases, since it is equal to σ_G / \sqrt{T} , and thus an increasingly smaller portion of the distribution crosses above 0 (Figure 2.22). By the same token, if u_G is greater than 0, then as time goes toward infinity, the probability of extinction approaches 0 (Lewontin and Cohen 1969).

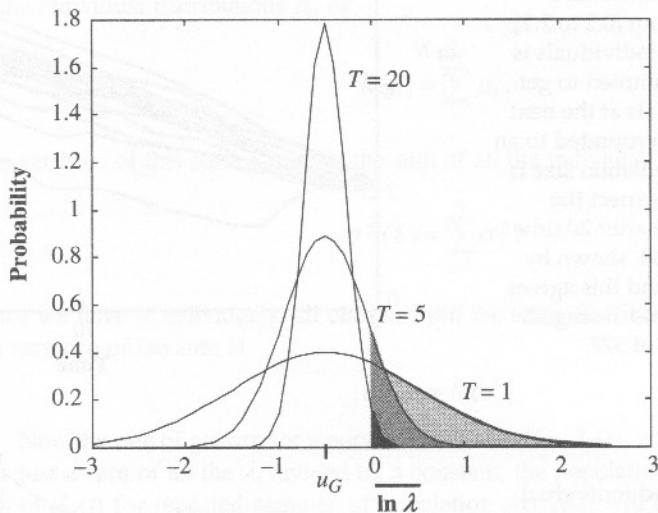
Figure 2.23 shows 100 replicate populations for the case of Fig 2.21; λ_i each year is a random variable uniformly distributed between 0.1 and 2.1. For this range the arithmetic mean $\bar{\lambda}$ is greater than 1 but the geometric mean is less than 1. Each population begins with only 2 individuals. The observed mean population size, 277.4, is close to the predicted size $(2)(1.1)^{50} = 234.7$, yet the vast majority of populations fell below a single individual, indicated by the horizontal line.

simulations in Figure 2.24, sampling error alone will lead to some deviation in the average growth rate of the population over time. This “temporal” variability is not, however, what we are calling environmental variability; this term is reserved for actual shifts in the universe distribution from year to year.

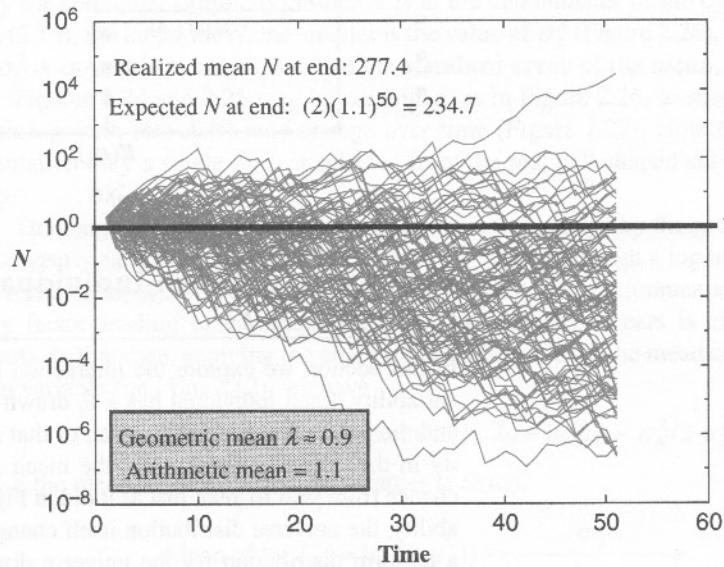
Note in Figure 2.24 that, early on when population sizes are low, the lines are jagged—populations sizes can actually dip, **despite the fact that the mean λ is 1.2**. But as time goes on and population sizes increase, the lines for each population smooth out and become nearly linear since there is less sampling error.

Figure 2.22

Each normal curve gives the probability density function for $(\ln \lambda)_T$ (the mean of the $\ln \lambda_i$ after T years); $T = 1, 5$, and 20 . The \ln of the geometric mean $\bar{\lambda}$ for these years is equal to this mean. In this example, $\ln \lambda_i$ for each year is drawn from a universe distribution with a negative mean: $u_G = -0.5$ and a standard deviation of 1 . Hence the average λ is less than 1 ($e^{-0.5} = 0.6065$). The shaded regions represent the probability that $(\ln \lambda)_T$ is greater than 0 , which corresponds to a population that has increased in size after T years. As time goes on, this probability decreases. When the geometric mean $\bar{\lambda}$ is less than 1 , the typical population declines to extinction as T increases.

**Figure 2.23**

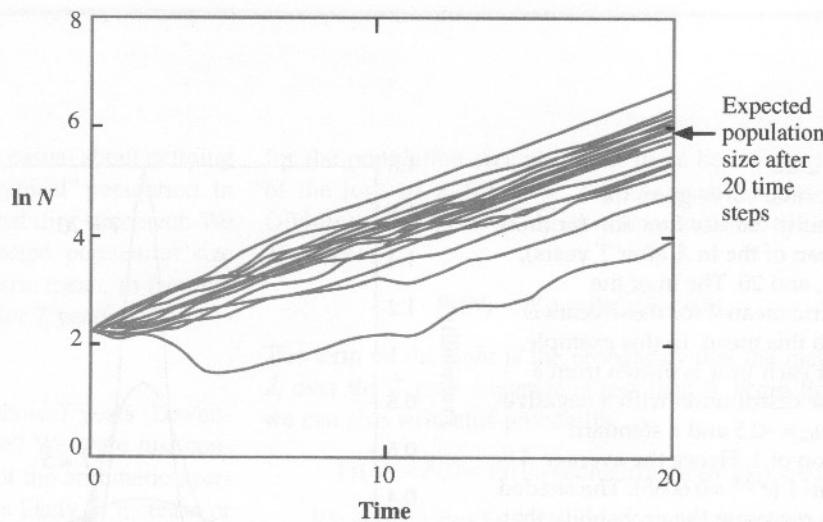
An example of a situation where the mean population size increases geometrically, but most populations decline to extinction. Here λ is drawn randomly from a uniform distribution [0.1 to 2.1]. The red lines show 100 replicate populations beginning from $N_0 = 2$. The black line marks a population size of one individual.



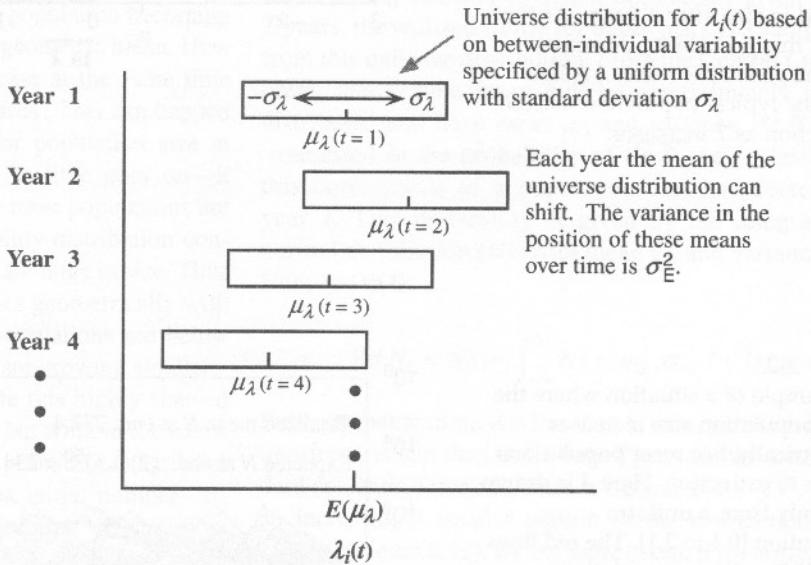
One last word of caution: even though the mean population is expected to grow with rate λ in a given time step, there is still some finite probability that a particular population will become extinct even if $\mu_\lambda > 1$, just as there is some finite probability that you might go home a winner from a Las Vegas casino even though the odds are stacked against you. A complete development of these probabilities is beyond the scope of this primer, but interested students can learn more from Pielou (1969) and Nisbet and Gurney (1982).

Figure 2.24

A simulation of 20 populations responding to the same demographic variability. For each individual in a population, its λ_i is chosen from a uniform distribution from [0.2 to 2.2]; thus the mean λ across individuals is 1.2. These λ_i are then summed to get the number of individuals at the next time step (which is then rounded to an integer). The initial population size is 10. From Eq. (2.14), we expect the average population size after 20 time steps to be $10(1.2)^{20} = 383$, shown by the arrow at the right, and this agrees well with the actual value averaged over these 20 replicates of 377.

**Figure 2.25**

Combining temporal and individual variability. Each rectangle is the universe distribution for λ_i in a given year. The grand arithmetic mean of all the yearly means is $E(\mu_\lambda)$. The variance in the yearly means, σ_E^2 , provides a measure of the temporal environmental variability.



Combining Between-Individual and Temporal Variability (ADVANCED)

In this section we explore the interaction between temporal variability and individual variability. Each individual has a λ_i drawn from the universe distribution for that year, and the population $\lambda(t)$ is the mean of that sample. Even without any temporal variability in the universe distribution, the mean λ for a sample of individuals can differ by chance from year to year, just as it did in Figure 2.24. With temporal environmental variability, the universe distribution itself changes over time. To keep things simple, we use a uniform distribution for the universe distribution and simply shift the mean μ_λ randomly each year while keeping the range the same. In this way, the shape and variance, σ_λ^2 , of the universe distribution do not change over time. To accomplish these temporal random shifts in the mean, we specified yet another uniform distribution in the section on “Temporal variability alone.” Here we leave the details of this distribution vague, except to say that it has a variance, σ_E^2 . This situation is illustrated in Figure 2.25.

Each year we can determine the population size for the next year by selecting λ_i from the universe distribution for each of the $N(t)$ individuals. When $N(t)$ is very large, the sample is very large, and $\lambda(t)$ will typically be similar to the mean of the universe distribution $\mu_\lambda(t)$ for that year t . Let’s now consider the distribution of these sample means when $N(t)$ is not necessarily large.

The Central Limit Theorem states that the sum (call it S) of a number (N) of independent random variables (x_i) approaches a **normal** distribution as n increases, even if the individual variables being summed have nonnormal distributions and different means. Furthermore, the expected value of the sum, $E(S)$, equals the sum of the means of the individual distributions μ_i , or

$$E(S) = \sum_i^N \mu_i.$$

The variance of this sum, S , equals the sum of all the individual variances, or

$$\sigma^2(S) = \sum_{i=1}^N \sigma_i^2.$$

Since we have N individuals, all chosen from the same distribution with variance σ^2 , the variance of the sum is

$$\sigma^2(S) = N\sigma^2.$$

Now the rate of growth for a population of size N is $\lambda_N(t)$, which is a sample mean; it is just a sum of all the λ_i divided by a constant, the population size N . The distribution of $\lambda_N(t)$ for repeated samples of population size $N(t)$ will thus be approximately normal, with an expected value equal to the mean of the universe distribution $\mu_\lambda(t)$. Its variance can be found by invoking one additional rule for functions of random variables: if S is any random variable with a variance σ^2 and k is any constant, then the variance of kS is $k^2 \sigma^2$. In our case, the constant k is $1/N$ and $k^2 = 1/N^2$. Hence we have

$$\sigma_N^2 = \frac{N\sigma_\lambda^2}{N^2} = \frac{\sigma_\lambda^2}{N}, \quad (2.15)$$

where σ_N^2 is the variance in λ_N for a population of size N (note that we dropped the $t(s)$ only for notational simplicity). Since N is in the denominator of the right-hand side of Eq. (2.15), the larger the N , the smaller is the value of σ_N^2 (Figure 2.26). The square root of σ_N^2 is σ_N and in statistics is called the **standard error of the mean**.

Figures 2.24 and 2.25 may be combined, as in Figure 2.26, to show how the population growth rate $\lambda_N(t)$ may change over time (Figure 2.27). Note that for a single population only a single $\lambda_N(t)$ is selected from the red, bell-shaped curves at each time step.

The long-term growth rate of a population is determined by the geometric mean of these yearly sample means over time, which are related through a log transformation to the mean of $\ln(\lambda_N)$, as we developed earlier. Without any environmental variability, the only factor leading to variation in sample means across years is chance sampling effects. In that case, applying the approximation formula for the mean of the \ln of a random variable (i.e., Eq. 2.12), we have

$$\ln(\text{geometric mean}) = \text{mean of } \ln \lambda_N \approx \ln(\mu_\lambda) - \sigma_N^2/2 \mu_\lambda^2.$$

Since the mean λ across years and samples is $E(\mu_\lambda)$,

$$\text{Mean of } \ln(\lambda_N) \approx \ln(E(\mu_\lambda)) - \frac{\sigma_\lambda^2}{2N(t)[E(\mu_\lambda)]^2}.$$

It is difficult to evaluate this formula because $N(t)$ is changing over time in response to the value of λ at each time step. Nevertheless, for large N the second term is negligible, and therefore the mean of $\ln \lambda_N$ is only slightly less than $\ln(E(\mu_\lambda))$, which would be the \ln of the population growth rate in an unchanging environment.

Environmental variability, the change in the mean of the universe distribution from year to year, provides an additional source of variation in $\ln \lambda_N$, which arises from σ_E^2 (Figure 2.25). The total variance in $\ln \lambda_N$ from sampling error and temporal environmental variability is just the sum $(\sigma_\lambda^2/N) + \sigma_E^2$ because variances of independent variables are additive (See Appendix 6). Again applying the approximation formula for the

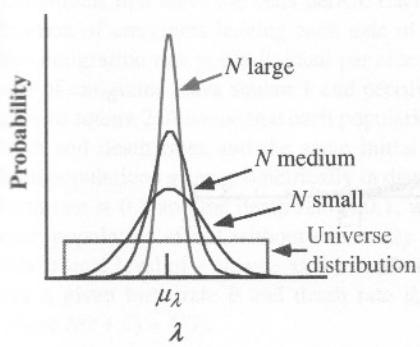


Figure 2.26

The probability plotted is that of obtaining λ with a sample of N individuals whose λ_i are drawn from the universe distribution. The larger the sample size N , the smaller is the standard error for the estimate of the mean in the universe distribution μ_λ . Regardless of the shape of the universe distribution, which in this case is rectangular, the density function for the mean of a sample from the universe is approximately a normal distribution with mean μ_λ .

Figure 2.27 Each year the universe distribution for λ_i shifts (the rectangles) and therefore so does the distribution for the mean, λ_N , for a population of size N sampled from this universe (in red). We chose a rectangular distribution for the universe distribution solely to make it conceptually clear and graphically distinct from the sample mean distribution, not because a uniform distribution is necessarily a more realistic assumption than, say, a normal distribution.

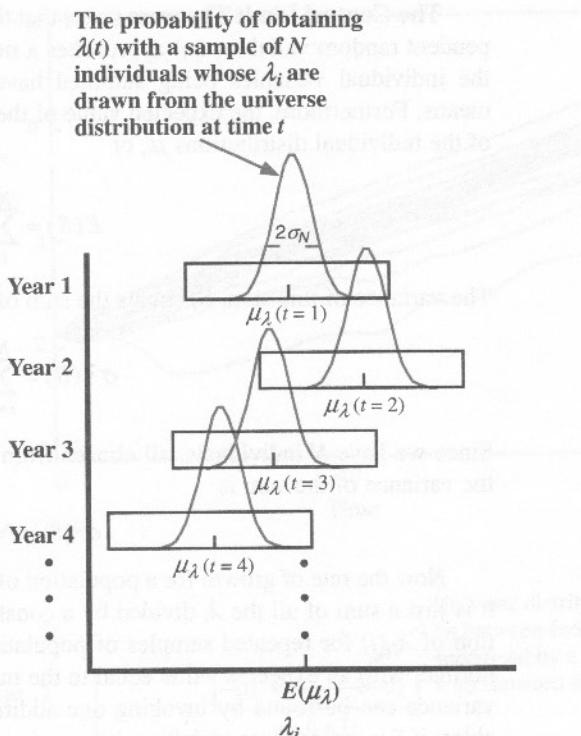
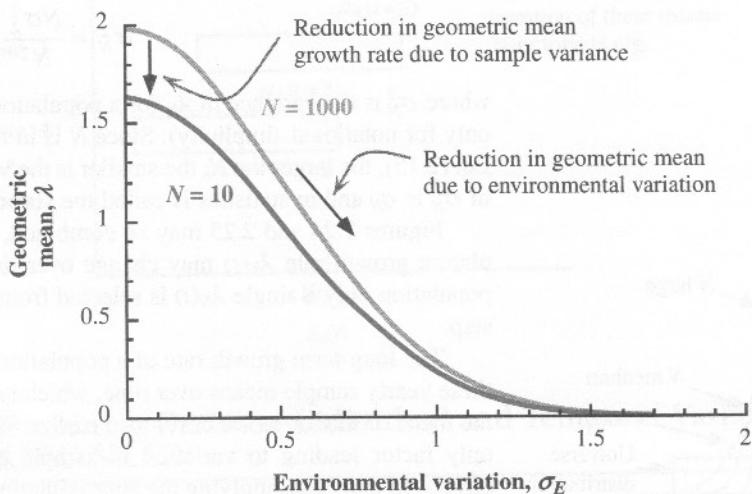


Figure 2.28
The geometric mean rate of growth declines with environmental variance and with decreases in population size; $E(\mu_\lambda) = 2$, and $\sigma_\lambda = 1$.



mean of the \ln of a random variable (Eq. 2.12) and noting that the arithmetic mean λ across years and samples is the grand mean $E(\mu_\lambda)$, we finally reach

$$\ln(\text{geometric mean } \lambda_N) = \text{mean of } \ln(\lambda_N) \approx \ln(E(\mu_\lambda)) - \frac{\sigma_E^2}{2[E(\mu_\lambda)]^2}. \quad (2.16)$$

The addition of environmental variability, σ_E^2 , in the numerator always increases the value of the fraction on the right and thus decreases the geometric mean. This function is graphed in Figure 2.28 for some selected parameter values. The greater the temporal environmental variability specified by σ_E^2 , the lower is the geometric growth rate of the average population. The sample variance also reduces the geometric mean—but to a significant degree only when N is small. The conclusion that we can draw is that small populations face a greater threat of chance extinction than do large populations from environmental variability.

both demographic and temporal environmental variability. However, in large populations, the role of environmental variability is proportionately more important in determining their dynamic behavior.

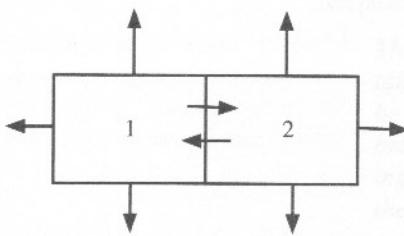
For some types of models of population growth, it is possible to derive formulas for the probability of extinction after a fixed number of years (e.g., Pielou 1969, Nisbet and Gurney 1982, Goodman 1987, Lande 1993), but doing so is often not easy and we are often forced to rely on simulation models. However, under no situation does the addition of temporal variability alone stabilize a population by preventing it from ultimately climbing toward infinity or collapsing to zero. This stabilization requires some sort of density dependence in the growth rate such that λ tends to get smaller as N gets larger, a theme developed in Chapter 5.

PROBLEMS

- Suppose that populations are governed by the equation

$$N(t+1) = N(t) + \text{births} + \text{immigrants} - \text{deaths} - \text{emigrants}.$$

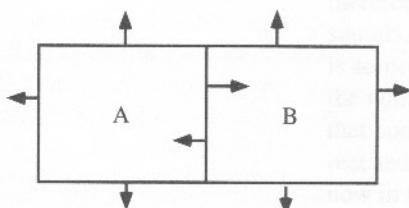
Consider two populations found in two adjacent patches (cells) with the following geometry.



Individuals that leave the cells perish. Each population has the same fraction of emigrants leaving each side of the square per year. Call this emigration rate per individual per side of each cell e . Thus three sets of emigrants leave square 1 and perish and one set of emigrants goes to square 2. Assume that each population has the same per capita birth and death rates and the same initial population size. Further, both populations grow geometrically in discrete time. If the per capita birth rate is 0.8 and the death rate is 0.1, what emigration rate e can each population afford without eventually going extinct? How does this critical level of e change as the birth rate and death rate change? For a given birth rate b and death rate d , find the emigration rate where $N(t+1) = N(t)$.

- Per capita growth parameters for a population that exists in two adjacent patches are:

Patch	Birth rate	Death rate	Emigration rate
A	0.33	0.1	0.06 in each direction
B	0.2	0.1	0.04 in each direction



Assume that both populations grow exponentially and that $r = \text{births} - \text{deaths}$. Emigrants leaving A's right side all enter B as immigrants and vice versa (as shown by the arrows). If both populations start with equal numbers of individuals, will they persist? If patch A is eliminated, will patch B persist? If patch B is eliminated, will patch A persist?

- Another formula for the diffusion coefficient D involves the mean dispersal radius of recaptured individuals after t time units (rather than the square of these distances as in Eq. 2.4). This is a measurable quantity in field ecology and can best be determined by putting small transmitters on animals to help find them. Let's call this distance measure $U(t)$, which is related to the diffusion coefficient D as $U(t)^2 = \pi D t$ (see, e.g., Shigesada and Kawasaki 1997, page 38). If the λ for muskrats is approximately 4/yr and the population has been expanding by 12 km/yr, what is $U(t)$ per year? (Hint: use the formula above and Eq. 2.6).

- An exotic species of elf ant has recently been introduced to the fictional island of Qualam (area = 200,000 acres). The ant population grows geometrically with a λ of 1.5 and expands into new territory as it spreads, according to a diffusion model. The natives have calculated its occupancy of territory as

1999: Just introduced;

2006: Area of Qualam occupied = 400 acres.

At this rate of spread, how much area of Qualam is likely to be occupied by 2001? When will all of Qualam be colonized by elf ants? (What a Qualamity!).

- A population of birds is influenced by its environment such that two-thirds of the time the population increases by 50% per year and the other one-third of the time the population decreases by 50% per year. What happens to the size of this population as time goes toward infinity?

- (Advanced) What is the long-term expectation of N for a population growing geometrically when λ each year is a random variable with a normal distribution whose mean is 1.1 and whose variance is 2? (Assume no individual variation.)

- Two individuals—one a male and the other a female—found a new population. This pair produces exactly 4 offspring that year; then both adults die. Offspring sex is determined by the flip of a coin with equal probability for males and females. What is the probability that this population will become extinct at the end of the first year because of a sex ratio imbalance?