Modeling the Dynamics of Life: Calculus and Probability for Life Scientists

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Chapter 1

Vectors

When we measure several values simultaneously, we can store them as a list of numbers, or a **vector**. Like many objects in mathematics, vectors have a whole set of algebraic and geometric properties, and are among the most widely useful tools in mathematics. We used vectors in a simplified form as direction arrows in Chapter 5, and begin their study from the geometric viewpoint, then in dynamical systems, and finally in the context of probability and Markov chains.

1.1 Introduction to vectors

A vector is the mathematical version of an arrow. An arrow is described by three things: where it starts, how far it goes horizontally, and how far it goes vertically. The vector labeled $\vec{v}$ in figure 1.1.1 starts at $(1, 3)$ (called the **base point**) and goes across 2 and up 1. The 2 is called the **horizontal component** and the 1 is the **vertical component**. We write

$$\vec{v} = (2, 1).$$

The arrow over **v** indicates that v is a vector. For most applications, the starting point $(1, 3)$ is not mentioned explicitly. Vectors with positive horizontal components ($\vec{w}$ and $\vec{v}$ in figure 1.1.1) point to the right while those with negative horizontal components ($\vec{u}$) point to the left. Vectors with positive vertical components ($\vec{v}$) point up and those with negative vertical components ($\vec{w}$ and $\vec{u}$) point down.

Vectors can be added together and multiplied by constants. Vectors are added component by component. We add $\vec{v} = (2, 1)$ and $\vec{w} = (3, -2)$ as

$$\vec{v} + \vec{w} = (2 + 3, 1 - 2) = (5, -1).$$

This corresponds to a geometric rule. To find the sum of $\vec{v}$ and $\vec{w}$ on a graph, complete the parallelogram and draw the diagonal, as shown in figure 1.1.2.

Vectors can be multiplied by numbers (called **scalars** in this context) component by component. For example, we multiply $\vec{v}$ by 3 as

$$3\vec{v} = (3 \times 2, 3 \times 1) = (6, 3).$$

The base point and direction remain the same. The vector $3\vec{v}$ now points from $(1, 3)$ to $(1+6, 3+3) = (7, 6)$.

Figure 1.1.1: Examples of vectors

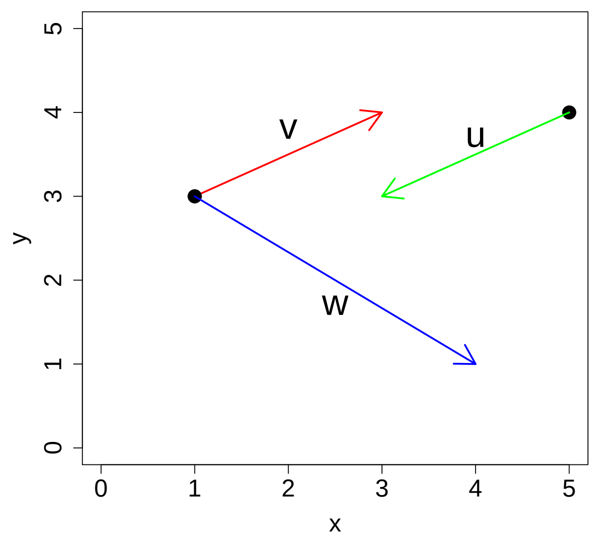


Figure 1.1.2: Adding vectors

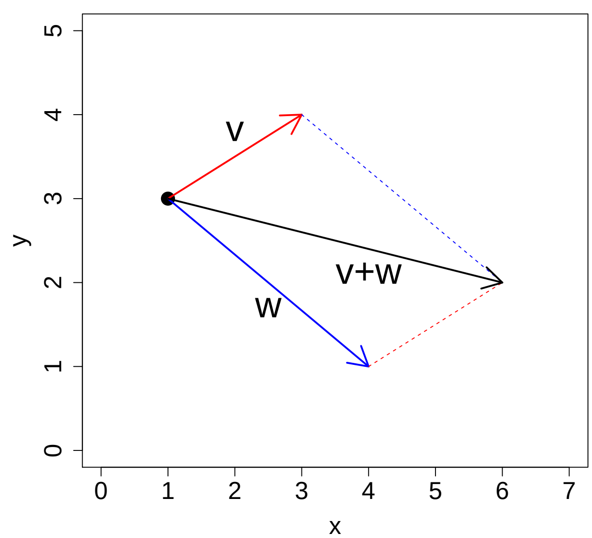
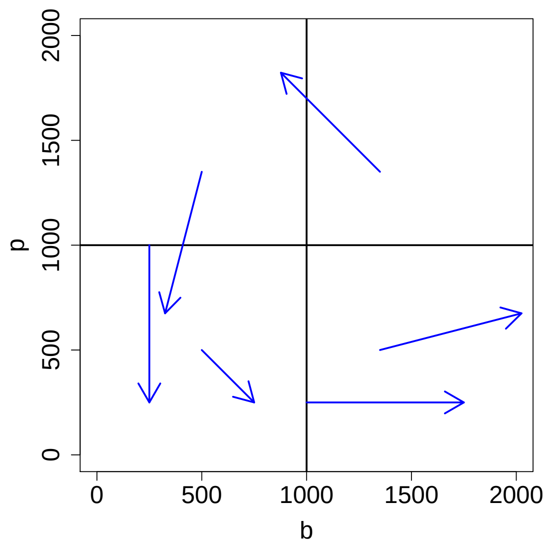


Figure 1.2.1: Some phase plane vectors for the predator-prey system



1.2 Phase plane vectors

Consider the system of differential equations for the predator-prey system from Chapter 5. With the parameter values $\lambda = \delta = 1.0$ and $e = h = 0.001$, the equations are

$$\frac{db}{dt} = (1.0 - 0.001p)b$$
$$\frac{dp}{dt} = (-1.0 + 0.001b)p.$$

We found direction arrows by checking the signs of the rates of change in the regions defined by the nullclines.

We can convert direction arrows into **phase plane vectors** with horizontal component equal to the rate of change of b and vertical component equal to the rate of change of p starting from the point (b, p).

At the point $b = 500$ and $p = 500$ in the phase plane, we compute the rates of change by from the differential equations, finding

$$\frac{db}{dt} = (1.0 - 0.001 \cdot 500)500 = 250$$
$$\frac{dp}{dt} = (-1.0 + 0.001 \cdot 500)500 = -250.$$

These components correspond to the vector $(250, -250)$ starting at the point $(500, 500)$ in the phase plane (figure 1.2.1). Like the direction arrow in this region, this vector points down and to the right.

What happens to phase plane vectors on the nullclines or at an equilibrium? When $p = 1000$, we are on the b-nullcline. Suppose we would like to draw the phase plane vector at $(250, 1000)$. We find

$$\begin{aligned}\frac{db}{dt} &= (1.0 - 0.001 \cdot 1000)750 = 0\\ \frac{dp}{dt} &= (-1.0 + 0.001 \cdot 750)1000 = -250.\end{aligned}$$

The phase plane vector points straight down. The horizontal component, indicating how b is changing, is zero. This is consistent with the fact that this point is on the b-nullcline.

The point $(1000, 250)$ lies on the p-nullcline. We find

$$\begin{aligned}\frac{db}{dt} &= (1.0 - 0.001 \cdot 250)1000 = 750\\ \frac{dp}{dt} &= (-1.0 + 0.001 \cdot 1000)500 = 0.\end{aligned}$$

This phase plane vector points straight to the right. The vertical component is zero, meaning that p is not changing. Finally, at the equilibrium $(1000, 1000)$,

$$\begin{aligned}\frac{db}{dt} &= (1.0 - 0.001 \cdot 1000)1000 = 0\\ \frac{dp}{dt} &= (-1.0 + 0.001 \cdot 1000)1000 = 0.\end{aligned}$$

Both components of the phase plane vector are zero, indicating that this point is an equilibrium. The phase plane vector has zero length.

1.3 Vectors and trigonometry

Instead of thinking of vectors in terms of their horizontal and vertical **components**, it is often useful to think instead about their **magnitude** and **direction**. We convert between these two viewpoints with trigonometry.

There are four numbers associated with every vector: the horizontal component x, the vertical component y, the length r and the angle θ it makes with the horizontal (figure 1.3.1). Trigonometric functions express the relationships among these four numbers, with the basic facts

$$\begin{aligned}x &= r\cos(\theta)\\ y &= r\sin(\theta).\end{aligned}$$

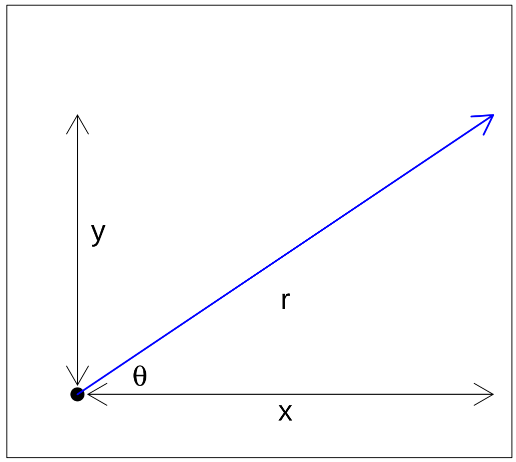
These equations are effectively the definitions of cosine and sine. By solving for the cosine,

$$\cos(\theta) = \frac{x}{r}.$$

This is the "adjacent over hypotenuse" definition used in trigonometry classes. Similarly, the vertical component y is the product of the length with the sine of the angle. By solving for the sine,

$$\sin(\theta) = \frac{y}{r},$$

Figure 1.3.1: Trigonometry and vectors



the "opposite over hypotenuse" definition of trigonometry.

The other trigonometric function useful for analyzing vectors is the tangent, defined by

$$\tan(\theta) = \frac{\sin(\theta)}{\cos(\theta)}.$$

From the definition,

$$\tan(\theta) = \frac{y/r}{x/r} = \frac{y}{x}.$$

The tangent is the "opposite over the adjacent".

Suppose that $r = 5.0$ and $\theta = \pi/3$. The horizontal and vertical components x and y are

$$\begin{aligned} x &= 5\cos(\pi/3) = 2.5 \\ y &= 5\sin(\pi/3) = 5\frac{\sqrt{3}}{2} = 4.33. \end{aligned}$$

The signs of the components depend on the angle. The horizontal component is positive when θ is between $-\pi/2$ and $\pi/2$ and the vertical component is positive when θ is between 0 and π.

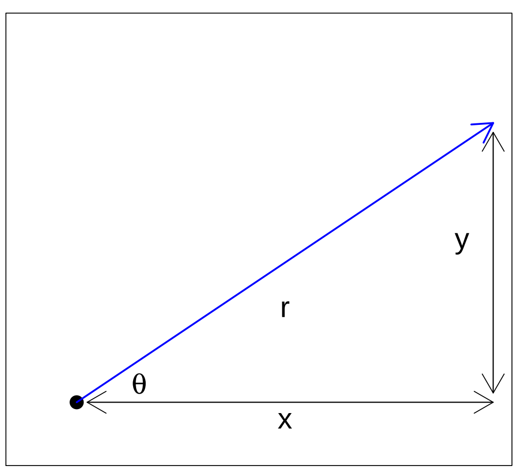
Many vectors are more conveniently described by r and θ than by the components x and y. The length r is called the **magnitude** and the angle θ is called the **direction**. Our next task is to compute the magnitude and direction from the components. The magnitude of a vector can be found from its components with the Pythagorean theorem (figure 1.3.2). The vector is the hypotenuse of a right triangle with legs of length x and y. If we denote the length by r, we have

$$r^2 = x^2 + y^2,$$

Table 1.1: Signs of the trigonometric functions

Range	Sign of sine	Sign of cosine	Sign of tangent
$0 < \theta < \frac{\pi}{2}$	$+$	$+$	$+$
$\frac{\pi}{2} < \theta < \pi$	$+$	$-$	$-$
$\pi < \theta < \frac{3\pi}{2}$ $-\pi < \theta < -\frac{\pi}{2}$	$-$	$-$	$+$
$\frac{3\pi}{2} < \theta < 2\pi$ $-\frac{\pi}{2} < \theta < 0$	$+$	$-$	$-$

Figure 1.3.2: Finding the magnitude and direction of vectors



and can find r by taking the positive square root.

For example, the vector $\vec{v} = (\sqrt{3}, 1)$ with components $x = \sqrt{3}$ and $y = 1$,

$$r = ||\vec{v}|| = \sqrt{\sqrt{3}^2 + 1^2} = \sqrt{3+1} = 2.$$

The double lines around $\vec{v}$ are meant to be reminiscent of absolute value. Just as the absolute value of a number is the distance from 0 to that number, the length of a vector is the distance from its base to its tip. In general, the magnitude of the vector $\vec{v} = (x, y)$ is

$$||\vec{v}|| = \sqrt{x^2 + y^2}.$$

If a vector is multiplied by a constant, the magnitude is multiplied by the absolute value of that constant, or

$$||c\vec{v}|| = \sqrt{(cx)^2 + (cy)^2} = |c|\sqrt{x^2 + y^2}.$$

The absolute value bars around c mean the both vectors $3\vec{v}$ and $-3\vec{v}$ have magnitude three times that of $\vec{v}$ itself.

To find the direction of a vector from its components we use the tangent function. For the vector $\vec{v} = (\sqrt{3}, 1)$, the angle θ satisfies

$$\tan(\theta) = \frac{1}{\sqrt{3}}.$$

We solve this equation with the inverse tangent function $\tan^{-1}$, finding

$$\theta = \tan^{-1}\left(\frac{1}{\sqrt{3}}\right) = \frac{\pi}{6}.$$

This equation has many solutions, differing from each other by multiples of π. For example, it solutions at

$$\theta = \ldots, -\frac{11\pi}{6}, -\frac{5\pi}{6}, \frac{\pi}{6}, \frac{7\pi}{6}, \frac{13\pi}{6}, \ldots$$

Which is the right one? Angles differing by multiples of 2π represent the same angle and pose no major problem. Angles differing by π, however, correspond to vectors with opposite directions. A vector with direction $\theta = 7\pi/6$ points down and to the left, exactly opposite to $\vec{v}$. To choose the right value, we make sure that the signs of the components match the results in table 1.1. In this case, both components are positive, so the direction must lie in the range 0 to $\pi/2$.

In general, the direction θ of the vector $\vec{v} = (x, y)$ satisfies

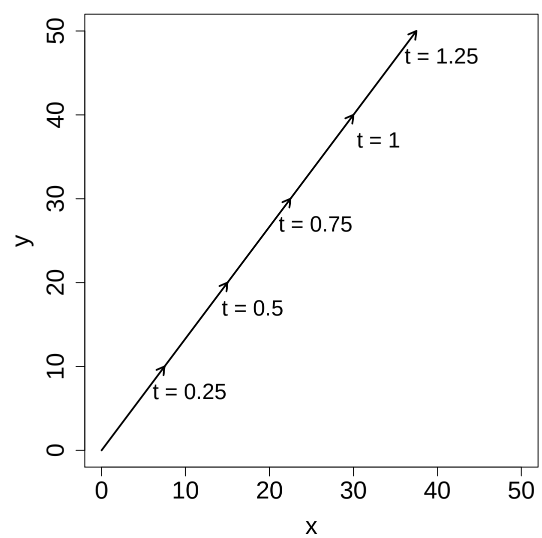
$$\tan(\theta) = \frac{y}{x}$$

or

$$\theta = \tan^{-1}\left(\frac{y}{x}\right).$$

Most calculators and computers return answers that lie between $-\pi/2$ and $\pi/2$. To get the correct direction, we check with table 1.1. A calculator returns the right answer when the vector points to the right. It gives an answer off by π when the vector points left. A sure way to get the right

Figure 1.4.1: Position as a function of time and the velocity vector



direction is to add π to your result if the vector points left, which occurs when the horizontal component is negative.

Consider the vector $(-1, 1)$. A calculator would return

$$\theta = \tan^{-1}(-1) = -\frac{\pi}{4}.$$

Because the horizontal component is negative, we add π to this direction to find $\theta = 3\pi/4$. In contrast, the vector $(1, -1)$ has direction $-\pi/4$ as our calculator says.

Multiplication by a positive constant does not change the direction of a vector. The direction of the vector (cx, cy) satisfies the same equation

$$\tan(\theta) = \frac{cy}{cx} = \frac{y}{x},$$

as (x, y). Multiplication by a negative constant switches the direction of a vector. It leaves the tangent of the angle unchanged, but switches the sign of the horizontal component and requires us to add π.

1.4 Velocity and parametric curves

Just as numbers measure quantities with magnitude, vectors measure quantities with both magnitude and direction. A familiar example is **velocity**. Imagine a bug walking along with eastward speed of 30 mm/sec and northward speed of 40 mm/sec (figure 1.4.1). The velocity vector of this bug has components $x = 30$ and $y = 40$.

The **speed** is the magnitude of the velocity vector. In this case, the speed is $\sqrt{30^2+40^2}=50$ mm/sec. The direction of motion of the bug is

$$\theta = \tan^{-1}\left(\frac{4}{3}\right) = 0.9273 \text{ radians} = 53.13 \text{ degrees}.$$

Because the horizontal component is positive, this is the correct direction.

How could we find the velocity and speed if we were given the horizontal and vertical positions of our bug as functions of time? The equations

$$\begin{aligned} x(t) &= 30t \\ y(t) &= 40t. \end{aligned}$$

exactly describe the bug in figure 1.4.1. It starts at $(0,0)$ and walks up and to the right. The speed in the x direction at time t is the derivative of the position in the x direction at time t, or

$$\text{speed in the } x \text{ direction } = x'(t).$$

Similarly, the speed in the y direction at time t is the derivative of the position in the y direction at time t, or

$$\text{speed in the } y \text{ direction } = y'(t).$$

In this case, $x'(t) = 30$ and $y'(t) = 40$, giving a velocity vector with x component 30 and y component 40.

Consider now a flying fish that has leapt from the water and followed the path shown in figure 1.4.2. Its position at time t is

$$\begin{aligned} x(t) &= 10.0t \\ y(t) &= -4.9t^2 + 8.0t \end{aligned}$$

if its initial horizontal speed is 10.0 m/sec, its initial vertical speed is 8.0 m/sec and gravity acts to accelerate downward at 9.8 m/s^2.

The velocity vector $\vec{v}$ at time t has components equal to the derivatives of each of the components of position, so

$$\vec{v} = (x'(t), y'(t)) = (10.0, -9.8t + 8.0).$$

The speed s is the magnitude of the velocity vector, so

$$\begin{aligned} s &= \sqrt{x'(t)^2 + y'(t)^2} \\ &= \sqrt{100.0 + (-9.8t + 8.0)^2}. \end{aligned}$$

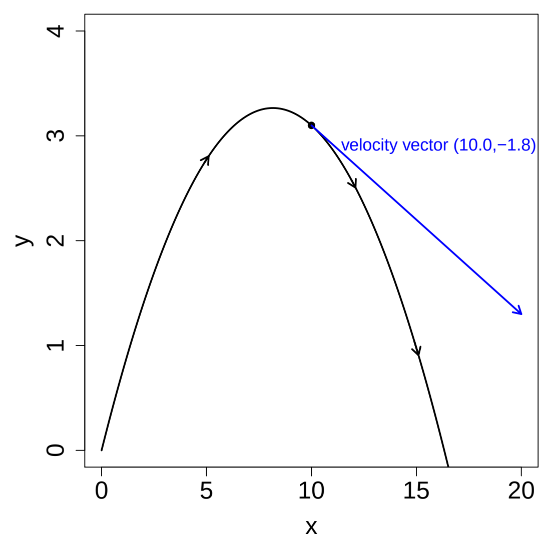
The direction at time t is

$$\theta = \tan^{-1}\left(\frac{-9.8t + 8.0}{10.0}\right).$$

At $t = 1$, the velocity vector is

$$\vec{v} = (x'(1), y'(1)) = (10.0, -9.8 \cdot 1.0 + 8.0) = (10.0, -1.8).$$

Figure 1.4.2: The horizontal and vertical position of a fish



The speed is

$$\text{speed} = \sqrt{10.0^2 + (-1.8)^2} = 10.16.$$

At $t = 1$, the direction is

$$\theta = \tan^{-1}\left(\frac{-1.8}{10.0}\right) = -0.178.$$

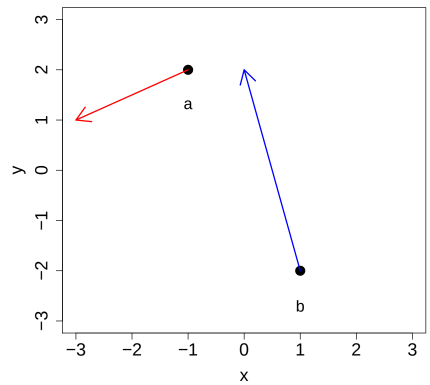
Because the fish is moving to the right, this is the correct direction. The fish is moving down by this time. The velocity vector is always tangent to the parametric curve for position, and will be different at every time for any object that is accelerating.

Summary

Vectors, the mathematical version of arrows, describe quantities that involve more than one measurement. They can be specified by their **horizontal** and **vertical components**. We used **phase plane vectors** to better understand the dynamics of two dimensional systems of coupled autonomous differential equations. Using the trigonometric functions, we have written vectors in terms of their **magnitude** and **direction**. One familiar example of a vector quantity is the **velocity** of an object. The magnitude of the velocity vector is the **speed**.

1.5 Exercises

• EXERCISE **1.1**
Find the components and starting points of the vectors in the following picture.



• EXERCISE **1.2**
Draw the following vectors.

a. The vector $(1, 3)$ starting from $(0, 0)$.
b. The vector $(3, 1)$ starting from $(0, 0)$.
c. The vector $(3, 4)$ starting from $(1, 3)$.
d. The vector $(-1, 3)$ starting from $(1, 3)$.

• EXERCISE **1.3**
Find and graph the sum of the following vectors.

a. The vectors $(1, 3)$ and $(3, 1)$ starting from $(0, 0)$.
b. The vectors $(3, 4)$ and $(-1, 3)$ starting from $(1, 3)$.

• EXERCISE **1.4**
Set $\alpha = 0.1$ and $\alpha_2 = 0.02$ in the equations for Newton's law of cooling in Chapter 5. Draw phase plane vectors at the following points (if your vectors seem too long or too short, multiply or divide by a suitable constant).

a. $H = 5.0$, $A = 1.0$.
b. $H = 1.0$, $A = 5.0$.
c. $H = 1.0$, $A = 0.0$.
d. $H = 2.0$, $A = 30.0$.

• EXERCISE **1.5**
Set $\lambda = \mu = 1.0$, $K_a = 10^3$, $K_b = 10^4$ in the competition equations from Chapter 5. Draw the phase plane vector at the following points (if the vectors seem to be too long or too short to see, multiply or divide them by a suitable constant).

a. $a = 10^3$, $b = 10^3$.
b. $a = 5 \times 10^2$, $b = 10^2$.
c. $a = 10^3$, $b = 5 \times 10^3$.
d. $a = 5 \times 10^3$, $b = 5 \times 10^3$.

• EXERCISE **1.6**
Convert the following angles.

a. Find 50 degrees, 150 degrees and 250 degrees in radians.
b. Plot each of these angles.

c. Find 1, 2, 3, 4, 5 and 6 radians in degrees.
d. Plot each of these angles.

• EXERCISE **1.7**
Compute the sines, cosines and tangents of each of the angles in exercise 1.6.

• EXERCISE **1.8**
Find the horizontal and vertical components of the following vectors. Graph the vectors.

a. $\vec{v}$ has length 6.0 and direction 1.2.
b. $\vec{v}$ has length 6.0 and direction 4.2.
c. $\vec{v}$ has length 0.1 and direction 2.2.
d. $\vec{v}$ has length 11.1 and direction -2.2.

• EXERCISE **1.9**
Find the magnitude and direction of the vectors in exercise 1.1.

• EXERCISE **1.10**
Consider the fish described in the text.

a. Find when the fish hits water (solve $y(t) = 0$ for t).
b. Find when the speed is a minimum. Find the speed and direction at this time.
c. Find the speed and direction when the fish takes off.
d. Find the speed and direction when the fish hits the water.
e. The acceleration is the derivative of the velocity. Find the acceleration vector for this fish.

• EXERCISE **1.11**
Suppose a bird is moving according to the formula

$$\frac{dx}{dt} = t - t^2$$
$$\frac{dy}{dt} = 3t - t^2 + 1.$$

a. Find the horizontal and vertical velocity at time t.
b. Draw the velocity vector at $t = 0$. Find the direction and speed.
c. Draw the velocity vector at $t = 1$. Find the direction and speed.
d. Draw the velocity vector at $t = 2$. Find the direction and speed.
e. Suppose the bird starts at $(0, 0)$. Find the position of the bird at time t. (Solve each of the equations as a pure-time differential equation).
f. Find the acceleration of this bird (the derivative of the velocity). What does this mean?

• EXERCISE **1.12**
Suppose an organism is moving according to the formula

$$x(t) = \cos(t)$$
$$y(t) = \sin(t).$$

a. Find the horizontal and vertical velocity at time t. Use the facts

$$\frac{d\sin(t)}{dt} = \cos(t)$$
$$\frac{d\cos(t)}{dt} = -\sin(t).$$

b. Draw the velocity vector at $t = 0$. Find the direction and speed.
c. Draw the velocity vector at $t = 1$. Find the direction and speed.
d. Draw the velocity vector at $t = 2$. Find the direction and speed.
e. Find the acceleration vector at these three times.

Chapter 2

Vectors and Discrete Dynamics

The previous section focussed on the geometric interpretation of vectors, including the important application to velocity. However, thought of as a list of numbers, vectors can be used to describe any set of related measurements. In particular, we can use vectors to write updating functions that track the dynamics of two or more measurements in discrete time. We will use **linear updating systems**, **column vectors** and **matrices** to study the dynamics of a population and a chemical.

2.1 Population dynamics

The bacteria described by the basic dynamical system

$$b_{t+1} = rb_t$$

are ready to divide every hour. What if they need two hours to grow and mature before they can divide? It takes two numbers to describe this population: the number of "juvenile" bacteria and the number of "adult" bacteria. We set

$$\begin{aligned} j_t &= \text{the number of juvenile bacteria at the beginning of a generation} \\ b_t &= \text{the number of adult bacteria at the beginning of a generation.} \end{aligned}$$

We need formulas for j_{t+1} and b_{t+1}, the numbers at the beginning of the next generation, in terms of j_t and b_t.

In the basic system, each adult produces r surviving offspring. These offspring are juveniles, so

$$j_{t+1} = rb_t.$$

Suppose a fraction σ of juveniles mature and the rest perish. Then

$$b_{t+1} = \sigma j_t.$$

If $r = 2$ each adult produces two juveniles, and if $\sigma = 0.5$ half the juvenile bacteria survive to maturity. If we start with 2.0×10^5 adults and 3.0×10^5 juveniles and $r = 2.0$ and $\sigma = 0.5$, we end up with 4.0×10^5 juveniles (double the old number of adults) and 1.5×10^5 adults (half the old number of juveniles).

Table 2.1: Chemical in the lung and the ambient air

Step	Volume	Chemical	Concentration
Air in lung before breath	V	$c_t V$	c_t
Ambient air before breath	MV	$\gamma_t MV$	γ_t
Air exhaled	qV	$qc_t V$	c_t
Air inhaled	qV	$q\gamma_t V$	γ_t
Air in lung after breathing	V	$(1-q)c_t V + q\gamma_t V$	$(1-q)c_t + q\gamma_t$
Ambient air after breathing	MV	$\gamma_t MV + c_t qV - q\gamma_t V$	$(1-\frac{q}{M})\gamma_t + \frac{qc_t}{M}$

We call these equations an **updating system**, written

$$\begin{aligned} j_{t+1} &= rb_t \\ b_{t+1} &= \sigma j_t. \end{aligned}$$

Computing the new number of juveniles requires knowing the old number of adults, and computing the new number of adults requires knowing the old number of juveniles. The dynamics of the two measurements are **coupled**.

The populations described by the equations

$$\begin{aligned} a_{t+1} &= sa_t \\ b_{t+1} &= rb_t, \end{aligned}$$

are **uncoupled**. The a population can be tracked without knowing the b population and vice versa. We transformed this updating system into an updating function by studying the fraction p of type a.

Both of these updating systems are **linear**. In each, new populations can be computed from old using only addition and multiplication by constants. If the per capita growth of each population decreases according to a law rather like the Ricker model, we might find

$$\begin{aligned} a_{t+1} &= sa_t e^{-\alpha(a_t+b_t)} \\ b_{t+1} &= rb_t e^{-\beta(a_t+b_t)}, \end{aligned}$$

This updating system is **nonlinear** because computing new populations from old requires exponentiation. Nonlinear systems are much more difficult to analyze.

2.2 Discrete diffusion

In Chapter 5, we modeled diffusive chemical exchange between two vessels with differential equations. In Chapter 1 we modeled chemical exchange in a lung but ignored changes in the ambient air.

We can emulate the reasoning of Chapter 1 to compute the change in the ambient concentration. Suppose the ambient air has volume M times that of lung. Table 2.1 outlines the steps to derive the updating system

$$\begin{aligned} c_{t+1} &= (1-q)c_t + q\gamma_t \\ \gamma_{t+1} &= \frac{q}{M}c_t + (1-\frac{q}{M})\gamma_t. \end{aligned}$$

The equation for the internal concentration c_{t+1} matches our original equation. The equation for the external concentration γ_{t+1} has the same form, but the fraction exchanged is q/M rather than q, a factor of M smaller. Change in the larger vessel is buffered.

For instance, if $c_t = 2.0\times10^{-5}$, $\gamma_t = 5.0\times10^{-5}$, $q = 0.6$ and $M = 4$, we find

$$\begin{aligned} c_{t+1} &= 0.4\cdot 2.0\times10^{-5} + 0.6\cdot 5.0\times10^{-5} = 3.8\times10^{-5} \\ \gamma_{t+1} &= 0.15\cdot 5.0\times10^{-5} + 0.85\cdot 2.0\times10^{-5} = 2.45\times10^{-5}. \end{aligned}$$

The concentration changes only 1/4 as much in the larger vessel.

This updating system is also linear. The state variables experience nothing more mathematically traumatic than multiplication by constants, addition, and subtraction.

2.3 Writing linear systems with vectors and matrices

Linear updating systems can be written with the notation of vectors and **matrices**. We write our state variables as a **column vector** which looks like

$$\begin{pmatrix} j_t \\ b_t \end{pmatrix}.$$

Stacking the variables in a column reminds us that we stacked the equations in the updating system. We now write

$$\begin{pmatrix} j_{t+1} \\ b_{t+1} \end{pmatrix} = \begin{pmatrix} 0 & r \\ \sigma & 0 \end{pmatrix}\begin{pmatrix} j_t \\ b_t \end{pmatrix}.$$

The block of numbers and letters is a **matrix**. This is shorthand for the full updating system. How do we decode this shorthand?

The right hand side is called **multiplication of a vector by a matrix**. The procedure works as follows. Rotate the column vector and lay it on top of the matrix. Multiply each term in the vector by the adjacent term in the matrix and add them up. We find

$$0\cdot j_t + r\cdot b_t$$

This is the upper element in the product column vector, so

$$j_{t+1} = 0\cdot j_t + r\cdot b_t = rb_t.$$

This matches our original equation. To find the bottom element of the product column vector, lay the rotated column vector on top of the bottom row of the matrix. Again, multiply each term in the vector by the neighboring term in the matrix and add them up. We find

$$b_{t+1} = \sigma\cdot j_t + 0\cdot b_t = \sigma j_t,$$

again matching our original equation. The process of multiplication of a vector by a matrix is defined to make the shorthand work.

How can we write the equations for chemical exchange in matrix shorthand? We need to find the matrix $\boldsymbol{N}$ that fits in the equation

$$\begin{pmatrix} c_{t+1} \\ \gamma_{t+1} \end{pmatrix} = \boldsymbol{N} \begin{pmatrix} c_t \\ \gamma_t \end{pmatrix}.$$

The top left element of $\boldsymbol{N}$ is $1-q$, the coefficient of c_t (the top element of the old column vector) in the expression for c_{t+1} (the top element of the new column vector). The top right element of $\boldsymbol{N}$ is q, the coefficient of γ_t in the equation for c_{t+1}. The bottom left element of $\boldsymbol{N}$ is the coefficient $\frac{q}{M}$ of c_t in the equation for γ_{t+1} and the bottom right element of $\boldsymbol{N}$ is the coefficient $1-\frac{q}{M}$ of γ_t in the equation for γ_{t+1}. In matrix notation,

$$\begin{pmatrix} c_{t+1} \\ \gamma_{t+1} \end{pmatrix} = \begin{pmatrix} 1-q & q \\ \frac{q}{M} & 1-\frac{q}{M} \end{pmatrix} \begin{pmatrix} c_t \\ \gamma_t \end{pmatrix}.$$

The matrix is a block of numbers consisting of the coefficients of our updating system.

To check, rotate the old column vector, place it on the top row of the matrix, multiply the adjacent terms, and add them up. c_t lines up with $1-q$ and γ_t lines up with q, giving

$$c_{t+1} = (1-q)c_t + q\gamma_t,$$

consistent with our updating system. Laying the old column vector on top of the bottom row of the matrix, c_t lines up with $\frac{q}{M}$ and γ_t lines up with $1-\frac{q}{M}$. Multiplying and adding, we find

$$\gamma_{t+1} = \frac{q}{M}c_t + (1-\frac{q}{M})\gamma_t,$$

again consistent with the updating system. Matrices and column vectors provide compact way to write linear updating systems.

Summary

We have found **updating systems** describing the dynamics of pairs of population and concentration measurements. When the new measurements depend on each other, the system is **coupled**. **Linear systems**, in which old measurements are only added or multiplied by constants, can be written with **column vectors** and **matrices**, and interpreted with the technique of **multiplying a column vector by a matrix**.

2.4 Exercises

• EXERCISE **2.1**

Find new values of j and b from the bacterial updating system in the following circumstances. Do you think the population will grow or decline?

a. $j_t = 2.0\times10^5$, $b_t = 4.0\times10^5$, $r = 2.0$, $\sigma = 0.75$.

b. $j_t = 4.0\times10^5$, $b_t = 2.0\times10^5$, $r = 2.0$, $\sigma = 0.75$.

c. $j_t = 7.0{\times}10^5$, $b_t = 4.0{\times}10^5$, $r = 1.5$, $\sigma = 0.75$.
d. $j_t = 3.0{\times}10^5$, $b_t = 9.0{\times}10^5$, $r = 1.5$, $\sigma = 0.75$.

• EXERCISE **2.2**
We can use the technique of converting dynamical systems to fractions to find an updating function for the fraction of juveniles described by the updating system for bacteria.

a. Define p_t as the old fraction of juveniles.
b. Write an equation for p_{t+1} in terms of j_t and b_t.
c. Use the trick of dividing top and bottom by $j_t + b_t$ to find the p_{t+1} in terms of p_t.
d. For the case $r = 2.0$, $\sigma = 0.75$, graph the updating function.
e. Find the equilibrium. Is it stable?

• EXERCISE **2.3**
Find all the quantities in table 2.1 in the following cases.

a. $c_t = 2.0{\times}10^{-5}$, $\gamma_t = 5.0{\times}10^{-5}$, $q = 0.5$, $V = 2.0$ liters, $M = 5.0$.
b. $c_t = 2.0{\times}10^{-5}$, $\gamma_t = 5.0{\times}10^{-5}$, $q = 0.9$, $V = 2.0$ liters, $M = 5.0$.
c. $c_t = 2.0{\times}10^{-5}$, $\gamma_t = 5.0{\times}10^{-5}$, $q = 0.5$, $V = 2.0$ liters, $M = 20.0$.

• EXERCISE **2.4**
Consider the matrices $\boldsymbol{M}$ and $\boldsymbol{N}$ and the column vectors $\vec{\boldsymbol{v}}$ and $\vec{\boldsymbol{u}}$,

$$\boldsymbol{M} = \begin{pmatrix} 2 & 3 \\ 1 & 4 \end{pmatrix},\ \boldsymbol{N} = \begin{pmatrix} 2 & 4 \\ -1 & 0 \end{pmatrix},\ \vec{\boldsymbol{v}} = \begin{pmatrix} 2 \\ 1 \end{pmatrix},\ \vec{\boldsymbol{u}} = \begin{pmatrix} 4 \\ -2 \end{pmatrix}.$$

Compute the following.

a. $\boldsymbol{M}\ \vec{\boldsymbol{v}}$.
b. $\boldsymbol{M}\ \vec{\boldsymbol{u}}$.
c. $\boldsymbol{N}\ \vec{\boldsymbol{v}}$.
d. $\boldsymbol{N}\ \vec{\boldsymbol{u}}$.

• EXERCISE **2.5**
Consider a population of pairs of rabbits, consisting of juveniles and adults. After a month, each juvenile grows to maturity. Each adult pair produces a pair of juveniles and itself survives.

a. Find the updating system for this population.
b. Find the associated matrix.
c. Suppose the population starts with 1 adult pair. Compute the number of juvenile and adult rabbits after 1 month, 2 months, up to 5 months.
d. Can you see the pattern?

Chapter 3

Matrices and Eigenvalues

We continue our study of matrices by introducing **matrix multiplication**, the method for composing linear updating systems. The structuring quantity behind the long-term dynamics of these systems is not the equilibrium, but the **stable distribution** or **eigenvector** and its associated **eigenvalue**.

3.1 Matrix multiplication

A matrix is like a function. It takes the old column vector as input and returns the new one as output. To understand updating functions, we **composed** the function with itself to figure out what happened to the state variable after a long time. The process of composing linear updating systems can be conveniently expressed in matrix notation with **matrix multiplication**.

Consider the updating system for the lung with $q = 0.4$ and $M = 4$. The updating matrix is

$$\begin{pmatrix} 0.6 & 0.4 \\ 0.1 & 0.9 \end{pmatrix}.$$

Suppose the initial conditions are $c_0 = 1.0$ and $\gamma_0 = 4.0$. We find the concentrations after one breath, c_1 and γ_1, by multiplying

$$\begin{aligned} \begin{pmatrix} c_1 \\ \gamma_1 \end{pmatrix} &= \begin{pmatrix} 0.6 & 0.4 \\ 0.1 & 0.9 \end{pmatrix} \begin{pmatrix} 1.0 \\ 4.0 \end{pmatrix} \\ &= \begin{pmatrix} 0.6 \cdot 1.0 + 0.4 \cdot 4.0 \\ 0.1 \cdot 1.0 + 0.9 \cdot 4.0 \end{pmatrix} \\ &= \begin{pmatrix} 2.2 \\ 3.7 \end{pmatrix}. \end{aligned}$$

We find the concentrations after another breath in the same way, as

$$\begin{aligned} \begin{pmatrix} c_2 \\ \gamma_2 \end{pmatrix} &= \begin{pmatrix} 0.6 & 0.4 \\ 0.1 & 0.9 \end{pmatrix} \begin{pmatrix} c_1 \\ \gamma_1 \end{pmatrix} \\ &= \begin{pmatrix} 0.6 & 0.4 \\ 0.1 & 0.9 \end{pmatrix} \begin{pmatrix} 2.2 \\ 3.7 \end{pmatrix} \end{aligned}$$

$$= \begin{pmatrix} 0.6 \cdot 2.2 + 0.4 \cdot 3.7 \\ 0.1 \cdot 2.2 + 0.9 \cdot 3.7 \end{pmatrix} = \begin{pmatrix} 2.8 \\ 3.55 \end{pmatrix}.$$

How can we find c_2 and γ_2 in one step, without finding c_1 and γ_1? To do so with updating functions, we used composition. To compose linear updating systems with **matrix multiplication**, we follow the same contortions used to multiply a vector by a matrix. Treat the second matrix as two column vectors sitting side by side. In particular

$$\begin{aligned} \begin{pmatrix} 0.6 & 0.4 \\ 0.1 & 0.9 \end{pmatrix} \begin{pmatrix} 0.6 & 0.4 \\ 0.1 & 0.9 \end{pmatrix} &= \begin{pmatrix} 0.6 \cdot 0.6 + 0.4 \cdot 0.1 & 0.6 \cdot 0.4 + 0.4 \cdot 0.9 \\ 0.1 \cdot 0.6 + 0.9 \cdot 0.1 & 0.4 \cdot 0.1 + 0.9 \cdot 0.9 \end{pmatrix} \\ &= \begin{pmatrix} 0.4 & 0.6 \\ 0.15 & 0.85 \end{pmatrix} \end{aligned}$$

To find the top left element of the product, we laid the left column of the second matrix on the top row of the first. The top right element combines the right column of the second matrix with the top row of the first and so forth. This process is designed to exactly match our original result. If we multiply the product matrix by the column vector $\begin{pmatrix} c_0 \\ \gamma_0 \end{pmatrix} = \begin{pmatrix} 1.0 \\ 4.0 \end{pmatrix}$,

$$\begin{pmatrix} 0.4 & 0.6 \\ 0.15 & 0.85 \end{pmatrix} \begin{pmatrix} 1.0 \\ 4.0 \end{pmatrix} = \begin{pmatrix} 2.8 \\ 3.55 \end{pmatrix} = \begin{pmatrix} c_2 \\ \gamma_2 \end{pmatrix}.$$

Matrix multiplication in general works as follows. We write a matrix $\boldsymbol{A}$ as

$$\boldsymbol{A} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}.$$

The a's are called the **elements** of the matrix. The numbering is standard. Try not to get confused about which element is a_{12} and which is a_{21}. The product of the two matrices $\boldsymbol{A}$ and $\boldsymbol{B}$ is

$$\begin{aligned} \boldsymbol{AB} &= \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix} \\ &= \begin{pmatrix} a_{11}b_{11} + a_{12}b_{21} & a_{11}b_{12} + a_{12}b_{22} \\ a_{21}b_{11} + a_{22}b_{21} & a_{21}b_{12} + a_{22}b_{22} \end{pmatrix}. \end{aligned}$$

For example, if

$$\boldsymbol{A} = \begin{pmatrix} 2 & 3 \\ 1 & 4 \end{pmatrix}, \ \boldsymbol{B} = \begin{pmatrix} -2 & 5 \\ -1 & 0 \end{pmatrix}$$

we find

$$\boldsymbol{AB} = \begin{pmatrix} 2 \cdot -2 + 3 \cdot -1 & 2 \cdot 5 + 3 \cdot 0 \\ 1 \cdot -2 + 4 \cdot -1 & 1 \cdot 5 + 4 \cdot 0 \end{pmatrix} = \begin{pmatrix} -7 & 10 \\ -6 & 5 \end{pmatrix}.$$

In contrast

$$\begin{aligned} \boldsymbol{BA} &= \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix} \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \\ &= \begin{pmatrix} b_{11}a_{11} + b_{12}a_{21} & b_{11}a_{12} + b_{12}a_{22} \\ b_{21}a_{11} + b_{22}a_{21} & b_{21}a_{12} + b_{22}a_{22} \end{pmatrix} \end{aligned}$$

With $\boldsymbol{A}$ and $\boldsymbol{B}$ from above,

$$\boldsymbol{BA} = \begin{pmatrix} -2\cdot 2+5\cdot 1 & -2\cdot 3+5\cdot 4 \\ -1\cdot 2+0\cdot 1 & -1\cdot 3+0\cdot 4 \end{pmatrix} = \begin{pmatrix} 1 & 14 \\ -2 & -3 \end{pmatrix},$$

which is not equal to $\boldsymbol{AB}$. Like functions, matrices generally do not **commute**.

3.2 Equilibria of updating systems

An equilibrium for an updating system, as with a discrete-time dynamical system or differential equation, is a point where the state variables are unchanged by the updating. For the lung model, nothing happens if

$$\begin{aligned} c_{t+1} &= c_t \\ \gamma_{t+1} &= \gamma_t \end{aligned}$$

or

$$\begin{aligned} c_t &= (1-q)c_t + q\gamma_t \\ \gamma_t &= (1-\frac{q}{M})\gamma_t + \frac{q}{M}c_t. \end{aligned}$$

As in Chapter 5, finding solutions of these **simultaneous equations** can be a tricky business, even when the updating function is a matrix. Techniques for handling this problem are treated in courses in **linear algebra**. In this case, we solve the first equation in the two dimensional lung updating system for c_t and find that $c_t = \gamma_t$ (as long as $q \neq 0$). We solve the second equation for γ_t, and find the same thing, $\gamma_t = c_t$. As before, when the internal and ambient concentrations are equal, exchange changes nothing, whatever the concentrations are.

Assume, as is true, that the internal and ambient concentrations converge to be equal (proving this requires more linear algebra or some tricks). How do we find the value? The total amount of chemical remains unchanged by the exchange process. The final concentrations are the total amount divided by the total volume.

In our example, suppose the volume of the smaller vessel is 1.0 liters. There are initially $c_0V = 1.0$ moles inside and $\gamma_0 MV = 4.0\cdot 4\cdot 1 = 16.0$ moles outside, giving a total of 17.0 moles. Dividing this evenly between the total volume of 5.0 liters in the two vessels gives 3.4 moles/liter.

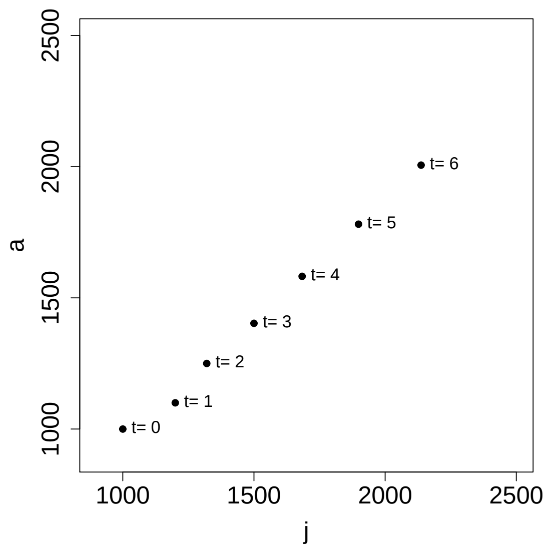
3.3 Eigenvectors and stable distributions

Equilibria often do not help make sense of population growth models. Like our basic equation for bacterial population growth, these models exhibit exponential growth or decay, with only a few exceptions.

Bacteria differ from other organisms in that adults vanish upon reproduction. Consider a population of asexually reproducing organisms where offspring born in the spring and are not ready to reproduce until they are two years old. Three numbers describe this population: the number of juveniles produced per adult (r), the probability that a juvenile successfully matures into an adult (σ), and the probability that an adult survives (p). Adult survival is the process missing from our original updating system. Letting j represent the number of juveniles and a the number of adults, we have the updating system

$$\begin{aligned} j_{t+1} &= ra_t \\ a_{t+1} &= \sigma j_t + pa_t. \end{aligned}$$

Figure 3.3.1: Population vectors from times $t = 0$ through $t = 6$



In matrix form,

$$\begin{pmatrix} j_{t+1} \\ a_{t+1} \end{pmatrix} = \begin{pmatrix} 0 & r \\ \sigma & p \end{pmatrix} \begin{pmatrix} j_t \\ a_t \end{pmatrix}.$$

The matrix is called a **Leslie matrix** in ecological and demographic theory.

What happens if we run this system for a long time? Suppose $r = 1.2$, $\sigma = 0.4$ and $p = 0.7$. The Leslie matrix is

$$\begin{pmatrix} 0 & 1.2 \\ 0.4 & 0.7 \end{pmatrix}.$$

Will the population survive? If so, how will it grow? Suppose the population starts with 1000 adults and 1000 juveniles. Applying the matrix repeatedly, we find

$$\begin{aligned} \begin{pmatrix} j_1 \\ a_1 \end{pmatrix} &= \begin{pmatrix} 1200 \\ 1100 \end{pmatrix}, \begin{pmatrix} j_2 \\ a_2 \end{pmatrix} = \begin{pmatrix} 1320 \\ 1250 \end{pmatrix}, \begin{pmatrix} j_3 \\ a_3 \end{pmatrix} = \begin{pmatrix} 1500 \\ 1403 \end{pmatrix} \\ \begin{pmatrix} j_4 \\ a_4 \end{pmatrix} &= \begin{pmatrix} 1684 \\ 1582 \end{pmatrix}, \begin{pmatrix} j_5 \\ a_5 \end{pmatrix} = \begin{pmatrix} 1898 \\ 1781 \end{pmatrix}, \begin{pmatrix} j_6 \\ a_6 \end{pmatrix} = \begin{pmatrix} 2137 \\ 2006 \end{pmatrix}. \end{aligned}$$

These results are easiest to visualize graphically. The column vectors are plotted as ordered pairs in figure 3.3.1. The points eventually move off in the same direction. The ratio of j_t to a_t is approaching a limit, or, equivalently, that the fraction of juveniles is approaching a limit. Denoting the fraction of juveniles at time t by p_t, we find that

$$\begin{aligned} p_0 &= 0.5000,\ p_1 = 0.5217,\ p_2 = 0.5136,\ p_3 = 0.5167, \\ p_4 &= 0.5155,\ p_5 = 0.5160,\ p_6 = 0.5158. \end{aligned}$$

This unchanging fraction is called a **stable age distribution**. About 51.6% of the organisms are juveniles and the remaining 48.4% are adults. Although the total population is growing, the fraction of juveniles remains the same.

Furthermore, the number of juveniles is increasing by a roughly constant factor. Letting λ_t be the increase in the number of juveniles between generations $t-1$ and t, we find

$$\begin{aligned}\lambda_1 &= 1.2000,\ \lambda_2 = 1.1000,\ \lambda_3 = 1.1364,\\ \lambda_4 &= 1.1224,\ \lambda_5 = 1.1276,\ \lambda_6 = 1.1257.\end{aligned}$$

Mathematically, the stable age distribution is called an **eigenvector** and the constant increase of the juvenile population is an **eigenvalue**. Eigenvectors and eigenvalues are the focus of linear algebra, and are the tools needed to find the stability of equilibria of high dimensional differential equations and updating systems and much more.

In general, an **eigenvector** $\vec{\boldsymbol{v}}$ of a matrix $\boldsymbol{A}$ is any vector $\vec{\boldsymbol{v}}$ that satisfies

$$\boldsymbol{A}\vec{\boldsymbol{v}} = \lambda\vec{\boldsymbol{v}}.$$

for some **eigenvalue** λ. An eigenvector and eigenvalue are associated with a particular matrix. Most matrices have more than one eigenvector and associated eigenvalue (our matrices have 2). Multiplying an eigenvector by the matrix preserves the direction and changes the magnitude by a factor of λ. If $\lambda < 0$, the direction is reversed.

In our example, the vector $\vec{\boldsymbol{v}} = \begin{pmatrix} 820.3 \\ 769.8 \end{pmatrix}$ is an eigenvector. Techniques for finding eigenvectors are a key part of linear algebra. We find

$$\begin{pmatrix} 0 & 1.2 \\ 0.4 & 0.7 \end{pmatrix}\begin{pmatrix} 820.3 \\ 769.8 \end{pmatrix} = \begin{pmatrix} 923.8 \\ 867.05 \end{pmatrix} = 1.1262\begin{pmatrix} 820.3 \\ 769.8 \end{pmatrix}.$$

The eigenvalue is 1.1262, meaning that the population grows by a factor of 1.1262 when it reaches its stable age distribution. The total population will eventually grow exponentially, but, unlike a one dimensional population, will not do so immediately. The total population is compared with this exponential rate in figure 3.3.2.

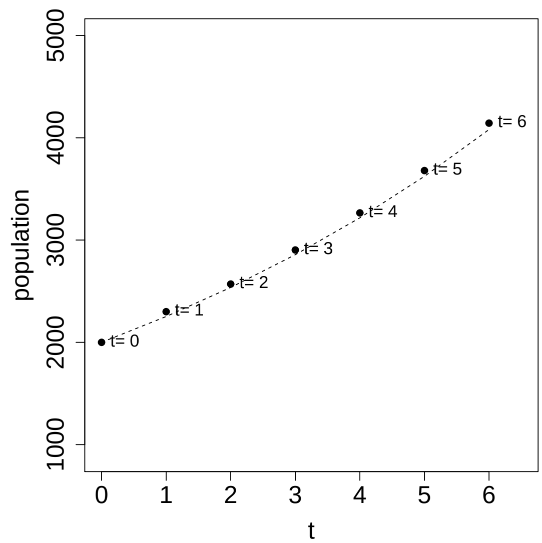
Summary

We have composed linear updating systems, **matrices**, with **matrix multiplication**. Like ordinary functional composition, matrices generally do not **commute**. Although equilibria can be found in the same way as in one dimension, they often give little insight about the solutions. For **Leslie matrices** that describe growth of populations broken into different age classes, the **stable age distribution** or **eigenvector** and the associated growth rate or **eigenvalue** best describe the long-term behavior of the population.

3.4 Exercises

• EXERCISE **3.1**
Suppose $r = 2.0$ and $\sigma = 0.6$, and that $j_0 = 1.0\times10^6$ and $b_0 = 5.0\times10^7$.

Figure 3.3.2: The growth of a bacterial population compared with an exponential function



a. Find the matrix for the updating system.

b. Find j_1 and b_1.

c. Find j_2 and b_2.

d. Find the two step updating system by multiplying the matrix by itself.

e. Find j_2 and b_2 using the result of **d**.

• EXERCISE **3.2**

Suppose $q = 0.2$, $M = 5.0$, $V = 2.5$ liters, $c_0 = 2.0{\times}10^{-2}$ moles/liter and $\gamma_0 = 7.0{\times}10^{-2}$ moles/liter in the lung model.

a. Write the matrix for the updating system.

b. Find c_1 and γ_1.

c. Find c_2 and γ_2.

d. Find the two step updating system by multiplying the matrix by itself.

e. Find c_2 and γ_2 using the result of **d**.

f. Find the three step updating system (multiply the matrix from **d** by the original matrix).

g. Find c_3 and γ_3 using the result of **f** and compare with the result found by multiplying the original matrix by $\begin{pmatrix} c_2 \\ \gamma_2 \end{pmatrix}$.

• EXERCISE **3.3**

Consider the updating system for bacteria without plugging in specific values for r and σ.

a. Find the two step updating system by multiplying the matrix by itself.

b. Find j_2 and b_2 as functions of j_0 and b_0.

• EXERCISE **3.4**
Suppose $a_{11} = 11$, $a_{12} = 12$, $a_{21} = 21$, $a_{22} = 22$ and

$$\boldsymbol{B} = \begin{pmatrix} 1 & 3 \\ 2 & 4 \end{pmatrix}, \vec{\boldsymbol{v}} = \begin{pmatrix} 3 \\ 7 \end{pmatrix}.$$

a. Write $\boldsymbol{A}$ as a matrix.
b. Find the components of $\boldsymbol{B}$.
c. Find $\boldsymbol{B}\vec{\boldsymbol{v}}$.
d. Multiply the result of **c** by $\boldsymbol{A}$.
e. Find $\boldsymbol{AB}$.
f. Multiply $\vec{\boldsymbol{v}}$ the result of **e**.
g. Find $\boldsymbol{BA}$. Do the matrices commute?

• EXERCISE **3.5**
Write the Leslie matrices in the following circumstances. Compute populations after 3 generations.

a. $r = 0.4$, $\sigma = 0.8$, $p = 0.9$, $j_0 = 1000$, $a_0 = 1000$.
b. $r = 0.4$, $\sigma = 0.8$, $p = 0.9$, $j_0 = 0$, $a_0 = 1000$.
c. $r = 0.4$, $\sigma = 0.8$, $p = 0.9$, $j_0 = 1000$, $a_0 = 0$.
d. $r = 0.9$, $\sigma = 0.8$, $p = 0.4$, $j_0 = 1000$, $a_0 = 1000$.

• EXERCISE **3.6**
Apply Leslie matrix theory to exercise 2.5.

a. Write the Leslie matrix.
b. Find the number of juvenile and adult pairs after 1, 2, up to 5 months starting from 1 adult pair and no juveniles.
c. Find the fraction of juveniles at each of these times.
d. Find the growth rates of the juvenile and adult populations.
e. Take a guess at the eigenvalue.

• EXERCISE **3.7**
Some birds inhabit two nearby islands. Each year, a fraction q of the birds on the first island leave for the second island and a fraction p of the birds on the second island leave for the first. The rest stay put. Suppose $p = 0.2$, $q = 0.8$, and that there are initially 1000 birds on each island.

a. How many birds are on each island after 1, 2, and 3 years?
b. Write the updating system giving the number of birds on each island.
c. Write the associated matrix.
d. Does this matrix resemble the one for a very different model?

• EXERCISE **3.8**
The solution of the updating system with the matrix $\begin{pmatrix} 1 & 1 \\ 0 & 1 \end{pmatrix}$ are one of the rare cases that does not grow or decay exponentially. Try to find the solution and describe what it does. Do you have any idea why this is an exception to the rule?

Chapter 4

Matrices and Markov Chains

We can think of Markov chains as updating systems, and describe their dynamics with matrices. This compact notation can be used to find equilibrium probabilities for Markov chains and to describe Markov chains with more than two possible states.

4.1 Matrices and conditional distributions

Recall the Markov chain describing a molecule hopping in and out of a cell. Letting I_t indicate that the molecule is inside and O_t that it is outside during minute t, we expressed the model with conditional probability notation as

$$\begin{aligned}
\Pr(\mathrm{I}_{t+1}|\mathrm{I}_t) &= 0.98 \\
\Pr(\mathrm{I}_{t+1}|\mathrm{O}_t) &= 0.01 \\
\Pr(\mathrm{O}_{t+1}|\mathrm{I}_t) &= 0.02 \\
\Pr(\mathrm{O}_{t+1}|\mathrm{O}_t) &= 0.99.
\end{aligned}$$

Let p_t designate the probability that the molecule is inside and q_t the probability that the molecule is outside at time t. According to the law of total probability,

$$\begin{aligned}
p_{t+1} &= \Pr(\mathrm{I}_{t+1}|\mathrm{I}_t)\Pr(\mathrm{I}_t) + \Pr(\mathrm{I}_{t+1}|\mathrm{O}_t)\Pr(\mathrm{O}_t) \\
&= 0.98p_t + 0.01q_t \\
q_{t+1} &= \Pr(\mathrm{O}_{t+1}|\mathrm{I}_t)\Pr(\mathrm{I}_t) + \Pr(\mathrm{O}_{t+1}|\mathrm{O}_t)\Pr(\mathrm{O}_t) \\
&= 0.02p_t + 0.99q_t.
\end{aligned}$$

These two equations define a linear updating system. Knowing the probabilities at time t, we can compute the probabilities at time $t+1$ using only addition and multiplication by constants.

We can rewrite the equations in matrix and vector notation as

$$\begin{pmatrix} p_{t+1} \\ q_{t+1} \end{pmatrix} = \begin{pmatrix} 0.98 & 0.01 \\ 0.02 & 0.99 \end{pmatrix} \begin{pmatrix} p_t \\ q_t \end{pmatrix}. \tag{4.1.1}$$

The left hand side is computed by multiplying the matrix by the vector. We compute the upper element in the product column vector (p_{t+1}) by rotating the original column vector, laying it on top of the matrix, multiplying adjacent terms, and adding up. Similarly, the lower element of the product column vector is computed by laying the original column vector on the lower row of the matrix, multiplying adjacent terms and adding up.

If $\begin{pmatrix} p_t \\ q_t \end{pmatrix} = \begin{pmatrix} 0.8 \\ 0.2 \end{pmatrix}$, meaning that the molecule has an 80% chance of being inside and a 20% of being outside at time t, the probabilities that it is in or out at time $t+1$ are

$$\begin{aligned} \begin{pmatrix} p_{t+1} \\ q_{t+1} \end{pmatrix} &= \begin{pmatrix} 0.98 & 0.01 \\ 0.02 & 0.99 \end{pmatrix} \begin{pmatrix} 0.8 \\ 0.2 \end{pmatrix} \\ &= \begin{pmatrix} 0.98 \cdot 0.8 + 0.01 \cdot 0.2 \\ 0.02 \cdot 0.8 + 0.99 \cdot 0.2 \end{pmatrix} \\ &= \begin{pmatrix} 0.786 \\ 0.214 \end{pmatrix}. \end{aligned}$$

Matrices and vectors describing Markov chains have special properties. The vector lists the probabilities that the system is in a particular state (“In” or “Out”). Because the molecule must be somewhere, the elements of the vector must add to 1. Vectors with elements that add to 1 are called **probability vectors**. The columns of the matrix are conditional distributions. The first column gives the probability distribution at time $t+1$ conditional on the molecule being inside at time t. The second column gives the probability distribution at time $t+1$ conditional on the molecule being outside at time t. Because the elements of a conditional probability distribution add to 1, the elements in each column of the matrix add to 1. Matrices with columns that add to 1 are called **probability matrices**. Every Markov chain with only a finite number of states can be summarized in a probability matrix.

In general, suppose a system can be in states designated 1 and 2. Let

$$a_{ij} = \Pr(\text{state is } i \text{ at time } t+1 | \text{state is } j \text{ at time } t).$$

For our molecule, the states are “In” and “Out”. Designating “In” as state 1 and “Out” as state 2, this translates to

$$\begin{aligned} a_{11} &= 0.98 \\ a_{12} &= 0.01 \\ a_{21} &= 0.02 \\ a_{22} &= 0.99. \end{aligned}$$

Let $p_i(t)$ denote the probability that the system is in state i at time t. We can write the general two state Markov chain as

$$\begin{pmatrix} p_1(t+1) \\ p_2(t+1) \end{pmatrix} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} p_1(t) \\ p_2(t) \end{pmatrix}.$$

Because this matrix describes a Markov chain, it must be a probability matrix and satisfy $a_{11}+a_{21} = 1$ and $a_{12} + a_{22} = 1$.

A word of warning is required here. Some authors write the matrices describing Markov chains “sideways,” with rows that add to 1. The vectors are written as **row vectors** and multiplied on the left hand side. This creates endless confusion. To avoid it, make sure that you understand how a book or paper defines the matrix, and rewrite it if it is sideways.

4.2 Equilibria of Markov chains

What does all this fancy notation do for us? In Chapter 6, we used the fact that $q_t = 1 - p_t$ to rewrite the updating system 4.1.1 as an updating function. We used the techniques from the first quarter to find an equilibrium probability that the molecule is inside the cell of 1/3. If many molecules followed this process, about 1/3 would be inside (and 2/3 outside) after a long time. Equilibrium does not mean that the molecule is sitting still, just that its position, on average, is the same.

With the updating system, the long term behavior is again described by the equilibrium. Unlike the updating systems for population dynamics, updating systems defined by probability matrices almost always have equilibrium values (the exception is when all moves occur with probability 1 and the object jumps around indefinitely).

We can get an idea of the value of the equilibrium by running the system for a while. Suppose we start the updating system 4.1.1 with a molecule known to be inside the cell, or

$$\begin{pmatrix} p_0 \\ q_0 \end{pmatrix} = \begin{pmatrix} 1 \\ 0 \end{pmatrix}.$$

We can find the probabilities at later times by repeatedly applying equation 4.1.1. In this case,

$$\begin{pmatrix} p_1 \\ q_1 \end{pmatrix} = \begin{pmatrix} 0.98 \\ 0.02 \end{pmatrix}, \begin{pmatrix} p_2 \\ q_2 \end{pmatrix} = \begin{pmatrix} 0.9606 \\ 0.0394 \end{pmatrix}, \begin{pmatrix} p_3 \\ q_3 \end{pmatrix} = \begin{pmatrix} 0.9418 \\ 0.058 \end{pmatrix}$$

and so forth. Were we to do this for many iterations, we would find p_t getting closer and closer to 0.333 and q_t getting closer and closer to 0.667.

We solve for the equilibrium by finding values p^* and q^* which remain unchanged by the dynamics, or

$$\begin{aligned} p^* &= 0.98p^* + 0.01q^* \\ q^* &= 0.02p^* + 0.99q^*. \end{aligned}$$

If the probabilities p^* and q^* satisfied these equations, they would remain the same at time $t+1$. We attack these **simultaneous equations** by solving the first for q^* in terms of p^*. Moving the $0.98p^*$ to the left hand side and dividing by 0.02, we find $q^* = 2p^*$. Next, we plug this into the second equation, finding

$$\begin{aligned} 2p^* &= 0.02p^* + 0.99 \cdot 2p^* \\ &= 2p^*. \end{aligned}$$

We were hoping to solve for p^* and ended up with an equation that works for any value of p^*. What went wrong? To solve for the equilibrium probabilities in a Markov chain, we must use the fact that $\begin{pmatrix} p^* \\ q^* \end{pmatrix}$ is a probability vector, or that $p^* + q^* = 1$. Plugging in $q^* = 2p^*$,

$$p^* + 2p^* = 1$$

which has solution $p^* = 0.333$. Furthermore, $q^* = 2p^* = 0.666$.

We can check our solution by trying $\begin{pmatrix} p^* \\ q^* \end{pmatrix} = \begin{pmatrix} p_t \\ q_t \end{pmatrix}$ in equation 4.1.1,

$$\begin{pmatrix} 0.98 & 0.01 \\ 0.02 & 0.99 \end{pmatrix} \begin{pmatrix} p^* \\ q^* \end{pmatrix} = \begin{pmatrix} 0.98 & 0.01 \\ 0.02 & 0.99 \end{pmatrix} \begin{pmatrix} 0.333 \\ 0.666 \end{pmatrix} = \begin{pmatrix} 0.333 \\ 0.666 \end{pmatrix}.$$

We have indeed found the equilibrium probabilities. Molecules will spend twice as much time, on average, outside as inside the cell.

4.3 Generalized Markov chains

Why write a Markov chain as a matrix when we can find the same result with a single equation by solving for $q = 1 - p$? First, equation 4.1.1 presents all the probabilities in an easily read format. Second, this notation works for Markov chains with more than two possible states. Consider the situation where a molecule can be transferred among three cells in different arrangements. Suppose it transfers among cells according to the following rules.

- If it is in cell 1, it remains there with probability 0.92, moves to cell 2 with probability 0.06, and to cell 3 with probability 0.02.
- If it is in cell 2, it remains there with probability 0.91, moves to cell 1 with probability 0.04, and to cell 3 with probability 0.05.
- If it is in cell 3, it remains there with probability 0.96, moves to cell 1 with probability 0.01, and to cell 2 with probability 0.03.

Let $p_i(t)$ represent the probability that the molecule is in cell i at time t. We can describe the probabilities at time $t + 1$ with the law of total probability. There are 3 ways a molecule could come to be in cell 1: it could have been in cell 1 and stayed (probability $0.92p_1(t)$), been in cell 2 and moved to cell 1 (probability $0.04p_2(t)$), or been in cell 3 and moved to cell 1 (probability $0.01p_3(t)$). Applying the same reasoning to each of the other cells, we find

$$\begin{aligned} p_1(t+1) &= 0.92p_1(t) + 0.04p_2(t) + 0.01p_3(t) \\ p_2(t+1) &= 0.06p_1(t) + 0.91p_2(t) + 0.03p_3(t) \\ p_3(t+1) &= 0.02p_1(t) + 0.05p_2(t) + 0.96p_3(t). \end{aligned}$$

These equations define a linear updating system for three probabilities simultaneously.

The probabilities are arranged like a matrix, exactly as with 2 states. We write

$$\begin{pmatrix} p_1(t+1) \\ p_2(t+1) \\ p_3(t+1) \end{pmatrix} = \begin{pmatrix} 0.92 & 0.04 & 0.01 \\ 0.06 & 0.91 & 0.03 \\ 0.02 & 0.05 & 0.96 \end{pmatrix} \begin{pmatrix} p_1(t) \\ p_2(t) \\ p_3(t) \end{pmatrix}. \tag{4.3.1}$$

This matrix-vector expression encodes the dynamical system in matrix form. The method for matrix multiplication is the same as before. If we started a molecule in the first cell (so $p_1(0) = 1$,

$p_2(0) = 0$ and $p_3(t) = 0$), we use equation 4.3.1 to find the probabilities at time 1 as

$$\begin{aligned}
\begin{pmatrix} p_1(1) \\ p_2(1) \\ p_3(1) \end{pmatrix} &= \begin{pmatrix} 0.92 & 0.04 & 0.01 \\ 0.06 & 0.91 & 0.03 \\ 0.02 & 0.05 & 0.96 \end{pmatrix} \begin{pmatrix} p_1(0) \\ p_2(0) \\ p_3(0) \end{pmatrix} \\
&= \begin{pmatrix} 0.92 & 0.04 & 0.01 \\ 0.06 & 0.91 & 0.03 \\ 0.02 & 0.05 & 0.96 \end{pmatrix} \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix} \\
&= \begin{pmatrix} 1 \cdot 0.92 + 0 \cdot 0.04 + 0 \cdot 0.01 \\ 1 \cdot 0.06 + 0 \cdot 0.91 + 0 \cdot 0.03 \\ 1 \cdot 0.02 + 0 \cdot 0.05 + 0 \cdot 0.96 \end{pmatrix} \\
&= \begin{pmatrix} 0.92 \\ 0.06 \\ 0.02 \end{pmatrix}.
\end{aligned}$$

The molecule has a 92% chance of being in the first cell, a 6% chance of being in the second and a 2% chance of being in the third. We follow the same procedure to find the probabilities at time 2 as

$$\begin{aligned}
\begin{pmatrix} p_1(2) \\ p_2(2) \\ p_3(2) \end{pmatrix} &= \begin{pmatrix} 0.92 & 0.04 & 0.01 \\ 0.06 & 0.91 & 0.03 \\ 0.02 & 0.05 & 0.96 \end{pmatrix} \begin{pmatrix} 0.92 \\ 0.06 \\ 0.02 \end{pmatrix} \\
&= \begin{pmatrix} 0.92 \cdot 0.92 + 0.06 \cdot 0.04 + 0.02 \cdot 0.01 \\ 0.92 \cdot 0.06 + 0.06 \cdot 0.91 + 0.02 \cdot 0.03 \\ 0.92 \cdot 0.02 + 0.06 \cdot 0.05 + 0.02 \cdot 0.96 \end{pmatrix} = \begin{pmatrix} 0.8490 \\ 0.1104 \\ 0.0406 \end{pmatrix}.
\end{aligned}$$

If we continued this procedure for a very long time, the results would converge to an equilibrium.

Can we find the equilibrium more efficiently? The equations for equilibrium encode the usual idea; things remain the same. Letting p_i^* be the equilibrium probability that the molecule lies in cell i,

$$\begin{aligned}
p_1^* &= 0.92p_1^* + 0.04p_2^* + 0.01p_3^* \\
p_2^* &= 0.06p_1^* + 0.91p_2^* + 0.03p_3^* \\
p_3^* &= 0.02p_1^* + 0.05p_2^* + 0.96p_3^*.
\end{aligned}$$

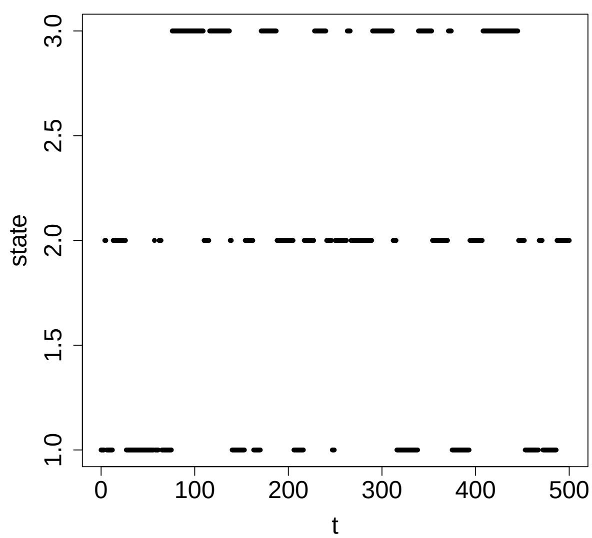
As before, we solve these step by step, ending by using the fact that $p_1^* + p_2^* + p_3^* = 1$. We solve the first equation for p_1^* in terms of p_2^* and p_3^*, finding

$$\begin{aligned}
p_1^* &= 0.92p_1^* + 0.04p_2^* + 0.01p_3^* \\
0.08p_1^* &= 0.04p_2^* + 0.01p_3^* \\
p_1^* &= 0.5p_2^* + 0.125p_3^*.
\end{aligned}$$

Plugging into the second equation, we can find p_2^* in terms of p_3^* as

$$p_2^* = 0.06(0.5p_2^* + 0.125p_3^*) + 0.91p_2^* + 0.03p_3^*$$

Figure 4.3.1: The position of a molecule over time



$$\begin{aligned} &= 0.03p_2^* + 0.0075p_3^* + 0.91p_2^* + 0.03p_3^* \\ &= 0.94p_2^* + 0.0375p_3^* \\ 0.06p_2^* &= 0.0375p_3^* \\ p_2^* &= 0.625p_3^*. \end{aligned}$$

Plugging into the previous equation, we find

$$p_1^* = 0.5 \cdot 0.625p_3^* + 0.125p_3^* = .4375p_3^*.$$

Now, we use the fact that the probabilities add to 1,

$$1 = p_1^* + p_2^* + p_3^* = 0.4375p_3^* + 0.625p_3^* + p_3^* = 2.0625p_3^*.$$

Dividing by 2.0625, we find $p_3^* = 0.485$. Working backwards, $p_2^* = 0.303$ and $p_1^* = 0.212$. Although there is a general drift of molecules toward the third cell, only about half of them will be there after a long time. The position of an individual molecule over time is plotted in figure 4.3.1. Even though the molecule spends a bit more time in cell 3, it continues to jump among the cells.

Summary

We have seen how to write the conditional probabilities describing a Markov chain in matrix form as an updating system. The probabilistic equilibria of these systems can be found by solving a pair of **simultaneous equations**. The method can be extended to Markov chains describing systems which can take on more than two states.

4.4 Exercises

• EXERCISE **4.1**
Using the updating system in equation 4.1.1, find the probability that a molecule that starts in the first cell at time 0 is in the first cell at time 3.

• EXERCISE **4.2**
A very clean bird fanatically preens itself when it gets even one louse, and therefore never has as many as two. Suppose the probability of it getting rid of a louse in a day is 0.2, but the probability of getting a louse when it has none (and lessens its vigilance) is 0.4 in a day.

a. Write the matrix describing this system.
b. If the bird starts out with no lice, what is the probability it has a louse on day 1, day 2 and day 3?
c. What is the equilibrium probability that the bird has a louse?

• EXERCISE **4.3**
Consider Markov chains describing the occupancy of two islands. On the first, the population goes extinct with probability 0.01 when occupied, and is founded again with probability 0.01 when extinct. On the second, the population goes extinct with probability 0.3 when occupied and is founded again with probability 0.3 when extinct.

a. Write the matrices describing these two islands.
b. Find the equilibrium fraction of time they are occupied.
c. How would observations of these two islands to differ?

• EXERCISE **4.4**
Using the probabilities in equation 4.3.1, find the following.

a. If a molecule is in cell 2 at time 0, find the probability vector at times 1 and 2.
b. If a molecule is in cell 3 at time 0, find the probability vector at times 1 and 2.

• EXERCISE **4.5**
A slightly less clean bird than in exercise 4.2 only cleans itself fanatically when it has two lice. In particular, the probability that it gets a new louse when it has 0 or 1 is 0.4. It never gets 2 lice in one day or loses a louse when it has 1. When it has 2, it removes one with probability 0.2 and both with probability 0.3.

a. Draw a diagram illustrating what this bird does.
b. Write the matrix describing this process.
c. Find the equilibrium vector.
d. Find the average number of lice on this bird.

• EXERCISE **4.6**
Assume that $\boldsymbol{A}$ is a probability matrix and $\vec{\boldsymbol{v}}$ is a probability vector. Prove that the product $\boldsymbol{A}\vec{\boldsymbol{v}}$ is a probability vector.

• EXERCISE **4.7**
Assume that $\boldsymbol{A}$ is a probability matrix with elements a_{ij}. We will find a general expression for the associated equilibrium vector.

a. Using the fact that $\boldsymbol{A}$ is a probability matrix, write a_{11} in terms of a_{21} and a_{22} in terms of a_{12}.
b. Write the equations for the equilibrium probabilities p_1^* and p_2^*.
c. Solve these equations and try to write your solution in as simple a form as possible.
d. Interpret your answer. The idea is that the denominator represents the total switching rate and the numerator the rate of switching into a particular state.

Answers

1.1.

- **a.** Starting point is (-1,2). Horizontal component is -2, vertical component is -1.
- **b.** Starting point is (1,-2). Horizontal component is -1, vertical component is 4.

1.5.

- **a.** Vector starts at $(10^3, 10^3)$ and has horizontal component -10^3 and vertical component 800. I divided the length by 5 to get it to look nice.
- **b.** Vector starts at $(5{\times}10^2, 10^2)$ and has horizontal component 200 and vertical component 94. This one looks nice without dividing.

1.6.

- **a.** 50 degrees = 0.87266 radians.
- **c.** 1 radian = 57.296 degrees.

1.8.

- **a.** Horizontal component is 2.174 and vertical component is 5.592.
- **b.** Horizontal component is -2.942 and vertical component is -5.229.

1.9.

- **a.** Magnitude $\sqrt{(-2)^2 + (-1)^2} = 2.236$, direction $= \pi + \tan^{-1}(0.5) = 3.605$.
- **b.** Magnitude $\sqrt{(-1)^2 + 4^2} = 4.123$, direction $= \pi + \tan^{-1}(-4.0) = 1.816$.

1.10.

- **a.** The fish hits when $-4.9t^2 + 8.0t = 0$ or $t = 1.633$.
- **c.** The velocity vector at $t = 0$ is $(10.0, 8.0)$. The speed is the magnitude of this vector, or 12.81 and the direction is 0.675 radians (or 38.7 degrees).

1.12.
2.1.

- **a.** $b_{t+1} = 0.75 \cdot j_t = 1.5{\times}10^5$. $j_{t+1} = 2.0 \cdot b_t = 8.0{\times}10^5$. This population will probably grow, because each adult produces 1.5 offspring that survive to adulthood.

2.3.

a.

Step	Volume	Chemical	Concentration
Air in lung before breath	2.0 liters	4.0×10^{-5} moles	$2.0\times10^{-5}\frac{\text{moles}}{\text{liter}}$
Ambient air before breath	10.0 liters	5.0×10^{-4} moles	$5.0\times10^{-5}\frac{\text{moles}}{\text{liter}}$
Air exhaled	1.0 liters	2.0×10^{-5} moles	$2.0\times10^{-5}\frac{\text{moles}}{\text{liter}}$
Air inhaled	1.0 liters	5.0×10^{-5} moles	$5.0\times10^{-5}\frac{\text{moles}}{\text{liter}}$
Air in lung after breathing	2.0 liters	7.0×10^{-5} moles	$3.5\times10^{-5}\frac{\text{moles}}{\text{liter}}$
Ambient air after breathing	10.0 liters	4.7×10^{-4} moles	$4.7\times10^{-5}\frac{\text{moles}}{\text{liter}}$

2.4.

a. $\begin{pmatrix} 7 \\ 6 \end{pmatrix}$.

b. $\begin{pmatrix} 2 \\ -4 \end{pmatrix}$.

2.5.

a.

$$\begin{aligned} j_{t+1} &= a_t \\ a_{t+1} &= j_t + a_t. \end{aligned}$$

b. $\begin{pmatrix} 0 & 1 \\ 1 & 1 \end{pmatrix}$.

c. Starts at $\begin{pmatrix} 0 \\ 1 \end{pmatrix}$, then goes $\begin{pmatrix} 1 \\ 1 \end{pmatrix}$, $\begin{pmatrix} 1 \\ 2 \end{pmatrix}$, $\begin{pmatrix} 2 \\ 3 \end{pmatrix}$, $\begin{pmatrix} 3 \\ 5 \end{pmatrix}$, $\begin{pmatrix} 5 \\ 8 \end{pmatrix}$.

d. The number of adult is the sum of the number the previous month with the number a month before that.

3.1.

a. $\begin{pmatrix} 0 & 2.0 \\ 0.6 & 0 \end{pmatrix}$.

b. $\begin{pmatrix} j_1 \\ b_1 \end{pmatrix} = \begin{pmatrix} 1.0\times10^{8} \\ 6.0\times10^{5} \end{pmatrix}$.

c. $\begin{pmatrix} j_2 \\ b_2 \end{pmatrix} = \begin{pmatrix} 1.2\times10^{6} \\ 6.0\times10^{7} \end{pmatrix}$.

d. $\begin{pmatrix} 1.2 & 0 \\ 0 & 1.2 \end{pmatrix}$.

e. $\begin{pmatrix} j_2 \\ b_2 \end{pmatrix} = \begin{pmatrix} 1.2\times10^6 \\ 6.0\times10^7 \end{pmatrix}$.

3.5.

a. $\begin{pmatrix} 0 & 0.4 \\ 0.8 & 0.9 \end{pmatrix}$. Population is $j_3 = 740$, $a_3 = 2209$.

b. $\begin{pmatrix} 0 & 0.4 \\ 0.8 & 0.9 \end{pmatrix}$. Population is $j_3 = 452$, $a_3 = 1305$.

3.6.

a. The Leslie matrix is $\begin{pmatrix} 0 & 1 \\ 1 & 1 \end{pmatrix}$.

b. $\begin{pmatrix} 0 \\ 1 \end{pmatrix}, \begin{pmatrix} 1 \\ 1 \end{pmatrix}, \begin{pmatrix} 1 \\ 2 \end{pmatrix}, \begin{pmatrix} 2 \\ 3 \end{pmatrix}, \begin{pmatrix} 3 \\ 5 \end{pmatrix}, \begin{pmatrix} 5 \\ 8 \end{pmatrix}$.

c. The fraction of juveniles goes 0.0, 0.5, 0.333, 0.667, 0.6, 0.625.

d. The growth rates for juveniles are 1.0, 2.0, 1.5, 1.667. For adults, they are 2.0, 1.5, 1.667, 1.6.

e. The eigenvalue is around 1.62.

3.8.

4.2.

a. $\begin{pmatrix} 0.6 & 0.2 \\ 0.4 & 0.8 \end{pmatrix}$.

b. 0.4 on day 1, 0.56 on day 2 and 0.624 on day 3.

c. 0.666.

4.4.

a.

$$\begin{aligned}
\begin{pmatrix} p_1(1) \\ p_2(1) \\ p_3(1) \end{pmatrix} &= \begin{pmatrix} 0.92 & 0.04 & 0.01 \\ 0.06 & 0.91 & 0.03 \\ 0.02 & 0.05 & 0.96 \end{pmatrix} \begin{pmatrix} 0 \\ 1 \\ 0 \end{pmatrix} \\
&= \begin{pmatrix} 0 \cdot 0.92 + 1 \cdot 0.04 + 0 \cdot 0.01 \\ 0 \cdot 0.06 + 1 \cdot 0.91 + 0 \cdot 0.03 \\ 0 \cdot 0.02 + 1 \cdot 0.05 + 0 \cdot 0.96 \end{pmatrix} \\
&= \begin{pmatrix} 0.04 \\ 0.91 \\ 0.05 \end{pmatrix}
\end{aligned}$$

$$\begin{aligned}
\begin{pmatrix} p_1(2) \\ p_2(2) \\ p_3(2) \end{pmatrix} &= \begin{pmatrix} 0.92 & 0.04 & 0.01 \\ 0.06 & 0.91 & 0.03 \\ 0.02 & 0.05 & 0.96 \end{pmatrix} \begin{pmatrix} 0.04 \\ 0.91 \\ 0.05 \end{pmatrix} \\
&= \begin{pmatrix} 0.04 \cdot 0.92 + 0.91 \cdot 0.04 + 0.05 \cdot 0.01 \\ 0.04 \cdot 0.06 + 0.91 \cdot 0.91 + 0.05 \cdot 0.03 \\ 0.04 \cdot 0.02 + 0.91 \cdot 0.05 + 0.05 \cdot 0.96 \end{pmatrix} \\
&= \begin{pmatrix} 0.0737 \\ 0.8320 \\ 0.0943 \end{pmatrix}
\end{aligned}$$

4.5.

b. $\begin{pmatrix} 0.6 & 0.0 & 0.3 \\ 0.4 & 0.6 & 0.2 \\ 0.0 & 0.4 & 0.5 \end{pmatrix}.$

c. $\begin{pmatrix} p_1^* \\ p_2^* \\ p_3^* \end{pmatrix} = \begin{pmatrix} 0.25 \\ 0.417 \\ 0.333 \end{pmatrix}.$

d. $\bar{L} = 0 \cdot 0.25 + 1 \cdot 0.417 + 2 \cdot 0.333 = 1.083.$

4.6. Let the vector be $\begin{pmatrix} v_1 \\ v_2 \end{pmatrix}$ where $v_1 + v_2 = 1$. Then

$$\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} v_1 \\ v_2 \end{pmatrix} = \begin{pmatrix} a_{11}v_1 + a_{21}v_2 \\ a_{12}v_1 + a_{22}v_2 \end{pmatrix}.$$

To prove this is a probability vector, we must show that the elements add to 1. We find

$$a_{11}v_1 + a_{21}v_2 + a_{12}v_1 + a_{22}v_2 = (a_{11} + a_{12})v_1 + (a_{22} + a_{21})v_2 = v_1 + v_2 = 1$$

where we used the fact that $\boldsymbol{A}$ is a probability matrix.

4.7.

a. We can rewrite the matrix as

$$\begin{pmatrix} 1 - a_{12} & a_{12} \\ a_{21} & 1 - a_{21} \end{pmatrix}.$$

b.

$$\begin{aligned}
(1 - a_{12})p_1^* + a_{21}p_2^* &= p_1^* \\
a_{21}p_1^* + (1 - a_{21})p_2^* &= p_2^*.
\end{aligned}$$

c. The first equation has solution

$$p_2^* = \frac{a_{21}}{a_{12}} p_1^*.$$

Plugging into $p_1^* + p_2^* = 1$, we find

$$\begin{aligned} 1 &= p_1^* + \frac{a_{21}}{a_{12}} p_1^* = (1 + \frac{a_{21}}{a_{12}}) p_1^* \\ p_1^* &= \frac{1}{1 + \frac{a_{21}}{a_{12}}} = \frac{a_{12}}{a_{12} + a_{21}} \\ p_2^* &= \frac{a_{21}}{a_{12} + a_{21}}. \end{aligned}$$

a_{12} gives the rate at which things switch from state 2 into state 1. The fraction in state 1 is the ratio of this rate to the total switching rate. If $a_{12} < a_{21}$, $p_1^* < 1/2$ and $p_2^* > 1/2$.