Reference Readings ${ }^{8}$ Homework Exercises for

# Matrix Models 

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## 1 Vectors: Order Matters!

In the last section of this course we used discrete difference equations to generate sequences of numbers $x_{0}, x_{1}, x_{2}$, $x_{3}, \ldots$ We also examined systems of discrete difference equations, $x_{t+1}=f\left(x_{t}, y_{t}\right)$ and $y_{t+1}=g\left(x_{t}, y_{t}\right)$, where the generation of the sequence of $x$ values depends on previous values in the $y$ sequence and vice versa. In this section, we examine an extension of this idea of modeling two (or more) state variables ( $x$ and $y$ ) discretely through time using the mathematics of matrix algebra.

A central theme in biology is that biological objects of interest have structure that may affect the way those objects should be analyzed. Examples include the various components of cells, the cellular composition of tissue, the tissue composition of individual organisms, the composition of different individuals within a population, the species that make up a community/ecosystem, and the types of habitat across a landscape. Each of these biological entities has a substructure. As an example, think of the different substructures within a population of mammals. The population could be divided into males and females, but it could also be divided into age classes. In many mammals, an individual's age can be grouped into one of three categories: young ( $0-1$ years old), juvenile ( $1-2$ years old), and adult ( $>2$ years old). If a disease is spreading through a population, the individuals in the population could be sorted into groups based on their infection status (susceptible, infected, immune/recovered, removed/dead).

As a motivating example we will consider the patterns of species across a landscape. Think of taking aerial photographs of a plot of land once each decade. You will likely observe changes in the landscape over time. An example of this is shown in the aerial photos of Amazon Park in Eugene, Oregon in Figure 1. For each decade, you might be able to classify the proportion of area used for a certain purpose (natural state, agricultural, residential, commercial, industrial) or used by a certain class of species (decidious hardwoods, herbaceous, grasslands, marshlands, etc.) A description of this landscape at a particular time could look like a list of numbers giving the fraction of the landscape of each species. For example, if the landscape was $20 \%$ grass, $50 \%$ shrubs, and $30 \%$ tree, we could represent is as the vector

$$
\mathbf{v}=\left[\begin{array}{l}
0.2 \\
0.5 \\
0.3
\end{array}\right]
$$

where the first component represents the proportion of landscape that is grass, the second component the proportion of landscape that is shrub, and the third component the proportion that is trees. In these reference readings we use a boldface lowercase letter to denote a vector, i.e., v. However, when we are writing out vector notation by hand, we use a half arrow (sometimes also called a harpoon) above the lowercase letter, i.e. $\vec{v}$. The order of the elements within the vector matters because the way we describe the structure of the landscape depends on the order in which we list the number in the vector. Thus, the vectors

$$
\mathbf{v}=\left[\begin{array}{c}
0.2 \\
0.5 \\
0.3
\end{array}\right] \quad \text { and } \quad \mathbf{w}=\left[\begin{array}{c}
0.5 \\
0.2 \\
0.3
\end{array}\right]
$$

are distinctly different vectors. Let $g$ be the proportion of the landscape which is grass, $s$ the proportion which is


Figure 1: Aerial photos of Amazon Park in Eugene, Oregon (1936-2009). The photes taken from 1936 to 1995 were posted on [2], and the 2009 photo was created using Google Maps [3].
trees, and $t$ the proportion which is trees, then we could describe our vector as

$$
\left[\begin{array}{l}
g \\
s \\
t
\end{array}\right]
$$

For the vector $\mathbf{v}, g=0.2, s=0.5$, and $t=0.3$, but for $\mathbf{w}, g=0.5, s=0.2$, and $t=0.3$. These two vectors would represent different landscapes: the order of the number matters.

As time goes on (e.g. we have pictures/data of the landscape for every decade), the vector describing the fraction covered by each type of organism will change. If we can determine the rules by which this vector changes, we will have the basis for a model of the landscape's dynamics (called succession in ecology). From this model, we might then be able to determine, from only a few decades of data, what the landscape might look like many decades from now. There are two different notations that we can use to denote the vector changing through time, $\mathbf{v}_{t}$ and $\mathbf{v}(t)$. The first notation is similar to what we have used for discrete difference equations, and makes sense to use here since we are assuming discrete time steps (in this case one time step $=$ one decade). However, it is common to denote the elements of a vector with subscripts, i.e.,

$$
\mathbf{v}=\left[\begin{array}{l}
v_{1} \\
v_{2} \\
v_{3}
\end{array}\right]
$$

and so to avoid confusion we can use $\mathbf{v}(t)$, in which case we have

$$
\mathbf{v}(t)=\left[\begin{array}{l}
v_{1}(t) \\
v_{2}(t) \\
v_{3}(t)
\end{array}\right]
$$

GIS The field of study concerning landscape, how they can be described, and how they change is a part of the field of geography. The main tool used to analyze landscape changes is called Geographical Information Systems (GIS), which is software that allows you to view, build, manipulate, and analyze spatial maps. If you find this idea intriguing or are interesting in dealing with spatial data, I encourage you to take the GIS course here at Rhodes (INTD 225).

## Example 1

Consider the images of Amazon Park in Eugene, Oregon in Figure 1. For each year (1936, 1951, 1960, 1963, 1995, and 2009),
(a) Divide the image into 10 equal area sectors by sketching a grid with two columns and five rows on the image.
(b) Using the grid, determine the proportion of landscape in each year within the following four categories: Farmland, Forest, Industrial, Residential. Use a vector to indicate the landscape structure in the image.

The solutions to this example will be worked in class.

## Exercise 1 - A Finer Grid

In the previous example, the way we constructed our grid determined the values of each element within our vector. Repeat part (b) using a finer grid with 20 equal area sectors by sketching a grid with:
(a) four columns and five rows,
(b) two columns and ten rows.

How does the configuration of the grid change the resulting vectors? How does using a grid with a finer mesh (i.e. the area of each sector is smaller) change the resulting vectors?

## 2 Vector Algebra

If you have never worked with vectors before, this section will introduce you to the basic arithmetic of vectors and what those manipulations meeting biologically. We will consider the algebraic manipulations of adding and multiplying.

## Vector Addition \& Scalar Multiplication

We start with some notation and by making the distinction between a vector and a scalar. A vector, $\mathbf{v}$, is a one-dimensional array that contains a finite number of elements (usually real numbers). A scalar, $c$, is a real number. Note, the difference in notation between a vector and a scalar. Let

$$
\mathbf{u}=\left[\begin{array}{c}
u_{1} \\
u_{2} \\
\vdots \\
u_{n}
\end{array}\right] \quad \text { and } \quad \mathbf{v}=\left[\begin{array}{c}
v_{1} \\
v_{2} \\
\vdots \\
v_{n}
\end{array}\right]
$$

each be vectors of length $n$, i.e., they each have $n$ elements. Then we define vector addition as

$$
\mathbf{u}+\mathbf{v}=\left[\begin{array}{c}
u_{1} \\
u_{2} \\
\vdots \\
u_{n}
\end{array}\right]+\left[\begin{array}{c}
v_{1} \\
v_{2} \\
\vdots \\
v_{n}
\end{array}\right]=\left[\begin{array}{c}
u_{1}+v_{1} \\
u_{2}+v_{2} \\
\vdots \\
u_{n}+v_{n}
\end{array}\right]
$$

Let $c$ be a scalar, then we define scalar multiplication as

$$
c \mathbf{u}=c\left[\begin{array}{c}
u_{1} \\
u_{2} \\
\vdots \\
u_{n}
\end{array}\right]=\left[\begin{array}{c}
c u_{1} \\
c u_{2} \\
\vdots \\
c u_{n}
\end{array}\right] .
$$

To determine what these two operations mean biological, consider an example of describing the composition of a coastal wetlands. Coastal wetlands are areas near the coast where the soil is submerged or soaked with moisture either permanently or seasonally and include salt marshes, bottomland hardwood swamps, fresh marshes, mangrove swamps, and pocosins. Coastal wetlands are found between areas that are always wet (i.e., oceans, seas, bays, and estuaries) and areas that are always dry (i.e., grasslands and forests). Suppose you are considering 160 hectares of coastal wetlands which are protected as a national park. You are able to classify the wetlands into three different land classifications: submerged, seasonally submerged, and dry. If we let

- $a=$ proportion of wetlands that are always submerged,
- $s=$ proportion of wetlands that are seasonally submerged,
- $d=$ proportion of wetlands that are always dry,
then the vector $\mathbf{v}$ representing the coastal welands landscape composition would be

$$
\mathbf{v}=\left[\begin{array}{l}
a \\
s \\
d
\end{array}\right] .
$$

If at some particular time $t$ you determined $65 \%$ of the wetlands are always submerged, $30 \%$ a seasonally submerged, and $5 \%$ are always dry, then

$$
\mathbf{v}(t)=\left[\begin{array}{l}
0.65 \\
0.30 \\
0.05
\end{array}\right]
$$

To determine the total number of hectares that are always submerged we would multiple the total landscape size (160 ha) by the proportion in the always submerged category ( 0.65 ). If we did this for each landscape category we could determine the landscape composition in terms of area (ha). Mathematically, this is equivalent to multiplying each element in the vector $\mathbf{v}(t)$ by 160 ha, i.e.,

$$
160 \mathbf{v}(t)=160\left[\begin{array}{l}
0.65 \\
0.30 \\
0.05
\end{array}\right]=\left[\begin{array}{r}
104 \\
48 \\
8
\end{array}\right] .
$$

Now, suppose the non-profit organization the Nature Conservancy owns and protects 72 hectares of coastal wetlands right next to the national park. The Nature Conservancy's wetlands are $20 \%$ always submerged and $80 \%$ seasonally submerged. What is the landscape composition for the combined area (national park and Nature Conservancy) of protected coastal wetlands? To determine this we need to of the area within each landscape category. Mathematically,
this is equivalent to adding the two vectors that represent the landscape composition in terms of area (ha), i.e.,

$$
\mathbf{w}(t)=160 \mathbf{v}(t)+80 \mathbf{u}(t)=160\left[\begin{array}{c}
0.65 \\
0.30 \\
0.05
\end{array}\right]+80\left[\begin{array}{c}
0.20 \\
0.80 \\
0
\end{array}\right]=\left[\begin{array}{r}
104 \\
48 \\
8
\end{array}\right]+\left[\begin{array}{r}
16 \\
64 \\
0
\end{array}\right]=\left[\begin{array}{r}
120 \\
112 \\
8
\end{array}\right]
$$

where $\mathbf{u}(t)$ represents the landscape composition of the Nature Conservancy's 80 ha of coastal wetlands. If we want to convert the combined landscape composition vector $\mathbf{w}(t)$ to represent proportions, we must scale the elements in the vector by the total landscape area $160+80=240$ ha. We can think of this as dividing by a the scalar 240 or multiplying the scalar $1 / 240$,

$$
\frac{1}{240} \mathbf{w}(t)=\left[\begin{array}{c}
1 / 2 \\
7 / 15 \\
1 / 30
\end{array}\right]=\left[\begin{array}{c}
15 / 30 \\
14 / 30 \\
1 / 30
\end{array}\right] .
$$

Notice, that the elements of $1 / 240 \mathbf{w}(t)$ sum to 1 as they should since the elements of the vector represent the different proportions of the combined protected coastal wetlands.

## Exercise 2 - Dorylus laevigatus Ant Colony

The term army ants is applied to over 200 different species of ants, and refers to these species agressive and predatory foraging behavior in which millions of ants forming an "ant trail" up to 20 m wide and 100 m long forage simultaneously in one location. Within each army ant colony there are there types of classes of ants: (1) queens, (2) males, and (3) workers. Workers are typically sterile females. Queens are also female, and in army ant colonies there is only ever one queen though other species of ants can have multiple queens in one colony. Male army ants have wings and typically fly to other colonies for mating after which they lose their wings.

The army ant species Dorylus laevigatus has two types of sterile female workers: large workers and small workers. The large workers ( $\sim 8.03 \mathrm{~mm}$ long, dry weight of 3.09 mg ) are soldiers and perform colony defense and incapacitation of large prey. The small workers ( $\sim 4.45 \mathrm{~mm}$ long, dry weight of 0.57 mg ). The large queens (up to 3 cm long) are mostly immobile. D. laevigatus males leave their natal colony at an early and seek out a different colony once they have reached sexual maturity.

The $D$. laevigatus colonies reproduce by a process known as colony fission. When the queen reproduces, she lays eggs which will become queens, males, and workers. When a newly grown virgin queen reaches sexual maturity and a male of sexual maturity enters the colony, the males wings are removed


Worker (female)


Figure 3: Three classes of ants. and he is carried to the virgin queen. They mate (possibly the queen mates with multiple males), and then the now fertile queen is carried by many colony workers to a new location to establish a new colony.

Suppose that one colony of $D$. laevigatus contains one queen, 300,000 small workers, and 25,000 large workers.
(a) Create a vector that represents the population structure of the workers (small and large).
(b) Suppose that during a colonial fission, a newly fertile queen takes $20 \%$ of the existing colony with her. Assuming she take $20 \%$ of the small workers, and $20 \%$ of the soldiers, how many workers of each type are left in the original colony?
(c) Suppose that the queen of the original colony has a brood of 150,000 larva that have matured into their adult forms. The structure of brood is $30 \%$ males, $40 \%$ small workers, and $30 \%$ large workers.
(i) Create a vector that represents the number of males and females in the brood.
(ii) Find the new population structure of workers in the colony (the final vector should represent proportions).

## Dynamics: Vectors Changing over Time

Consider again our coastal wetlands example. Suppose that we are looking at a total area of 100 hectares, which is initially always submerged. Every 10 years, $5 \%$ of submerged wetlands become seasonally submerged, and $12 \%$ of the seasonally submerged wetlands become dry. All hectares that are dry remain dry. This is an example of aquatic succession (see Figure 4). Let us calculate how much of the land is always submerged, seasonally submerged, and always dry after 10 years and after 20 years.

For notation, we will let the vector

$$
\mathbf{v}(t)=\left[\begin{array}{l}
a(t)  \tag{1}\\
s(t) \\
d(t)
\end{array}\right]
$$

represent the composition of the 100 hectares of wetlands where $a(t)$ is the proportion of the wetlands that is always submerged in decade $t, s(t)$ is the proportion of wetlands that is seasonally submerged in decade $t$, and $d(t)$ is the proportion of wetlands that is always dry in decade $t$.

Given the description of aquatic succession of the coastal wetlands, we could construct a discrete difference equation model with multiple states. In the $(t+1)^{t h}$ decade, the proportion of always submerged wetlands, $a(t+1)$, is the amount from the $t^{t h}$ decade, $a(t)$, minus the $5 \%$ of always submerge wetlands that become seasonally submerged, that is,

$$
a(t+1)=a(t)-0.05 a(t)=0.95 a(t)
$$

Similarly, in the $(t+1)^{t h}$ decade, the proportion of seasonally submerged wetlands, $s(t+1)$, is the amount from the $t^{t h}$ decade, $s(t)$, plus the $5 \%$ of always submerged wetlands that becomes seasonally submerged, minus the $12 \%$ of seasonally submerged wetlands that become dry land, that is,

$$
\begin{aligned}
s(t+1) & =s(t)+0.05 a(t)-0.12 s(t) \\
& =0.05 a(t)+0.88 s(t)
\end{aligned}
$$

Lastly, in the $(t+1)^{t h}$ decade, the proportion of dry land, $d(t+1)$, is the amount from the $t^{t h}$ decade, $d(t)$, plus the $12 \%$ of seasonally submerged wetlands that become dry land, that is,

$$
d(t+1)=d(t)+0.12 s(t)
$$

This system of discrete difference equations describes the change in the coastal wetlands composition from


Figure 4: Depiction of aquatic succession. In the top image shows a body of water (lake or pond). The ground beneath the lake is always submerged with only the edges of the lake being seasonally submerged. As time progresses and more sediment collects in the lake, the lake becomes shallower and the outer edges which used to be seasonally submerged are not always dry land. Eventually, the entire lake is filled in with sediment, and where the lake used to be is now dry land.
one decade to the next. We can rewrite this system of discrete difference equations in such a way that we can take advantage of the vector structure in Equation (1):

$$
\begin{align*}
a(t+1) & =0.95 a(t)+0.00 s(t)+0.00 d(t)  \tag{2}\\
s(t+1) & =0.05 a(t)+0.88 s(t)+0.00 d(t)  \tag{3}\\
d(t+1) & =0.00 a(t)+0.12 s(t)+1.00 d(t) \tag{4}
\end{align*}
$$

Using the coefficients of $a(t), s(t)$, and $d(t)$ in Equations (2)-(4), we can form a two-dimensional array of real numbers with three rows and three columns. We will call this a $3 \times 3$ matrix, and we will represent this matrix as

$$
\left[\begin{array}{ccc}
0.95 & 0 & 0 \\
0.05 & 0.88 & 0 \\
0 & 0.12 & 1
\end{array}\right]
$$

where each row corresponds to the coefficients in one each equation, and each column corresponds to the coefficients of one land classification. For example, the second row gives the coefficients in Equation (3), and the second column gives the coefficients of $s(t)$ for each of the three Equations (2)-(4). Notice, that the entries along the diagonal (shown in red) are the proportion of land in each land classification that remain in the same land classification during a single decade. The entries in the matrix which are not along the diagonal tell us how land changes from one class to another:

\[

\]

Equations (2)-(4) are written as a system discrete difference equations, but we can use the $3 \times 3$ matrix of coefficients and the notation of Equation (1) to rewrite the system as a matrix model:

$$
\left[\begin{array}{l}
a(t+1)  \tag{5}\\
s(t+1) \\
d(t+1)
\end{array}\right]=\left[\begin{array}{ccc}
0.95 & 0 & 0 \\
0.05 & 0.88 & 0 \\
0 & 0.12 & 1
\end{array}\right]\left[\begin{array}{c}
a(t) \\
s(t) \\
d(t)
\end{array}\right] \quad \text { or } \quad \mathbf{v}(t+1)=\left[\begin{array}{ccc}
0.95 & 0 & 0 \\
0.05 & 0.88 & 0 \\
0 & 0.12 & 1
\end{array}\right] \mathbf{v}(t)
$$

The operation on the right-hand size of the equal sign in Equation (5) is matrix multiplication. The $3 \times 3$ matrix in Equation (5) is sometimes referred to as a transfer matrix since it describes how the landscape is transferred from one state to another. Transfer matrices can be easily represented using a flow diagram, such as the one in Figure 5. Notice, that each column in the transfer matrix sums to 1 .


Figure 5: Flow diagram of the transfer matrix in Equation (5).

More generally, if we have $n$ classes describing a landscape (or whatever other structure we might be modeling), then
we can write the vector describing the composition of the landscape at time step $t$ as

$$
\mathbf{v}(t)=\left[\begin{array}{c}
v_{1}(t) \\
v_{2}(t) \\
\vdots \\
v_{n}(t)
\end{array}\right]
$$

where the $k^{t h}$ entry $v_{k}(t)$ is the proportion of the landscape that is of class $k$ at time step $t$. Since this is a proportion, we must have

$$
0 \leq v_{k}(t) \leq 1 \text { for all } k
$$

Additionally, since each class is a proportion of the total landscape, the sum of the proportions over all classes must equal 1 , that is,

$$
\sum_{k=1}^{n} v_{k}(t)=v_{1}(t)+v_{2}(t)+\cdots+v_{n}(t)=1
$$

The matrix describing how landscape composition changes between time steps will have $n$ rows and $n$ columns (an $n \times n$ matrix) ,

$$
\mathbf{A}=\left[\begin{array}{cccc}
a_{11} & a_{12} & \cdots & a_{1 n} \\
a_{21} & a_{22} & \cdots & a_{2 n} \\
\vdots & \vdots & \ddots & \vdots \\
a_{n 1} & a_{n 2} & \cdots & a_{n n}
\end{array}\right]
$$

where $a_{i j}$ is the proportion of class $j$ that becomes or moves into class $i$. Note, that each column of the matrix $\mathbf{A}$ must sum to 1 , that is

$$
\sum_{i=1}^{n} a_{i j}=1 \text { for each } j
$$

That matrix model describing how the landscape composition changes from one time step to the next is

$$
\mathbf{v}(t+1)=\mathbf{A} \mathbf{v}(t)
$$

## Example 2

Suppose that we want to model how the composition of a coastal wetland changes over time, but the dynamics are a bit more complex than the example we previously worked through. The composition of the coastal wetlands still consists of always submerge, seasonally submerged, and dry land, however the each decade the composition of the wetlands changes according to the flow diagram below.


Construct a matrix model that describes how the composition of these coastal wetlands changes every 10 years.
The solutions to this example will be worked in class.

Example 3


Figure 6: Vegetative zones of a freshwater shoreline.

The vegetative zones along the shoreline of a freshwater lake, natural pond, storm water pond, or estuary are the littoral zone (which contains plants that are completely submerged), the emergent zone (which contains plants that are partially submerged), the riparian zone (which contains plants which are not typically submerged but may become submerged when water levels are high), and the upland zone (which contains plants that are never submerged). See Figure 6 for a graphical depiction.

Aquatic succession occurs along the freshwater shoreline according to the flow diagram below where $L$ is the littoral zone, $E$ is the emergent zone, $R$ is the riparian zone, and $U$ is the upland zone. Construct a matrix model that describes how the composition of these freshwater shoreline vegetation zones changes every 10 years.


The solutions to this example will be worked in class.

## Example 4

During the fall semester last year, a particular dormitory had a common cold epidemic. During the epidemic, individuals could be classified as either being susceptible to acquiring the common cold, or already infected with the common cold. Each day, $4 \%$ of the dorm residents became infected with the cold, while $20 \%$ recovered from the cold and became susceptible again. The dynamics of the epidemic are shown in the flow diagram below.

(a) Construct a matrix model that describes how the population structure of the dormitory changes each day during the epidemic.
(b) Now suppose that recovery from the cold provides immunity from the virus for one year. How can the model be modified to account for this? Construct a new flow diagram and new matrix model to reflect the changes you have made to the model.

The solutions to this example will be worked in class.

## Exercise 3 - Herpes Simplex Virus

Herpes simplex virus (HSV) is a virus that causes the disease herpes. One of the simplest population models for HSV (without including treatment) is to divide the population into three categories: (1) susceptible, (2) infected and shedding virus (people in this class can infect other individuals), and (3) quiescent (people in this class are infected but not shedding virus and thus cannot infect others).
(a) After completing a survey of the population, researchers discovered that $65 \%$ if the population is suceptible, $20 \%$ are currently shedding virus, and the remaining proportion of the population are in the quiescent phase. Construct a vector that represents what proportion of the population is in each category.
(b) Suppose each year that $2 \%$ of the susceptible population becomes infected and moves into the infected and shedding virus category. Additionally, each day, $28.6 \%$ of those infected and shedding the virus more into the quiescent stage, and $2.9 \%$ of those in the quiescent state start to shed the virus again. Note that the units are not the same for each of the given transfer rates.
(i) Draw flow diagram to represent the dynamics of HSV in the population. Be sure to label your diagram carefully.
(ii) Construct a transfer matrix to represent how the population structure of susceptible, shedding, and quiescent individuals changes each day.

## Exercise 4 - Strontium-90 Cycling

Strontium-90 is a radioactive by-product produced by the nuclear fission of uranium and plutonium. The atmospheric nuclear weapons tests of the 1950s and 1960s produces a substantial amount of strontium-90 as radioactive fallout and was dispersed into ecosystems around the world. When an organism ingests strontium-90 from contaminated food or water, most of the compound is excreted, but $20-30 \%$ becomes deposited in the organisms bones and bone marrow. This can lead to bone cancer, and leukemia. However, strontium- 90 is also used a radioactive source for the radiotherapy used to treat some cancers and eye diseases, and as a heat source for thermoelectric devices used in navigational beacons, remote weather stations, and space vehicles.

We can model the "movement" of Strontium-90 through an ecosystem using a matrix model. The ecosystem is divided into grasses $(G)$, soil $(S)$, streams and waterways $(W)$, and dead organic matter $(O)$. In this model, we assume that the amount of strontium- 90 ingested by organisms (other than grasses) is negligible, and that the time period over which we will examine the model is short compared to the half-life of strontium-90 (28.8 years). Within the ecosystem, each month $5 \%$ of the strontium- 90 in the grass leaches into the soil, but $1 \%$ of the strontium-90 in the soil is absorbed into the grass through growth. Each month, $10 \%$ of the strontium- 90 in the grasses moves to dead organic matter as the grasses die, $20 \%$ of the strontium- 90 in organic matter moves to soil as the organic matter decomposes, and $1 \%$ of the strontium-90 in the soil moves to the waterways through runoff.
(a) Create a flow diagram that represents the dynamics of the strontium-90 cycling in the ecosystem.
(b) Construct a transfer matrix which represents the movement of strontium-90 through the ecosystem each month.

## 3 Matrix Algebra

Recall that the matrix model for describing how the structural composition of a landscape or population (with $n$ classes) changes from one time step to the next is

$$
\mathbf{v}(t+1)=\mathbf{A v}(t)
$$

where $\mathbf{v}(t)$ is a vector of length $n$ where element $v_{k}(t)$ is the proportion in class $k$ at time $t$, and $\mathbf{A}$ is a $n \times n$ transfer matrix. If we know $\mathbf{v}(0)$, then

$$
\begin{aligned}
\mathbf{v}(1) & =\mathbf{A v}(0) \\
\mathbf{v}(2) & =\mathbf{A v}(1)=\mathbf{A}(\mathbf{A v}(0))=\mathbf{A}^{2} \mathbf{v}(0) \\
\mathbf{v}(2) & =\mathbf{A v}(2)=\mathbf{A}\left(\mathbf{A}^{2} \mathbf{v}(0)\right)=\mathbf{A}^{3} \mathbf{v}(0) \\
& \vdots \\
\mathbf{v}(t) & =\mathbf{A}^{t} \mathbf{v}(0)
\end{aligned}
$$

Note, we worked a similar derivation for a discrete difference equation model. So, now we have a formula for how to find the population structure at any future time step without iteration through all previous time steps. However, what does $\mathbf{A}^{t}$ mean? That is, what does it mean to multiply a matrix by itself once, twice, or $t$ times? How is this operation defined? We saw how to multiply a matrix by a vector in the previous section. Now, we examine the more general case of multiplying a matrix by a matrix. For completeness, we also examine matrix addition and scalar multiplication.

## Matrix Addition

Let $\mathbf{A}$ and $\mathbf{B}$ be $m \times n$ matrices, then

$$
\mathbf{A}+\mathbf{B}=\left[\begin{array}{ccc}
a_{11} & \cdots & a_{1 n} \\
\vdots & \ddots & \vdots \\
a_{m 1} & \cdots & a_{m n}
\end{array}\right]+\left[\begin{array}{ccc}
b_{11} & \cdots & b_{1 n} \\
\vdots & \ddots & \vdots \\
b_{m 1} & \cdots & b_{m n}
\end{array}\right]=\left[\begin{array}{ccc}
a_{11}+b_{11} & \cdots & a_{1 n}+b_{1 n} \\
\vdots & \ddots & \vdots \\
a_{m 1}+b_{m 1} & \cdots & a_{m n}+b_{m n}
\end{array}\right]
$$

Notice that to find the sum of two matrices they must have the same size (i.e. both matrices must have the same number of rows, and both must have the same number of columns). The sum for two matrices that are not of the same size is not defined. Thus, adding a $3 \times 2$ matrix to a $3 \times 2$ matrix will results in a $3 \times 2$ matrix, but the action of adding a $3 \times 2$ matrix to a $2 \times 3$ matrix is not defined. Notice also that adding matrices is a more general version of adding vectors. A vector with $n$ elements is simply an $n \times 1$ matrix.

## Matrix Scalar Multiplication

Let $\mathbf{A}$ be an $m \times n$ matrix and $c$ be a real number. Then

$$
c \mathbf{A}=c\left[\begin{array}{ccc}
a_{11} & \cdots & a_{1 n} \\
\vdots & \ddots & \vdots \\
a_{m 1} & \cdots & a_{m n}
\end{array}\right]=\left[\begin{array}{ccc}
c a_{11} & \cdots & c a_{1 n} \\
\vdots & \ddots & \vdots \\
c a_{m 1} & \cdots & c a_{m n}
\end{array}\right]
$$

Again, notice that matrix scalar multiplication is a more general version of multiplying a scalar by a vector.
We can use matrix scalar multiplication and matrix addition to define the difference between two matrices (of the same size):

$$
\mathbf{A}-\mathbf{B}=\mathbf{A}+(-1) \mathbf{B}
$$

where the matrix $\mathbf{B}$ is being multiplied by the scalar -1 .

Properties of Matrix Addition Let $\mathbf{A}, \mathbf{B}$, and $\mathbf{C}$ be $m \times n$ matrices, and $a$ and $b$ be real numbers. Additionally, let $\mathbf{0}$ denote an $m \times n$ matrix where all the entries are 0 . Then

1. Commutative Property: $\mathbf{A}+\mathbf{B}=\mathbf{B}+\mathbf{A}$
2. Associative Property: $\mathbf{A}+(\mathbf{B}+\mathbf{C})=(\mathbf{A}+\mathbf{B})+\mathbf{C}$
3. Distributive Property: $a(\mathbf{A}+\mathbf{B})=a \mathbf{A}+a \mathbf{B}$ and $(a+b) \mathbf{A}=a \mathbf{A}+a \mathbf{B}$
4. Identity Property: $\mathbf{A}+\mathbf{0}=\mathbf{A}$ or $\mathbf{A}-\mathbf{A}=\mathbf{0}$

## Matrix Multiplicaiton

Let $\mathbf{A}$ be an $m \times n$ matrix and $\mathbf{B}$ an $n \times p$ matrix, then the product is an $m \times p$ matrix denoted $\mathbf{A B}$. If $\mathbf{C}=\mathbf{A B}$, and $c_{i j}$ denotes the entry in matrix $\mathbf{C}$ in the $i^{\text {th }}$ row and $j^{\text {th }}$ column, then

$$
c_{i j}=\sum_{k=1}^{n} a_{i k} b_{k j}=a_{i 1} b_{1 j}+a_{i 2} b_{2 j}+\cdots+a_{n 1} b_{n j}
$$

for each pair $(i, j)$ with $1 \leq i \leq m$ and $1 \leq j \leq p$. If you are familiar with dot products (or inner products), the value of each $c_{i j}$ is the inner product of the vector formed by the $i^{\text {th }}$ row of $\mathbf{A}$ by the vector formed by the $j^{\text {th }}$ column of $\mathbf{B}$. Figure 7 gives a visual depiction of matrix multiplication.


Notice in order to multiply two matrices together (i.e. in order for the matrix product to be defined), the number of columns of the matrix being multiplied on the left must equal the number of rows of the matrix being multiplied on the right. Additionally, the product of the two matrices will have the same number of rows as the matrix being multiplied on the left and the same number of columns as the matrix being multiplied on the right. Thus,

$$
\overbrace{(m \times \underbrace{n) \cdot(n}_{\text {equal }} \times p)}^{\text {product is an }} m \times p \text { matrix }
$$

Returning to our examples of transfer matrix models, let $\mathbf{A}$ be an $n \times n$ transfer matrix, and $\mathbf{v}(0)$ represent the initial system structure. Recall that $\mathbf{v}(1)=\mathbf{A v}(0)$. Since $\mathbf{A}$ is $n \times n$ and $\mathbf{v}(0)$, the product $\mathbf{A v}(0)$ is an $n \times 1$ matrix, which makes sense because it is equivalent to the matrix $\mathbf{v}(1)$. Recall that $v(2)=\mathbf{A}^{2} \mathbf{v}(0)$. Here, notice that the product $\mathbf{A}^{2}=\mathbf{A A}$ is also $n \times n$. In fact, we could multiply $\mathbf{A}$ by itself as many times as we wanted and the resulting matrix would always by $n \times n$.

Properties of Matrix Multiplication Let $\mathbf{A}, \mathbf{B}$, and $\mathbf{C}$ be matrices, and $a$ and $b$ be real numbers. Additionally, let I denote the identity matrix

$$
\mathbf{I}=\left[\begin{array}{cccc}
1 & 0 & \cdots & 0 \\
0 & 1 & \cdots & 0 \\
\vdots & \vdots & \ddots & \vdots \\
0 & 0 & \cdots & 1
\end{array}\right]
$$

Provided that the following matrix multiplications are defined, then

1. Not Commutative: generally $\mathbf{A B} \neq \mathbf{B A}$
2. Associative Property: $\mathbf{A}(\mathbf{B C})=(\mathbf{A B}) \mathbf{C}$
3. Distributive Property: $\mathbf{A}(\mathbf{B}+\mathbf{C})=\mathbf{A B}+\mathbf{A C}$ and $(\mathbf{B}+\mathbf{C}) \mathbf{A}=\mathbf{B A}+\mathbf{C A}$ and $(a \mathbf{A})(b \mathbf{B})=a b \mathbf{A B}$
4. Identity Property: $\mathbf{A I}=\mathbf{A}$

Exercise 5 - Matrix Multiplication is NOT Commutative
To prove to yourself that the matrix multiplication is not commutative, consider the following two examples.
(a) Let $\mathbf{A}=\left[\begin{array}{ccc}1 & 0 & 2 \\ -1 & 3 & 1\end{array}\right]$ and $\mathbf{B}=\left[\begin{array}{ll}3 & 1 \\ 2 & 1 \\ 1 & 0\end{array}\right]$. Determine $\mathbf{A B}$ and $\mathbf{B A}$ if defined. Does $\mathbf{A B}=\mathbf{B A}$ ?
(b) $\mathbf{C}=\left[\begin{array}{ll}1 & 0 \\ 2 & 1\end{array}\right]$ and $\mathbf{x}=\left[\begin{array}{c}3 \\ -1\end{array}\right]$. Determine $\mathbf{C x}$ and $\mathbf{x} \mathbf{C}$ if defined. Does $\mathbf{C x}=\mathbf{x} \mathbf{C}$ ?

## 4 Long-Term Dynamics and Equilibria

An important question in epidemiology (the study of the causes and impacts of the spread, or lack thereof, of infectious diseases in human populations) is whether an outbreak of an infectious disease will lead to a sustained epidemic or will die out after some time. Will the dynamics of the disease in the population lead to future outbreaks? If an outbreak will lead to an epidemic, are there measures (vaccination, quarantine, improved sanitation, etc.) that can reduce the proportion of the population that becomes infected, or eventually lead to eradication of the disease in the population? In essence, what is the long-term "behavior" of the disease in the population?

An important question in landscape ecology is whether, overall, the fraction of the landscape in each class is always changing or whether the landscape stabilizes. You can certainly think of simple cases in which a landscape has been completely urbanized so there is not longer any forest, or in which a region is dammed so that the area that was forest is now underwater and forms a lake. In these cases, it is easy to intuit what happens in the long term, but in many situations where land is changing back and forth between different classes, it is harder to determine if the proportion in each class is remaining constant.

A biological system that stays mostly unchanged over time is said to be at equilibrium, and it is stable if it returns to this equilibrium following a small change in the system. Recall from our study of discrete difference equations that mathematically, for a single discrete difference equation, $x^{*}$ is an equilibrium of the difference equation $x_{t+1}=f\left(x_{t}\right)$ if $x^{*}=f\left(x^{*}\right)$. For a system of two difference equations $x_{t+1}=f\left(x_{t}, y_{t}\right)$ and $y_{t+1}=g\left(x_{t}, y_{t}\right)$, the point $\left(x^{*}, y^{*}\right)$ is an equilibrium point if $x^{*}=f\left(x^{*}, y^{*}\right)$ and $y^{*}=g\left(x^{*}, y^{*}\right)$. This can be further extrapolated to systems of $3,4, \ldots, n$ difference equations. Recall that the matrix equation $\mathbf{v}(t+1)=\mathbf{A v}(t)$ represents the system of discrete difference equations,

$$
\begin{aligned}
v_{1}(t+1) & =a_{11} v_{1}(t)+a_{12} v_{2}(t)+\cdots+a_{1 n} v_{n}(t) \\
v_{2}(t+1) & =a_{21} v_{1}(t)+a_{22} v_{2}(t)+\cdots+a_{2 n} v_{n}(t) \\
& \vdots \\
v_{n}(t+1) & =a_{n 1} v_{1}(t)+a_{n 2} v_{2}(t)+\cdots+a_{n n} v_{n}(t)
\end{aligned}
$$

If the vector

$$
\mathbf{v}^{*}=\left[\begin{array}{c}
v_{1}^{*} \\
v_{2}^{*} \\
\vdots \\
v_{n}^{*}
\end{array}\right]
$$

satisfies the equation $\mathbf{v}^{*}=\mathbf{A} \mathbf{v}^{*}$, or written as difference equations satisfies the set of equations,

$$
\begin{aligned}
v_{1}^{*} & =a_{11} v_{1}^{*}+a_{12} v_{2}^{*}+\cdots+a_{1 n} v_{n}^{*} \\
v_{2}^{*} & =a_{21} v_{1}^{*}+a_{22} v_{2}^{*}+\cdots+a_{2 n} v_{n}^{*} \\
& \vdots \\
v_{n}^{*} & =a_{n 1} v_{1}^{*}+a_{n 2} v_{2}^{*}+\cdots+a_{n n} v_{n}^{*},
\end{aligned}
$$

then $\mathbf{v}^{*}$, called an eigenvector, represents an equilibrium point of the system represent by the transfer matrix $\mathbf{A}$. Note, if $\mathbf{v}^{*}$ is an eigenvector for a system, then $c \mathbf{v}^{*}$ where $c$ is a real number, is also an eigenvector for the system. When the eigenvector $\mathbf{v}^{*}$ is scaled such that the sum of the elements in $\mathbf{v}^{*}$ is 1 , we refer to this form of the eigenvector as the normalized eigenvector (i.e., it has been normalized with respect to the sum total of the vector).

Consider the aquatic succession model described by Equation (5). What would we expect to happen over many decades? If we examine the flow diagram of the model in Figure 5, we see that the arrows are pointing in one direction, and we would expect that eventually all of the wetlands become dry land. Thus, we would expect the eigenvalue of the system to be

$$
\mathbf{v}^{*}=\left[\begin{array}{l}
0 \\
0 \\
1
\end{array}\right] .
$$

Let us check if our intuition is correct. Let

$$
\mathbf{v}^{*}=\left[\begin{array}{l}
a \\
s \\
d
\end{array}\right],
$$

where $a$ is the proportion of wetlands always submerged when the system is at equilibrium, $s$ is the proportion which is seasonally submerged at equilibrium, and $d$ is the proportion which is always dry at equilibrium. Then to determine the values of $a, s$, and $d$ we must solve the equation

$$
\left[\begin{array}{l}
a \\
s \\
d
\end{array}\right]=\left[\begin{array}{ccc}
0.95 & 0 & 0 \\
0.05 & 0.88 & 0 \\
0 & 0.12 & 1
\end{array}\right]\left[\begin{array}{l}
a \\
s \\
d
\end{array}\right]=\left[\begin{array}{c}
0.95 a \\
0.05 a+0.88 s \\
0.12 s+d
\end{array}\right],
$$

which yields the three equations

$$
\begin{align*}
a & =0.95 a  \tag{6}\\
s & =0.05 a+0.88 s  \tag{7}\\
d & =0.12 s+d \tag{8}
\end{align*}
$$

The only value of $a$ that satisfies Equation (6) is $a=0$, and thus Equation (7) becomes $s=0.88 s$. The only value of $s$ that satisfies this equation is $s=0$, and thus Equation (8) becomes $d=d$ which is obviously true. Thus, we have that $a=0$ and $s=0$, but what is the value of $d$ ? Since the values in the vector $\mathbf{v}^{*}$ represent proportions of a total landscape, all the values in the vector must sum to 1 . This implies that $d=1$, and thus (just as we
hypothesized),

$$
\mathbf{v}^{*}=\left[\begin{array}{l}
0 \\
0 \\
1
\end{array}\right]
$$

Therefore, according to our model, all of the wetlands will eventually become dry land.
In the above example, it was fairly easy to predict, without finding an eigenvalue, the long-term behavior of the wetlands systems since from the flow diagram we could see that eventually all the land would become dry land. Now, let us consider a more complex example, where the flow diagram show "movement" back and forth between two classes. Recall in Example 4, we constructed a matrix model of a the dynamics of the common cold spreading through a dormitory. In the model, individuals were either susceptible $(S)$ or infected $(I)$. Each day $4 \%$ of the susceptible dorm residents became infected with the cold, while $20 \%$ of the infected dorm residents recovered and became susceptible again. The dynamics of the disease are represented by the matrix model,

$$
\left[\begin{array}{l}
S(t+1) \\
I(t+1)
\end{array}\right]=\left[\begin{array}{ll}
0.96 & 0.20 \\
0.04 & 0.80
\end{array}\right]\left[\begin{array}{c}
S(t) \\
I(t)
\end{array}\right] .
$$

Let $S^{*}$ and $I^{*}$ represent the proportions of the dormitory population in the susceptible and infected states, respectively, at equilibrium. Then, the eigenvector representing the equilibrium state can be found by solving the set of equations

$$
\begin{align*}
S^{*} & =0.96 S^{*}+0.20 I^{*}  \tag{9}\\
I^{*} & =0.04 S^{*}+0.80 I^{*} \tag{10}
\end{align*}
$$

Solving either Equation (9) or (10) for $S^{*}$, we obtain $S^{*}=5 I^{*}$. Since the $S^{*}$ and $I^{*}$ represent proportions of a population $S^{*}+I^{*}=1$, (or $\left.S^{*}=1-I^{*}\right)$. Thus,

$$
1-I^{*}=5 I^{*} \quad \Rightarrow \quad I^{*}=1 / 6 \quad \Rightarrow \quad S^{*}=5 / 6, \quad \text { and the eigenvector is }\left[\begin{array}{l}
5 / 6 \\
1 / 6
\end{array}\right]
$$

We can interpret this as the model predicting that in the long-term, $1 / 6$ or roughly $17 \%$ of the dormitory population will always be infected with the cold. Note, it will not always be the same individuals who are infected, but there will always be some individuals in the dorm who have the cold.

## Example 5

Recall that in Example 2 we considered a more complex aquatic succession model where the movement along the flow diagram was not all in one direction. Dry land could become seasonally or always submerged again.

(a) Use Matlab to calculate the proportion of wetlands in each class after 5, 10, 20, 50, 100, 150, 200, and 250 decades assuming you start with all the wetlands as always submerged.
(b) Use Matlab to calculate the proportion of wetlands in each class after 5, 10, 20, 50, 100, 150, 200, and 250 decades assuming you start
with $60 \%$ as always submerged, $20 \%$ as seasonally submerged, and $20 \%$ as always dry.
(c) Use Matlab to calculate the proportion of wetlands in each class after 5, 10, 20, 50, 100, 150, 200, and 250 decades assuming you start with $5 \%$ as always submerged, $90 \%$ as seasonally submerged, and $5 \%$ as always dry.
(d) Given your answers to (a), (b), and (c) make a hypothesis about the equilibrium of the wetland system according to this model.
(e) Calculate the eigenvector which represents the long-term structure of the wetlands system (i.e. the proportion in each class over the long term).
(f) When the system reaches this structural equilibrium will a given hectare of land no longer change from one class to another? Explain.

The solutions to this example will be worked in class.

## Example 6

Recall that in Example 3 we considered a model for the aquatic succession that occurs along freshwater shorelines, according to the flow diagram below where $L$ is the littoral zone, $E$ is the emergent zone, $R$ is the riparian zone, and $U$ is the upland zone.

(a) Use Matlab to calculate the proportion of freshwater shoreline in each class after 5, 10, 20, 50, 100, 150, 200, and 250 decades assuming you start with all of the "shoreline" in the littoral zone.
(b) Use Matlab to calculate the proportion of freshwater shoreline in each class after 5, 10, 20, 50, 100, 150, 200, and 250 decades assuming you start with $50 \%$ in the littoral zone and $50 \%$ in the emergent zone.
(c) Use Matlab to calculate the proportion of freshwater shoreline in each class after 5, 10, 20, 50, 100, 150, 200, and 250 decades assuming you start with $30 \%$ in the littoral zone, $30 \%$ in the emergent zone, $30 \%$ in the riparian zone, and $10 \%$ in the upland zone.
(d) Given your answers to (a), (b), and (c) make a hypothesis about the equilibrium of the freshwater shoreline system according to this model.
(e) Calculate the eigenvector which represents the long-term structure of the freshwater shoreline system (i.e., the proportion in each class over the long-term).

The solutions to this example will be worked in class.

## Exercise 6 - Herpes Simplex Virus Equilibrium

Recall from Exercise 3 that HSV is a virus that cause the disease herpes. In Exercise 3 we considered one of the simplest population models for HSV (without treatment) which divided the population into three categories: (1) susceptible, (2) infected and shedding virus (i.e., infectious), and (3) quiescent (infected but not shedding virus and thus not infectious). The model was is described by the flow diagram below.

(a) Use Matlab to calculate the proportion of the population in each state (susceptible, infectious, and quiescent) after $1,5,10,20,50$, 100, 250, and 500 years. Note: The matrix model constructed in Exercise 3 calculates the change in infection status each day. Use your results to hypothesize the equilibrium structure of the population.
(b) Calculate the eigenvector which represents the long-term structure of the population in terms of individuals infections status (i.e., the proportion of susceptibles, infectious, and quiescents over the long-term.)
(c) Is this model biologically reasonable over $1,5,10,20,50,100,250$, or 500 years? Explain why or why not.

## Exercise 7 - Strontium-90 Cycling Equilibrium

Recall from Exercise 4 that strontium-90 is a radioactive by-product produced by the nuclear fission of uranium and plutonium. Strontium90 cycles through ecosystems, and this dynamic process can be describe by a matrix model as represented by the flow diagram below where the ecosystem is divided into grasses $(G)$, soil $(S)$, streams and waterways $(W)$, and dead organic matter $(O)$.


Calculate the eigenvector which represents the long-term structure of the population in terms of the proportion of the strontium-90 in each class of the ecosystem. Interpret your result in biological terms.

## 5 Leslie Matrix Models

The matrix models we have considered so far, using transfer matrices, are limited by the assumption that nothing is created or destroyed. Each area on a landscape may change from one class to another, and each individual in a population changes only from one disease status to another. We did not consider the case of a population in which new individuals are born or individuals die. So in these models, each component (area or individuals) changes only in state. In the landscape succession examples, we never created or destroyed land, but each area on the landscape could change from one state to another. In the disease model, there were not births or deaths, but individuals could move between infected and susceptible states. Much of biology deals with systems in which the entities (cells or individuals) can be born and can die. We will now explore matrix models that take into account births and deaths, and develop methods to see what happens to the structure of the biological system in the long-term.

Intuitively, unless we can somehow match up the number of births and deaths within a population at each time step, that population will either grow or decline (depending on if there are more births or more deaths). This should happen no matter how we structure the population. When we represent the structure of a population, we must account for the death rate and reproductive rate within each class of the structure, as well as the rate of movement between each classes.

As a motivating example, suppose we want to study how a population of locusts changes over time. Locusts have three distinct stages in their life cycle: (1) egg, (2) nymph, and (3) adults (see Figure 8). Not all locust eggs will survive to become adults. Some will die while they are still eggs; others will die while they are nymphs. Females locusts are able to reproduce (lay eggs) only during the adult stage of their life.


Figure 8: Life stages of a locust: (a) egg, (b)nymph, and (c) adult. Note the nymph does not have wings, but the adult does.

Suppose that in a particular population of locusts, each year $2 \%$ of the eggs survive to become nymphs, $5 \%$ of the nymphs survive to become adults, and adults die soon after they reproduce (i.e., they do not survive to the next year). Additionally, a female adult locust will produce (on average) 2000 eggs before she dies.

Since it is the female that reproduces, we will model only the females of the population and assume there are an equal number of males within each life stage. Let $x_{1}(t)$ be the number of female eggs in the locust population at time step $t$ (measured in years), let $x_{2}(t)$ be the number of female nymphs in the locust population at time step $t$, and let $x_{3}(t)$ be the number of female adults in the locust population at time step $t$. Recall that with transfer matrix models we model the proportion (not the total number) in each class; this is one of the ways in which this matrix model differs from transfer matrix models. We can describe how the population changes each year with a system of discrete difference equations:

$$
\begin{align*}
x_{1}(t+1) & =1000 x_{3}(t),  \tag{11}\\
x_{2}(t+1) & =0.02 x_{1}(t)  \tag{12}\\
x_{3}(t+1) & =0.05 x_{2}(t) \tag{13}
\end{align*}
$$

Equation (11) shows that at time step $t+1$ each female adult from the previous time step produced 1000 female eggs (we assume that half of 2000 eggs per female adult are female eggs). Equation (12) shows that $2 \%$ of the eggs from time step $t$ survive and move to the nymph class by time step $t+1$. Equation (13) shows that $5 \%$ of the nymphs from time step $t$ survive to move to the adult class by time step $t+1$ and none of the adults survive from time step $t$ to $t+1$ (i.e. $\left.x_{3}(t+1)=0.05 x_{2}(t)+0.00 x_{3}(t)\right)$. If we rewrite Equations (11) - (13) as

$$
\begin{align*}
x_{1}(t+1) & =0 x_{1}(t)+0 x_{2}(t)+1000 x_{3}(t)  \tag{14}\\
x_{2}(t+1) & =0.02 x_{1}(t)+0 x_{2}(t)+0 x_{3}(t)  \tag{15}\\
x_{3}(t+1) & =0 x_{1}(t) 0.05 x_{2}(t)+0 x_{3}(t) \tag{16}
\end{align*}
$$

it should be clear from the construction of our transfer matrix models that we can express this model as the matrix equation

$$
\begin{align*}
{\left[\begin{array}{l}
x_{1}(t+1) \\
x_{2}(t+1) \\
x_{3}(t+1)
\end{array}\right] } & =\left[\begin{array}{ccc}
0 & 0 & 1000 \\
0.02 & 0 & 0 \\
0 & 0.05 & 0
\end{array}\right]\left[\begin{array}{l}
x_{1}(t) \\
x_{2}(t) \\
x_{3}(t)
\end{array}\right] \\
\mathbf{x}(t+1) & =\left[\begin{array}{ccc}
0 & 0 & 1000 \\
0.02 & 0 & 0 \\
0 & 0.05 & 0
\end{array}\right] \mathbf{x}(t) . \tag{17}
\end{align*}
$$

## Example 7

Given the matrix model of the locust population in Equation (17), how doe the population of locusts change over the course of 6 years if
(a) there are only 50 adults at the initial time (no eggs and no nymphs)?
(b) there are 50 eggs, 100 nymphs, and 50 adults at the initial time?

Based on your answers to (a) and (b), what do you expect to happen to the locust population over the long-term? Will there be an eigenvector corresponding to the an equilibrium population structure? Does the population size remain constant? The solutions to this example will be worked in class.

The type of matrix model for populations that takes into account the births and survival rates of each class or stage within a population is known as a Leslie matrix model, named after population biologist Patrick H. Leslie. In general, Leslie matrix models have the form $\mathbf{x}(t+1)=\mathbf{A x}(t)$, where

$$
\mathbf{A}=\left[\begin{array}{ccccc}
F_{1} & F_{2} & F_{3} & \cdots & F_{n} \\
S_{1} & 0 & 0 & \cdots & 0 \\
0 & S_{2} & 0 & \cdots & 0 \\
\vdots & \vdots & \vdots & \ddots & \vdots \\
0 & 0 & 0 & S_{n-1} & S_{n}
\end{array}\right]
$$

where $F_{i}$ is the average number of female offspring born to a female individual in class $i$ in one time step, and $S_{i}$ is the fraction of individuals in class $i$ that survive to class $i+1$ per time step for $i<n$. For $i=n, S_{n}$ is the proportion of individuals in class $n$ that survive a subsequence time period (with the same proportion of surviving for each future time period). The parameter $F_{i}$ is known as the fecundity rate, and the parameter $S_{i}$ is known as the survival rate. Note that the first row gives the coefficients of the difference equation corresponding to the first life stage or class $x_{1}$ (like eggs or newborns). In Leslie matrix models, we assume that the "instance" of the time step occurs after reproduction and that only females are counted. In relating this to the collection of field data, this represents when we would census the population. Note, if $S_{n}=0$, then individuals in the last stage do not spend more than one time step in that stage. The survival and fecundity rates are assumed to be constant over time and independent of the total population size. Thus, Leslie matrix models do not account for density-dependent phenomenon such as carrying-capacities which prevent overcrowding.

## Example 8



Figure 9: Herd of American bison.

Suppose we can model a population of American bison (Bison bison) using a Leslie matrix model,

$$
\mathbf{x}(t+1)=\left[\begin{array}{ccc}
0 & 0 & 0.42 \\
0.60 & 0 & 0 \\
0 & 0.75 & 0.95
\end{array}\right] \mathbf{x}(t)
$$

where $x_{1}(t)$ is the number of female calves (age is less than 1 year) in the herd at time $t, x_{2}(t)$ is the number of female yearlings (age is between 1 and 2 years) in the herd at time $t$, and $x_{3}(t)$ is the number of female adults (age is 2 years or greater) in the herd at time $t$. In this model, the size of one time step is one year.
(a) Which class in the herd is the reproductive class? On average, how many female calves are born to a female in the reproductive class each year? If you assume an even sex ratio in the herd, on average, how many calves (male and female) are born to a female in the reproductive class each year? Does every female in the reproductive class reproduce every year?
(b) What proportion of calves survive to become yearlings? What proportion of yearlings survival to become adults? What proportion of adults survive to another year?
(c) What is the death rate of the calves? of the yearlings? of the adults?
(d) Create a table of the population structure of the herd over the next 5 years assuming the herd starts with 200 adult bison half of which are female. In your table, indicate the total number of female each year, and the total herd size each year.
(e) Using the table created in (d), calculate the proportion (to the nearest 0.0001 ) of the herd in each class over the next 5 years.
(f) Using the values in the tables you created in (d) and (e) make a hypothesis about what happens to the total herd size over time, and what happens to the proportion in each class over time.
(g) Use Matlab to plot the total herd size and the proportion in each class over the next 30 years. Do the results match your predictions?

The solutions to this example will be worked in class.

## Long-Term Growth Rates \& Population Structures

For transfer matrices we were able to determine if the long-term population structure of a system approach an equilibria by examining the normalized eigenvector. For Leslie matrices we do the same, but we must account for whether the population is growing or declining.

Let $\mathbf{x}(t)$ denote the population structure at time $t$. If the population size is at equilibrium (i.e., the population is neither growing nor declining), then $\mathbf{x}(t+1)=\mathbf{x}(t)$. However, if the the population is growing or declining, but the population structure is at equilibrium, then $\mathbf{x}(t+1)=\lambda \mathbf{x}(t)$, where $\lambda$ is a constant. To see why this is the case, suppose

$$
\mathbf{x}(t)=\left[\begin{array}{l}
a \\
b \\
c
\end{array}\right] \quad \text { and } \quad a+b+c=N,
$$

then the proportion in each class is $a / N, b / N$, and $c / N$. If $\mathbf{x}(t+1)=\lambda \mathbf{x}(t)$, then

$$
\mathbf{x}(t+1)=\left[\begin{array}{l}
\lambda a \\
\lambda b \\
\lambda c
\end{array}\right] \quad \text { and } \quad \lambda a+\lambda b+\lambda c=\lambda N .
$$

Thus, the proportion in each class is

$$
\frac{\lambda a}{\lambda N}=\frac{a}{N}, \quad \frac{\lambda b}{\lambda N}=\frac{b}{N}, \quad \text { and } \quad \frac{\lambda c}{\lambda N}=\frac{c}{N} .
$$

Thus, even though the total population size increased or decreased by a factor of $\lambda$, the proportion in each class remained the same.

Note if $\lambda>1$, then the population size will be increasing, but if $0<\lambda<1$, then the population size will be decreasing. If at population structure equilibrium the population is growing by $5 \%$ each time step, then $\lambda=1.05$. If instead the population is declining by $5 \%$ each time step, then $\lambda=0.95$. In the special case where $\lambda=1$, the population size remains the same. The transfer matrices fall into this special case because they are set up such that the population size (or total land area) always remains the same.

Suppose that $\mathbf{A}$ is a Leslie matrix, then the Leslie matrix model is $\mathbf{x}(t+1)=\mathbf{A x}(t)$. If there is a long-term population structure equilibrium, let $\mathbf{x}^{*}$ denote the normalized population structure at this equilibrium (i.e., the $i^{\text {th }}$ element of $\mathbf{x}^{*}$ represents the proportion of the population in class $i$ when the population is at the structural equilibrium). When the population is at a structural equilibrium

$$
\mathbf{x}(t+1)=\mathbf{A} \mathbf{x}(t), \quad \text { and } \quad \mathbf{x}(t+1)=\lambda \mathbf{x}(t) .
$$

Combining these two equations, we find that

$$
\mathbf{A} \mathbf{x}(t)=\lambda \mathbf{x}(t) \quad \Rightarrow \quad \mathbf{A} \mathbf{x}(t)-\lambda \mathbf{x}(t)=\mathbf{0} \quad \Rightarrow \quad(\mathbf{A}-\lambda \mathbf{I}) \mathbf{x}(t)=\mathbf{0} .
$$

Recall that $\mathbf{0}$ is the vector or matrix where all the elements are 0 .

The determinant is a function that takes a square matrix as an input variable and returns a real number. The function is defined recursively for matrices of increasing size, i.e. the determinant of a $3 \times 3$ matrix is defined using the determinant of $2 \times 2$ matrices; the determinant of a $4 \times 4$ matrix is defined using the determinant of $3 \times 3$ matrices; and so on. The determinant of a matrix $\mathbf{A}$ is denoted $\operatorname{det}(\mathbf{A})$.

Determinant for a $2 \times 2$ : If $\mathbf{A}=\left[\begin{array}{ll}a & b \\ c & d\end{array}\right]$, then $\operatorname{det}(\mathbf{A})=\left|\begin{array}{ll}a & b \\ c & d\end{array}\right|=a d-b c$.
Determinant for a $3 \times 3$ : If $\mathbf{A}=\left[\begin{array}{lll}a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33}\end{array}\right]$, then
$\operatorname{det}(\mathbf{A})=\left|\begin{array}{lll}a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33}\end{array}\right|=a_{11}\left|\begin{array}{ll}a_{22} & a_{23} \\ a_{32} & a_{33}\end{array}\right|-a_{12}\left|\begin{array}{ll}a_{21} & a_{23} \\ a_{31} & a_{33}\end{array}\right|+a_{13}\left|\begin{array}{ll}a_{21} & a_{22} \\ a_{31} & a_{32}\end{array}\right|$.
Determinant for a $4 \times 4$ : If $\mathbf{A}=\left[\begin{array}{llll}a_{11} & a_{12} & a_{13} & a_{14} \\ a_{21} & a_{22} & a_{23} & a_{24} \\ a_{31} & a_{32} & a_{33} & a_{34} \\ a_{41} & a_{42} & a_{43} & a_{44}\end{array}\right]$, then

$$
\operatorname{det}(\mathbf{A})=\left|\begin{array}{llll}
a_{11} & a_{12} & a_{13} & a_{14} \\
a_{21} & a_{22} & a_{23} & a_{24} \\
a_{31} & a_{32} & a_{33} & a_{34} \\
a_{41} & a_{42} & a_{43} & a_{44}
\end{array}\right|=a_{11}\left|\begin{array}{lll}
a_{22} & a_{23} & a_{24} \\
a_{32} & a_{33} & a_{34} \\
a_{42} & a_{43} & a_{44}
\end{array}\right|-a_{12}\left|\begin{array}{lll}
a_{21} & a_{23} & a_{24} \\
a_{31} & a_{33} & a_{34} \\
a_{41} & a_{43} & a_{44}
\end{array}\right|+a_{13}\left|\begin{array}{lll}
a_{21} & a_{22} & a_{24} \\
a_{31} & a_{32} & a_{34} \\
a_{41} & a_{42} & a_{44}
\end{array}\right|-a_{14}\left|\begin{array}{lll}
a_{21} & a_{22} & a_{23} \\
a_{31} & a_{32} & a_{33} \\
a_{41} & a_{42} & a_{43}
\end{array}\right| .
$$

Determinant for an $n \times n$ matrix where all elements are zero: If $\mathbf{A}=\mathbf{0}$, then $\operatorname{det}(\mathbf{A})=0$.

From the to the equation $(\mathbf{A}-\lambda \mathbf{I}) \mathbf{x}(t)=\mathbf{0}$, we see that either $\mathbf{x}(t)=\mathbf{0}$ or $(\mathbf{A}-\lambda \mathbf{I})=\mathbf{0}$. If $\mathbf{x}(t)=\mathbf{0}$ then the population went extinct and the population can be neither increasing nor decreasing. In this case, the population structure equilibrium is $\mathbf{x}^{*}=\mathbf{0}$. If $\mathbf{A}-\lambda \mathbf{I}=\mathbf{0}$, then we need to find the value of $\lambda$ in order to determine the population structure equilibrium $\mathbf{x}^{*}$.

By a property of determinants if $\mathbf{A}-\lambda \mathbf{I}=\mathbf{0}$, then $\operatorname{det}(\mathbf{A}-\lambda \mathbf{I})=0$. We will use this equation to determine the value of $\lambda$. Any value $\lambda$ that satisfies the equation $\operatorname{det}(\mathbf{A}-\lambda \mathbf{I})=0$ is called an eigenvalue of $\mathbf{A}$. If $\mathbf{A}$ is an $n \times n$ matrix, it will have $n$ eigenvalues. The eigenvalue with the largest absolute magnitude is the dominant eigenvalue, i.e. if $\lambda_{1}, \lambda_{2}, \ldots, \lambda_{n}$ are all eigenvalues of $\mathbf{A}$, then $\lambda_{i}$ is the dominant eigenvalue if $\left|\lambda_{i}\right| \geq\left|\lambda_{k}\right|$ for all $k=1,2, \ldots, n$. For a given eigenvalue $\lambda$, any vector $\mathbf{v}$ that satisfying the equation $\mathbf{A v}=\lambda \mathbf{v}$ is the eigenvector associated with the eigenvalue $\lambda$.

For Leslie matrix models the dominant eigenvalue determines whether the population is growing or declining and represents the long-term growth rate or the structural equilibrium growth rate. The eigenvector associated with the dominant eigenvalue is represents the population structure equilibrium. Note that for transfer matrix models, the dominant eigenvalue is always 1 .

As a simple example, consider the Leslie matrix

$$
\mathbf{A}=\left[\begin{array}{cc}
1 & 4 \\
0.5 & 0
\end{array}\right]
$$

We can determine whether the population will be growing or declining when at population structure equilibrium by solving the equation $\operatorname{det}(\mathbf{A}-\lambda \mathbf{I})=\mathbf{0}$ for $\lambda$. Notice, since $\mathbf{A}$ is a $2 \times 2$ matrix, we should expect to find 2
eigenvalues,

$$
\begin{aligned}
0 & =\operatorname{det}(\mathbf{A}-\lambda \mathbf{I})=\operatorname{det}\left(\left[\begin{array}{cc}
1 & 4 \\
0.5 & 0
\end{array}\right]-\left[\begin{array}{ll}
\lambda & 0 \\
0 & \lambda
\end{array}\right]\right) \\
& =\left|\begin{array}{cc}
1-\lambda & 4 \\
0.5 & -\lambda
\end{array}\right| \\
& =(1-\lambda)(-\lambda)-(4)(0.5) \\
& =\lambda^{2}-\lambda-2 \\
& =(\lambda-2)(\lambda+1)
\end{aligned}
$$

Thus, the two eigenvalues are $\lambda_{1}=2$ and $\lambda_{2}=-1$. Since $\left|\lambda_{1}\right|>\left|\lambda_{2}\right|, \lambda_{1}$ is the dominant eigenvalue. Furthermore, since $\lambda_{1}=2>1$, the population is increasing (doubling, in fact) when it reaches its structural equilibrium. Using the long term growth rate (the dominant eigenvalue) we can determine the population structure equilibrium:

$$
\mathbf{A} \mathbf{x}=2 \mathbf{x} \quad \Rightarrow \quad\left[\begin{array}{cc}
1 & 4 \\
0.5 & 0
\end{array}\right]\left[\begin{array}{l}
x_{1} \\
x_{2}
\end{array}\right]=\left[\begin{array}{l}
2 x_{1} \\
2 x_{2}
\end{array}\right]
$$

Thus, the eigenvector representing the equilibrium state can be found by solving the set of equations

$$
\begin{align*}
x_{1} 4 x_{2} & =2 x_{1}  \tag{18}\\
0.5 x_{1} & =2 x_{2} \tag{19}
\end{align*}
$$

Solving either Equation (18) or (19) for $x_{1}$, we obtain $x_{1}=4 x_{2}$. To find the proportion in each state at the structural equilibrium, we let $x_{1}+x_{2}=1$, thus

$$
1=x_{1}+x_{2}=4 x_{2}+x_{2}=5 x_{2} \quad \Rightarrow \quad x_{2}=1 / 5 \quad \Rightarrow \quad x_{1}=4 / 5
$$

and the eigenvector corresponding to the dominant eigenvalue is $\left[\begin{array}{l}4 / 5 \\ 1 / 5\end{array}\right]$.
Example 9
Find all the eigenvalues for the transfer matrix $\mathbf{A}=\left[\begin{array}{ccc}0.95 & 0 & 0 \\ 0.05 & 0.88 & 0 \\ 0 & 0.12 & 1\end{array}\right]$, and verify that the dominant eigenvalue is 1 .
The solutions to this example will be worked in class.

## Example 10

Recall from Example 10 that we modeled a population of American bison using the Leslie matrix model,

$$
\mathbf{x}(t+1)=\left[\begin{array}{ccc}
0 & 0 & 0.42 \\
0.60 & 0 & 0 \\
0 & 0.75 & 0.95
\end{array}\right] \mathbf{x}(t)
$$

where $x_{1}(t)$ is the number of female calves (age is less than 1 year) in the herd at time $t, x_{2}(t)$ is the number of female yearlings (age is between 1 and 2 years) in the herd at time $t$, and $x_{3}(t)$ is the number of female adults (age is 2 years or greater) in the herd at time $t$. In this model, the size of one time step is one year.
(a) Find all the eigenvalues of the Leslie matrix. Which eigenvalue is the dominant eigenvalue?
(b) Is the population growing or declining when it reaches structural equilibrium? Does this match your analysis from Example 8?
(c) Find the normalized eigenvector corresponding to the dominant eigenvalue. What do the values in this vector represent? How do the values in this vector correspond with the predictions you made in Example 8?

The solutions to this example will be worked in class.

## Oscillating Populations

If the dominant eigenvalue represents the long-term growth rate of a population for Leslie matrix models where the population approaches a structural equilibrium, what about the Leslie matrix models for which no structural equilibrium is approached? Recall the model for Leslie matrix model for the locust population,

$$
\mathbf{x}(t+1)=\left[\begin{array}{ccc}
0 & 00 & 1000 \\
0.02 & 0 & 0 \\
0 & 0.05 & 0
\end{array}\right] \mathbf{x}(t)
$$

where $x_{1}(t)$ is the number of female locust eggs at time $t, x_{2}(t)$ is number of female nymphs at time $t$, and $x_{3}(t)$ is the number of female adult locusts at time $t$. In Example 7 we saw that this population oscillates through time, never approaching a structural equilibrium. What can the eigenvalues of the Leslie matrices in these oscillating population tell us?

Let $\mathbf{A}$ be an $n \times n$ Leslie matrix where $d$ of the $n$ eigenvalues have the same absolute magnitude whose value is greater than the absolute magnitudes of the remaining $n-d$ eigenvalues. Then $d$ is called the index of imprimitivity, and the state structure of the population modeled by $\mathbf{A}$ does not converge to a structural equilibrium but instead oscillates with a period of $d$. In this case, the position of "dominant eigenvalue" is filled by $d$ of the eigenvalues; here we might refer to the dominant eigenvalue of having a multiplicity of $d$. In the case where $d>1$, the biological interpretation of the value of the dominant eigenvalues is a bit more complex.

Suppose that $\lambda_{1}, \ldots, \lambda_{d}$ are the dominant eigenvalues.

- If $\left|\lambda_{1}\right|=\cdots=\left|\lambda_{d}\right|=1$, then the population will oscillate with period $d$ through the same values each period.
- If $\left|\lambda_{1}\right|=\cdots=\left|\lambda_{d}\right|>1$, then the population will oscillate with period $d$, but the values will increase each period.
- If $\left|\lambda_{1}\right|=\cdots=\left|\lambda_{d}\right|<1$, then the population will oscillate with period $d$, but the values will decrease each period.


## Example 11

Find the index of imprimitivity (and period of oscillation) determine if the population size overall is increasing or decreasing over time for each of the following variants of the locust model:
(a) $\left[\begin{array}{ccc}0 & 0 & 1000 \\ 0.02 & 0 & 0 \\ 0 & 0.05 & 0\end{array}\right]$; Original locust population model
(b) $\left[\begin{array}{ccc}0 & 0 & 500 \\ 0.02 & 0 & 0 \\ 0 & 0.05 & 0\end{array}\right]$; female adults produce half as many eggs each time step
(c) $\left[\begin{array}{ccc}0 & 0 & 1000 \\ 0.02 & 0 & 0 \\ 0 & 0.05 & 0.25\end{array}\right] ; 25 \%$ of female adults survive to live another year

Create a plot showing the population structure over time in Matlab for each model. Use 50 eggs, 100 nymphs, and 50 adults as the starting condition; plot over 10 years.

The solutions to this example will be worked in class.

## Exercise 8 - Wild Horses

Wild horses on a large ranch are divided into foals, yearlings, and adults. Data indicates that $70 \%$ of the foals survive the first year to become yearlings, while $80 \%$ of the yearlings mature into adults. In addition, $90 \%$ of adults survive a given year, and an average adult female produces a single foal every 5 years.
(a) Construct a Leslie matrix representing the dynamics of the wild horse population.
(b) Assuming the wild population started with 20 adults, create tables showing the number of females in each class and the proportion in each class over the first 7 years.
(c) Find all of the eigenvalues for the Leslie matrix. Indicate which is the dominant eigenvalue. If the index of imprimitivity is greater than 1 , give its value.
(d) Based on your answer in (c), doe the population reach a stable population structure? If so, is the population increasing or decreasing once the structural equilibrium is reached, and what is the population structure at said equilibrium?

## Exercise 9 - Spotted Owl Conservation

In an attempt to save the endangered northern spotted owl (Strix occidentalis caurina), in the 1989 the U.S. Fish and Wildlife Service imposed strict guidelines for the use of 12 million acres of Pacific Northwest forest. This decision led to a national debate between the logging industry and environmentalists. Mathematical ecologists have created a mathematical model to analyze the population dynamics of the north spotted owl by dividing the female owl population into three categories: juvenile (up to 1 year old), subadult ( 1 to 2 years old), and adult (over 2 years old). the female owl population can be modeled by the Leslie matrix model

$$
\left[\begin{array}{l}
j(t+1) \\
s(t+1) \\
a(t+1)
\end{array}\right]=\left[\begin{array}{ccc}
0 & 0 & 0.33 \\
0.18 & 0 & 0 \\
0 & 0.71 & 0.94
\end{array}\right]\left[\begin{array}{c}
j(t) \\
s(t) \\
a(t)
\end{array}\right]
$$


(a) If there are currently 4000 female northern spotted owls made up of 900 juveniles, 500 subadults, and 2600 adults, to determine the number of female owls in each class for the next 5 years. Round each answer to the nearest whole owl.
(b) Determine the long-term growth rate of the spotted owl population. What can you conclude about the long-term survival of the northern spotted owl?
(c) Notice that only $18 \%$ of the juveniles become subadults. If the U.S. Fish and Wildlife Service improved the habitat of the northern spotted owls through their strict guidelines such that the survival rate of the juveniles increased to $40 \%$, what would be the fate of the northern spotted owl?

## Exercise 10 - Livestock Management

A herd of carefully managed beef cattle can be divided up into calves (less than one year old), yearlings (between 1 and 2 years old), and adults (older than 2). Only the adults birth calves. On average each adult female produces 1.2 female calves per year. The survival rate of the calves and the yearlings is $90 \%$. However, after the two-year-old adults give birth, they are "processed" into beef.
(a) Construct the Leslie matrix describing the herd of beef cattle.
(b) Will the population approach a structural equilibrium? Why or why not?
(c) Is the population size stable? Should the manager of the herd worry about having a growing or declining population of cattle?

## Exercise 11 - How often do you oscillate?

For the following two (contrived) scenarios: (i) Construct a Leslie matrix model describing the population, (ii) find all the eigenvalues, the index of imprimitivity, and the dominant eigenvalue, and (iii) describe what will happen to the population over time.
(a) Consider a population with three stages: babies, juveniles, and adults. Each female has (on average) 5 female offspring per year. the yearly survival rate of the babies and juveniles is $50 \%$. No adults survive longer than 1 year.
(b) Consider a population with four stages. Stage 2 and 4 reproduce with females in stage 2 producing (on average) 1 female offspring per time step, and females in stage 4 producing (on average) 2 female offspring per time step. The survival rates of stages 1-3 are $50 \%$ per time step. No individuals in stage 4 survival longer than one time step.

## A Modification of the Leslie Matrix Model

Recall that the Leslie matrix models have the form $\mathbf{x}(t+1)=\mathbf{A} \mathbf{x}(t)$, where

$$
\mathbf{A}=\left[\begin{array}{ccccc}
F_{1} & F_{2} & F_{3} & \cdots & F_{n} \\
S_{1} & 0 & 0 & \cdots & 0 \\
0 & S_{2} & 0 & \cdots & 0 \\
\vdots & \vdots & \vdots & \ddots & \vdots \\
0 & 0 & 0 & S_{n-1} & S_{n}
\end{array}\right]
$$

where $F_{i}$ is the average number of female offspring born to a female individual in class $i$ in one time step, and $S_{i}$ is the fraction of individuals in class $i$ that survive to class $i+1$ per time step for $i<n$. This model assumes that individuals in each age class either survive and moves up to the next age class, or they die. However, sometimes it is more convenient to consider size classes in which individuals do not necessarily spend the same amount of time. Thus, we must consider some individuals in each size class that survive, but remain in the same size class. For these models
we use $\mathbf{x}(t+1)=\mathbf{A} \mathbf{x}(t)$, where

$$
\mathbf{A}=\left[\begin{array}{ccccc}
P_{1} & F_{2} & F_{3} & \ldots & F_{n} \\
G_{1} & P_{2} & 0 & \cdots & 0 \\
0 & G_{2} & P_{3} & \cdots & 0 \\
\vdots & \vdots & \vdots & \ddots & \vdots \\
0 & 0 & 0 & G_{n-1} & P_{n}
\end{array}\right]
$$

where $F_{i}$ is the average number of female offspring born to a female individual in class $i$ in one time step, $P_{i}$ is the proportion of size class $i$ that survive and remain in size class $i$, and $G_{i}$ is the proportion of size class $i$ that survive and move up to size class $i+1$. Note, the survival rate of size class $i$ is $S_{i}=P_{i}+G_{i} \leq 1$.

## References

[1] E.N. Bodine, S. Lenhart, and L.J. Gross. Mathematics for the Life Sciences. Princeton University Press, 2014.

## Web Resources

[2] http://www.cyber-dyne.com/~tom/03/natural_amazon.htm
[3] htt://maps.google.com
[4] http://www.antweb.org/antblog/2010/04/what-is-the-largest-ant-in-the-world-luke-from-chicago-il-usa. html
[5] http://www.epa.gov/superfund/health/contaminants/radiation/pdfs/strontium.pdf
[6] http://www.clemson.edu/extension/hgic/water/resources_stormwater/shoreline_plants_in_south_ carolina_waterfronts.html

## Answer Key to Exercises

Exercise 2 - Dorylus laevigatus Ant Colony
(a) $\left[\begin{array}{l}s \\ l\end{array}\right]=\left[\begin{array}{c}12 / 13 \\ 1 / 13\end{array}\right]$,
(b) $\left[\begin{array}{r}300,000 \\ 25,000\end{array}\right]-0.2\left[\begin{array}{r}300,000 \\ 25,000\end{array}\right]=\left[\begin{array}{r}240,000 \\ 18,750\end{array}\right] \Rightarrow\left[\begin{array}{c}64 / 69 \\ 5 / 69\end{array}\right]$
(c) (i) $\left[\begin{array}{l}m \\ f\end{array}\right]=\left[\begin{array}{r}45,000 \\ 105,000\end{array}\right]$, (ii) $\left[\begin{array}{r}300,000 \\ 25,000\end{array}\right]+150,000\left[\begin{array}{l}0.4 \\ 0.3\end{array}\right]=\left[\begin{array}{r}360,000 \\ 70,000\end{array}\right] \Rightarrow\left[\begin{array}{c}36 / 43 \\ 7 / 43\end{array}\right]$

Exercise 3 - Herpes Simplex Virus
(a) $\left[\begin{array}{l}S \\ I \\ Q\end{array}\right]=\left[\begin{array}{l}0.65 \\ 0.20 \\ 0.15\end{array}\right]$
(b) (i)

(ii) $\left[\begin{array}{ccc}0.999945 & 0 & 0 \\ 0.000055 & 0.714 & 0.029 \\ 0 & 0.286 & 0.971\end{array}\right]$

Exercise 4 - Strontium-90 Cycling
(a)

(b) $\left[\begin{array}{cccc}0.85 & 0.01 & 0 & 0 \\ 0.05 & 0.98 & 0 & 0.2 \\ 0 & 0.01 & 1 & 0 \\ 0.1 & 0 & 0 & 0.8\end{array}\right]\left[\begin{array}{c}G \\ S \\ W \\ O\end{array}\right]$

Exercise 5 - Matrix Multiplication is NOT Commutative
(a) $\mathbf{A B}=\left[\begin{array}{ll}5 & 1 \\ 4 & 2\end{array}\right] ; \mathbf{B A}=\left[\begin{array}{lll}2 & 3 & 7 \\ 1 & 3 & 5 \\ 1 & 0 & 2\end{array}\right] ; \mathbf{A B} \neq \mathbf{B} \mathbf{A}$, in fact, they are not even the same size
(b) $\mathbf{C x}=\left[\begin{array}{l}3 \\ 5\end{array}\right] ; \mathbf{x C}$ is not defined; $\mathbf{C x} \neq \mathbf{x} \mathbf{C}$ since $\mathbf{x} \mathbf{C}$ is not even defined!

Exercise 6 - Herpes Simplex Virus Equilibrium

| Year | $S$ | I | $Q$ |
| :---: | :---: | :---: | :---: |
| 1 | 0.9801 | 0.0020 | 0.0179 |
| 5 | 0.9045 | 0.0089 | 0.0866 |
| 10 | 0.8181 | 0.0169 | 0.1650 |
| 20 | 0.6693 | 0.0306 | 0.3001 |
| 50 | 0.3665 | 0.0584 | 0.5751 |
| 100 | 0.1343 | 0.0797 | 0.7860 |
| 250 | 0.0066 | 0.0915 | 0.9019 |
| 500 | 0.0000 | 0.0921 | 0.9079 |
| 1000 | 0.0000 | 0.0921 | 0.9079 |

Hypothesis: At equilibrium none of the population will be susceptible (i.e., everyone is infected), $9.21 \%$ of the population will be infectious, and $90.79 \%$ will be quiescent.
(b) $\left[\begin{array}{c}S^{*} \\ I^{*} \\ Q^{*}\end{array}\right]=\left[\begin{array}{c}0 \\ 29 / 315 \\ 286 / 315\end{array}\right]$
(c) This is a model for a human population in which, presumably, individuals age and die and new individuals are born. However, this model does not take that into account. Thus, though this model might provide a reasonable approximation over 1 or 5 years (maybe even 10 years), the farther out this model is extended, the less realistic it becomes. Note that the eigenvector shows us that eventually everyone is infected (i.e. there are no more susceptible individuals). However, if we assume that individuals are not born infected, then we can assume new susceptible individuals are created each time step, and this is not accounted for in this model. Additionally, each time step, it would also be reasonable to assume that some individuals in each class have died, but this is also not accounted for in this model. In mathematical modeling, we would refer to the population in this model as a "closed population" indicating that no individuals are entering (through birth or immigration) or exiting (through death or emigration) the population.

Exercise 7 - Strontium-90 Cycling Equilibrium
$\left[\begin{array}{c}G^{*} \\ S^{*} \\ W^{*} \\ O^{*}\end{array}\right]=\left[\begin{array}{l}0 \\ 0 \\ 1 \\ 0\end{array}\right] \quad \begin{aligned} & \text { which can be interpreted as, "eventually all the strontium-90 ends up in the streams and waterways } \\ & \text { through runoff." }\end{aligned}$

Exercise 8 - Wild Horses
(a) $\left[\begin{array}{ccc}0 & 0 & 0.2 \\ 0.70 & 0 & 0 \\ 0 & 0.80 & 0.90\end{array}\right]$

| Numbers |  |  |  |
| :---: | :---: | :---: | :---: |
| $t$ | $F$ | $Y$ | $A$ |
| 0 | 0.00 | 0.00 | 20.00 |
| 1 | 4.00 | 0.00 | 18.00 |
| 2 | 3.60 | 2.80 | 16.20 |
| 3 | 3.24 | 2.52 | 16.82 |
| 4 | 3.36 | 2.27 | 17.15 |
| 5 | 3.43 | 2.35 | 17.25 |
| 6 | 3.45 | 2.40 | 14.41 |
| 7 | 3.48 | 2.42 | 17.59 |


| Proportions |  |  |  |
| :---: | :---: | :---: | :---: |
| $t$ | $F$ | $Y$ | $A$ |
| 0 | 0.000 | 0.000 | 1.000 |
| 1 | 0.182 | 0.000 | 0.818 |
| 2 | 0.159 | 0.124 | 0.717 |
| 3 | 0.143 | 0.112 | 0.745 |
| 4 | 0.148 | 0.099 | 0.753 |
| 5 | 0.149 | 0.102 | 0.749 |
| 6 | 0.148 | 0.103 | 0.749 |
| 7 | 0.148 | 0.103 | 0.749 |

(c) $\lambda_{1}=-0.0549+0.3285 i, \lambda_{2}=-0.0549-0.3285 i, \lambda_{3}=1.0098 ;\left|\lambda_{3}\right|>\left|\lambda_{1}\right|=\left|\lambda_{2}\right|$, thus $\lambda_{3}$ is the dominant eigenvalue; the index of imprimitivity is 1 .
(d) Since the index of imprimivitity is 1 , a structural equilibrium is reached. The eigenvector associated with the dominant eigenvalue gives the population structure at the structural equilibrium:

$$
\left[\begin{array}{l}
0.148 \\
0.103 \\
0.749
\end{array}\right] .
$$

Exercise 9 - Spotted Owl Conservation

(a) | $t$ | $j(t)$ | $s(t)$ | $a(t)$ |
| :---: | :---: | :---: | :---: |
| 0 | 900 | 500 | 2600 |
| 1 | 858 | 162 | 2799 |
| 2 | 924 | 154 | 2746 |
| 3 | 902 | 166 | 2691 |
| 4 | 888 | 163 | 2648 |
| 5 | 874 | 160 | 2605 |

(b) The dominant eigenvalue (and long-term growth rate) is $\lambda=0.9836$. This indicates that the northern spotted owl population will decline over time eventually reaching extinction.
(c) By changing only the survival rate of the juveniles, the Leslie matrix becomes

$$
\left[\begin{array}{ccc}
0 & 0 & 0.33 \\
0.40 & 0 & 0 \\
0 & 0.71 & 0.94
\end{array}\right]
$$

. The new matrix has a dominant eigenvalue (and long-term growth rate) of 1.0286 , which means that the owl population will increase over time and not become extinct.

Exercise 10 - Livestock Management
(a) $\left[\begin{array}{ccc}0 & 0 & 1.2 \\ 0.9 & 0 & 0 \\ 0 & 0.9 & 0\end{array}\right]$
(b) The eigenvalues for the model are $\lambda_{1}=-0.4953+0.8579 i, \lambda_{2}=-0.4953-0.8579 i$, and $\lambda_{3}=0.9906$. Since $\left|\lambda_{1}\right|=\left|\lambda_{2}\right|=\left|\lambda_{3}\right|=0.9906$, the index of imprimitivity is 3 . The population will oscillate with a period of 3 , and decline (slightly) with each period.
(c) The population declining slightly with each period of the oscillation. However, the since 0.9906 is very close to 1 , the decline in the population each cycle will be marginal. We could hypothesize that the population will be relative stable for many years.

Exercise 11 - How often do you oscillate?
(a) (i) $\left[\begin{array}{ccc}0 & 0 & 5 \\ 0.5 & 0 & 0 \\ 0 & 0.5 & 0\end{array}\right]$, (ii) $\lambda_{1}=1.0772, \lambda_{2}=-0.5386+0.9329 i, \lambda_{2}=-0.5386-0.9329 i$; $d=3$; the dominant eigenvalue is 1.0772 , (iii) Oscillates with a period of 3 , but increases with each period.
(b) (i) $\left[\begin{array}{cccc}0 & 1 & 0 & 2 \\ 0.5 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.5 & 0\end{array}\right]$, (ii) $\lambda_{1}=0.8995, \lambda_{2}=-0.8995, \lambda_{3}=0.5559 i, \lambda_{4}=-0.5559 i$; $d=2$; the dominant eigenvalue is 0.8995 , (iii) Oscillates with a period of 2 , but declines each period and will eventually reach extinction.

