

## 5 Koster's Curse

Major concepts:

- **Stage-structured population models** classify individuals by size or other life stages. In many populations size is a better predictor of an individual's demographic contribution to population growth than is age. The **Life cycle graph** is a useful way to understand the demographic processes in stage structured populations.
- The rate at which individuals progress from one stage to the next is captured in the demographic **transition matrix**, which is based on the survival, growth, and fecundity of individuals in different stages.
- The rules of matrix algebra can be used to project the population size over time and calculate the asymptotic growth rate of the population ( $\lambda$ ).
- One use of this demographic model is to investigate various future scenarios, by altering elements of the transition matrix and seeing how that affects the population growth rate.
- For example, one possibility to control the spread of Koster's curse, an invasive shrub in Hawaii might be to introduce herbivorous insects that feed on the plant. The demographic model shows that very large reductions in survival would be necessary to prevent the spread of this species.

In the late 1800s some seeds of the plant *Clidemia hirta* were accidentally introduced onto the island of Fiji, probably with a shipment of coffee plants. *Clidemia* is a shrub in the family Melastomataceae that is native to Central and South America. Normally it is not a common species. It is often found in disturbed sites, but rarely at high density and rarely in the forest understory. However on Fiji things changed. The plant grew prolifically and by the 1920s it became a major pest in coffee and coconut plantations, forming dense monospecific stands that shaded out all of the other vegetation. It is now known as "Koster's Curse", named for the unfortunate person whose coffee plantation was the site of the original introduction. It has spread to most of the Pacific Islands and is listed as one of the 100 worst invasive species in the world.

Like most islands, Hawaii is very susceptible to invasive species. Over 1000 plant species have been identified as invasive in the Hawaiian Islands. Koster's Curse was first observed in Hawaii in 1941 and by the 1980s it had spread to most of the major islands. Its growth and spread has been prolific. On the island of Oahu it covered less than 100 ha in 1950, about 38000 ha in the 1970s and 100,000 ha in 1990s.

Various volunteer groups have attempted to control the plant by pulling it by hand, generally without success. Each fruit produces hundreds of seeds, so even if the aboveground plants are removed, there are often plenty of seeds in the soil to reestablish the population.

Figure 5.1 Koster's Curse, *Clidemia hirta*



<http://tncweeds.ucdavis.edu/photos/clihi01.jpg>

### 5.1 Why has it become invasive?

Dr. Saara DeWalt, then a graduate student at Louisiana State University, wanted to determine why it was so invasive in Hawaii and what could be done about it. She came up with several possible hypotheses. First, perhaps Hawaiian plants are particularly vigorous varieties that grow faster than their counterparts on the mainland. To test that, she grew plants from Costa Rica and Hawaii next to each other in experimental gardens and there was no difference in the growth of the two types. So she could discount that hypothesis.

Perhaps it has escaped from specialist herbivores or parasites that reduce the plant's abundance in its native range? If those herbivores and parasites are not present in Hawaii, then populations of *Clidemia* would grow faster and make the plant "invasive". To test that, she planted test plots in Hawaii and Costa Rica and then experimentally excluded insects and fungi by spraying randomly chosen sets of plants with insecticide, fungicide, or both. She found that on the mainland, there was 5 times more damage to leaves by herbivores than in Hawaii (where less than 1% of the leaf area was damaged). Moreover, the sprayed plants had higher survival, at least in the understory (Fig 5.2). These data suggest that escape from herbivores and pathogens may be part of the reason that the species has become invasive in Hawaii, and part of the reason why it has expanded its ecological range into the forest understory. In Hawaii, there are no native plants from the family Melastomataceae, so the islands have few insects that naturally feed on *Clidemia*.

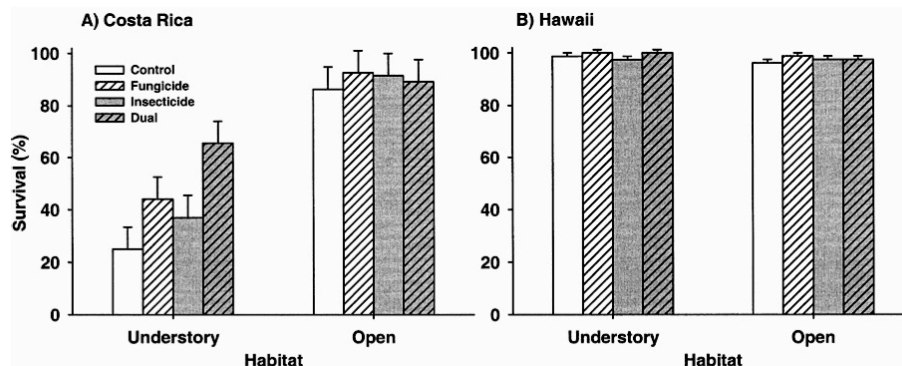


Figure 5.2. Fungicides and insecticides increase survival in understory forests on the mainland but not on Hawaii where overall damage rates are low. (from DeWalt 2004)

From the data in Fig. 5.2, what is the evidence that the survival differences in the Understory in Costa Rica are caused by insect and fungal damage?

Why is there no difference among the treatments in Hawaii?

These results suggest that one approach to control the spread of this aggressive invader would be to introduce insects or pathogens to Hawaii that feed on the plant. There is an active program to identify insects that could be released in Hawaii that feed on *Clidemia*, but at the same time would not threaten native plant species. Several insects appear promising. The thrips *Liothrips urichi* was released in 1953 because it had been shown to be effective in Fiji, at least in open habitats. More recently, other insect species have been identified as candidates to control the spread of *Clidemia*. The fungus *Colletotrichum gloeosporioides* was introduced in 1986 and

appears successful at reducing the survival of infected plants. Here are some of the insects and fungi that are promising candidates as biocontrol agents (Table 5.1):

*Table 5.1 Some potential biological control agents for Clidemia hirta.*

	<b>Species</b>	<b>Feeds on:</b>
Thrips	<i>Liothrips urichi</i>	shoots
Moths	<i>Carposina bullata</i>	flowers and fruits
	<i>Mompha trithalama</i>	flowers and fruits
	<i>Antiblemma acclinalis</i>	leaves
	<i>Ategumia matutinalis</i>	leaves
Beetle	<i>Lius Poseidon</i>	leaves
Fungus	<i>Colletotrichum gloeosporioides</i>	leaves

Of those species, some feed on flowers and fruits and thus reduce the seed production of *Clidemia*. Others feed on leaves and reduce plant growth or survival. We know that both survival and reproduction contribute to the population growth rate, but which is more important? Would it be more effective to reduce the growth of seedlings to adults? or the survival of adults? or the fecundity of adults? In other words, which class of insects is more likely to be an effective biological control agent?

One way to answer that question is to develop a model of population growth of *Clidemia*, and use that model to try out different scenarios. With a model that captures the basic biology of the system, we can systematically alter particular factors (such as fecundity or survival) and see how much of a change is needed to prevent the growth of the population.

So what should the model look like? We want a model with just enough detail to capture the system, but one that is simple enough that it is easy to understand. For this invading species, we are primarily concerned with whether the population will continue growing exponentially or not, so we can initially ignore density dependence. On the other hand, not all individuals are equal. In the previous chapter we used life tables to explore the growth of age-structured populations. Here we will use a different technique based on size rather than age, because sometimes size is a better predictor of the demographic contribution of an individual. That is particularly true for species with indeterminate growth (such as plants). Regardless of their age, the reproductive output and survival of large plants is much higher than that of small plants. So we will need a model that keeps track of large, medium and small plants separately.

## 5.2 Life-cycle graph and stage structured matrices

One of the most useful ways to begin to look at the demography of populations when there are several important life stages is to construct a “life cycle graph”.

Imagine that there is a hypothetical plant species that can be divided into several size classes (small, medium, large, extra large). We’ll imagine that we census the population once a year, and record the fate of each individual.

What are the possible fates of individuals in each size class of plants? Small individuals can either survive and grow to become medium plants, survive but stay small, or die. Thus there is an arrow connecting small plants to the medium size class, and a circular arrow connecting small plants back to the same size class. We do not need an explicit arrow for the dead plants since they are not observed at the next census.

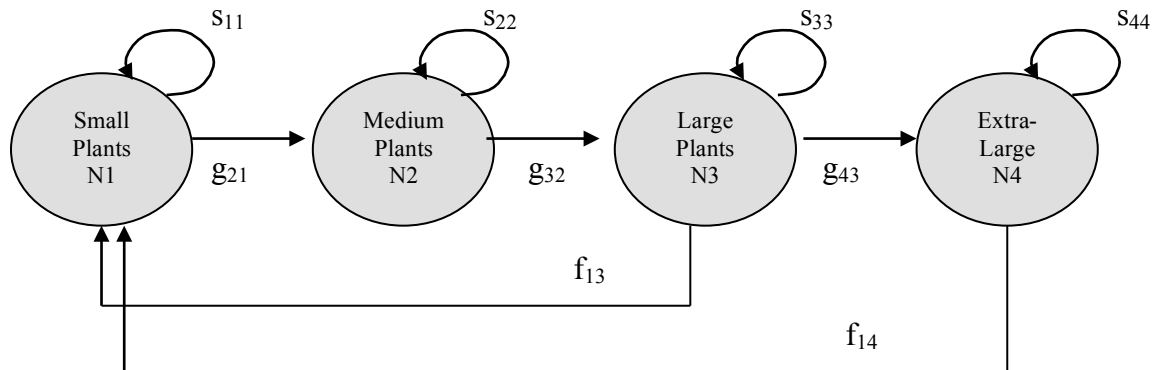


Figure 5.3 An example life cycle graph.

Similarly medium plants can stay at that size or grow to become large plants or die. Large and Extra large plants can also reproduce to produce new small plants, so there are arrows from those sizes back to size 1. The lack of an arrow from size 2 to size 1 in our hypothetical example implies that the medium plants are not yet large enough to reproduce.

In this simple graph, the “g” terms are the probability of surviving and growing into the next size class, the “s” terms are the probability of surviving and staying in the same size class and the “f” terms are the fecundities: the number of seedlings that are produced by each size class *and* survive to be counted in the next census.

This is just one possible life cycle. Under some conditions, it is possible for a plant to grow so fast it traverses two or more size classes in a single year. In that case there would be additional arrows that go directly from size 1 to 3 or from size 2 to 4. Or, sometimes a plant can be eaten or damaged so it loses biomass and shrinks from a larger to a smaller size class. In that case there could be additional arrows pointing backwards from a larger to a smaller size class.

*Steps for constructing the life cycle graph:*

- ♦ Identify the important life stages. Each of the life stages becomes a node on the graph
- ♦ Decide on a census interval (commonly 1 yr).
- ♦ Connect the nodes with arrows showing the possible transitions from one stage to another that can occur during a single census interval.
- ♦ Label the arrows with either the transition probabilities (for survival and growth arrows) or fecundities (for arrows leading back to the first size class).

We can then use the information in this life cycle graph to predict the numbers of individuals in a particular size class at the next census time. For example, what will be the number of medium individuals next year? There are two possible sources. Some individuals that are small plants this year will grow to become medium plants next year, and some individuals that are medium

this year will remain medium plants next year. For this particular life cycle graph there are no other ways to produce medium individuals. Therefore, the number of medium plants next year will be the current number of small plants times the probability that they survive and grow to become medium plants, plus the current number of medium plants times the probability that they survive and stay medium plants.

$$N_{2,t+1} = N_{1,t}g_{21} + N_{2,t}s_{22}$$

What will be the number of small plants next year? There are three possible ways to produce small plants: small plants can stay small, or they can be new recruits that were produced by either large or extra large plants. Thus,  $N_{1,t+1} = N_{1,t}s_{11} + N_{3,t}f_{13} + N_{4,t}f_{14}$ .

We can do the same for each of the size classes and end up with this set of equations:

$$\begin{aligned} N_{1,t+1} &= s_{11}N_{1,t} & + & & + f_{13}N_{3,t} & + f_{14}N_{4,t} \\ N_{2,t+1} &= g_{21}N_{1,t} & + s_{22}N_{2,t} & & & \\ N_{3,t+1} &= & g_{32}N_{2,t} & + s_{33}N_{3,t} & & \\ N_{4,t+1} &= & & g_{43}N_{3,t} & + s_{44}N_{4,t} & \end{aligned} \quad \text{eqs. 5.1}$$

Filling in zeros for all of the possible transition arrows that are not on the life cycle graph, you get

$$\begin{aligned} N_{1,t+1} &= s_{11}N_{1,t} & + 0 N_{2,t} & + f_{13}N_{3,t} & + f_{14}N_{4,t} \\ N_{2,t+1} &= g_{21}N_{1,t} & + s_{22}N_{2,t} & + 0 N_{3,t} & + 0 N_{4,t} \\ N_{3,t+1} &= 0 N_{1,t} & + g_{32}N_{2,t} & + s_{33}N_{3,t} & + 0 N_{4,t} \\ N_{4,t+1} &= 0 N_{1,t} & + 0 N_{2,t} & + g_{43}N_{3,t} & + s_{44}N_{4,t} \end{aligned}$$

You may notice that there is a consistent structure to this system of equations. Each of the equations has set of transition probabilities multiplied by exactly the same set of N's. We can collect all of the transition probabilities into a single matrix (**A**) and collect all of the numbers of individuals into a vector of population size, which we will call **N**. The boldface symbols are used to indicate that **A** and **N** are matrices.

$$A = \begin{bmatrix} s_{11} & 0 & f_{13} & f_{14} \\ g_{21} & s_{22} & 0 & 0 \\ 0 & g_{32} & s_{33} & 0 \\ 0 & 0 & g_{43} & s_{44} \end{bmatrix} \quad \mathbf{N} = \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix} \quad 5.2$$

Using the rules of matrix algebra, we can rewrite that system of equations as the product of two matrices:

$$\begin{bmatrix} N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \\ N_{4,t+1} \end{bmatrix} = \begin{bmatrix} s_{11} & 0 & f_{13} & f_{14} \\ g_{21} & s_{22} & 0 & 0 \\ 0 & g_{32} & s_{33} & 0 \\ 0 & 0 & g_{43} & s_{44} \end{bmatrix} \begin{bmatrix} N_{1,t} \\ N_{2,t} \\ N_{3,t} \\ N_{4,t} \end{bmatrix} \quad \text{eq. 5.3}$$

so this whole set of equations can be written as simply:

$$\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t \quad \text{eq. 5.4}$$

Why do we bother putting this into a matrix form? There are several advantages. First, it clearly separates the demographic and life history information that is contained in matrix  $\mathbf{A}$  from the population numbers, contained in  $\mathbf{N}$ . Regardless of the starting conditions or the particular population size, the eventual *dynamics* depends only on the transition probabilities in matrix  $\mathbf{A}$ . Second, it is easy to change the elements of  $\mathbf{A}$  to reflect changes in the biology, but the basic formulae and analytical procedures stay exactly the same. The matrix formulation is applicable to any system simply by changing the values and or dimensions of the matrices. Finally, if you know matrix algebra you can take advantage of those well-developed analytical tools to solve the system of equations and analyze the population dynamics.

### 5.3 The data

In order to estimate the transition probabilities between size classes, it is necessary to mark individuals and monitor them for several years. DeWalt chose two study sites, Waiakea and Laupahoehoe, both on the big island of Hawaii. At each site she marked and measured 300 plants in June of 1998 in a small rectangular plot. Then she returned each summer for three consecutive years to follow the fate of those plants. Each year she revisited each of the marked plants and determined the size of each surviving plant by measuring its height and stem diameter. She also counted and marked all of the new seedlings that appeared.

For analysis, she divided the plants into five size classes based on their biomass. Her life cycle graph for *Clidemia* looked like this:

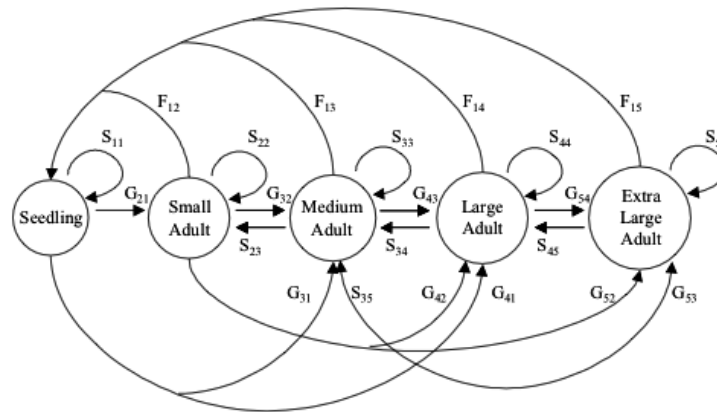


Figure 5.4 DeWalt's life cycle graph for *Clidemia hirta*.

This graph includes all possible transitions between size classes. Determining the growth and survival transition probabilities was straightforward. Because she knew the size of each individual each year, she could simply count the number of individuals that grew from one size class to the next. Thus  $g_{21}$  is simply the number of plants that survived and grew from size 1 to size 2, divided by the total number of plants that were in size class 1 at the previous census. Similarly,  $s_{11}$  is simply the proportion of size 1 plants that were still alive and in size 1 the next year.

Determining fecundity was slightly more complicated. From other plants at nearby sites, she developed a prediction equation that she could use to predict the biomass and number of seeds produced as a function of plant size. She then allocated the total number of new seedlings to the proportional contribution of each size plant. Therefore the fecundity arrows incorporate both the total seed production and the fraction of seeds that survive to be counted as seedlings in the next census.

#### 5.4 Model parameters for *Clidemia*

From her censuses of the *Clidemia* population at Laupahoehoe, DeWalt was able to determine the transition probabilities from each stage class to all others. For this population some of the transition probabilities were zero, because they were never observed. Most of the growth transitions were increases from one size class to the next larger class. Occasional plants grew very quickly and were able to skip a stage. A few other plants lost size and moved to a smaller size class (growth transitions above the diagonal).

Table 5.2. Transition matrix for the Laupahoehoe population of *Clidemia*. Reproductive transitions are shown in green, survival and stasis in bright blue, and growth transitions are shown in dark blue.

		This year				
		Seedling <10 g	Small 10-50 g	Medium 50-100 g	Large 100-200g	Extra- large >200 g
Next year	Seedling	0.56	0.47	2.71	5.48	14.75
	Small	0.24	0.22	0.02	0.00	0.00
	Medium	0.05	0.26	0.18	0.02	0.01
	Large	0.02	0.35	0.52	0.36	0.04
	Extra- large	0.00	0.05	0.27	0.62	0.95

In normal mathematical form, the transition matrix for Laupahoehoe is

$$\mathbf{A} = \begin{bmatrix} 0.56 & 0.47 & 2.71 & 5.48 & 14.75 \\ 0.24 & 0.22 & 0.02 & 0.00 & 0.00 \\ 0.05 & 0.26 & 0.18 & 0.02 & 0.01 \\ 0.02 & 0.35 & 0.52 & 0.36 & 0.04 \\ 0.00 & 0.05 & 0.27 & 0.62 & 0.95 \end{bmatrix}$$

What is the meaning, in words, for the fourth element in row 1 (it has the value 5.48)?

Use the numbers from that transition matrix to label the magnitude of each arrow in the life cycle graph for *Clidemia* (Fig 5.4).

In order to predict the number of plants in future years, we need to specify the starting conditions. Let  $\mathbf{N}_0$  be:

$$\mathbf{N}_0 = \begin{bmatrix} 223 \\ 37 \\ 23 \\ 13 \\ 12 \end{bmatrix}$$

How many extra-large plants are present at time zero? \_\_\_\_\_



Now, using equation 5.4 and the rules for multiplying matrices (Appendix 5A), we can compute the number of plants in each size class in the next generation:

$$\mathbf{N}_1 = \mathbf{A}\mathbf{N}_0$$

$$\begin{bmatrix} 452.8 \\ 62.1 \\ 25.2 \\ 34.5 \\ ??? \end{bmatrix} = \begin{bmatrix} 0.56 & 0.47 & 2.71 & 5.48 & 14.75 \\ 0.24 & 0.22 & 0.02 & 0.00 & 0.00 \\ 0.05 & 0.26 & 0.18 & 0.02 & 0.01 \\ 0.02 & 0.35 & 0.52 & 0.36 & 0.04 \\ 0.00 & 0.05 & 0.27 & 0.62 & 0.95 \end{bmatrix} \begin{bmatrix} 223 \\ 37 \\ 23 \\ 13 \\ 12 \end{bmatrix} \quad \text{eqs. 5.5}$$

As a check on your understanding of eqs. 5.5, how did we get the number of size 2 individuals next year (62.1)? Those plants can be seedlings that grew from size 1 to size 2, plants that remained size 2, or a few plants that shrunk from size 3 to size 2.  $62.1 = 0.24 \cdot 223 + 0.22 \cdot 37 + 0.02 \cdot 23$ .

Using the same rules for multiplying matrices, fill in the last element of  $\mathbf{N}$ . How many extra large plants are predicted at the next time step? \_\_\_\_\_

To project the population size at time 2, we simply need to use the population size at time 1 as input and multiply it by the same transition matrix:  $\mathbf{N}_2 = \mathbf{A}\mathbf{N}_1$ . We can project the population size for as many generations into the future as we want using the relationship:  $\mathbf{N}_t = \mathbf{A}\mathbf{N}_{t-1}$ . Here are the first 10 generations:

Table 5.3. Population projection for *Laupahoehoe*:

Time	Seedlings	Small	Medium	Large	Extra-Large	Total	$N_{t+1}/N_t$
0	223	37	23	13	12	308.0	--
1	452.8	62.1	25.3	34.5	27.5	602.3	1.96
2	946.4	122.9	44.3	57.5	57.5	1228.5	2.04
3	1870.5	255.1	89.0	108.0	108.3	2430.9	1.98
4	3597.9	506.8	179.1	216.1	206.6	4706.5	1.94
5	6969.9	978.6	350.3	428.5	403.9	9131.2	1.94
6	13618.2	1895.1	678.6	834.5	792.8	17819.1	1.95
7	26622.2	3698.8	1320.4	1620.6	1548.2	34810.2	1.95
8	51942.4	7229.5	2578.4	3159.0	3016.5	67925.8	1.95
9	101278.2	14108.2	5034.2	6167.8	5880.9	132469.4	1.95
10	197532.6	27511.3	9820.4	12036.9	11473.6	258374.8	1.95

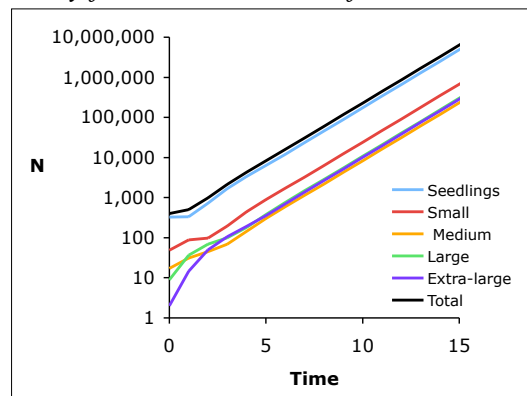
Notice that this is an exponential growth model, so the population will continue to grow without bounds. The population growth rate,  $\lambda$  ( $= N_{t+1}/N_t$ ) fluctuates a little bit for the first few generations, but eventually stabilizes at  $\lambda = 1.95$ . That is the asymptotic growth rate for this

population.<sup>1</sup> Lambda is a property of the transition matrix, **A**. Any population with a particular transition matrix will eventually grow at the same rate, regardless of the starting conditions.

The population obviously cannot keep growing at that rate forever. So, what our model is doing is making a “projection” of what *would* happen to the population *if* all of the demographic rates stay the same. (That is different from a “forecast” of the actual population size some time in the future.) Nevertheless  $\lambda$  is a useful way to describe the growth potential of the population under the current transition probabilities.

The change in numbers of plants in each size class is shown in Figure 5.5. The rate of increase is linear on the graph of  $\log(N)$  vs. time, which is typical of exponential growth. You can also see that the growth trajectories for plants in each size class are parallel. Just as an age-structured model will eventually settle into a stable age distribution, this stage-structured model eventually achieves a stable stage distribution. After several generations the proportion of seedlings, small, medium, and large plants is consistently 76%, 11%, 4%, 5% and 4% of the population.

Figure 5.5. Population trajectory for each size class of *Clidemia hirta* at Laupahoehoe.



### 5.5 Does this model capture the observed changes in density at Laupahoehoe?

Our demographic model predicts an asymptotic growth rate of  $\lambda=1.95$ . How does that match the observed population dynamics at Laupahoehoe? Here are her results of the observed population size and the predicted size given a growth rate of 1.95. As you can see, this is a population that appears to be growing approximately exponentially, as predicted by our simple model.

Given the predicted asymptotic growth rate of  $\lambda=1.95$  and a starting density of 1655 plants per hectare, predict the number of plants in the next three years. How does that match the observed density?

Table 5.4 Observed and predicted plant density for *Clidemia* at Laupahoehoe.

Year	Observed density per ha	Predicted, $\lambda=1.95$
1998	1655	1655
1999	3154	<input type="text"/>

<sup>1</sup> If you know matrix algebra,  $\lambda$  is the dominant eigenvalue of the transition matrix **A**.

2000	5935	
2001	13623	

(Disclaimer: this is a circular test, because the demographic rates were in part determined by the observed changes in population size. But the dynamics based on the transition probabilities are at least consistent with the observed changes in abundance)

### 5.6 Use the model to investigate various scenarios

Now we are finally ready to actually use our model to answer our original questions! Remember that our initial motivation was to assess whether herbivorous insects could control the growth of *Clidemia* populations. Now that we have a model that captures the current population dynamics of *Clidemia* at Laupahoehoe, we can use it to ask “what if” questions about possible ways to control the spread of *Clidemia*. In particular, we want to evaluate whether biological control insects that feed on flowers and fruits (and thus reduce fecundity) will be more or less effective than leaf-feeding insects or fungi that reduce survival. Under current conditions, the population is projected to almost double each year ( $\lambda=1.95$ ). However, if the biological control insects could reduce  $\lambda$  to less than 1.0, the population would be predicted to eventually go extinct.

#### Scenario 1: reduce fecundity

If flower-feeding insects are introduced to control *Clidemia*, we expect the fecundities to be reduced. From eq. 5.2, those are the quantities in the top row of matrix **A**, (except for  $A_{11}$  because we assume that seedlings are too small to reproduce). How much of a reduction in fecundity would be required to produce  $\lambda < 1.0$ ?

To test that scenario, we can imagine that all of the fecundity elements are reduced by  $x\%$  and determine what the asymptotic population growth rate would be. We can then vary the level of fecundity reduction to see how large a reduction is necessary to produce  $\lambda < 1.0$ .

Table 5.5 Potential effect of biocontrol insects that reduce fecundity.

Fecundity reduction	$\lambda$
10%	1.90
20%	1.86
50%	1.69
75%	1.49
90%	1.30
99%	1.06

For this population, even a 99% reduction in fecundity would not be enough to cause extinction of *Clidemia*, but it may be possible to slow the rate of population growth.

#### Scenario 2: reduce growth transitions

We'll assume that leaf-feeding insects primarily reduce the growth rate of the plants.

Which elements of the transition matrix show *growth* from one stage to the next?

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Again we can hypothetically reduce the growth transitions by 10, 20, 30% and see what effect that has on the projected population growth rate.

Table 5.6

Growth reduction	$\lambda$
10%	1.85
20%	1.75
50%	1.42
75%	1.13
90%	0.98
99%	0.95

The hypothetical reductions in growth are more effective. It is possible to drive the population extinct if the leaf damage is sufficient to reduce growth by 90%, but that would probably require a very high density of leaf-feeding insects.

### Scenario 3: reduce survival

Third, we might assume that pathogenic fungi and or leaf-feeding insects reduce the survival of *Clidemia*. That would affect all of the non-fecundity transition elements. How much of a decrease in survival would be necessary to control the population?

Table 5.7

Survival reduction	$\lambda$
10%	1.79
20%	1.63
50%	1.14
60%	0.96
75%	0.68

Try out some other possible scenarios for controlling *Clidemia*. One possibility is to hand-pull all of the large and extra large plants (so the survival of those largest plants is close to 0).

How would you modify the transition matrix to model the effect of hand pulling large and extra large plants? \_\_\_\_\_

How effective would that strategy be? \_\_\_\_\_

Another possibility might be releasing both flower-feeding and leaf-feeding insects at the same time. Would that be more effective in controlling *Clidemia*? \_\_\_\_\_

We have used the stringent criterion of  $\lambda < 1.0$  as our definition of “control”. While local extinction would be nice, smaller reductions in  $\lambda$  may also be worthwhile.

### 5.7 Other considerations

The projected growth rate for this model is an asymptotic growth rate. Eventually the rate of increase will converge on the asymptotic growth rate, but the first few generations may be quite different. It will only reach the asymptotic  $\lambda$  when the number of plants in each stage is at the stable stage distribution. What use is asymptotic lambda when modeling a rapid invasion, a situation that is clearly not at a steady state?

In addition, there is no density dependence in our matrix model. The projections show the population quickly increasing to extremely large population size, and density dependent limitations on growth will almost surely become important before the asymptotic growth rate is achieved. So as an explicit prediction about the fate of a particular population and its future size this model is probably not very useful. Instead the model tells us about the current growth *potential* of the population. We can then use that index of growth potential to compare the *relative* effectiveness of two scenarios, or to determine which life cycle stages have the greatest effect on population growth.

### 5.8 Your turn:

DeWalt also collected demographic data for another site on Hawaii, Waiakea, where the population was growing less quickly. Here is her transition matrix for Waiakea. How effective would the biocontrol insects be at stopping the spread of *Clidemia* at this site? Which type would be most effective?

Table 5.8. Transition matrix for *Clidemia hirta* Waiakea (from DeWalt 2004).

		This year				
		Seedling <10 g	Small 10-50 g	Medium 50-100 g	Large 100-200g	Extra- large >200 g
Next year	Seedling	0.78	0.26	0.93	1.99	3.12
	Small	0.18	0.61	0.07	0.00	0.00
	Medium	0.00	0.33	0.51	0.03	0.03
	Large	0.00	0.05	0.42	0.67	0.00
	Extra- large	0.00	0.00	0.00	0.30	0.97

Use the information in this matrix to sketch a life-cycle diagram for *Clidemia* at Waiakea.

Assume that the population starts with 120 seedlings, 20 small plants, and 5 each of medium, large and extra large plants. What is the projected asymptotic growth rate of this population if it continues as is? (project the population size for at least 3 generations).

Try out one scenario for control and see if it will be effective at reversing the population growth of *Clidemia* at this site.

**5.9 Further reading:**

- Caswell, H. 1989. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts, USA
- DeWalt, S J. 2004. Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. *Ecology* 85:471-483.
- DeWalt, S. 2006. Population dynamics and potential for biological control of an exotic invasive shrub in Hawaiian rainforests. *Biological Invasions* 8:1145-1158.
- Shea, K. and D. Kelly. 1998. Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications* 8: 824-832

**5.10 Practice Problems (will add 5-10 questions here)**

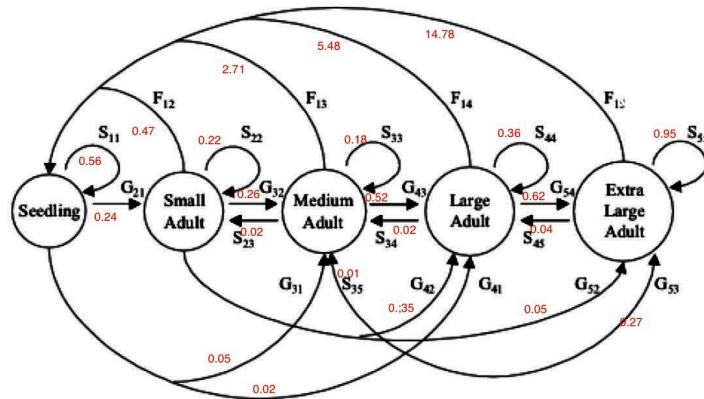
**Answers**

p. 2 The key inference from Figure 5.2 is that in the Costa Rica understory plant survival is higher when they are sprayed with fungicide or insecticide. The comparison of the experimental treatments to the control allowed her to detect the survival increase when insects and fungi are excluded.

In Hawaii, survival is high for all plants and there is no difference among treatments. Presumably that is because the damaging insects and fungi are not present.

p 8. Element A[1,4] gives the transition from large plants to seedlings.

It is the expected fertility of large plants: the number of seeds that they produce that then survive to be counted as seedlings in the next census.



There are 12 extra large plants at time 0.

p 9. After one time step, there will be 27.52 extra large plants.  $(0 \cdot 223 + 0.05 \cdot 37 + 0.27 \cdot 23 + 0.62 \cdot 13 + 0.95 \cdot 12 = 27.52)$ .

p 10

Year	Obs.	Predicted, $\lambda=1.95$
1998	1655	1655
1999	3154	3227
2000	5935	6293
2001	13623	12272

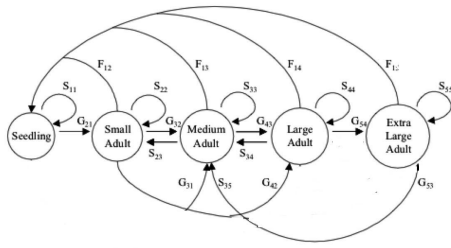
p 11. The growth transition elements of **A** are all of the elements below the diagonal.

p 12. To model hand-pulling of large and extra large plants, you could reduce the transition elements in the fourth and fifth columns of **A**. If you assume that 100% are pulled up before they reproduce, then all of the elements in those columns would become 0.

In that case the asymptotic growth rate becomes  $\lambda=1.07$ . The population would still be growing, but much more slowly.

If you want to model the inclusion of both flower and leaf feeding insects (i.e. reduce growth and survival) you could reduce all of the transition elements below the first row.

p 13. Your Turn: the Waiakea population.  
Lifecycle graph for Waiakea:



After 3 generations,  $\lambda=1.3$ . The asymptotic estimate is  $\lambda =1.33$



### 5.11 Appendix A: General rules for multiplying matrices

Assume there is a matrix **A** with  $k$  rows and  $m$  columns, and a matrix **B** with  $m$  rows and  $n$  columns. By convention, boldface symbols are used to indicate that **A**, **B**, and **Y** are matrices.

The product of those two matrices will have dimensions  $k \times n$ .

In symbols, we can write that as  $\mathbf{Y}_{k \times n} = \mathbf{A}_{k \times m} \mathbf{B}_{m \times n}$

To find the element  $\mathbf{Y}_{ij}$ , you sum the products of the elements in row  $i$  of **A** and the corresponding elements of column  $j$  of **B**.

$$\mathbf{Y}_{ij} = \sum_k^m \mathbf{A}_{ik} \mathbf{B}_{kj}$$

Here is a numerical example:

$$\begin{bmatrix} 22 & 28 \\ \mathbf{49} & 64 \\ 76 & 100 \\ 103 & 136 \end{bmatrix} = \begin{bmatrix} 1 & 2 & 3 \\ \mathbf{4} & \mathbf{5} & \mathbf{6} \\ 7 & 8 & 9 \\ 10 & 11 & 12 \end{bmatrix} \cdot \begin{bmatrix} \mathbf{1} & 2 \\ \mathbf{3} & 4 \\ \mathbf{5} & 6 \end{bmatrix}$$

The element in the second row and first column of **Y** ( $\mathbf{Y}_{21}$ ) is the sum of the products of elements in the second row of **A** and the first column of **B**:  $4*1 + 5*3 + 6*5 = 49$ . Similarly, the element in the third row and second column of **Y**, will be the sum of the products of elements in the third row of **A** and the second column of **B**:  $7*2 + 8*4 + 9*6 = 100$ .

Often one of the matrices will have a single row or column, but the general procedure is exactly the same. If matrix **B** has only a single column then **Y** will also have only a single column. But just as before, the element in the third row and first column of **Y** will be the sum of the products of the elements in the third row of **A** and the first column of **B**.

$$\begin{bmatrix} . \\ . \\ \mathbf{50} \\ . \end{bmatrix} = \begin{bmatrix} 1 & 2 & 3 \\ 4 & 5 & 6 \\ \mathbf{7} & \mathbf{8} & \mathbf{9} \\ 10 & 11 & 12 \end{bmatrix} \cdot \begin{bmatrix} \mathbf{1} \\ \mathbf{2} \\ \mathbf{3} \end{bmatrix}$$

$$7*1 + 8*2 + 9*3 = 50.$$

What are the other three elements of **Y** in this example? \_\_\_\_\_

Notice that the dimensions must be compatible. To multiply matrices, the number of columns of the first matrix must equal the number of rows of the second. The result will have the same number of rows as the first matrix and the same number of columns as the second.

Therefore  $\mathbf{A}_{4 \times 3} \mathbf{B}_{3 \times 1}$  is valid because the number of columns of **A** and rows of **B** match. The reverse ( $\mathbf{B}_{3 \times 1} \mathbf{A}_{4 \times 3}$ ) is not allowed.

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Answer:  $\mathbf{Y}' = [14, 32, 50, 68]$