

# POPULATION VIABILITY ANALYSIS

## Introduction

Over the last few lectures we've talked about the stochastic threats to persistence in small populations. We identified five classes of threats and some of their qualitative properties:

1. Genetic stochasticity — Not a problem in populations with  $N_e$  greater than a few hundred. Therefore, not likely to be a problem in populations large enough to buffer environmental stochasticity
2. Demographic stochasticity — Unlikely to be a problem in populations with more than 50–100 individuals
3. Environmental stochasticity — Likely to be a problem unless population sizes are on the order of 1000–10,000
4. Demographic heterogeneity — In the one case I am aware of where the magnitude of environmental stochasticity, demographic stochasticity, and demographic heterogeneity were compared, demographic heterogeneity contributed more to variability in population growth rate than either of the other two, suggesting that populations must be on the order of several thousand to buffer against this source of heterogeneity.
5. Natural catastrophes — No single populations can ever be large enough to buffer against natural catastrophes

These general guidelines are useful, but suppose you're asked to design a recovery plan for the northern spotted owl.<sup>1</sup> How do you go about determining

- How many breeding pairs are necessary to provide a reasonable chance of long-term survival?
- What are the prospects for *increasing* the number of breeding pairs?

---

<sup>1</sup>We'll talk in some detail about the northern spotted owl next time.

- What management manipulation will be most necessary to prevent extinction?
- What are the most critical stages of the life-cycle, i.e., have the largest impact on population dynamics?

Recall that the models we've discussed so far are based on very general assumptions. To answer these questions for *any* specific species, perhaps even for any *population*, a demographic model describing the dynamics of *that* species or population is necessary. The approach a conservation biologist takes to answering is (or should be) the same that a population ecologist takes to answering those questions.

1. Identify life history stages.<sup>2</sup>
2. Determine rates of transition between these life history stages.
3. Project future population sizes from these observations.

There are, however, two significant differences between how conservation biologists and population biologists approach their tasks.

1. Population biologists choose a particular species for study, at least in part, because they think that the species they have chosen will allow them to address broad, general issues of conceptual importance in population biology. Conservation biologists have the species chosen for them by circumstances — the circumstances of endangerment.

One consequence of this difference is that it may be much more difficult for conservation biologists than for population biologists to get complete demographic information.<sup>3</sup> Population biologists choose species that allow them to get the information they need. Conservation biologists have to figure out how to get the information they need from species that were chosen for them.

2. Population biologists are often satisfied with discovering the factors that limit population size, population growth rate, or species distribution. Conservation biologists *use* that information to project the fate of populations/species and to decide among management strategies. That requires conservation biologists to squeeze a lot more from their data than population biologists typically do.

---

<sup>2</sup>Recently, population ecologists have begun to use integral projection models [3] that don't require you to specify discrete life-history stages. We won't discuss them here, but feel free to ask me about them if you're interested.

<sup>3</sup>We'll return to approaches conservation biologists can use to overcome the information deficit they face. But for the next hour or two, we're going to ignore this problem.

How do we do those projections? Well, we've noted over the last couple of lectures that there are many stochastic processes that affect population size. We can't just measure birth and death rates and make a simple projection. We have to take account of the variability in birth and death rates. Two principles guide our approach.

1. Any finite population will eventually go extinct.
2. We cannot predict population size with certainty. We can only specify the probability of particular outcomes.

## Population Viability Analysis

Population viability analysis (PVA) began life as an attempt to answer the question, "How large must a population be for it to have a reasonable chance of survival for a reasonably long period of time?" A reasonable chance of survival was often taken as 95%.<sup>4</sup> A reasonably long period was often taken to be 100 years.<sup>5</sup> In its early life population viability analyses were used in an attempt to identify the smallest population that would have a reasonable chance of survival for a reasonable period of time—the minimum viable population size (MVP). Although, as we'll see, assessing the viability of any population is far from easy, estimating an MVP may be a useful exercise because it crystallizes several other ideas:

- It identifies the *population* as the critical unit for conservation purposes.<sup>6</sup> Until about 25 years ago conservationists tended to focus only on protecting land, not on managing the populations of plants and animals that occur there. Moreover, even with the recent shift in emphasis to "ecosystem-level" conservation, we mustn't forget that the species that make up an ecosystem are found in populations, and management of some populations may still be necessary.
- The term "viability" stresses that we're concerned with persistence of the population over some reasonably long period of time. Furthermore, it emphasizes that we're interested in the prospects that the population can be self-sustaining.
- The idea of "minimum" emphasizes the idea that there are certain critical aspects of the interaction of a species with its environment. If the population gets too small, it

---

<sup>4</sup>For no better reason than we accept a 95% confidence level as "reasonable" evidence against a null hypothesis in statistical tests.

<sup>5</sup>For no better reason than that 10 years seemed too short and 1000 years seemed unrealistic.

<sup>6</sup>We'll see later that this restriction gets broadened to include sets of interacting populations. These sets of interacting populations are known as metapopulations.

may no longer be able to cope. There may be a threshold below which a population is doomed to extinction. That it has survived its current decline is not evidence that it can suffer a further decline.

There are, however, several problems associated with the idea of *minimum* viable populations.

1. The first is the practical problem that if we identify the minimum size of a population that is sufficient for conservation purposes, that's all we're likely to get.
2. The second, and more fundamental, is that because of the enormous uncertainties associated with forecasting the fate of populations,<sup>7</sup> we're unlikely to be able to provide a good estimate of an MVP. Unless MVPs are determined with a large safety factor, specifying an MVP might actually promote extinction, rather than retard it.
3. Morris and Doak [6, p. 43] go so far as to argue that "no good PVA should attempt to evaluate the risk of utter extinction." There are so many things that can go wrong and so many uncertainties that we're better off focusing on *quasi-extinction*, the number of individuals below which the population is likely to be immediately and critically imperiled.
4. Perhaps most fundamentally of all, populations of a species may cease performing the ecological functions they provide well before they become extinct. Kent Redford [7] points out, for example, that a botanically intact forest will cease to exist if the animal communities responsible for pollination and seed dispersal go extinct or become so rare that pollination and seed dispersal success declines to a point where it is insufficient to allow their persistence.<sup>8</sup>

Today we'll be talking about the principles of population viability analysis. Over the following two lectures we'll examine two applications of the principles: the northern spotted owl and the bay checkerspot butterfly. What we've seen in the last several lectures reminds us that we'll need to take account of stochastic processes in these populations. Before we can start talking about including that stochasticity, however, we have to take a detailed look at the deterministic models to which we will add probabilistic components. Today I'll give

---

<sup>7</sup>Some of which we've already seen and more of which we're about to encounter.

<sup>8</sup>More precisely, those components of the community that depend on these animals will go extinct. Other components may persist, but the community that persists will be quite different from the one currently in place.

an overview of age- and stage-structured demographic models, because they are the most widely used and most widely applicable.<sup>9</sup> There are several reasons for doing this:

1. You have to have a good understanding of the basic model before you can understand what it's like when randomness is added to it.
2. Recall that many threats to population persistence are systematic. Analysis of deterministic a model helps to identify those systematic threats, especially if they're not immediately obvious.
3. Analysis of a deterministic model also allow us to identify the life-history stages that are most critical in determining individual abundance so that we can focus management efforts where they are likely to be most successful.
4. Even if a complete PVA is not necessary or possible, knowing what one would include helps to structure thinking about management options and leads to the design of management programs that can be expanded into a full PVA if needed.

## Leslie matrix models

The simplest model is one first described Lotka in the 1920's and formalized in the 1940's by Leslie. It is based on age-specific survival and fecundity rates.<sup>10</sup>

$p_i$	probability of surviving from age $i$ to age $i + 1$
$f_i$	number of offspring per individual of age $i$
$n_i^{(t)}$	number of individuals in age class $i$ at time $t$

We take  $n_0^{(t)}$  as the number of newly-born individuals at time  $t$ . Thus

$$n_0^{(t+1)} = \sum_{i=0}^T n_i^{(t)} f_i \quad ,$$

---

<sup>9</sup>Insects and annual plants, though they pose their own problems for conservationists, are fairly simple to deal with demographically.

<sup>10</sup>The discussion of Leslie and Lefkovitch matrices found here draws extensively on material in [1, Chapters 2–4].

where  $T$  is the maximum age to which individuals can survive. The number of individuals in other age categories is determined purely by the number of individuals that survive from the preceding year. Specifically,

$$n_i^{(t+1)} = p_{i-1}n_{i-1}^{(t)} \quad .$$

This completely specifies the demographics of the population, assuming for the moment that the  $p_i$  and  $f_i$  don't vary from one year to the next. This can be written in matrix form as

$$\begin{pmatrix} n_0^{(t+1)} \\ n_1^{(t+1)} \\ n_2^{(t+1)} \\ \vdots \\ n_T^{(t+1)} \end{pmatrix} = \begin{pmatrix} f_0 & f_1 & f_2 & \cdots & f_T \\ p_0 & 0 & 0 & \cdots & 0 \\ 0 & p_1 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & p_{T-1} & 0 \end{pmatrix} \begin{pmatrix} n_0^{(t)} \\ n_1^{(t)} \\ n_2^{(t)} \\ \vdots \\ n_T^{(t)} \end{pmatrix}$$

More compactly

$$\begin{aligned} \mathbf{n}^{(t)} &= \mathbf{A}\mathbf{n}^{(t-1)} \\ &= \mathbf{A}^t\mathbf{n}(0) \end{aligned}$$

This model is usually referred to as a Leslie matrix model. It's important properties (as far as we're concerned) are:

- All yearly age classes are identified, each with their own age-specific survival and fecundity rates.
- All members of a year class have the same probability of surviving to the next year and produce the same number of offspring.<sup>11</sup>
- *Linear* — The population will either grow geometrically or decline geometrically
- Mathematical properties
  - All age classes eventually grow (or shrink) at the same rate

---

<sup>11</sup>In the models we'll be considering today, we also ignore demographic stochasticity, so the probability of surviving from one year to the next is equal to the fraction that actually survive. Notice that we're also ignoring demographic heterogeneity, i.e., the possibility that the probabilities in the matrix may vary from individual to individual.

- Initial growth depends on the age structure of the population
- Early reproduction contributes much more to population growth rate than late reproduction.

In humans a woman who has three children starting at age 15 contributes as much to population growth as one who has five children starting at age 30.

## Lefkovitch matrix models

Although Leslie matrix models have the longer history, an alternative approach introduced in the mid-1960's by Lefkovitch is often more useful. Rather than being based on *age*-specific survival and fecundity rates, it is based on *stage*-specific survival rates. Lefkovitch models are often more useful for several reasons:

- It's often difficult or impossible to age animals and plants accurately.
- In some organisms, especially perennial plants, survivorship and fecundity are more closely related to size (or some other variable by which a population might be stage-classified) than to age.
- In some organisms, especially herbaceous perennial plants, individuals may actually revisit stages they already left, e.g., they may get smaller from one season to the next.
- Focusing on life-cycle stages helps to focus attention on identifying the critical life-history transitions that may provide opportunities for management.

## Constructing a life-cycle graph

The easiest way to understand Lefkovitch models is to talk about the construction of a *life cycle graph*.

1. Choose a *projection interval*, commonly a year.
2. Identify life-cycle stages and define a node for each.
3. Draw a directed line from each node to any other node into which it can move in a single time step.
4. Label each line with a coefficient reflecting either the probability of the transition or reproductive outputs (for lines leading to the initial life stage).

You can see an example of this in the life cycle graph for teasel (Figure 1).

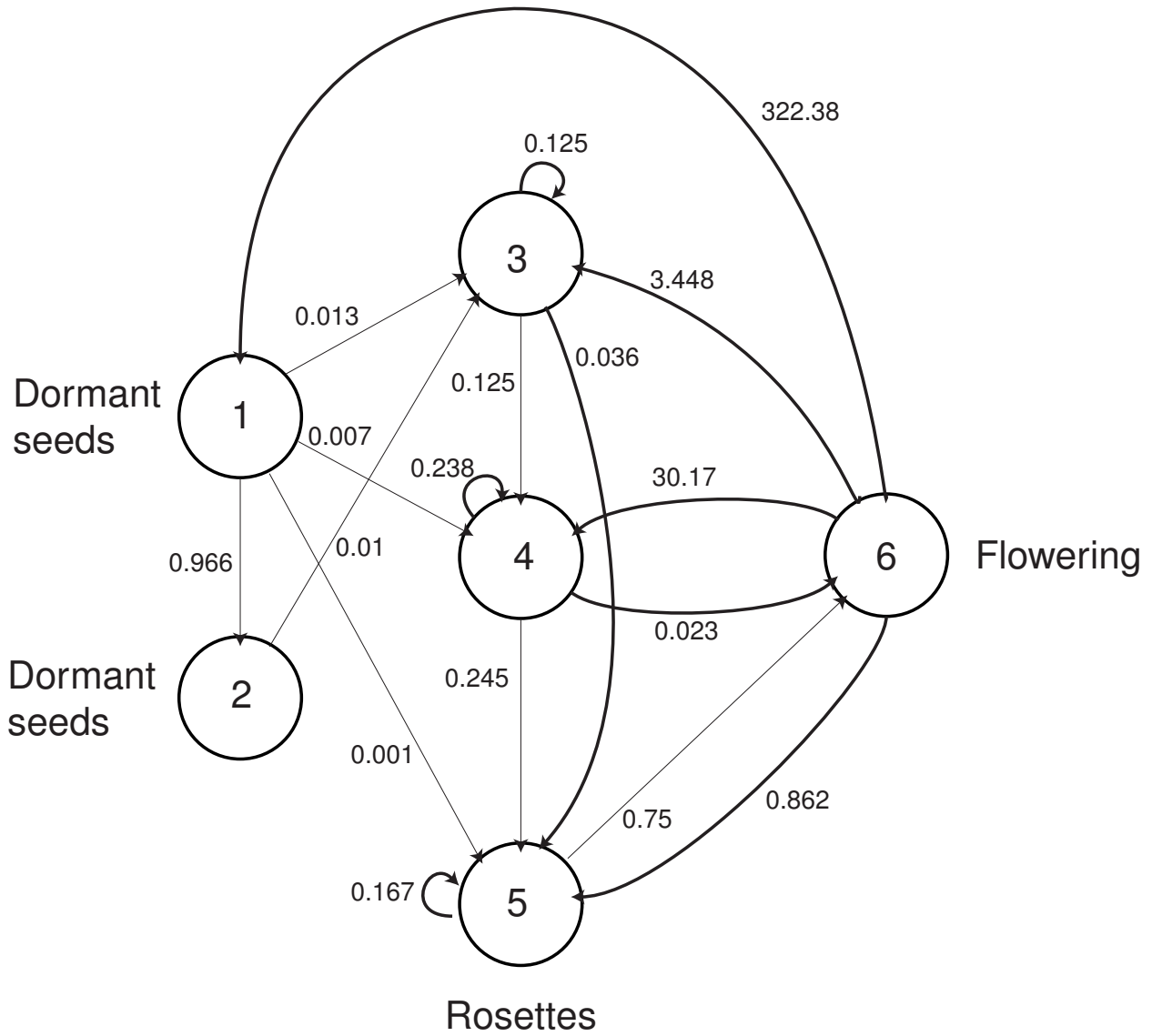


Figure 1: A life cycle graph for teasel (*Dipsacus sylvestris*, redrawn from Figure 4.4 of [1]).

## Converting a life-cycle graph to a matrix

This life cycle graph can be translated into a matrix,  $\mathbf{A}$ , and the number of individuals in the next time step can be calculated as

$$\mathbf{n}^{(t)} = \mathbf{A}\mathbf{n}^{(t-1)}$$

(cf. the equation for Leslie matrices). The matrix corresponding to the life-cycle graph in Figure 1 is:

$$\begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 322.38 \\ 0.966 & 0 & 0 & 0 & 0 & 0 \\ 0.013 & 0.010 & 0.125 & 0 & 0 & 3.448 \\ 0.007 & 0 & 0.125 & 0.238 & 0 & 30.170 \\ 0.001 & 0 & 0.036 & 0.245 & 0.167 & 0.862 \\ 0 & 0 & 0 & 0.023 & 0.750 & 0 \end{pmatrix}$$

## A Digression into Matrix Algebra

One way to project the behavior of populations with these matrices is simply to write a little program, throw in the numbers and see what happens. It is possible, however, to be a bit more sophisticated. For any  $n \times n$  matrix  $\mathbf{A}$  there are  $n$  pairs of scalars  $\lambda_k$  and vectors  $\mathbf{x}_k$  satisfying the following equation

$$\mathbf{A}\mathbf{x}_k = \lambda_k\mathbf{x}_k$$

The  $\lambda_k$  are conventionally numbered from the largest in absolute value to the smallest, and  $\lambda_k$  is referred to as the  $k$ th eigenvalue, while  $\mathbf{x}_k$  is the corresponding eigenvector.

Let  $\mathbf{X}$  be the  $n \times n$  matrix in which column  $k$  is composed of  $\mathbf{x}_k$ , and let  $\mathbf{\Lambda}$  be a diagonal matrix in which the  $k$ th diagonal element is  $\lambda_k$ .<sup>12</sup> Then

$$\begin{aligned} \mathbf{A}\mathbf{X} &= \mathbf{X}\mathbf{\Lambda} \\ \mathbf{A} &= \mathbf{X}\mathbf{\Lambda}\mathbf{X}^{-1} \end{aligned}$$

Thus,

$$\begin{aligned} \mathbf{A}^t &= (\mathbf{X}\mathbf{\Lambda}\mathbf{X}^{-1})^t \\ &= \mathbf{X}\mathbf{\Lambda}\mathbf{X}^{-1}\mathbf{X}\mathbf{\Lambda}\mathbf{X}^{-1}\dots\mathbf{X}\mathbf{\Lambda}\mathbf{X}^{-1} \end{aligned}$$

---

<sup>12</sup>To keep things (relatively) simple, I'm assuming that all eigenvalues are distinct.

$$\begin{aligned}
&= \mathbf{X}\Lambda^t\mathbf{X}^{-1} \\
&= \sum_{k=1}^n \lambda_k^t \mathbf{x}_k \mathbf{x}_k^{-1} \quad ,
\end{aligned}$$

where  $\mathbf{x}_k^{-1}$  refers to the vector forming the  $k$ th row of  $\mathbf{X}^{-1}$ .

We can apply these results to the projection of populations from one generation to the next. Recall that with both Leslie and Lefkovich matrices the population dynamics can be summarized as

$$\mathbf{n}(t) = \mathbf{A}\mathbf{n}(t-1) \tag{1}$$

$$= \mathbf{A}^t \mathbf{n}(0) \tag{2}$$

$$\tag{3}$$

Thus,

$$\mathbf{n}(t) = \sum_{k=1}^n \lambda_k^t \mathbf{x}_k \mathbf{x}_k^{-1} \mathbf{n}(0)$$

All of the age categories grow asymptotically at the rate  $\lambda_1$ , because if  $\lambda_1 > \lambda_k$ , then  $\lambda_1^t \gg \lambda_k^t$ , which implies that  $\mathbf{n}(t) \approx \lambda_1 \mathbf{n}(t-1)$ . The largest eigenvalue gives the asymptotic rate of population increase. Moreover,  $\mathbf{n}(t) \approx \lambda_1 \mathbf{n}(t-1)$  implies that  $\mathbf{n}(t-1) \propto \mathbf{x}_1$ . When the population has reached its asymptotic growth rate, the age-structure of the population is proportional to  $\mathbf{x}_1$ . The eigenvector corresponding to the largest eigenvalue gives the stable age structure.

## Sensitivity and Elasticity Analyses

One approach to determining how much various life-history stage transitions affect the population dynamics is by examining how changes in a particular stage affect the magnitude of the leading eigenvalue. The advantage of this approach is that once you've done all the work to measure the transition rates you don't have to *experimentally* manipulate the rates and watch for the effect, you can *mathematically* manipulate the rates and determine the effect.

Consider the following simple Leslie matrix

$$\begin{pmatrix} 0 & 1 & 4 \\ .7 & 0 & 0 \\ 0 & .5 & 0 \end{pmatrix}$$

For this matrix  $\lambda_1 = 1.32528$ . Suppose we subtract 0.1 from  $a_{12}$  making it 0.9. Then  $\lambda_1 = 1.30493$ , a change of 0.02035.

Suppose we subtract 0.1 from  $a_{21}$  making it 0.6. Then  $\lambda_1 = 1.24923$ , a change of 0.07605.

It appears that the population growth rate,  $\lambda_1$ , is more sensitive to changes in first year-survivorship,  $a_{21}$ , than to changes in second-year reproduction,  $a_{12}$ .

We can formalize this by saying that the *sensitivity* coefficient of  $a_{ij}$  is

$$\frac{\partial \lambda}{\partial a_{ij}}$$

For the above matrix

Coefficient	Sensitivity	
$a_{12}$	0.2030	$\approx 0.02035/0.1$
$a_{13}$	0.0766	
$a_{21}$	0.7278	$\approx 0.07605/0.1$
$a_{32}$	0.6128	

This analysis suggests that survivorship from age 1 to age 2 ( $a_{21}$ ) and from age 2 to age 3 ( $a_{32}$ ) are the most important stages in the life history. A unit change in either of these produces a corresponding change three or more times as great as increasing the fecundity of individuals in age-class 2 and nine to ten times as great as increasing the fecundity of individuals in age-class 3.

One problem with this approach is that some of the variables, i.e., survival rates, are intrinsically restricted in their range to values between 0 and 1, while others, i.e., fecundities, may be very large. Elasticity is a measure of “proportional” effect, i.e., the effect that a change in a given matrix element has as a *proportional* to the change in that element:

$$\frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}$$

Coefficient	Sensitivity	Elasticity <sup>13</sup>
$a_{12}$	0.2030	0.1532
$a_{13}$	0.0766	0.2312
$a_{21}$	0.7278	0.3844
$a_{32}$	0.6128	0.2312

The importance of some measure of proportional effect is illustrated by this very similar matrix:

$$\begin{pmatrix} 0 & 1000 & 4000 \\ .7 & 0 & 0 \\ 0 & .5 & 0 \end{pmatrix}$$

Coefficient	Sensitivity	Elasticity
$a_{12}$	<b>0.0124</b>	<b>0.4507</b>
$a_{13}$	0.0002	0.0329
$a_{21}$	<b>18.9318</b>	<b>0.4836</b>
$a_{32}$	<b>1.8027</b>	0.0329

## Limitations of these analyses

- Projections vs. forecasts
  - A projection says what would happen *if current trends continue*.
  - A forecast says what will happen.
  - It is best to regard these analyses as projections, because we know that populations can't grow at a geometric rate forever. They are tools for assessing the current condition of the population and for identifying critical stages.
- Large statistical uncertainties associated with estimates of leading eigenvalue.
- Elasticities vs. sensitivities vs. management possibilities
  - Elasticities provide a sense of *proportional* effect.
  - Sensitivities provide a sense of *numerical* effect.
  - What we really need is a measure of effect over the range of possible management options.
- Frequent focus on leading eigenvalue may be misplaced. It indicates the *asymptotic* properties of population growth rate, but the trend in the next few generations may be much more important (and much different).

- No environmental or demographic stochasticity
- Single isolated populations

Still, these analyses are useful.

- Only under very special conditions can a species be viable long-term unless at least one of its constituent populations is also viable.
- Help identify focus for management efforts. If individual populations are viable, focus should be on protection of habitat. If individual populations are not viable, some of them must also be managed to restore viability (or at least to prevent extinction).
- Provide a framework to which extensions including environmental and demographic stochasticity and migration among populations is easily added.
- Provide a focus for identifying critical life-history stages, even in the absence of a complete demographic analysis. Identify the life-history stages at which intervention is most likely to be useful.

## Things that are really critical to understand

- What goes in the matrix, how it's constructed.
- Initial growth depends on the age structure of the population.
- All age classes eventually grow at the same rate
  - This asymptotic rate of growth is  $\lambda_1$ , the leading eigenvalue.
  - The proportional representation of each age class is given by  $x_1$ , the eigenvector associated with  $\lambda_1$ .
- Early reproduction contributes more to the population growth rate than late reproduction.

## What do we do with limited data?

What I've just shown you is wonderful stuff, but we can only use it if we have data on survival probabilities and fecundities for every age or stage in our population. When you consider that the elements of the matrix are likely to vary from season to season<sup>14</sup> and that

---

<sup>14</sup>We ignored environmental stochasticity, remember.

to make reasonable forecasts about the fate of the population we'd need good data on both the mean and the variance of every element in the matrix, it seems as if we're doomed. Only a few of the most important endangered species will ever have enough data collected to do a complete analysis. Does that mean we should give up on population viability analysis? Obviously, I don't think so, or I wouldn't be lecturing about it, but how should we proceed?

One possibility is to construct an explicit simulation model that incorporates as much of the biology of the species you're concerned with as possible, to select a broad range of plausible values for the parameters in that model with values based on best guesses (derived from existing data, comparison with related species, or back-of-the-envelope calculations), and to do an extensive simulation study incorporating all of the plausible parameter estimates. You would probably then try to find a combination of management alternatives that made the worst-case scenario the most unlikely, but there are other alternatives.

Another alternative, a variant of which we'll see applied to the northern spotted owl, is to do some relatively simple calculations based on a minimal amount of data [5]. Dennis et al. [2] propose a relatively simple model of population dynamics based on the observation that age-structured populations are well-approximated by a stochastic, discrete time model with exponential growth. They illustrate how to calculate extinction properties of a population from such a model knowing only the mean rate of population growth and its variance.<sup>15</sup> Holmes [5] presents a relatively simple method for estimating  $\bar{R}$  and  $\sigma_R^2$  from a time series of population censuses. Her simulations show that the method she proposes provides reasonable estimates of extinction parameters when compared with projections based on fully-specified age-structured models. Morris and Doak [4, pp. 434] suggest two rules in conducting a PVA that I urge you to remember:<sup>16</sup>

1. **Let the available data tell you how complex your PVA should be.** We've seen that a complete demographic analysis, even for a plant or animal with a fairly simple life cycle requires measuring a *lot* of stage transitions, ideally for at least 4-5 years. If you don't have that much data, don't try to make a precise, quantitative model. Explore simpler alternatives, try some plausibility analyses, and don't overinterpret your results. They will be a qualitative guide to action more than a quantitative prediction.
2. **Make sure you understand what the model is doing.** If you're collaborating with someone who says "Don't worry about the model. I'll handle that," make sure you understand what that person is up to. You don't need to know how eigenvalues

---

<sup>15</sup>Remember the simple relationships I told you about a couple of lectures ago. Their results are quite similar.

<sup>16</sup>I'd urge you to recite them to yourself every night before you go to bed, but that's a bit much.

were calculated, but you *must* understand how your data are being fed into the model, what assumptions are embedded in the model, and how to interpret the output. *And* you need to do a “gut check” of the output. If the results don’t seem plausible, don’t dismiss them out of hand, but examine the inputs and the structure of the model very carefully before accepting a projection that doesn’t match your instincts.

## References

- [1] H Caswell. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Sunderland, MA, 2nd edition, 2001.
- [2] B Dennis, P L MunHolland, and J M Scott. Estimation of growth and extinction parameters for endangered species. *Ecological Monographs*, 61:115–143, 1991.
- [3] S P Ellner and M Rees. Integral projection models for species with complex demography. *American Naturalist*, 176(3):410–428, 2006.
- [4] M Groom, G K Meffe, and C R Carroll. *Principles of Conservation Biology*. Sinauer Associates, Sunderland, MA, 3rd edition, 2005.
- [5] E E Holmes. Estimating risks in declining populations with poor data. *Proceedings of the National Academy of Sciences USA*, 98:5072–5077, 2001.
- [6] William F Morris and Daniel F Doak. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer Associates, Sunderland, MA, 2002.
- [7] K H Redford. The empty forest. *BioScience*, 42:412–422, 1992.

## Creative Commons License

These notes are licensed under the Creative Commons Attribution-NonCommercial-ShareAlike License. To view a copy of this license, visit <http://creativecommons.org/licenses/by-nc-sa/3.0/> or send a letter to Creative Commons, 559 Nathan Abbott Way, Stanford, California 94305, USA.