

Using the Leslie Matrix to Project Population Dynamics

There are four steps involved in making a basic stochastic projection model.

1. Collect *demographic data*
2. Analyse the data to obtain *age- and sex-specific survivorship and fecundity*
3. Use age-specific survivorship and fecundity to *project population dynamics using Leslie matrix*.
4. Incorporate *variance* to shift from deterministic to stochastic model.
5. This basic stochastic projection model ($N_t = N_0\lambda^t$) assumes exponential growth: the next step is to incorporate *limiting factors*. Step five is the subject of the case study lectures that follow.

BASIC DEMOGRAPHIC DATA - getting l_x and m_x curves.

A **Population** is a group of individuals of the ¹*same species*, ²*living sufficiently close together* that ³*intermating is possible*, and therefore ⁴*sharing a common gene pool*.

Study of population parameters is also called **demography**, from Greek root for population, 'deme'.

Difficulties with defining a population:

1. In practice, can be hard to identify a population; often a study area is defined and this defines a 'study population'. Care is needed when a population is defined in this way, b/c immigration and emigration can affect estimates of survival and reproduction. (open vs. closed populations). Especially a problem for animals that live at low density, large ranges.
2. Population size and geographic extent vary through time
3. Definition cannot be applied to asexual organisms - for these, the focus is on proximity

Population-level variables depend on the properties of individuals that compose the population. The two most basic parameters of a population are an individual's likelihood of **surviving** and an individual's likelihood of **breeding**. A quick glance at the world reveals that both of these depend on the individual's age, in most species. (E.g. very young and very old individuals often don't breed, and very young individuals often have high odds of dying.)

These basic parameters are combined in a **life-table**, as **age-specific survivorship** and **age-specific fecundity**. From these two parameters, we can derive considerable information, which falls into two categories:

1. Demographic information allows measurement of the rate of population growth and projection of future population sizes.

2. Demographic information allows analysis of 'life-history tactics'. For example, some species breed once and die, while others breed many times. Some species mature quickly while others wait years before reproducing. Demographic data allows quantitative analyses of the fitness trade-offs involved in the evolution of life-history tactics.

Continuous vs. Discrete events. Many life-history processes are continuous, but are broken into discrete units for the purpose of demographic analysis. Example is aging. *Age* is a **continuous** variable, but it is generally broken into discrete **age-classes** in demographic analyses.

(Fig. 3.1 Gotelli)

As long as the discrete units are not too long, this approach usually works well. E.g. most vertebrates have a distinct annual breeding season, so life-tables for vertebrates are based on discrete one-year age-classes, each potentially including a bout of reproduction.

In this class, all of the equations are given in the discrete form that is most widely used. However, all of these equations can be written in continuous form using integration rather than summation - that is the only real difference.

First step in life table is determining age-classes to be used. Age class (x) is the first column of life table.

Survivorship Schedule or l_x curve

Describes the probability of surviving (or dying, equivalently) through each age class. Can be determined in two basic ways.

Cohort method is to observe a set of individuals through time, from birth to death, recording how many still alive in each age class (at beginning of class usually, but can also be at mid-point of age class). E.g. Start with 500 newborns. $N_0 = 500$. 400 still alive at age 1, so $N_1 = 400$. 200 still alive at age 2 so $N_2 = 200$. Continue until all are dead, $N_\omega = 0$. ω (omega) is typical symbol for oldest age attained.

Static method (Pianka calls this segment method) is to record # of individuals of each age class present in population at one time. $N_0 = 500$ juveniles, $N_1 = 400$ 1-year olds, $N_2 = 200$ 2-year olds, etc. As Gotelli notes, this method assumes that the population has a **stable age distribution**.

(Fig. 8.1 Pianka)

| Age class | Number in | Survivorship | Age-specific |
|-----------|------------------|-------------------|-----------------|
| x | age class: N_x | from birth: l_x | survival: s_x |
| 0 | 500 | 1.00 | 0.80 |
| 1 | 400 | 0.80 | 0.50 |
| 2 | 200 | 0.40 | 0.25 |
| 3 | 50 | 0.10 | 0.00 |
| 4 | 0 | 0.00 | --- |

Survivorship from birth to age-class x , is denoted l_x . (l for life)

$$l_x = N_x/N_0 \quad (\text{N for number})$$

This is the likelihood of living to a given age. Interesting for some questions, but for others we want to know the probability of dying during a specific age-class, or s_x .

Age-specific survival is denoted s_x . (s for survival)

$$s_x = N_{x+1}/N_x \quad (= l_{x+1}/l_x)$$

l_x decreases continually through age classes, but this does not mean that old animals are more likely to die than young animals. Use s_x values to compare the risk of death for different age classes.

But need to use l_x to ask questions about benefit of reproducing at different ages (because it is l_x that determines whether an individual will be alive to reproduce at a given age).

Survivorship curves: three general types are often described (Deevey 1947), based on shape of log-linear plot of N_x vs x .

Type II is a straight line: constant probability of death (birds)

Type I: survive well until senescence (large mammals, humans)

Type III: heavy juvenile mortality (inverts, fish, plants)

Though these types are useful descriptors, real survivorship curves are often more complex in shape, and there are MANY exceptions to the general pattern. Knowing the types is useful, but it is not safe to assume (for example) that a bird population will have type II survival.

(Fig. 8.3 and 8.4 Pianka)

For example, mammals are often said to have Type I survival, but many mammals also have big pulse of mortality among juveniles, giving curve like that for Dall sheep in Fig. 8.3 Pianka). Other mammals have Type II constant mortality, as in dwarf mongooses:

(Fig 20.2 Waser et al.)

Good example of practical problems with measuring l_x comes from fish, where differences in catchability of age-classes makes early survival almost impossible to measure in ordinary ways.

(Fig. 2.1 Ricker - numbers apparently increase across early age classes, which is impossible)

Fecundity Schedule or m_x curve.

m_x = $1/2$ number of offspring born to parent of age x .

For each offspring produced, male and female parent each credited with $1/2$ of an offspring produced. To see the logic of this, remember that in sexual organism, each individual must leave 2 offspring for exact replacement.

In practice, m_x is usually measured as **female offspring per female of age x** (m for maternity). This is simply because paternity is usually unknown, so numbers of offspring per male can't be measured. In some cases, male reproduction is known, and m_x is measured as $1/2$ of total # offspring for each parent.

α (alpha) → typical symbol for age at which breeding begins.

ω (omega) → typical symbol for age at which breeding ends

(Fig 20.2 Waser et al: typical m_x curves for mammal that breeds repeatedly - iteroparous)

Can combine m_x and l_x schedules to determine several measures of population growth:

| x | N_x | l_x | m_x | $l_x m_x$ | $x l_x m_x$ |
|-----|-------|-------|---------------------------|-------------------------------------|--------------------------|
| 0 | 500 | 1 | 0 | 0 | 0 |
| 1 | 400 | 0.80 | 2 | 1.6 | 1.6 |
| 2 | 200 | 0.40 | 3 | 1.2 | 2.4 |
| 3 | 50 | 0.10 | 1 | 0.1 | 0.3 |
| 4 | 0 | 0 | 0 | 0.0 | 0.0 |
| | | | $\Sigma m_x = 6$ (GRR) | $\Sigma l_x m_x = 2.9$ (R_0) | $\Sigma x l_x m_x = 4.3$ |

Gross reproductive rate = Σm_x . Total lifetime reproduction in the absence of mortality. This is the average lifetime reproduction of an individual that lives to senescence, useful in considering potential population growth if all ecological limits (predation, competitors,

disease, starvation) were removed for a population. GRR is rarely if ever attained in nature, but useful to consider how far below this a population is held by ecological limits.

Net reproductive rate, $R_0 = \sum l_x m_x$. Average number of offspring produced by an individual in its lifetime, taking normal mortality into account. l_x is the odds of living to age x , m_x is the average # of kids produced at that age, so the product $l_x m_x$ is the average number of kids produced by individuals of age x . Summed across all ages, this is average lifetime reproduction.

R_0 is also called the **replacement rate**:

$R_0 < 1$ individuals not fully replacing themselves, population shrinking

$R_0 = 1$ individual exactly replacing themselves, population size stable

$R_0 > 1$ individuals more than replacing themselves, population growing

The schedule of reproduction (m_x curve) can be used to determine the **generation time, T** . Need to know generation time in order to convert R_0 into a population growth rate measured in time units such as years (or days, etc)

Semelparous species = big bang breeders, which breed only once in life (e.g. salmon, many insects) T = egg to egg time, or newborn to newborn time (obviously).

But in **iteroparous** species, T is more complex.

$$T = \frac{\sum x l_x m_x}{\sum l_x m_x} = 4.3/2.9 = 1.48$$

To understand this, think first about the numerator. $l_x m_x$ is the average number of offspring born to female at age x , as discussed above. If we weight each offspring by the age of the mother, x , and then sum across all ages, then we have the **mother's age when each offspring was born, summed across all offspring born in her life**.

The denominator ($\sum l_x m_x$) is equal to the total number of offspring born. Dividing the numerator by the denominator gives the mean age of a female when each of her children was born. In other words, the whole expression is just a weighted average — if most offspring are produced when mothers are young, T will be short; if most offspring are produced when mothers are old, T will be long.

The denominator is equal to R_0 . In a stable population, $R_0 = 1$, so the denominator has no effect on generation time. In a growing population, $R_0 > 1$ and T is decreased, because it takes less time for a cohort to 'replace' itself. In a shrinking population, $R_0 < 1$ and T is increased, because it takes longer for a cohort to 'replace' itself.

Relationship of net reproductive rate (R_0) to intrinsic rate of increase, (r):

Defined population growth in terms of R_0 above. But R_0 measures reproduction on the basis of *individual lifetimes* (offspring produced per individual per lifetime), and most models of population growth measure growth on the basis of *births - deaths per unit time*, where time doesn't have to be a generation - often years are the units. The most common measure of population growth is the *intrinsic rate of increase, r*.

$$r \approx \frac{\ln R_0}{T} = \ln(2.9)/1.48 = 0.72 \text{ individuals/individual/year (growing rapidly)}$$

when $R_0 = 1, r = 0$, stable population
 $R_0 < 1, r < 0$, shrinking
 $R_0 > 1, r > 0$, growing

remember that $r = b - d$ where $b = \text{births/unit time}$ and $d = \text{deaths/unit time}$. So units of r are individuals produced per unit time.

The equation $r \approx \ln R_0 / T$ only give accurate results when $R_0 \approx 1$ ($r \approx 0$). The exact solution comes from Euler's equation.

$$1 = \sum e^{-rx} l_x m_x$$

This is solved by iteration, a polite way of saying 'hunt and peck'. Many computer packages (including MS Excel) have numerical 'solvers' that will do this for you → the following explains what these 'solvers' do.

1. Use the approximate solution to get a close estimate of r .

$$r \approx \frac{\ln R_0}{T} = \ln(2.9)/1.48 = 0.72 \text{ individuals/individual/year}$$

2. Make an e^{-rx} column.

3. Make an $e^{-rx} l_x m_x$ column and sum it.

| x | N_x | l_x | m_x | $l_x m_x$ | $x l_x m_x$ | e^{-rx} | $e^{-rx} l_x m_x$ |
|-----|-------|-------|-------|-----------|-------------|-----------|-------------------|
| 0 | 500 | 1 | 0 | 0 | 0 | 1 | 0 |
| 1 | 400 | 0.80 | 2 | 1.6 | 1.6 | 0.487 | 0.779 |
| 2 | 200 | 0.40 | 3 | 1.2 | 2.4 | 0.237 | 0.284 |
| 3 | 50 | 0.10 | 1 | 0.1 | 0.3 | 0.115 | 0.012 |
| 4 | 0 | 0 | 0 | 0.0 | 0.0 | 0.056 | 0 |
| | | | | | | | $\Sigma=1.075$ |

4. $\Sigma e^{-rx}l_xm_x = 1.075$, so first estimate of $r = 0.72$ is too small. (We are summing terms raised to a negative exponent of r , so $\uparrow r$ will \downarrow sum). Adjust estimate of r and try again. As a guess, try $r = 0.75$

| x | N_x | l_x | m_x | l_xm_x | xl_xm_x | e^{-rx} | $e^{-rx}l_xm_x$ |
|-----|-------|-------|-------|----------|-----------|-----------|------------------|
| 0 | 500 | 1 | 0 | 0 | 0 | 1 | 0 |
| 1 | 400 | 0.80 | 2 | 1.6 | 1.6 | 0.472 | 0.755 |
| 2 | 200 | 0.40 | 3 | 1.2 | 2.4 | 0.223 | 0.268 |
| 3 | 50 | 0.10 | 1 | 0.1 | 0.3 | 0.105 | 0.011 |
| 4 | 0 | 0 | 0 | 0.0 | 0.0 | 0.050 | 0 |
| | | | | | | | $\Sigma = 1.034$ |

5. $\Sigma e^{-rx}l_xm_x = 1.034$, so estimate of r (0.75) is still too small. Increase it and try again. By repeating this process, will home in on $r = 0.776$, which gives $\Sigma e^{-rx}l_xm_x = 1$

| x | N_x | l_x | m_x | l_xm_x | xl_xm_x | e^{-rx} | $e^{-rx}l_xm_x$ |
|-----|-------|-------|-------|----------|-----------|-----------|------------------|
| 0 | 500 | 1 | 0 | 0 | 0 | 1 | 0 |
| 1 | 400 | 0.80 | 2 | 1.6 | 1.6 | 0.460 | 0.736 |
| 2 | 200 | 0.40 | 3 | 1.2 | 2.4 | 0.212 | 0.254 |
| 3 | 50 | 0.10 | 1 | 0.1 | 0.3 | 0.097 | 0.010 |
| 4 | 0 | 0 | 0 | 0.0 | 0.0 | 0.045 | 0 |
| | | | | | | | $\Sigma = 1.000$ |

The true intrinsic rate of increase is $r = 0.78$, compared with original estimate of $r = 0.72$. This is **a difference of 8%**, which is big enough to matter in practical applications.