

Age and stage structure

Key concepts

- Static and cohort life tables
- Survivorship curves
- Gross *vs.* net reproductive growth
- Transient dynamics and the stable age distribution
- Projection matrices
- Reproductive value
- Age- *vs.* stage-structure

So far, we've assumed that all individuals in a population are the same with regard to the forces that change population size (particularly births and deaths). A moment's thought about our own species convinces us that reproductive potential and probability of dying vary with age. This chapter reviews how we collect and organize data concerning heterogeneity in reproduction and survivorship as a function of age or stage of life, and explores the consequences of such structure on population dynamics.

Static *vs.* cohort life table data

Obtaining information about age- or stage-specific survivorship and fecundity can be a lifetime's work. There are two complementary approaches that can reveal important information about a species. *Static* life table data is typically one snapshot in time. It allows an estimation of the age-distribution in a population.

Cohort life table data is obtained by following a cohort (a group of individuals of the same species born at approximately the same time). The cohort is tracked until there are no more survivors.

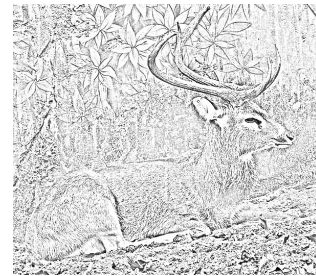


Figure 1: Hainan Eld's deer (*Cervus eldi hainanus*).

Life table basics

The first three columns of Table 1 are the raw data we can hope to obtain from following a cohort through its life. The other columns are calculated from the raw data. The proportion of the initial cohort still alive at age x , (l_x) reveals the nature of the survivorship function. The age-specific fecundity (m_x) is calculated as the average number of offspring per female in age-class x . The sum of this column tracks the reproductive output of a hypothetical female that lives to the maximum observed age. This sum is called the gross reproductive ratio (GRR).

$$GRR = \sum_x m_x. \tag{1}$$

In order to track the reproductive output of typical female (rather than one that lives to the maximum observed age) we can take the product of survivorship (to age x) and reproductive output (at age x) and sum over all ages x .

Age	Total alive	No. offspring	l_x	m_x	$l_x m_x$
0	49	0	1	0	0
1	45	0	0.918	0	0
2	39	10	0.796	0.256	0.204
3	29	12	0.592	0.414	0.245
4	23	11	0.469	0.478	0.224
5	18	10	0.367	0.556	0.204
6	12	7	0.245	0.333	0.082
7	8	2	0.163	0.25	0.041
8	7	1	0.143	0.143	0.020
9	5	1	0.102	0.2	0.020
10	2	1	0.041	0.5	0.020
11	1	0	0.020	0	0
12	0	-	-	-	-
			$GRR = 3.13$		$R_0 = 1.06$

This quantity is called the net reproductive ratio R_0 , and tells us how many offspring a typical individual will have.

$$R_0 = \sum_x l_x m_x. \tag{2}$$

Like the value λ derived previously, we see that a population will grow if $R_0 > 1$ and decline if $R_0 < 1$.

Survivorship curves

The way in which survivorship (l_x) drops off with age can be broadly classified in to three different survivorship profiles or functions:

Table 1: Dynamic life table of female Hainan Eld's deer *Cervus eldi hainanus*, from Nie et al. 2011

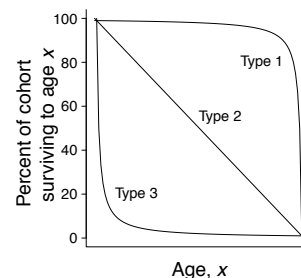


Figure 2: Survivorship functions

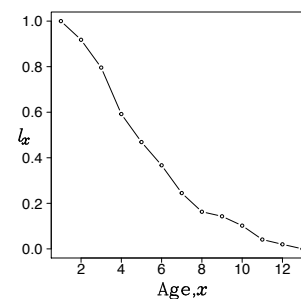


Figure 3: Survivorship profile of female Hainan Eld's deer

Type	Patterns	Example organism
1	Juvenile and middle-age mortality low Old-age mortality high	humans
2	Mortality approximately equal at all age classes	slider turtles
3	High juvenile mortality low Middle- and old-age mortality	oak trees

Table 2: Types of survivorship function

In the cases of Hainan Eld's deer, the survivorship profile could be classified as type 2 or 3.

Life expectancy

Additionally, the life table allows us to calculate life expectancy. We originally considered the l_x column to be the proportion of an initial cohort still alive at age x . This is equivalent to the probability that a single individual is still alive at age x (assuming that age is the only way in which individuals differ). In order to live to a given age, k , an individual must survive all the preceding age classes. The probability of surviving from birth to age k is given by the area under the survivorship curve up to age k . When we treat age as a continuously changing quantity, this area would be expressed by integration:

$$\int_0^k l_x dx. \quad (3)$$

For practical purposes, age is expressed in discrete classes. We can approximate the area under the survivorship curve by a series of right-angled trapezia, as illustrated in Figure 4.

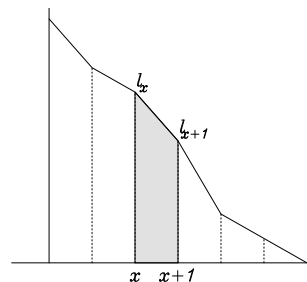
We say "approximate" because we assume that individuals that die in a certain age class do so at the halfway point. This assumption is made by drawing straight lines between adjacent survivorship values and is reasonable provided the interval represented by the age class is not too large.

Life expectancy at birth is the area under the whole curve, i.e.

$$e_x = \sum_{x=0}^{x=k} (l_{x+1} + l_x)/2. \quad (4)$$

We are not constrained to calculating life expectancy at birth, we can start at some later age, j . In this case we divide by the survivorship of the lowest age considered (l_j) because we assume (with probability 1) that individuals have reached age j . The revised formula

$$e_x = \frac{1}{l_j} \sum_{x=j}^{x=k} (l_{x+1} + l_x)/2, \quad (5)$$

Figure 4: Area under survivorship curve composed of trapezoids of area $(l_{x+1} + l_x)/2$.

where k is the maximum observed age, serves as a general formula, replacing equation (4), since $l_0 = 1$ by definition.

Age	l_x	e_x
0	1	4.35
1	0.918	3.70
2	0.796	3.19
3	0.592	3.11
4	0.469	2.80
5	0.367	2.44
6	0.245	2.41
7	0.163	2.38
8	0.143	1.64
9	0.102	1.09
10	0.041	0.99
11	0.020	0.5
12	0	0

Table 3: Calculation of life expectancy for female Hainan Eld's deer *Cervus eldi hainanus*, from Nie et al. 2011

Life expectancy (e_x) is defined as expected years of life in addition to current age x . Expected age at death is then

$$x + e_x. \quad (6)$$

Population dynamics and the stable age distribution concept

The information coded in a life table allows us to project population dynamics forward in time from a set of initial conditions (initial values of each age class). Consider a hypothetical life table with four age-classes (0, 1, 2 & 3).

Age	l_x	m_x	s_x
0	1	0	0.8
1	0.8	0	0.7
2	0.56	1	0.5
3	0.28	4	0
4	0	-	

Table 4: Hypothetical life table with three age classes, 0, 1, 2 & 3

We've introduced a new column s_x which represents the fraction of a given age class that survives to the next age

$$s_x = l_{x+1}/l_x. \quad (7)$$

As the discrete time formulation represents annual birth pulses, the "next" newborns (n_0) will come from "current" individuals in an age class x that successfully mature to the next age class and have the appropriate number of offspring (m).

$$n_0(t+1) = n_1(t)m_1 + n_2(t)m_2 + \dots \quad (8)$$

where the n_1, n_2, \dots are formed from survivors of the preceding age class

$$n_0(t+1) = s_0 n_0(t) m_1 + s_1 n_1(t) m_2 + \dots \quad (9)$$

Other age classes are simply determined by survivorship of the preceding age class. For our hypothetical life table, we expect populations to change according to

$$n_0(t+1) = 0n_0(t) + 0.7n_1(t) + 2.0n_2(t) + 0n_3(t) \quad (10)$$

$$n_1(t+1) = 0.8n_0(t) + 0n_1(t) + 0n_2(t) + 0n_3(t) \quad (11)$$

$$n_2(t+1) = 0n_0(t) + 0.7n_1(t) + 0n_2(t) + 0n_3(t) \quad (12)$$

$$n_3(t+1) = 0n_0(t) + 0n_1(t) + 0.5n_2(t) + 0n_3(t) \quad (13)$$

At this stage we will adopt a matrix notation to describe these dynamics, as this is useful for later analysis.

$$\begin{bmatrix} n_0 \\ n_1 \\ n_2 \\ n_3 \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0.7 & 2.0 & 0 \\ 0.8 & 0 & 0 & 0 \\ 0 & 0.7 & 0 & 0 \\ 0 & 0 & 0.5 & 0 \end{bmatrix} \begin{bmatrix} n_0 \\ n_1 \\ n_2 \\ n_3 \end{bmatrix}_t \quad (14)$$

The matrix, M , is the projection matrix.

Sometimes we also refer to a *Leslie* matrix, named for the mathematician credited with pioneering the technique

Population projection and transient dynamics

From an initial population state, n (e.g., 5 individuals in each class n_0, n_1, n_2 and n_3), we can project the population forward in time using the rule

$$n_{t+1} = Mn_t \quad (15)$$

The dynamics illustrated in Figure 5 have a *transient* phase (approximately the first ten years) when the population sizes appear to change erratically. Following this phase, the population sizes of each class increase at the same rate. This means that the proportion of individuals in a given age class does not change. We refer to this phenomenon as a *stable age distribution*. Although the simulation only projects forward twenty years, the model continues to exhibit the stable age distribution at all subsequent times (provided the numbers in the matrix don't change).

From an applied perspective (e.g., conservation or management) there is considerable value in knowing which age classes will dominate a population (or which will be rare). Models often predict that stable age distributions are reached fairly quickly. Assuming that the

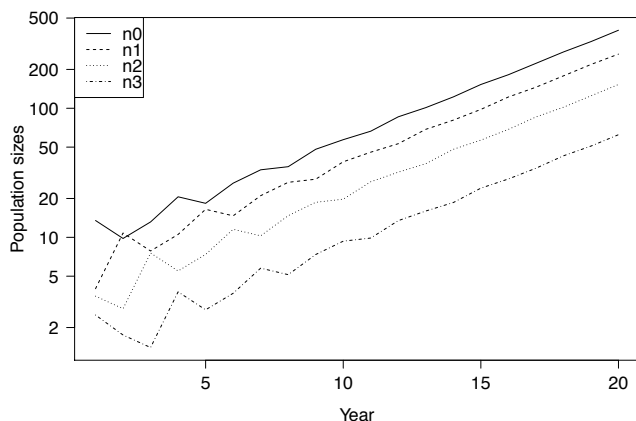


Figure 5: Population projection of equation 14 over 20 years

population has reached a stable age distribution allows for further information to be derived from life tables, including the generation time and intrinsic growth rate.

As in populations without age structure, we can project an arbitrary number of time steps forward from an initial state by raising the matrix to the appropriate power

$$n_t = M^t n_0.$$

Computers are able perform such matrix multiplication routinely, allowing us to estimate how populations (and their age-specific sub-populations) are expected to change far into the future, under a set of assumptions about the population processes.

Generation time and growth rate

The net reproductive ratio, R_0 , is a dimensionless quantity. It doesn't tell us anything about how quickly a population is growing or declining. To help us put a pace to population change, we can use a life table to estimate the generation time, T_G . First, we need a crisp definition. While the definition is not unique, the mean age of females when their offspring are born is popular and logical. From the life table we note that the realized fecundity of an age class is

$$l_x m_x, \quad (17)$$

and the proportion of overall fecundity attributable to an age class is

$$l_x m_x / R_0. \quad (18)$$

The mean age at which females give birth, T_G , is then the sum of all ages weighted by their proportional contribution to overall fecundity,

$$T_G = \frac{\sum_x x l_x m_x}{R_0}. \quad (19)$$

Provided the population is at its stable age distribution, then

$$R_0 = n_{T_G} / n_0. \quad (20)$$

When a population is growing or declining by a fixed factor, we know from the earlier chapter on “Growth and decline” that

$$R_0 = e^{rT_G} = \lambda^{T_G}, \quad (21)$$

and so

$$r = \frac{\ln(R_0)}{T_G} \quad (22)$$

and

$$\lambda = R_0^{1/T_G}. \quad (23)$$

Eigenvectors and eigenvalues

The matrix (14) is a square matrix (same number of rows and columns) and is used to calculate the sizes of age classes over time. Because we’re projecting current population sizes into the future, we refer to this matrix as a projection matrix. Certain attributes of the projection matrix allow us to make valuable assessments of the population whose dynamics it is describing. These attributes relate to the eigenvectors and eigenvalues of this matrix.

An eigenvector, v , is a set of numbers (e.g., population sizes of each age class) that when multiplied by the matrix, M , generates a vector that is a constant multiple, λ , of the original eigenvector, meaning each element of the vector is multiplied by the factor, λ . The multiplying factor λ is an eigenvalue of the matrix. Mathematically, we usually describe this as

$$Mv = \lambda v. \quad (24)$$

There are as many eigenvalues as there are age classes (in our case three). When there are only two or three age classes, eigenvalues can be calculated by hand. More generally, we use computers to calculate the eigenvalues of a matrix. The dominant eigenvalue is the one that is biggest in size (ignoring sign) and tells us the factor by which the population changes at each time step. In other words, the dominant

eigenvalue is the same as the annual reproductive ratio, λ , and it is not a coincidence that this symbol is used in eigenvalue notation.

Calculating stable age distributions and reproductive value

Each eigenvalue has a right and left eigenvector. The left eigenvector, u , satisfies

$$uM = u\lambda \quad (25)$$

which for our example is

$$\begin{bmatrix} u_0 & u_1 & u_2 & u_3 \end{bmatrix} \begin{bmatrix} 0 & 0.7 & 2 & 0 \\ 0.8 & 0 & 0 & 0 \\ 0 & 0.7 & 0 & 0 \\ 0 & 0 & 0.5 & 0 \end{bmatrix} = \begin{bmatrix} u_0 & u_1 & u_2 & u_3 \end{bmatrix} \lambda. \quad (26)$$

The right eigenvector, v , satisfies

$$Mv = \lambda v \quad (27)$$

which for our example is

$$\begin{bmatrix} 0 & 0.7 & 2 & 0 \\ 0.8 & 0 & 0 & 0 \\ 0 & 0.7 & 0 & 0 \\ 0 & 0 & 0.5 & 0 \end{bmatrix} \begin{bmatrix} v_0 \\ v_1 \\ v_2 \\ v_3 \end{bmatrix} = \lambda \begin{bmatrix} v_0 \\ v_1 \\ v_2 \\ v_3 \end{bmatrix}. \quad (28)$$

The reason we care about these eigenvectors is that for the dominant eigenvalue, the left eigenvector tells us the *reproductive value* of each age class and the right eigenvector tells us the *stable age distribution*.

We've already met the concept of the stable age distribution, and now we see that it can be extracted directly from the projection matrix without computer simulation (though, in practice we would still use a computer to calculate the eigenvectors). The numbers in the right eigenvector, once normalized (i.e., scaled to sum to one), tell us the proportion of the total population that will belong to any age class once the population dynamics have moved passed the transient phase.

Matrix (14) has a dominant eigenvalue of $\lambda \approx 1.21$ and the right eigenvector associated with this scales to $(0.46, 0.30, 0.17, 0.07)$ meaning that the population will ultimately be composed of 46% of the youngest age class, 30% of the second youngest age class, 17% of the second oldest age class and 7% of the oldest age class, which is consistent with Figure 5.

Reproductive value is defined as an individual's expected contribution to the population through both current and future reproduction, which will vary with age. For matrix (14) the normalized left

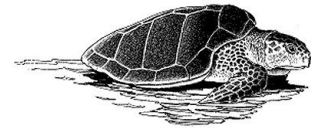


Figure 6: Loggerhead sea turtle (*Caretta caretta*).

eigenvector is $(0.24, 0.37, 0.39, 0.0)$, so although the youngest age class dominates the population its reproductive value is only third highest.

Stage-based structure: The conservation of loggerhead sea turtles

It is sometimes more practical to group individuals into life stages, which may be of unequal length. For example, the loggerhead sea turtle *Caretta caretta* has survivorship and fecundity values that are better related to stages of life than age (Table 5)

Class	Size* (cm)	Approx. ages	Annual sur- vivorship	Fecundity (eggs/yr)
1. eggs, hatchlings	<10	<1	0.6747	0
2. small juveniles	10.1-58.0	1-7	0.7857	0
3. large juveniles	58.1-80.0	8-15	0.6758	0
4. sub-adults	80.1-87.0	16-21	0.7425	0
5. novice breeders	>87.0	22	0.8091	127
6. 1st yr remigrants	>87.0	23	0.8091	4
7. mature breeders	>87.0	24-54	0.8091	80

Table 5: Loggerhead sea turtle life table (adapted from Crouse et al. 1987)

Much of the ideas about age structure apply to stage structure as well. One important difference is that as time progresses from t to $t + 1$ (where the time unit could be selected as days, months, years etc., depending on the organism) surviving individuals do not necessarily pass to the next stage as they did with age structure. To illustrate this, consider a generic three age class model

$$\begin{bmatrix} n_0 \\ n_1 \\ n_2 \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & f_1 & f_2 \\ s_0 & 0 & 0 \\ 0 & s_1 & 0 \end{bmatrix} \begin{bmatrix} n_0 \\ n_1 \\ n_2 \end{bmatrix}_t \quad (29)$$

where f_x is the age-specific fecundity and s_x is the between-age survivorship probability.

We note that at each time step individuals either age into the next category or die. If instead we assume a 3-stage class model, we include the possibility of staying in the stage at subsequent time steps

$$\begin{bmatrix} n_0 \\ n_1 \\ n_2 \end{bmatrix}_{t+1} = \begin{bmatrix} h_0 & f_1 & f_2 \\ g_0 & h_1 & 0 \\ 0 & g_1 & h_2 \end{bmatrix} \begin{bmatrix} n_0 \\ n_1 \\ n_2 \end{bmatrix}_t \quad (30)$$

Here, h_x is defined as within-stage survivorship, and g_x is the probability of developing to the next stage.

Test yourself

- In what ways is R_0 a summary of a typical individual?

The matrix describing stage-based dynamics is often named for the pioneer of the technique, *Lefkovich*

- What are transient dynamics?
- What is the difference between age-structured and stage-structured models?
- Supposing regression to a stage experienced by an individual at an earlier stage of life were possible (e.g. shrinkage in a size-structured plant population). How might this information be coded in a projection matrix?

Further reading

- Matrix Population Models, H. Caswell, 2001, Sinauer Press.
- H. Nie et al. 2011. Life history pattern and fitness of an endangered Hainan Eld's deer population. *Integrative Zoology* 6(1): 63-70.
- D. T. Crouse et al. 1987. A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation. *Ecology* 68(5): 1412-1423.

Homework

1. Calculate the life expectancy for all ages based on the data in Table 4
2. Using the data in Table 4 calculate R_0 , T_G , r and λ .
3. In less than 100 words, explain how stable age distributions and reproductive value are useful data in conservation biology

Hint: Relate their usefulness to their definitions for full credit