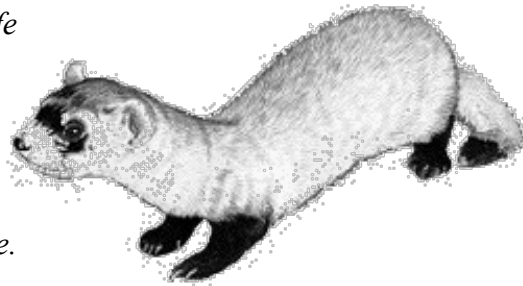


4 Growth of Age-Structured Populations: black-footed ferrets

Major concepts:

- Survival and fecundity rates often change with age. In such cases, an accurate understanding of population growth must take the age structure of the population into account. **Life tables** show how survivorship and reproduction change with age.
- Life tables for black-footed ferrets have been used to monitor and understand the growth of populations of that critically endangered species.
- The population **net reproductive rate** (R_0) is a measure of population growth and is computed from the life table as the expected number of female offspring per female over her entire life.
- The life table can also be used to calculate life expectancy, reproductive value and generation time.
- Different life history strategies (annual vs perennial, semelparous vs iteroparous) have different survivorship and fecundity schedules, which are reflected in the life table.



One of the great conservation successes in recent years has been the recovery of the Black Footed Ferrets (*Mustela nigripes*). Black footed ferrets were feared to be extinct until a single surviving colony was discovered in 1981 near the town of Meeteetse, Wyoming.

Immediately conservation biologists sprang into action to try to rebuild viable populations of a species that once thrived in the western US. All eighteen of the remaining ferrets were captured to serve as the founder stock for a captive breeding program. Since then the offspring of those captive ferrets have been released at several locations and the new populations appear to be rebounding. In this chapter we'll use data on the survival and fecundity of ferrets of different ages to predict the growth rate of ferret populations.

Black footed ferrets are medium sized mammals related to skunks and weasels. They are notable in that they are completely dependent on colonies of burrowing rodents commonly known as prairie dogs (*Cynomys* spp). Prairie dogs are the only food source for ferrets. The short legs and slender bodies of ferrets are ideal for entering the burrows of prairie dogs in search of prey.

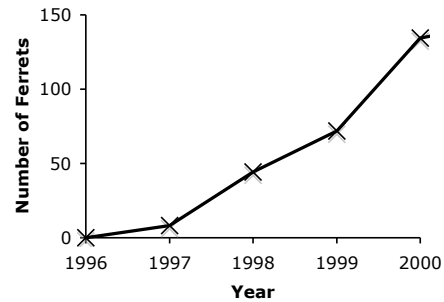


Prairie dogs were once common in the western US but they have long been considered pests. Although they are an important component of the shortgrass prairie ecosystem, the colonies form extensive networks of burrows that can make the landscape unsuitable for farming and other human uses. After a century of systematic prairie dog extermination programs, prairie dog colonies now occupy less than 2% of their original range.

Figure 4.1 Historical and current range of black footed ferrets. Ferrets are now known from only a few sites where they have been reintroduced.

The fate of the ferret was tied to the demise of prairie dog. In response to the elimination of prairie dog colonies the numbers of black-footed ferrets also plummeted and at one point they were believed to be extinct. Now, there have been several successful reintroductions of ferrets to the wild, in locations where there are still large and active prairie dog colonies. Some of those reintroduced ferret populations have shown a remarkable comeback.

Figure 4.2 Population size of black footed ferrets in the Conata Basin. (Data from MacDonald)



We've already seen examples of the power of exponential population growth and looked at simple population growth models. Those models are good abstractions, but make several simplifying assumptions. One important assumption is that they assume all individuals are identical. That allowed us to keep track of only the total population size (N) and ignore any differences among individuals. However, individuals are rarely identical. Most populations of animals have two sexes. Also, survival and reproduction usually change with age. Very often, survival is lower for newborns than it is for adults. And it is very common for organisms to have a pre-reproductive juvenile stage, and obviously those individuals can not produce any offspring. Those real differences among individuals mean that we need to keep track of animals of different ages in order to have an accurate gauge of the population growth potential.

Often the simple models are sufficient. When populations are large, it is often possible to use the simple models of exponential or logistic growth, knowing that they make simplifying assumptions that don't precisely hold. However, for small and medium populations when individuals have very different survival and reproductive output, more complicated models may be necessary.

In this chapter our approach will differ from the previous models of population growth that we saw in the first three chapters. Instead of fitting a population growth rate (r) to time series data, we will look at the underlying demographic processes of survival and reproduction, and then infer the potential population growth rate. Thus we will primarily be concerned with the fates of *individuals*: how long do they survive? how many offspring do they produce? We will then combine that information on individual behavior to see how the population as a whole is expected to grow.

To understand the growth of age-structured populations, it is necessary to know how individual survival and fecundity change with age. That means it is necessary to identify the age, sex, and reproductive status of particular individuals. Usually, that requires some kind of long-term census of marked individuals. The survivorship and fecundity schedules are then collected into a life table.

To keep things simple, we will assume that all give birth or die exactly on their birthday (in other words we will use a discrete model of population growth). We will then keep track of the probability of surviving from birth to their first, second, third or fourth birthday and the number of offspring that produced by females of each age.

4.1 How do you measure survival?

Black-footed ferrets occur in populations that are spread over a large area, they are nocturnal, and they spend most of their time underground. That makes them hard to count! One of the key parameters of our demographic model will be the **survivorship schedule** for the population, i.e. the fraction of individuals that survive to various ages. Measuring survival requires the researcher to follow individuals through time and record the number of deaths.

One way to do that is to follow a particular **cohort** (i.e. the set of individuals born at a particular time) through their life and record the fraction that remain after each time interval. Although that is conceptually easy, there are a couple of difficulties. First, for long-lived organisms it would take many years of study to monitor the entire life cycle. Second, because there is constant attrition of the cohort as individuals die, you would need to start with a very large initial sample in order to effectively measure the survival of the oldest individuals. Finally, any environmental variation may mask true survivorship schedule. Increases in mortality over time could be due to natural aging of the cohort, but it could also be due to deterioration of the environment.

For those reasons, it is more common to measure the short-term survival of individuals of different ages, and then combine that information into a composite survivorship schedule. That is relatively easy to do for stationary organisms like plants, but somewhat harder for mobile animals.

In the particular case of black footed ferrets, the usual approach is to go out at night with spotlights looking for the characteristic green reflections from the ferrets' eyes. Once a ferret is spotted researchers place a trap near the burrow to try to capture that animal later in the evening. Individual ferrets are then marked by implanting a tiny tag with a unique barcode number under the ferret's skin. When the ferret is later recaptured it's ID code can be read. Ferrets are captured and identified each year, and all new individuals are tagged. Thus the fate of most individuals in the population is known.

When you have complete knowledge of the fate of all individuals, measuring survival is easy: you simply record the fraction of individuals of a given age that are recaptured at the next census. However not every individual is encountered at each census, so not all disappearances are true deaths. Some of the animals may have just been missed by chance. Appendix 4A outlines a method for estimating survival that takes the capture probability into account.

The estimates of individual survival for animals of different ages are then collected into a **survivorship schedule**. The survivorship (l_x) is the probability of surviving from birth to age x . Because survival is multiplicative over time (individuals that survive two years must survive year 1 and survive year 2), the survivorship from birth to age x is: $l_x = s_0 \cdot s_1 \cdot \dots \cdot s_{x-1}$ or

$$l_x = \prod_{y=0}^{x-1} s_y \quad \text{eq. 4.2}$$

By definition, $l_0 = 1.0$, because all individuals are alive at birth.

Alternatively, you can calculate l_x sequentially as

$$l_{x+1} = l_x \cdot s_x \quad \text{eq. 4.3}$$

(In words, the survivorship to age $x+1$ is the survivorship to age x times the survival from age x to $x+1$.)

To be clear, the term "survivorship" (l_x) is used by ecologists to mean the survival probability from birth to age x . We will use the term "survival" (s) when we talk about any other time interval. Also remember that survivorship (l_x) is the probability of surviving from birth to the *start* of age x , and the age-specific survival (s_x) is the probability that individuals of age x survive the next year to the start of age $x+1$.

As an example, here are the age-specific survival results from annual censuses of one population of black footed ferrets. In these data 60% of newborns survived their first year, 50% of one year olds survived to age 2, etc. Complete the survivorship column for 3 and 4 year olds:

Table 4.1. Annual survival of ferrets in South Dakota.

Age x	Annual Survival s_x	Cumulative Survivorship l_x
0	0.6	1.0
1	0.5	0.6
2	0.4	0.3
3	0.3	
4	0	

4.2 How do you measure reproduction?

Reproduction is relatively easy to measure, at least for birds and mammals. Sometimes it is as easy as counting the number of offspring in a nest or den. However, female reproductive success is usually much easier to measure than male reproductive success. Often the male is no longer present when offspring are born. Even when a male is present on a territory, that male may or may not be the biological parent of all of the offspring.



Figure 4.3: Litter sizes of female black-footed ferrets

Because each offspring has two parents we need to make sure that we don't double-count the parents' reproductive output. In a sense, each of the two parents contributes only half. So when we construct the fertility schedule, we must credit only half of the offspring of a pair to the female parent and the other half to the male. Because female reproduction is so much easier to measure than male reproduction, it is customary to keep track only of *the number of female offspring per female*.

The fertility schedule shows how the expected number of offspring changes with age. The **age specific fecundity** (b_x) shown in the fertility schedule is the expected number of female offspring produced by females of age x .

Some females may not reproduce at all and it is important to include them when calculating the fertility schedule. The overall age specific fecundity will then be the proportion of females of age x that reproduce, times the average number of female offspring per litter.

Table 4.3 Fecundity schedule for black footed ferrets in South Dakota.

Age	Proportion reproducing	Average Total Litter size of females that reproduce (males+females)	Expected number of female offspring per female (assuming 50:50 sex ratio) b_x
0	0	0	0
1	0.98	3.0	1.47
2	0.98	3.4	1.67
3	0.98	3.6	
4	0.98	3.6	

Complete this fecundity schedule to calculate the fecundity of 3 and 4 year old ferrets. (Hint: remember that the probabilities are multiplicative. Therefore the expected number of female offspring per female is the probability of reproduction *times* the average litter size *times* the proportion of female offspring.)

The expected number of female offspring is what you expect to find *on average* for females of different ages. Because it is an average, the age specific fecundity (b_x) shown in the fertility schedule is usually not an integer.

Other species of insects, marine invertebrates, and plants have no parental care and therefore newborn offspring do not remain associated with parents. In that case individual fertilities can be very hard to measure. Sometimes seeds can be counted before they disperse. In other

cases the best you can do is to estimate an average fertility for the whole population from the total number of offspring divided by the total number of parents.

4.3 How can you predict population growth from the life table?

The rate of population growth will depend on both the survival and reproduction. The survival and fecundity schedules are therefore combined into a **life table**, which shows the expected survivorship and reproduction of individuals from birth through their entire life.

To determine the total number of offspring a female will produce, we will need to know the expected number of (female) offspring produced by a 1-year-old, times the probability that she survives to 1 year. Then we'll add the expected number of offspring produced when she is two years old, times the probability that she survives to age 2. We'll continue in a similar fashion for reproduction in years 3, 4, etc.

Table 4.4. Simplified life table for a population of Black Footed Ferrets

x	s_x	l_x	b_x	$l_x b_x$	$x l_x b_x$
0	0.6	1.000	0	0	0
1	0.5	0.600	1.5	0.90	0.90
2	0.4	0.300	1.7	0.51	1.02
3	0.3	0.120	1.8	0.22	0.65
4	0	0.036	1.8	0.065	0.26

Sum: 1.69 2.83

In the life table,

Which column shows the probability that a newborn will survive to age x ? _____

Which column shows the expected number of (female) offspring produced at age x ? _____

The life table also includes two additional columns that are used for calculating population growth parameters. The product $l_x b_x$ is the expected number of offspring produced by individuals of age x , taking survival to age x into account. From the perspective of a newborn, the expected reproduction at age x is the fertility at age x times the probability of surviving to age x . The last column shows the product $x l_x b_x$ and is used to calculate the generation time.

The total number of female offspring produced by a female during her entire life is called the **net reproductive rate** or the replacement rate of the population (R_0).

$$R_0 = \sum l_x b_x \quad \text{eg. 4.4}$$

R_0 is an important number because it is a measure of population growth rate. If the population size is to stay constant, then on average each female should produce one female offspring

over her entire life ($R_0 = 1$). If $R_0 > 1$, then some “excess” offspring are being produced and the population will grow. If $R_0 < 1$ then the population will decline.

What is the net reproductive rate for the ferret population in table 4.4? $R_0 =$ _____

Is the population expected to grow? _____

R_0 is similar in many ways to λ , the finite rate of increase of a population (see chapter 1). The key difference is that R_0 is measured on a time scale of *generations*. It shows the replacement rate or the proportional increase of a population over an entire generation, whereas λ describes the growth of a population on an absolute time scale (e.g. one year).

4.3.1 Generation time

A generation is the length of time from the birth of one generation until the birth of the next generation of offspring. In other words, the **generation time (G) is the average age of mothers when they give birth.**

The generation time is calculated as:

$$G = \frac{\sum x l_x b_x}{\sum l_x b_x} \quad \text{eq. 4.5}$$

Notice that the numerator is the sum of the final column of the life table and the denominator is equal to R_0 .

What is the generation time of the ferret population in table 4.4? $G =$ _____

One way to see that the generation time is in fact an average is to look at a simple example. Let's look at a very simple life table and let's imagine we start with a small cohort of only 10 newborns.

Table 4.5. Example life table.

x	l_x	b_x	Number remaining alive	Total number of offspring produced
0	1.0	0	10	0
1	0.5	0	5	0
2	0.2	1	2	2
3	0.1	2	1	2

Based on that example life table, there are a total of four offspring produced: two are produced by 2-year-old mothers and two are produced by 3-year-old mothers. We expect two of the ten newborns to still be alive at age 2, and each will produce one offspring. What is the average age of the mothers of those four offspring? $\frac{2+2+3+3}{4} = \frac{10}{4} = 2.5$ years

How does that compare to the generation time for that life table using equation 4.5? _____

4.4 Assumptions for the age-structured model

Most of our previous assumptions from chapter 1 still hold:

- There is a constant environment, so vital rates (survival and fecundity of each age class) do not change over time.
- Survival and reproduction do not depend on density.
- There is no immigration into or emigration out of the population.
- The only difference is that now we let survival and fecundity depend on the age of the individual.

Notice that we've added some complexity to the model by keeping track of ages of individuals, but we've ignored any kind of density dependence. This model can show whether the population is currently growing ($R_0 > 1$) or declining ($R_0 < 1$) and the parameter R_0 gives the rate of geometric increase. But we probably wouldn't want to use this model to make long-term projections of population growth since it contains no provision for density dependence.

4.5 How does R_0 relate to r ?

Two populations can have the same net reproductive rate (R_0) yet have different absolute rates of growth if the generation times of the two populations differ. For example, if $R_0 = 2$ then the population will double after one generation. That might be one month for a population of insects, but a decade for a large mammal. It is often useful to convert the net reproductive rate, R_0 , to the Malthusian parameter, r , which shows the population growth rate on an absolute time scale.

We have seen that R_0 is the proportional rate of increase over a time interval of one generation, so after G years

$$N_{t+G} = R_0 N_t$$

From equation 1.7 we also saw that under normal exponential growth the population size after G years would be

$$N_{t+G} = N_t e^{rG}$$

Equating those two and simplifying leads to

$$R_0 N_t = N_t e^{rG}$$

$$R_0 = e^{rG}$$

$$\ln(R_0) = rG$$

and finally

$$r \approx \frac{\ln(R_0)}{G} \quad \text{eq. 4.6}$$

What is the intrinsic population growth rate for our population of ferrets? $r =$ _____

Equation 4.6 is only approximately correct, because it does not consider *when* in a generation offspring are born. Offspring born early in a generation will themselves reproduce earlier than later-born offspring, and so will contribute more to the overall population growth rate. Even within a generation individuals are not equivalent.

The exact equation for r was worked out in 1760 by the mathematician Leonhard Euler who showed that

$$1 = \sum e^{rx} l_x b_x \quad \text{eq. 4.7}$$

Equation 4.7 can't be solved directly. But, starting with our approximation of r (above), we can use trial and error to find a value of r that satisfies the Euler equation such that the quantity $\sum e^{rx} l_x b_x$ is close to 1.0.

For ferrets, we found that that r was approximately 0.31 using eq 4.6. Now we can try several values of r near 0.31 and put them into equation 4.7 to see which comes closest to satisfying the equality:

r	Euler equation result
0.30	1.054
0.31	1.034
0.32	1.023
0.33	1.008
0.34	0.993

The exact solution for r for this life table is somewhere between 0.33 and 0.34 ($r=0.335$)

To see how the intrinsic growth rate (r) depends on generation time, consider this hypothetical example. Both populations have $R_0=2.0$, but population 2 has a shorter generation time and therefore has a higher intrinsic rate of increase.

Table 4.6, two hypothetical life tables.

Population 1, late reproduction					Population 2, early reproduction				
Age	lx	bx	lxbx	xlxbx	Age	lx	bx	lxbx	xlxbx
0	1	0	0	0	0	1	0	0	0
1	0.7	0	0	0	1	0.6	1	0.6	0.6
2	0.4	0	0	0	2	0.4	3	1.2	2.4
3	0.2	6	1.2	3.6	3	0.2	1	0.2	0.6
4	0.1	8	0.8	3.2	4	0.1	0	0	0
5	0	0	0	0	5	0	0	0	0
Sum			2	6.8	Sum			2	3.6

Complete the table by calculating R_0 , G and r for Population 2:

	R_0	G	Approximate r from eq 4.6
Population 1	2	3.40	0.20
Population 2			

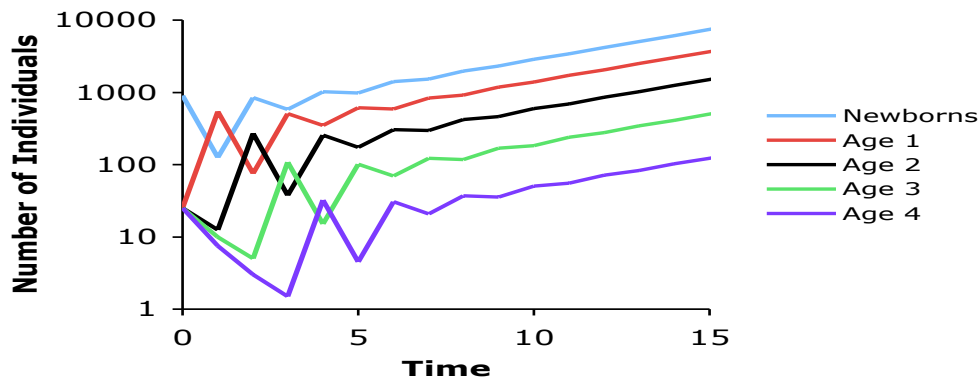
4.6 OPTIONAL: The life table can also be used to compute the stable age distribution, and the life expectancy and reproductive value of each age class.

4.6.1 Stable age distribution

Solving the life table to compute the population growth rate gives an asymptotic estimate that is accurate only when the population reaches its **stable age distribution**. In the short term, the population may grow at a rate that is very different from the predicted growth rate. For example, if you start a population with all adults of reproductive age, the initial population growth rate will be higher than if you start the population with only newborns. No new individuals can be added to the second population until the newborns reach reproductive age, so initially that population can only decrease in size. Eventually, however, the population will reach its stable age distribution and will grow at the predicted rate.

An example may be useful. Using the life table data for ferrets, this hypothetical population started with 900 newborns and 25 of each of the other ages. The relative abundance of animals of each age changes as those newborns become 1 year olds and 2 year olds, etc. but eventually the relative proportion stabilizes to a characteristic stable age distribution. When it reaches the stable age distribution the population size then increases at a constant geometric rate (e.g. it is linear on the log scale).

Figure 4.4



The stable age distribution implies that the *proportion* of individuals of each age is constant. But the overall population size will continue to grow at the rate r .

Once the stable age distribution is reached, the proportion of individuals of age x is given by:

$$c_x = \frac{l_x e^{-rx}}{\sum l_x e^{-rx}} \quad \text{eq. 4.8}$$

To calculate the stable age distribution by hand, it is most convenient to add one more column to the life table, showing the quantity $l_x e^{-rx}$ and then compute the sum of that column.

Table 4.7 Calculation of the stable age distribution.

x	s_x	l_x	b_x	$l_x b_x$	$x l_x b_x$	$l_x e^{-rx}$	c_x
0	0.6	1.000	0	0	0	1.00	
1	0.5	0.600	1.5	0.9	0.9	0.43	
2	0.4	0.300	1.7	0.51	1.02	0.15	0.10
3	0.3	0.120	1.8	0.216	0.648	0.04	0.03
4	0	0.036	1.8	0.0648	0.2592	0.01	0.01
Sum:				1.69	2.83	1.64	

What will be the proportion of newborns and 1-year-olds in this population when it reaches its stable age distribution?

newborns: $c =$ _____

1-year-olds: $c =$ _____

4.6.2 Life Expectancy

The life expectancy for any given age class of individuals is the expected number of additional years they are likely to survive, given that they have already survived to age x . Human demographers often report the life expectancy of a newborn when comparing different populations. But you can calculate the future life expectancy for an individual of any age. Life insurance companies use their calculations of future life expectancy when they determine insurance premiums. Insurance rates go up with age because older humans have shorter life expectancy.

In concept, the life expectancy is the expected number of additional person-years from age x

onward, divided by the expected number of individuals alive at age x : $\frac{\sum_{y=x} N_y}{N_x}$. If we divide

top and bottom by the number of newborns, that is equivalent to $\frac{\sum_{y=x} l_y}{l_x}$. However this

expression assumes that all individuals die on their birthday. In fact, some will die early in the year, just after their birthday, and others will die near the end of the year. On average, those that die during the interval live about 1/2 of the year. To correct for the different times of death, we need to calculate the midpoint survivorship, $L_x = l_{x+1/2}$. Remember that l_x is the proportion of the cohort that survives to the start of age x , and l_{x+1} is the proportion surviving to the start of the next age class. To get the midpoint survivorship, we just average the survivorships l_x and l_{x+1} :

$$L_x = \frac{l_x + l_{x+1}}{2}$$

The life expectancy for an individual of age x is then:

$$e_x = \frac{\sum_{y=x} L_y}{l_x} \quad \text{eq. 4.9}$$

Complete the table for life expectancy in the ferret population:

Age x	Survivorship l_x	Midpoint Survivorship L_x	$\sum_{y=x} L_y$	Life Expectancy e_x
0	1.000	0.8	1.556	
1	0.600	0.45	0.756	
2	0.300	0.21	0.306	1.02
3	0.120	0.078	0.096	0.80
4	0.036	0.018	0.018	0.50

In this population of ferrets, the life expectancy at birth is only 1.5 years. Nevertheless, a 2-year-old is still expected to live an additional 1 year. How is that possible? That two-year old ferret has already survived the early juvenile period. All that matters, given that it has survived to age 2, is the future survival probability.

4.6.3 Reproductive value

Another consequence of age specific fecundity and survival is that different age classes of individuals contribute unequally to future population growth. For example, the death of an old

individual may have little effect on the growth rate of the population because that individual has already completed most of its reproduction. By that reasoning we might expect that the reproductive value would be highest for a newborn, given that their entire reproductive potential is still ahead of them. However newborns have a substantial risk of dying before they reproduce at all. So they, too, have relatively little effect on future population growth.

The geneticist and mathematician Ronald Fisher developed the concept of **reproductive value** (V_x) to quantify the contribution an age class makes to the growth of the population. He noted that when there are tradeoffs between age-specific life history traits (e.g. juvenile vs adult survival or early vs late reproduction), natural selection will have the strongest effect on traits that affect age classes with high reproductive value. Age classes with the highest reproductive value will, on average, leave the most descendants in the future. For many populations, V_x is highest at the age of first reproduction. Those individuals have already survived the period of juvenile mortality yet still have their entire reproductive life ahead of them.

Reproductive value of an individual of age x is defined as the expected number of offspring produced in future years, given that the individual has already survived to age x .

$$\frac{\text{expected number of offspring produced at age } x \text{ and all future years}}{\text{probability of surviving to age } x}$$

which can be written as

$$V_x = \frac{1}{l_x} \sum_{y=x}^k l_y b_y \quad \text{eq. 4.10}$$

Equation 4.10 works for stable populations, but not for growing populations. The reason is that when populations are growing, an offspring produced now will comprise a relatively larger fraction of the total population than an offspring produced in the future when the overall population has grown. Therefore the value of future offspring needs to be "discounted" by the expected population growth. We can use the Euler equation (eq ??) to find the intrinsic growth rate of the population, r . After x years of growing at the rate r , the population will have grown by the fraction e^{rx} , so the future reproduction must be discounted by that expected increase population size. For a growing population,

$$V_x = \frac{e^{rx}}{l_x} \sum_{y=x}^k e^{-ry} l_y b_y \quad \text{eq. 4.11}$$

If the population is not growing ($r = 0$) show that eq 4.11 reduces to eq 4.10.

To calculate the reproductive value by hand, it is easiest to add some temporary columns to the life table, e^{rx} and $\sum_{y=x}^k e^{-ry} l_y b_y$

Complete the reproductive value calculations for black-footed ferrets: (using $r=0.335$)

x	lx	bx	lxbx	e^{rx}	$\sum_{y=x}^k e^{-ry} l_y b_y$	Vx
0	1.000	0	0	1.00	1.00	1.00
1	0.600	1.5	0.9	1.37	1.00	2.33
2	0.300	1.7	0.51	1.87	0.36	
3	0.120	1.8	0.216	2.57	0.10	
4	0.036	1.8	0.065	3.51	0.02	

Which age class of ferrets has the highest reproductive value? _____

4.7 How do survivorship and fecundity schedules differ among species?

The life table is a tidy way to summarize a lot about the basic demography and life history of a species. There are broad differences among species in the form of the life table. Some species "live fast and die young", meaning that they typically have low survivorship but high reproductive output. Other species have a more protracted life cycle, with delayed maturity but relatively higher survival and longer lifespans. Those different patterns are the result of inherent tradeoffs among different components of fitness. Clearly, a population would grow fastest if it had both high survival and high fecundity. But that is rarely possible. In general, resources that are used to support one process, like reproduction, are not available to support growth and survival.

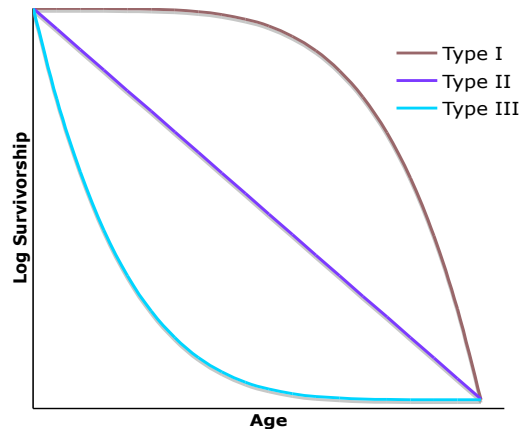
The most famous attempt to summarize the variation in life histories was the idea by Robert MacArthur and E. O. Wilson that organisms could be separated along an axis of "r and K selection". They argued that organisms that typically occurred in low or variable densities would be selected for rapid population growth (high r), high reproductive output and short generation times. Other species that typically occurred in high densities near the carrying capacity (K) of the environment would have fewer resources so selection would favor efficiency over rapid growth. Those species would have fewer, larger, offspring, delayed maturity, and higher adult survival. The r-K selection idea is intuitively appealing and it guided lots of ecological research during the 1960s and 1970s. It is too simplistic to hope that a single r vs. K axis can explain all of life history variation. But much can be learned by examining the survivorship and fecundity and how the influence other life history characters.

One way to think about the life history of an organism is to consider the overall shape of the survivorship curve. Some species have a constant risk of death over their entire life, whereas others have increased mortality during particular life stages (e.g. higher mortality rates among newborns). There are three general patterns of survivorship which have been given the creative names Type I, Type II, and Type III survivorship curves.

- In type I survivorship, there is high initial survival followed by increased mortality at the end of life as organism becomes senescent. Survivorship curves of this type are typical of long-lived mammals with extensive parental care.

- Type II survivorship curves show a constant risk of mortality. Each year the population declines by a constant proportion. Type II curves are sometimes seen in birds and other small vertebrates.
- Finally, Type III survivorship curves have low juvenile survival with long-lived adults. Type III curves are typical of many forest trees and marine invertebrates. Most seedlings die, but the few surviving adult trees can survive for many decades.

Figure 4.5 Type I, II, III survivorship curve.



Note the logarithmic scale on the y axis.

These types of survivorship curves are really ideals that highlight some common differences among survivorship schedules. Most real populations will have survivorship curves that are somewhat intermediate between those pure types. It is even possible to have mixtures. For example, many species have high juvenile mortality (as in type III) and also show a second increase in mortality among the oldest individuals (as in type I). It is important to not be overly concerned with the particular labels, and instead think about the biological processes that are implied by the shape of the survivorship curve. Is the risk of mortality constant or is it concentrated on the juvenile or adult stages?

What kind of survivorship curve do Ferrets have?

Imagine you start with a cohort of 100 newborns. In that case we would expect 60 survivors after 1 year, 30 after 2 years, etc. Graph the logarithm of the number of survivors, $\ln(N)$, vs age using the survivorship schedule for Ferrets. What kind of survivorship curve (Type I, Type II, Type III) do they have?

Fecundity schedules also differ dramatically among species. Some species reproduce only once and then die. They are said to be **semelparous**. Examples include salmon and giant lobelias. Other species have multiple episodes of reproduction and are said to be

iteroparous. There can also be large differences in the timing of reproduction. Some species have an extended juvenile stage and delay reproduction until they reach large size. We see that, for example, in humans or forest trees. Other species reproduce early in life.

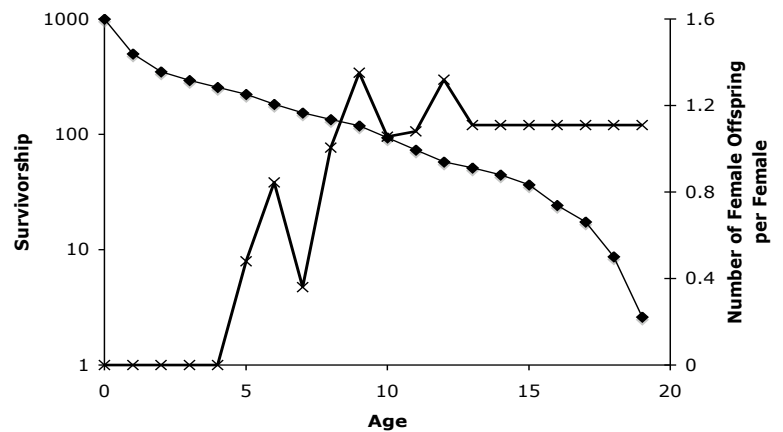
As we saw in the preceding section, the value of future reproduction is discounted by the rate of population growth. So, in rapidly growing populations selection would be expected to favor current reproduction over delayed reproduction. That is consistent with MacArthur and Wilson's idea of "r" selected species: fast growing populations reproduce early. Similarly, in populations with high mortality rates the reproductive value distribution is skewed toward younger ages. The reproductive value of older age classes is low because there is a relatively high probability of dying before that older reproduction is realized. Therefore, the survivorship schedule can have a large influence on the evolution of the fecundity schedule.

4.8 Your turn: Demography of Black Bears

Ferrets have a typical "fast" life cycle. They have relatively high annual mortality rates, and short lifespans, but they reproduce early and have a fairly high rate of population growth. In contrast, eastern black bears (*Ursus americanus*) have one of the slowest reproductive rates of any North American mammal. Females don't reproduce at all until they are 5 or 6 years old, they have small litters of 1-3 cubs, and they have an extended period of parental care.

Eastern Black Bears were once widely distributed in North America. While many populations are still strong, encroachment by humans has

fragmented the habitat and isolated some populations. Below are data from a large population of black bears from a relatively pristine environment in central Ontario, Canada. They are subject to hunting, so some of the adult mortality reflects hunting pressure. Bears were tagged and censused each year from 1969 to 1982 to estimate annual survival of bears of different ages. Newborn cubs were counted to estimate the reproductive output of females.



- Is this population projected to grow? How fast?
- What is the generation time (G) for this population of black bears.
- What is the life expectancy of a newborn?
- Which age class(es) have the highest reproductive value?
- What might a manager do to increase the growth rate of the population?

Age	$l(x)$	$b(x)$
0	1.000	0
1	0.500	0
2	0.350	0
3	0.294	0
4	0.256	0
5	0.223	0.48
6	0.182	0.84
7	0.153	0.36
8	0.135	1.01
9	0.119	1.35
10	0.094	1.06
11	0.073	1.08
12	0.058	1.32
13	0.051	1.11
14	0.045	1.11
15	0.037	1.11
16	0.024	1.11
17	0.017	1.11
18	0.009	1.11
19	0.003	1.11

4.9 Further Reading:

Beton, M., C. Townsend, and J. L. Harper. 2006. Ecology: from individuals to ecosystems 4th ed. Blackwell. (Chapter 4).

Grenier, M. B., D. B. MacDonald, S. W. Buskirk. 2007. Rapid population growth of a critically endangered carnivore. *Science* 317:779.

[USFWS] U.S. Fish and Wildlife Service. 1998. Black-footed Ferret: Return of a Native. Black-footed Ferret Recovery Implementation Team, U.S. Fish and Wildlife Service: Pierre, South Dakota.

4.10 Practice Problems (will add 5-10 questions here)

Appendix 4A: Estimating Survival through Mark-Recapture

The key ideas for estimating survival from mark-recapture experiments were developed by R. M. Cormack, G. M. Jolly and G. A. F. Seber in the early 1960s. In the simplest case, assume there is a set of marked individuals that is released into a closed population. Some of the animals are later recaptured on one or more occasions, in which case they are known to be alive. Others disappear from the population and are never again recaptured or resighted. Those may be dead, or they may have just been missed each time. How can you estimate the true survival rate?

One key is to recapture individuals on more than one occasion. Individuals that are recaptured or re-sighted at time 2 were, of course, also alive at time 1, even if they were not recaptured after the first time interval. Because we know those individuals were actually alive even though they were missed, we can use those data to estimate the fraction of individuals that are not recaptured during a given census. Ecologists have developed sophisticated statistical models to analyze mark-recapture data to estimate the population size, survival rates of different age classes, and emigration rates.

	Survival rate s_1	Capture probability c_1		Survival rate s_2	Capture probability c_2		
Mark and release	→	→	First recapture	→	→	Second recapture	→ etc.
Time 0			1			2	

Each animal will have an associated capture history. We'll denote captures with 1's and failure to sight that individual during a capture period with 0's. Our raw data will then be the number of animals observed with each kind of capture history. For example, imagine we mark and release 100 animals. We then recapture animals on two subsequent occasions. We might see something like this:

Capture sequence	N
1,1,1	70
1,1,0	10
1,0,1	9
1,0,0	11
Total	100

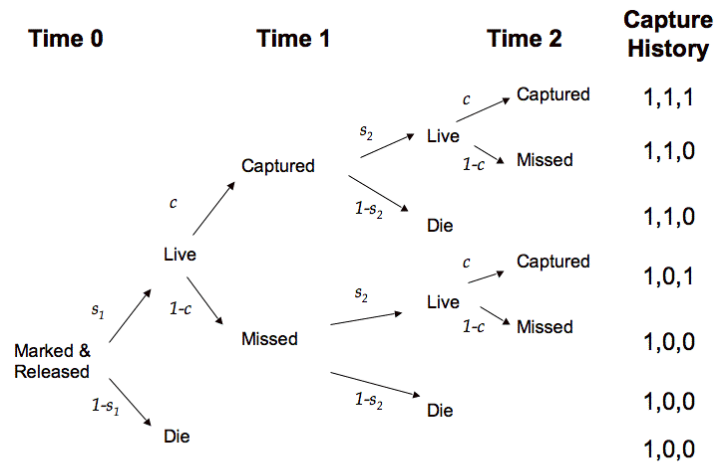
The first row shows that 70 of the 100 animals marked initially were recaptured on both subsequent censuses. The second row shows that 10 animals were recaptured once, but then not recaptured at the second census. Nine animals were missed at time 1 but then subsequently recaptured at time 2.

Finally, the last row shows that 11 animals were never seen again after the initial release.

How can we use those observations to estimate the underlying survival rates in the population?

The first thing to do is to write down how the underlying processes (survival and recapture) relate to the observations. To keep things simple, let's assume that the trapping program is set up consistently each time, so

there is a constant (but unknown) probability of capturing an individual during each trapping session. Survival, however, may be different in different time intervals. During each time interval an animal may either live (with probability s_i) or die (probability $(1-s_i)$). If the animal survives, it may then either be recaptured (with probability c) or missed (probability $(1-c)$). That gives a "decision tree" that shows the following possible recapture sequences:



To calculate the probability of a particular outcome, you multiply probabilities along the arrows of a particular path, and then sum the probabilities across all paths that produce a particular capture history.

Let's look at the capture sequence $\{1,0,0\}$. In that case the individual was captured and marked at the beginning but then never seen again. The decision tree shows that there are three ways an individual could end up with that capture history:

1. it could have died during the first interval. That will happen with probability $(1-s_1)$
2. it could have survived and been missed in the first re-capture period, but then died during the second time interval. That will occur with probability $s_1 \cdot (1-c) \cdot (1-s_2)$
3. it could have survived the whole time, but have been missed on both occasions. That occurs with probability $s_1 \cdot (1-c) \cdot s_2 \cdot (1-c)$ or $s_1 \cdot s_2 \cdot (1-c)^2$

Adding them up, the overall probability of finding a capture history $\{1,0,0\}$ would then be:

$$\Pr [\text{Capture history is } \{1,0,0\}] = (1-s_1) + s_1 (1-c) (1-s_2) + s_1 (1-c) s_2 (1-c)$$

In all, there are four distinct capture histories (111, 110, 101, and 100) and you can set up similar equations for each of them.

From the decision tree above, what is the probability of observing a capture history of $\{1,1,1\}$? _____

Hypothetical data:

Capture history	Observed number of animals with that capture history (N_{iii})	Probability (p_{iii})
1,1,1	70	
1,1,0	10	$s_1 c s_2 (1-c) + s_1 c (1-s_2)$
1,0,1	9	$s_1 (1-c) s_2 c$
1,0,0	11	$(1-s_1) + s_1 (1-c) (1-s_2) + s_1 (1-c) s_2 (1-c)$

The trick, then, is to pick values of the unknown parameters ($s_1 c s_2$) such that the predicted number of recaptures is close to the observed number. This could be done by trial and error, i.e. making a guess of the parameter values, seeing how close the prediction is to the observed value, and then adjusting your guesses.

Sometimes ratios can be useful to estimating some of the underlying processes. For example, what is the ratio of $\frac{p_{101}}{p_{111}}$? $\frac{p_{101}}{p_{111}} = \frac{s_1(1-c)s_2c}{s_1cs_2c} = \frac{(1-c)}{c}$ That ratio is solely dependent on the capture rate, so that provides one way to estimate c (but that method does not use all of the available information about c).

Usually, however, a simultaneous estimation of the parameters is done by computer using an optimization technique such as maximum likelihood. For example, you can calculate the log likelihood of the data, given a particular guess at the parameters as:

$$\text{LogLikelihood} = \text{Const} + N_{111} \text{Log}(P_{111}) + N_{110} \text{Log}(P_{110}) + N_{101} \text{Log}(P_{101}) + N_{100} \text{Log}(P_{100})$$

where the p_{iii} values are taken from the table above. The computer then searches for the parameter set that maximizes the log likelihood. Various computer programs are available to automate that process. For our example data, the maximum likelihood values are $s_1=0.90$, $s_2=0.99$, and $c=0.89$.

This basic framework can easily be extended to more complicated scenarios. For example, you might want to estimate survival rates separately for males and females, or for juveniles and adults. The equations get longer, but the basic procedure remains the same.

Assumptions for estimating survival via mark-recapture experiments:

- The population is closed. There is no immigration or emigration.
- The survival probability is the same for all individuals.
- Each individual has an equal probability of being captured.
- Marking does not affect survival.

Answers:

p 4. $l_3=0.12$

$l_4=0.036$

p 5. $b_3=1.76$

$b_4=1.76$

p 6. l_x shows the probability of survival to age x

b_x is the expected number of offspring at age x

p 7. $R_0=1.69$

$R_0>1$ so it will grow

$G=2.83/1.69 = 1.67$ years

p 8. using eq 4.5, $G=2.5$ yrs, the same as above.

p 9 $r=\ln(1.69)/1.67=0.31$

p 10. $R_0=2$, $G=1.8$, $r=0.385$

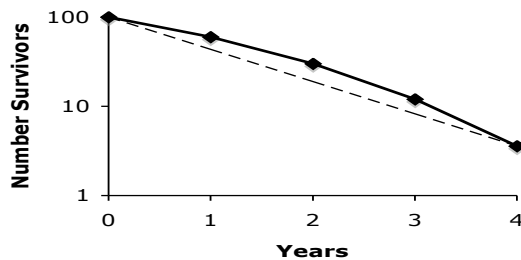
p 11. At the stable age distribution, 60% of the ferrets will be newborns and 26% will be 1 yr olds ($c_0=0.60$ $c_1=0.26$)

p 12. Life expectancy is 1.56 for newborns and 1.26 for 1 yr olds.

p 14. Reproductive value: $V_2=2.33$, $V_3=2.19$, $V_4=1.80$

One-yr-olds have the highest reproductive value (that is also the age of first reproduction)

p 15. The survivorship curve of ferrets is approximately linear, so it is close to a type II survivorship curve (although there is a slight increase in mortality with age, as in a type I curve).



p 17. **Black Bears**

$R_0=1.07$, so the population is growing

$G=9.5$ yrs

Life expectancy of a newborn is 3.1 yrs

The reproductive value is highest for 8-year-olds (5.48)

p 19. Appendix 4A. The probability of observing a capture sequence $\{1,1,1\}$ is $s_1 * c * s_2 * c$

Age	$l(x)$	$b(x)$	$lxbx$	$xlxbx$	$c(x)$	$E(x)$	$V(x)$
0	1.000	0	0.000	0.000	0.28	3.12	1.00
1	0.500	0	0.000	0.000	0.14	4.74	2.02
2	0.350	0	0.000	0.000	0.10	5.56	2.90
3	0.294	0	0.000	0.000	0.08	5.53	3.48
4	0.256	0	0.000	0.000	0.07	5.28	4.03
5	0.223	0.48	0.107	0.534	0.06	4.99	4.66
6	0.182	0.84	0.154	0.924	0.05	4.98	5.14
7	0.153	0.36	0.055	0.386	0.04	4.83	5.15
8	0.135	1.00	0.136	1.086	0.04	4.42	5.49
9	0.119	1.35	0.160	1.443	0.03	3.96	5.13
10	0.094	1.05	0.099	0.990	0.02	3.88	4.82
11	0.073	1.08	0.079	0.869	0.02	3.83	4.86
12	0.058	1.32	0.076	0.915	0.02	3.72	4.82
13	0.051	1.11	0.057	0.742	0.01	3.11	3.96
14	0.045	1.11	0.050	0.695	0.01	2.50	3.30
15	0.037	1.11	0.041	0.611	0.01	1.94	2.69
16	0.024	1.11	0.027	0.430	0.01	1.69	2.41
17	0.017	1.11	0.019	0.329	0.00	1.15	1.82
18	0.009	1.11	0.010	0.174	0.00	0.80	1.44
19	0.003	1.11	0.003	0.055	0.00	0.50	1.11