

DEMOGRAPHY

The ability to predict the abundance of a population would clearly be of value to a wildlife manager. Such predictions require knowledge of birth and death rates of the population in question, age and sex composition, and more. Since populations fluctuate in numbers, all of these parameters may also fluctuate. Thus, to make predictions concerning a dynamics population, one must understand population structure and the forces that mold that structure.

Tables and graphs of age specific mortality and of age specific fecundity are useful for understanding the dynamics of a population and for understanding differences between populations.

The following terminology is usually (but not always) used in these tables and graphs:

cohort - a group of individuals born simultaneously

x - age, usually in years for wildlife species but sometimes in months

l_x - the proportion of a cohort still living at age x , or the probability of a newborn living to be age x

m_x - the expected number of female offspring produced by a female of age x

R_0 - the expected number of female offspring a newborn female will produce during her lifetime.

N_t - population size at time t

r - intrinsic rate of natural increase for an uncrowded population (sometimes denoted r_{max})

T - generation time

v_x - reproductive value of a female of age x

d_x - the frequency of mortality for individuals of age x , or the difference between l_x and

l_{x+1}
 q_x - mortality rate from age x to age $x+1$

p_x - survival rate from age x to age $x+1$

l_x , d_x , q_x and p_x are not independent of each other but present the same information from different perspectives. Conversions among these 4 parameters are merely arithmetic exercises; tables of conversions may be found in many wildlife managements or ecology texts. Because the information presented by these parameters is redundant, we shall discuss l_x almost exclusively in this handout and deal with the others very little.

SURVIVAL RATE, l_x

It is not surprising that the chances of surviving to the next age class decrease as age increases. For a given species, however, survival rates can be quite variable, depending on the environment. Figure 1 shows as l_x curve that is typical of hooved mammals. For a species living in its optimum habitat, survival rates and the l_x curve will be elevated above the same statistics for the same species in less favorable habitat. The l_x curve for black-tailed deer in both chaparral and shrub land habitats in California are similar to the curve in figure 1 but the chaparral curve lies above the shrub land curve because chaparral is better black-tailed deer habitat in California than is shrub land. l_x curves for a single species in different habitat do not, however, always look the same. Sometimes they have very different shapes.

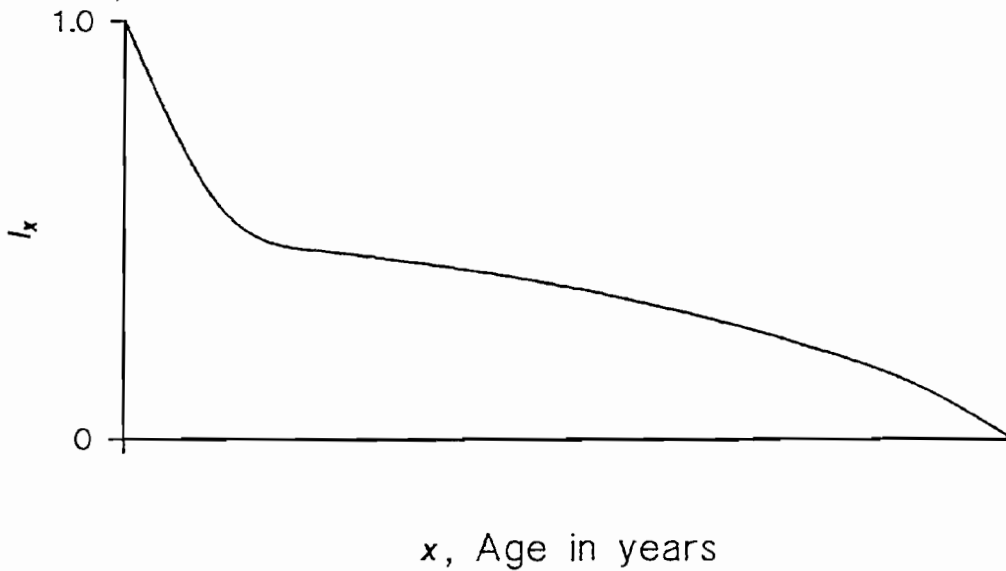


Figure 1. Typical l_x curve for hooved mammals, such as deer, sheep and goats

Figure 2 shows a specific example of an l_x curve, the l_x curve for a dall sheep population in Alaska.

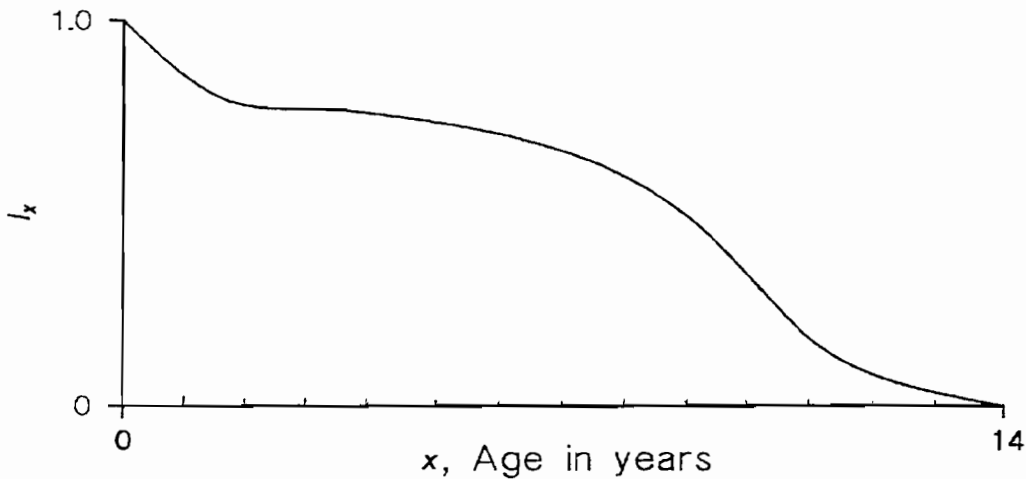


Figure 2. l_x curve for a wild dall sheep population in Alaska.

Mortality after birth is usually very high but is often difficult to measure. Very young and very old individuals are generally more vulnerable to natural mortalities than individuals of "prime" reproductive ages. Note that the l_x curves in Figures 1 and 2 both have plateaus during the "middle" years. Such a plateau is common in l_x curves of hooved animals. For many wildlife species, precision of l_x curves is limited by the reliability of age estimation. Data are often not available until young reach some "harvestable" age. For some birds, the ages of adults can not be estimated.

Two basic approaches exist for gathering age specific survival data. One used very little is to follow one (or preferably more than one) cohort through time until all are dead, noting the age at

cohorts are dead, noting the age at which each died. This is a sample of the dying. In extrapolating such data to the whole population, one assumes that the sampled cohorts were typical of all other cohorts. The more commonly used approach is to establish the proportion of the total population that individuals of each age class comprise at a specific time. These relative proportions should be monitored through one (or several) reproductive cycle(s). This results in a sampling of the living and requires crucial assumptions concerning age distributions and population growth that we shall discuss later. One major assumption is that the sampled year(s) or season(s) is (are) typical.

In practice, age specific data are often gathered from a variety of times, places, and methods. Using such diverse data sources does provide larger sample sizes than each data source independently provides but assuming that data of diverse origin can be lumped together is dangerous and can lead to false deductions. One must consider various types of data and how they can best be used. For example, if hunting is not biased towards a certain sex or ages, it can be used to obtain a sample of the living. When hunting is a major source of mortality, or the sole source of mortality, it may be used to obtain a sample of the dying. These sorts of factors must be kept in mind when collecting data and when lumping data from different sources.

FECUNDITY RATES, m_x

Individuals (and thus populations) exhibit considerable variation in timing and amount of reproduction. They vary in their ages of first reproduction, litter or clutch sizes, life expectancies, frequencies of reproduction, and more. Many populations with which we are familiar are seasonally and synchronously reproductively active (Figure 3); in the United States, most wildlife species produce young in the spring and early summer. Such synchrony results in regular fluctuations in the numbers of individuals in a population. Because production of young is seasonal and usually occurs in a benign season, population fluctuations are often associated with a regular fluctuations in environmental severity. Over an extended period, the numbers of individuals in a population will fluctuate around some mean value. In population analyses, it is convenient to think of all individuals born during one season (a cohort) as being born simultaneously. The conclusions drawn are generally applicable even to populations that do not reproduce in pulses or that have secondary pulses. Reproduction by an individual varies with age (Figures 4 and 5). Individuals of young ages typically contribute less to recruitment to the population than do older individuals. When conditions are unfavorable, young and very old members of a population are the first to curtail reproduction. Very old individuals may exhibit a reduction in reproduction even during good years,

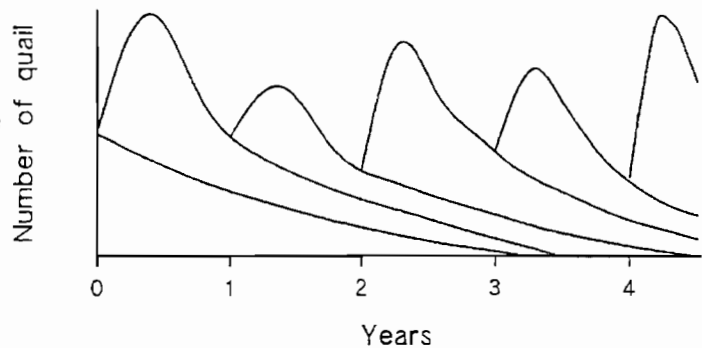


Figure 3. Change in population size of valley quail

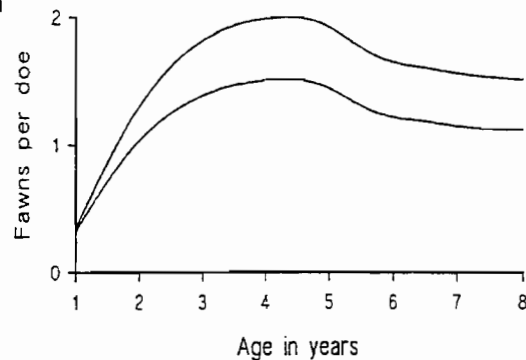


Figure 4. Reproductive rates for female white-tailed deer of different ages at 2 sites in Michigan

though this is not always the case.

Figures 3, 4, and 5 are not m_x curves. Figure 4, with each point divided by 2, would have shown m_x curves (remember, m_x is the expected number of female offspring). From here on we shall assume that sex ratios are 50:50 and, therefore, fecundity of the whole population is m_x : (2 sexes of adults)/(2 sexes of young).



Figure 5. Percent of captive dall sheep ewes of different ages that give birth to lambs (litter size is always 1).

Figure 6 shows l_x , m_x and $l_x m_x$ curves for an hypothetical dall sheep population. Remember, l_x is the probability of survival or the proportion of a cohort expected to be left alive at age x , m_x is the potential fecundity of female in terms of female offspring, and now -- $l_x m_x$ is the realized fecundity of a female in terms of female offspring. $l_x m_x$ incorporates both the expected number of offspring produced by l_x a female of age x and that female's chances of living to age x , thus $l_x m_x$ is realized fecundity.

The $l_x m_x$ curve shows the number of daughters a female is expected to produce at age x multiplied by the probability of the female living to be age x . The total area under the $l_x m_x$ curve, summed over all ages is,

$$R_0 = \sum_{x=0}^{\infty} l_x m_x$$

This is the total contribution (of daughters) to the next generation that is expected from one female. It is therefore also the ratio of females in 2 successive generations, and since the sex ratio is assumed to be 50:50, it is the ratio of total

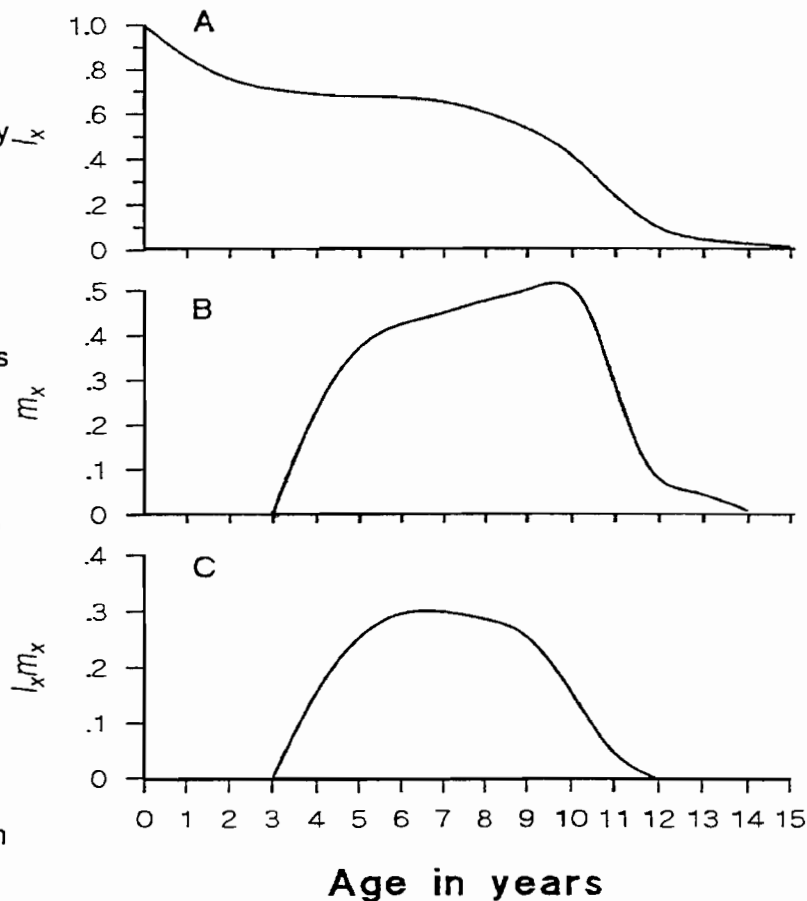


Figure 6. Life table curves for an hypothetical dall sheep population in Alaska; (A) l_x curve for wild dall sheep in Alaska, l_x always varies from 1.0 to 0.0; (B) m_x curve for captive dall sheep in Alaska, m_x varies dramatically between species, depending on age of first reproduction, litter or clutch sizes, and more; (C) assuming that the curves for captive and wild dall sheep are the same, this is the $l_x m_x$ curve for dall sheep in Alaska; this curve is made by simply taking the product of l_x and m_x at each age.

population sizes in 2 successive generations. Therefore:

$$\frac{N_T}{N_0} = R_0 = \sum_{x=0}^{\infty} l_x m_x$$

where N is the total population size at time 0 and N_T is the total population size one generation later. For the population of dall sheep graphed in Figure 6, R_0 is 1.83. This is probably an overestimate of R_0 for a real population because the m_x of wild sheep would probably be lower than that of captive sheep (Figure 4 shows how m_x curves for the same species can be different in different habitats - here captivity is a different habitat that experienced by a wild population). Even though this is probably an overestimate of a real R_0 , we shall follow it through this handout as an example.

Now, if R_0 is greater than 1 for any population of a species, and l_x and m_x do not change, then that population should grow, and continue to grow, indefinitely, because each female is expected to produce more than one female for the next generation. This brings us to age distribution or age structure.

AGE STRUCTURE or AGE DISTRIBUTION, S_x

The age distribution of a population is the proportion of the population found in each age class; you might call it the distribution among individuals among the different age classes. If the age distribution does not change over a long time, it is called a stable age distribution. A population with a stable age structure does not necessarily have a stable population size. The population size could be rapidly changing but the proportion of the population in each age class could stay the same.

An uncrowded population that is steadily growing will increase at a rate proportional to the population size. This can be represented by:

$$\begin{aligned} \frac{\text{rate of population growth}}{\text{population}} &= \frac{\text{change in population size}}{\text{change in time}} \\ &= \frac{dN}{dt} \\ &= rN \end{aligned}$$

where N equals the population size (Number present) and r is the constant of proportionality for this increase in population size, called the intrinsic rate of increase)

In a population with a stable age distribution, each age class will also grow at the same rate as the population. If $r = 0$, the population does not change in size; the rate of population growth is 0. If r is greater than 0, the population is growing; if r is less than 0, it is decreasing.

Now, for a population that has a stable age distribution, the relative numbers of individuals in each age class can be conveniently represented by the equation:

$$S_x = l_x e^{-rx}$$

Here S_x represents the age structure and e is the root of the natural logarithms. If $r = 0$, then

$$S_x = l_x$$

So, in the special case of population with both a stable population size and a stable age distribution, survival rates (the l_x distribution) can easily be calculated because it is the age distribution. All one has to do is determine the age distribution. In the special case of a population with a stable age distribution only, the survival rates can still be calculated from the age distribution and r .

These are very special cases. For example, if a population of white-tailed deer has a stable age distribution and a stable population size (age distribution and population size determined at the same time each year) and hunting mortality is a random sample from all age classes, then the age structure of the hunter killed deer gives the l_x table for the population. If, however, the population is either increasing or decreasing, then the age structure does not give the l_x table. Only if $r = 0$, does $S_x = l_x$. In a declining population, mortality is underestimated by age structure and survival is overestimated; in an increasing population the reverse is true. This relationship is particularly important for wildlife managers who deal with endangered species. If you must manage a decreasing population, you could be fooled into thinking that survival is greater than it really is if you estimate l_x as S_x .

If a population does not have a stable age distribution, surprising things can happen. The dall sheep population whose life table curves are shown in Figure 6 will increase in the long term and will continue to increase until l_x , m , or both change. But let's say, for example, that we have a population that for some reason has been reduced to 10 10-year-old ewes and just enough rams to breed with them. The future of this population is shown in Figure 7. This sort of change in population structure and population size is possible in real life again when we must manage endangered species whose population sizes have fallen to low levels. Even though we may initiate a management program that increases R_0 so that it is greater than 1, the species may still begin a marked decline in population size before beginning to increase in population size. Unfortunately, this initial population decline may be enough to lead to extinction before the species has a chance to recover. So, age structure of a population is very important.

GENERATION TIME, T

Let us go back to the equation for population growth in an uncrowded population:

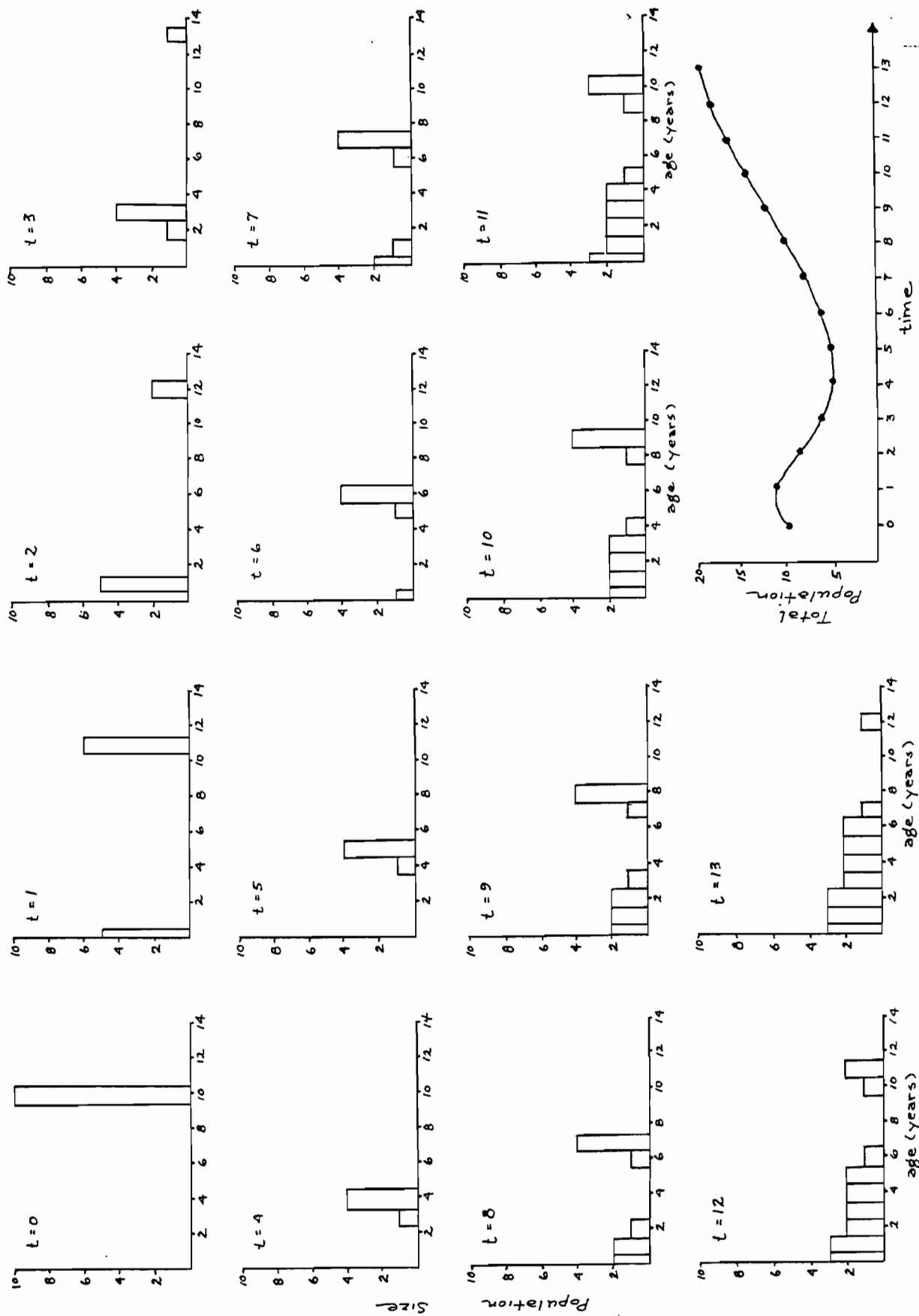
$$dN/dt = rN$$

This is a differential equation. We can solve it by separating the variables and integrating both sides. We shall integrate over one generation in time, T .

$$dN/dt = rN$$

$$dN/N = r dt$$

Figure 7. Population dynamics of a dall sheep population with an unbalanced age distribution. Note that even though R_0 is greater than 1, the population decreases before it begins its endless increase.



$$\frac{dN}{dt} = rN$$

$$\frac{dN}{N} = r dt$$

$$\int_{N=N_0}^{N_T} \frac{dN}{N} = r \left(\int_{t=0}^T dt \right)$$

$$\ln(N_T) - \ln(N_0) = r(T-0)$$

$$\ln\left(\frac{N_T}{N_0}\right) = rT$$

$$\frac{N_T}{N_0} = e^{rT}$$

Now, remember that $N_T/N_0 = R_0$. With this relationship, we now have a relationship between r (which we usually can not observe because few populations have stable age distributions) and l_x and m_x , both of which can be estimated.

Had we solved the equation from time 0 to any arbitrary time, t , we would have found

$$\frac{N_t}{N_0} = e^{rt}$$

$N_t = N_0 e^{rt}$ = population size at any arbitrary time, t .

For $t = 1$, we have

$$N_1 = N_0 e^r, \text{ and}$$

$$e^r = N_1/N_0 = \lambda$$

So e^r is the ratio of the numbers of animals in 2 successive units of time and λ (the Greek letter lambda) is the symbol often used for this ratio. But since

$$R_0 = e^{rT},$$

then,

$$e^r = \lambda = R_0^{1/T},$$

which is an exceedingly important relationship. It enables us to compare the importance of a female's total contribution of offspring (R_0) with her rate of growth to maturity (which influences T).

Notice: T is relatively much more important than R_0 because R_0 enters the equation as a factor but T enters the equation as an exponent (actually, $1/T$ is the exponent). The greater the size of R_0 with respect to T , the more important this relationship becomes. When R_0 and T are about the same size, then a 4-fold increase in R_0 will be completely offset by only a 2 fold increase in T . As R_0 gets relatively greater than T , the relative importance of T becomes greater. In our dall sheep example, $R_0 = 1.83$, T is very close to 7, and λ is about 1.09. Changing λ to 1.20 could be done by doubling R_0 or halving T . For cottontail rabbits where R_0 has the potential of being very high and T very small, a 10-fold decrease in R_0 could have the same effect on the population as only doubling T .

We do run into a problem here, though. How do we measure T ? We know that

$$R_0 = e^{rT},$$

but this equation has 2 unknowns, r and T . Several equations exist to estimate T but they all contain 2 unknowns, T and something else that usually reduces to r .

Another approach comes from the general "feel" for the meaning of generation time. Generation time is the time difference between ages of parents and offspring. Therefore generation time might be the age at which a female has just replaced herself with female offspring, or the T that solves the equation:

$$1 = \sum_{x=0}^T l_x m_x$$

This can not be solved algebraically for T but one can easily do some fiddling and come up with an approximate value for T . When one does come up with a value for T in this manner, it agrees very well with the T that satisfies the equation

$$R_0 = e^{rT}.$$

For our dall sheep example,

$$\sum_{x=0}^7 l_x m_x = 1.04$$

T estimated in this manner is really close to 6.7. And r is approximately equal to 0.0090.

But there is a problem with this technique, too. When R_0 is less than 1 (the population is decreasing), T is undefined by this technique, yet it is not undefined by the equation

$$R_0 = e^{rT}$$

This is where we have to leave generation time. The concept of generation time might seem reasonably easy to visualize and to define and to determine, but this is not the case. Generation time can and does cause trouble in many demographic studies.

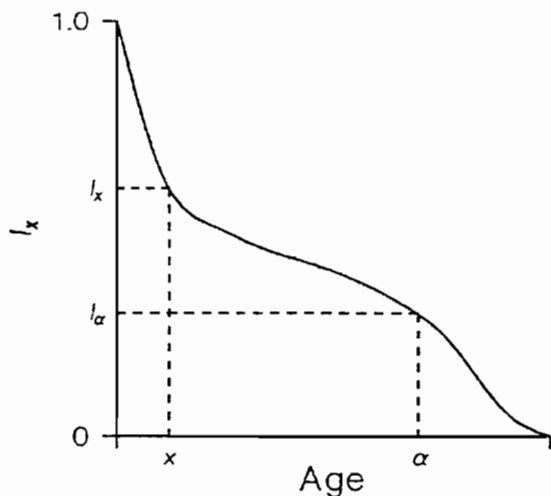
REPRODUCTIVE VALUE, v_x .

Perhaps the most interesting thing to do with r is to calculate v_x , the reproductive value of a female of age x . This can be done with a very hairy equation, which you need not understand completely. Look at it and at the explanation and try to get as much from it as you can, but do not worry if you can not see its derivation or exactly how it works.

$$v_x = \sum_{\alpha=x}^{\infty} \left(\frac{l_\alpha}{l_x} \right) m_\alpha \left(\frac{e^{-r\alpha}}{e^{-rx}} \right)$$

v_x ← reproductive value of a female of age x
 $\sum_{\alpha=x}^{\infty}$ ← summation over all ages (α) older than x
 $\left(\frac{l_\alpha}{l_x} \right)$ ← the probability of living to age α given that the female has already survived to age x
 m_α ← age specific fecundity for a female of age α
 $\left(\frac{e^{-r\alpha}}{e^{-rx}} \right)$ ← the "cost of waiting", a number between 0 and 1

We are now considering a female of age x and we want to quantify her contributions in female offspring at all future ages (α) greater than x . Just as $l_x/l_0 = l_x/1 = l_x$ is the probability of surviving to age x given that a female has survived to age 0 (that is, she was born), l_α/l_x is the probability that the female will survive to age α given that she has already survived to age x .



The "cost of waiting" refers to how soon a female has young or how she distributes the young she will have over her ages older than x . The sooner a female has the young she is going to produce, the sooner those young will also be reproducing. Consequently, the earlier a female reproduces, the greater her contribution of individuals and genes to future generations. The "cost of waiting" also quantifies a female's future reproduction relative to the rate that the population in which she lives is growing.

Notice that the reproductive value of a newborn female is 1. Substituting 0 for all x 's in the v_x equation produces

$$v_0 = 1$$

This means that the reproductive value (v_x) evaluates the future contributions of a female of any age in terms of an equivalent number of newborn females. At birth, $v_0 = 1$. v_x then climbs to a peak (which occurs before the peak in the m_x curve) and finally falls off again. The reason that the v_x curve is not at its highest point at birth is because not all young survive to the age of first reproduction. The reason it peaks before the m_x curve and then falls off is because a female's greatest future potential contribution of offspring comes shortly after she starts breeding or right around that time. The relationship between v_x and m_x for our dall sheep example is shown in

Figure 8. Note that the peak in the v_x curve is at age 4, the age of first reproduction, whereas the peak in the m_x curve is at ages 9 to 10. A 4 year old female is expected to contribute as much to future generations as about 2.5 newborn females. A 9 year old female is expected to contribute as much to future generations as a single new born. So, if you are interested in maintaining a population with the greatest potential for growth, you should be most interested in keeping the 2 to 6 year olds alive and healthy, and should have about as much interest in newborns as you have in 9 year olds, even though 9 year olds have the highest m_x .

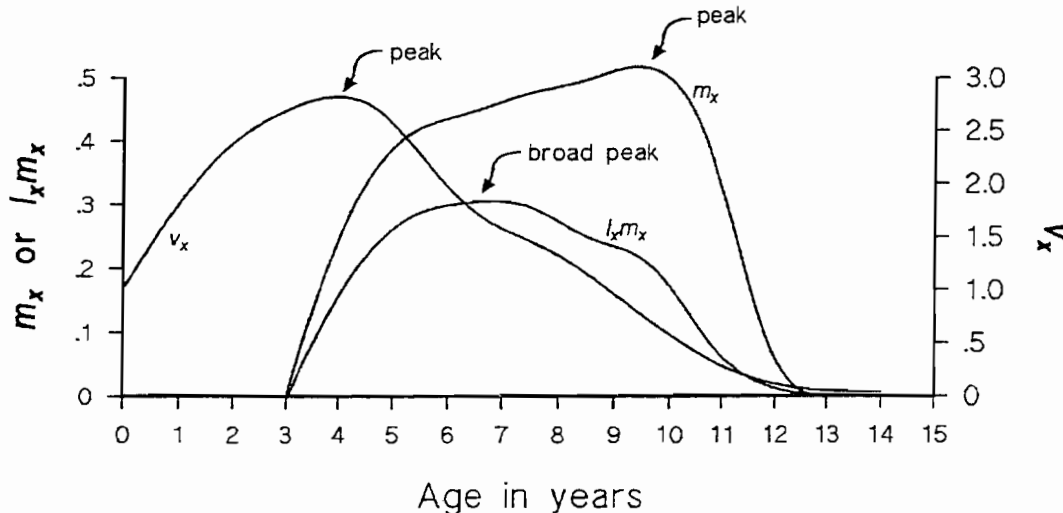


Figure 9. v_x , m_x and $l_x m_x$ curves for the dall sheep population graphed in Figure 6.

... As an aside, in humans there is an approximate permanent pair bond. In order for a male to reproduce he must choose some female and stay with her. It is expected that natural selection would favor those males that can best recognize females with maximum reproductive value because such males would then leave the maximum number of offspring. The age process brings about changes in external appearance of females and it is therefore expected that males would be very sensitive to these changes in appearance and have strong preferences for females whose ages coincide with maximum reproductive value. In some data for white Australians reported by R. A. Fisher in 1930, the maximum reproductive value occurred at 18½ years of age. All of which might be an evolutionary biologist's way of saying the "beauty lies in the eyes of the beholder". . . .

SOME APPLICATIONS

The main value of life table information is what it communicates about a population's strategies for survival. That is, what environmental factors influence birth and death rates over the short and the long term. Whether a manager seeks to reduce or increase a given population, he or she must identify life stages with the greatest variability and the life stages with greatest importance. This information can then be used as a basis for field experimentation or computer simulation to document or to estimate effects of management policies.

There are a few broad steps to take to determine why a population might decline:

- 1) Compare the declining population to a healthy population to discern obvious differences.

2) Determine if fecundity or breeding have been impaired, indicating whether low fecundity or high mortality are causing the decline:

3) Determine age classes with high mortality. If adult mortality is high and juvenile mortality normal, hunting pressure may be excessive. If mortality of juveniles or young adults is high, some aspect of habitat, probably food, is lacking. High mortality of juveniles or young adults is important because members of these age classes usually have high v_x and have the potential to make the greatest contributions to population growth.