

## Demography and Age-Structured Populations

### Outline

#### Population parameters

Discrete vs. continuous events, ages vs age-classes.

#### Life Tables

Cohort vs. Static (segment)

Survivorship:  $l_x$  and  $s_x$

Fecundity:  $m_x$

Net reproductive rate:  $R_0$

Generation time:  $T$

Intrinsic rate of increase:  $r$

Reproductive value:  $v_x$

Residual reproductive value

Trade-offs and optimal life-histories

Assumptions and limitations

Age distributions

Recall from lecture 1, a **Population** is a group of individuals of the *same species*, living *sufficiently close* together than *intermating is possible*, and therefore *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 other 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 seasons, so life-tables for vertebrates are based on discrete one-year age-classes, each potentially including a bout of reproduction.

In Pianka Chapter 8, all of the equations are given in the discrete form that is most widely used, and in continuous form using integration rather than summation - that is the only 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.**

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,  $N_\omega = 0$ .  $\omega$  (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.

(Fig. 8.1 Pianka)

Age class	Number in age class: $N_x$	Survivorship from birth: $l_x$	Age-specific 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)

(Fig 4.12 Begon et al.)

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)

Survivorship ( $l_x$ ) tables can be used to calculate **life expectancy,  $E_x$** , which is the **average lifespan remaining for an individual of age  $x$** .

$$E_x = \frac{\sum_{y=x}^{\omega} l_y}{l_x}$$



Example of calculation:

$$E_0 = (1 + 0.80 + 0.40 + 0.10)/1 = 2.30 \text{ years}$$

$$E_1 = (0.80 + 0.40 + 0.10)/0.8 = 1.63 \text{ years}$$

### ***Fecundity Schedule.***

$m_x$  =  $1/2$  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.

$\alpha$  (alpha) = typical symbol for age at which breeding begins.

(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** =  $\Sigma m_x$ . 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,  $R_0$**  =  $\Sigma l_x m_x$ . 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,  $T$** .

**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.

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

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’.

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  $e^{-rx}l_xm_x$  column and sum it.

$x$	$N_x$	$l_x$	$m_x$	$l_xm_x$	$xl_xm_x$	$e^{-rx}$	$e^{-rx}l_xm_x$
0	500	1	0	0	0	1	0
1	400	0.80	2	1.6	1.6	0.487	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.

### ***Reproductive Value, residual reproductive value and life-history tactics***

Life expectancy is the average life-span expected for an individual of age  $x$ . Extending this idea, one can ask what is the ***expected current and future reproductive output for an individual of age  $x$*** , which is termed ***reproductive value***,  $v_x$ .

$$v_x = \sum_{t=x}^{\omega} [(l_t/l_x) m_t]$$

The term  $l_t/l_x$  gives the probability of living from age  $x$  to age  $t$ , and  $m_t$  is the number of offspring produced by those that survive to age  $t$ .

Reproductive value initially increases with age, because each pre-reproductive year that an individual survives increases the probability that it will survive to reproductive age. RV usually peaks near the age of first reproduction ( $\alpha$ ), for two reasons: (1) At age  $\alpha$ , an individual has its entire reproductive span yet to come. A postreproductive animal has RV of 0, and RV usually declines more-or-less linearly from the peak to 0. (2) In addition to having fewer reproductive years to come as it ages, an individual's fecundity ( $m_x$ ) tends to decrease with age (as Pianka notes on page 154, but Pianka does not mention that, in mammals, fecundity usually *increases* for several years, *then* decreases until senescence).

(Fig 20.2 Waser et al. -  $m_x$  curves for dwarf mongooses)

In many fish, relationship of RV to age is even more complex, because fecundity depends on size, and they grow indeterminately, so  $m_x$  just keeps going up with age. (This does not apply to big-bang breeders.)

(Fig 169 Zale - example with blue tilapia)

Life-histories evolve. For example, as body size increases, the age of first reproduction usually shifts to a later age, to allow growth to finish before reproduction begins. In other words, selection would act against individuals that retained the tendency to breed young, if selection was also favoring longer or faster growth (because there would not be enough energy available to grow, reproduce and survive - the ***principle of allocation*** discussed in earlier lecture).

In general there are ***trade-offs*** between:

1. Reproduction and survival. A change in the  $m_x$  curve will affect the  $l_x$  curve, and vice-versa.
2. Current reproduction and future reproduction. An increase in current reproduction will decrease later reproduction.
3. Number of offspring and quality of offspring. Can produce 1-2 offspring at a time (like ungulates), a handful (like carnivores), thousands (like many fish) or millions (like



redwoods). The more produced, the more likely they are to die quickly, because little is invested in each.

Basically, an animal can gather only so much energy in a lifetime, and the optimal life-history allocates energy to (growth) survival and reproduction in a way that **maximizes lifetime reproductive success**.

To analyze the first two trade-offs simultaneously, one can partition reproductive value into **current reproduction** and **residual reproductive value**.

$$v_x = m_x + \sum_{t=x+1}^{\infty} (l_t/l_x)m_t$$

↑
↑
↘

RV = current reproduction + expected future reproduction.

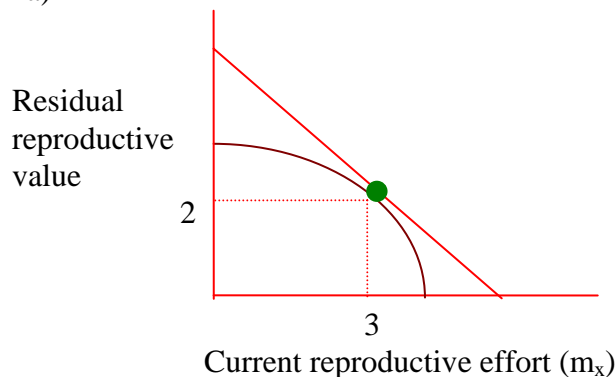
If there was no cost in terms of survival or future reproduction, it would obviously pay to breed early and often. But there are costs:

1. Increased reproduction reduces survival  
(Fig 8.10 Pianka - example with rotifer)
2. Increased reproduction reduces later reproduction

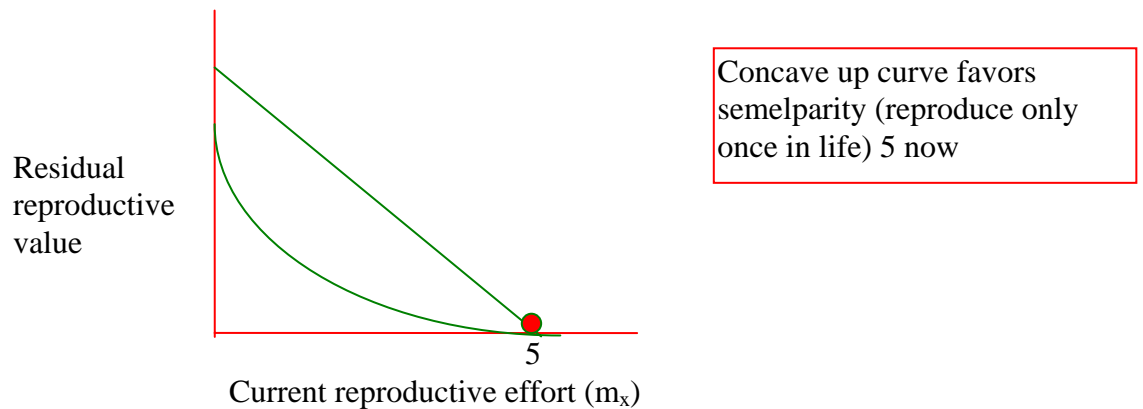
(Figure 8.9 Pianka - example with hens)  
(Figure 8.11 Pianka - example with rotifer)

For an individual *of specific age*, the optimal trade-off between current and future reproduction can be determined graphically by plotting residual reproductive value vs. current reproductive effort ( $m_x$ ), and finding point tangent to line with slope of -1. [This assumes that the population is stable, so that current and future offspring are equally valuable. In a growing population, current offspring are more valuable than future offspring, because each offspring forms a bigger percentage of the (currently small) population than it would later, in a bigger population]

(Fig. 8.12 Pianka)



Concave down curve favors iteroparity (reproduce more than once) 3 now and two later.



Over an *entire lifetime*, the approach is the same for each age, but there is a series of relationships (graphs) like these, one for each age. For each age, determine the optimal trade-off as just described. Then connect those optimal points across ages, to get the optimal life history, which maximizes lifetime reproductive success.

(Fig. 8.13 Pianka - iteroparous)

(Fig 8.14 Pianka - semelparous)

### *Optimal clutch or litter size*

Final trade-off to consider is number vs. quality of offspring. The more offspring produced, the lower the fitness of each individual offspring.

(Fig 8.17 Pianka - example with great tits)

(Fig. 8.16 Pianka)

If fitness of each offspring decreases as number of offspring goes up, there will be an optimal trade-off that maximizes the number of offspring that survive to reproduce. Plotting (#offspring\*offspring fitness) vs litter size gives the optimum number to produce. Of course, each individual offspring would do better if it got ALL the parental resources, so there is parent-offspring conflict with respect to allocation of resources.

### *Assumptions of life-table analysis.*

1. Closed population. If population is open to immigration and emigration, then must correct for this before calculating  $l_x$  and  $m_x$ . E.g. undetected emigration would cause estimated mortality to be erroneously high; undetected immigration could cause estimated mortality to be too low, or estimated reproduction to be too high.

2. Stable age distribution  $\Rightarrow$  the proportion of individuals in each age class is constant through time.

(Fig 4.24 Begon et al)

3. Mortality and fecundity curves are constant through time.

Most of these assumptions are not met perfectly in nature; for example, it is unusual for juvenile survival to be the same year after year - there are good years and bad years, dependant on weather, food availability, predators, epidemics. But violations of assumptions often small enough to have little effect on projections from life tables.

The exercise below is optional.

***Populus Simulation of Life Tables and Demography: Stable Age Distributions***

Use the age-structured population growth module in Populus, to show how constant  $l_x$  and  $m_x$  tables determine the age distribution at which populations stabilize. The Populus program is in the Biology 405 folder on the network drive. (See the Using Network Drives handout.) Copy the Populus folder to drive C, then run the program from drive C.

1. Select 'Population Growth' from the main menu.
2. Select 'Age-Structured Population Growth' from the pop-up menu.
3. Read the pop-up notes.
4. Modify the number of time intervals to be run, from 6 to 20 (or more). Accept the default values for all other variables. It does not matter which display you select in the data entry panel, because (after running the simulation), you can use the space bar to switch between displays, to examine all of them.
5. Write down the initial age-distribution, which is in the table under the column labeled  $N_{x0}$ . This column gives the Number of individuals of age  $x$  at time  $0$ . When the simulation is run, it will fill in columns for  $N_{x1}$ ,  $N_{x2}$  ....  $N_{x20}$ . These columns are the age distributions projected for the 20 time intervals, and they show how the age-distribution changes through time, for a given set of  $l_x$  and  $m_x$  schedules. (You'll examine these data using a graph, rather than the table itself.)
6. Run the simulation by hitting 'Enter'. Use the space bar to view all the available graphs, but pay particular attention to the 3-D plot that shows how the proportion of the population aged  $x$  changes through time. By time interval 20, the age distribution has stopped changing. Look at the age distribution for time interval 20, and write down the proportion of the population that is in each age class.
7. Hit ESC to return to the data entry panel.
8. Leaving all other settings the same (keeping the same  $l_x$  and  $m_x$  curves), change the initial age distribution (in the  $N_{x0}$  column). Write down your new starting age distribution.
9. Run the simulation. Once again, pay particular attention to the 3-D plot that shows how the proportion of the population aged  $x$  changes through time. As in step 6, write down the proportion of the population of each age at time interval 20.
10. Compare the final age distributions for the 2 runs. How do they compare? What does this mean? If this result surprises you, try several more initial age distributions and see what happens. Try strange

initial distributions, e.g. with more old individuals than young ones. (How would a population get an age distribution with more individuals in old age classes than in young ones?)

11. What happens to the stable age distribution if you alter the  $l_x$  and/or  $m_x$  schedule?