Lecture 10

Variation among Individuals and Population Structure

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Outline

1. Individual variation
2. Age structure
3. Life tables and R_0 calculations

Individual variation

- Going back to the very first question in the first exercise, we have so far assumed that individuals are identical represented by an average individual in the population.
- But of course, individuals within a population are not identical – individuals differ in sex, age, size, developmental stage, behavior, quality, etc.
- More importantly, from a population ecology point of view, individuals differ in their demographic performance – i.e., mortality risk (survival) and reproductive output (fecundity).
- This variation at the level of individuals would have consequences to population dynamics and growth – i.e., consequences at the level of populations.

Individual variation

- The most basic variation among individuals is that of variation in **individual fate**.
- Even in a population of identical individuals, some individuals will die younger, other will die older.
- Similarly, some would produce more offspring and some would produce less.
- These are outcomes of random chance – i.e., probabilistic events – e.g., being captured by a predator or not.
- This variation in fate provides a baseline level of individual variation within a population, which exists even if all individuals are otherwise identical.

Individual variation

- This variation in fate is called **unstructured variation** or **demographic stochasticity** – demonstrating that it is not associated with any systematic variation among individuals.
- But of course, no natural populations is made of identical individuals (though this situation can be approximated in the lab by growing clones born at exactly the same time).
- There is always additional variation (in age, stage, size, quality, etc.).
- So individuals will have systematic differences.
- Of special interest are those differences that are maintained for a long time – e.g., a relatively larger individual remains relatively larger also a year later, although all individuals have grown during that time.

Individual variation

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- There is always additional variation (in age, stage, size, quality, etc.).
- Of special interest are those differences that are maintained for a long time – e.g., a relatively larger individual remains relatively larger also a year later, although all individuals have grown during that time.
- This type of systematic variation is called **structured variation** or **population structure**.
- The consequent systematic variation in demographic performance is called **demographic heterogeneity**. E.g., relatively larger individuals demonstrate consistently lower mortality risk and higher fecundity.

Individual variation

- Intraspecific competition (and also interspecific) has important effects on individual variation.
- For example, an initially slightly larger individual will be able through interference and aggressive behavior to secure more food, better territory etc.
- Consequently it would grow more then the competitively inferior individuals.
- Under stronger crowding these differences and asymmetries among individuals tend to
- Although all individuals will suffer reduced performance (scramble-type competition), some will suffer less then others (contest-type competition).
- These differences will be exaggerated in more crowded conditions with stronger intraspecific competition.

Individual variation

An example: fecundity of female grasshoppers

(Wall & Begon 1987. *Ecol. Entomol.* 13:331)

Lifetime fecundity (no. eggs laid) of female grasshoppers, in two density treatments.

Although overall fecundity decreased (in high density, no female laid more than 40 eggs), there was also a large increase in bad performers (low fecundity females, laying less than 20 eggs).

Overall, the distribution of reproductive performance is wider and more bimodal in high density, showing more contest-like competition ("losers" and "winners").

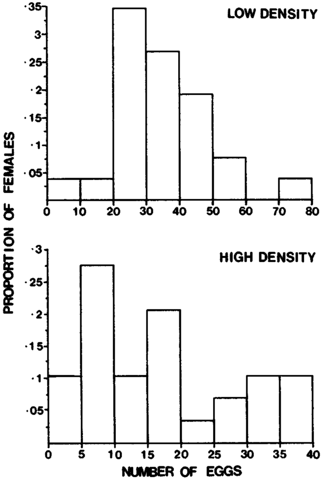
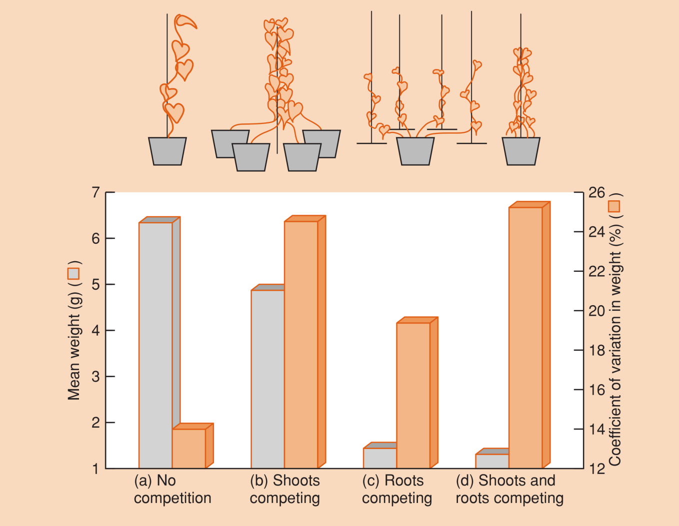


FIG. 3. The distribution of reproductive output in the low and high density treatments, as the proportion of the total number of females that produce eggs in ten and five egg-number classes respectively.

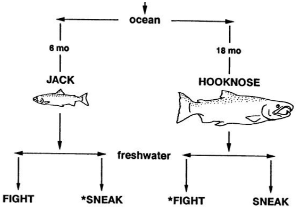
Individual variation

Another example – competition and individual variation in morning glory vines. (From reading material of exercise 3.)



Individual variation

- Intraspecific competition tends to exaggerate individual differences and demographic heterogeneity.
- This exaggeration causes competition effects to become more contest-like, superimposed on the scramble-like reduction in mean individual performance.
- Small initial advantages (e.g., due to differences in seed or egg size) can self-amplify during competition, and result in significant phenotypic variation in size, quality, behavior, etc.

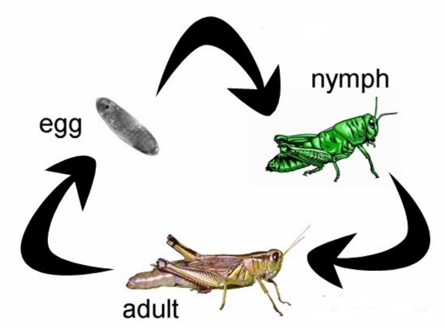


Population structure

- Division of a population into classes (i.e., subgroups) according to some structuring variable – age, sex, stage, size etc.
- We measure not only total population size, but also how individuals are divided among classes.
- We investigate how both population size and the division into classes is changing over time.
- For example, for the grasshopper lifecycle:

Population structure

- An illustrative example for the grasshopper lifecycle:
  - Winter: 100% eggs
  - Mid-spring: 10% eggs, 70% L1 nymph, 10% L2 nymph.
  - Early summer: 60% L4 nymph 30 % L5 nymph 10% adults.
  - Mid-summer: 30% eggs, 70% adults.
  - Late summer: 90% eggs 10% adults.



Population structure

- Each class has its own dynamics.
- For example, number of L1 nymphs increases as eggs hatch, and decreases as L1 nymphs progress to the next developmental stage (i.e., molt to L2 nymph).
- Each class is associated with different demographic parameters – i.e., contributes differently to overall population growth and dynamics.
- Leading to **age-/stage-/size-dependent mortality and fecundity.**
- An illustrative grasshopper example,
  - Eggs: 90% overwinter survival.
  - L1 nymphs: mortality rate of 15% per day.
  - L3 nymphs: mortality rate of 1% per day.
  - Adults: mortality rate of 0.05% per day; fecundity rate of 20 eggs per week.

Population structure

- Human populations are also structured.
- This structure is often also associated with variation in demographic rates (demographic heterogeneity):
  - In the past, hereditary social classes – e.g., nobles vs. commons – were also associated with different dempgraphic rates (E.g., significant differences in life expectancy between nobles and commoners).
  - Nowadays, socio-economic status is more flexible – people can move up an down the income quantiles. Often also associated with different reproductive rates.
- A much more basic structuring factor in populations of humans (which are long-lived perennial organisms) is **age**.
- Age has clear association with variation in mortality and fecundity.

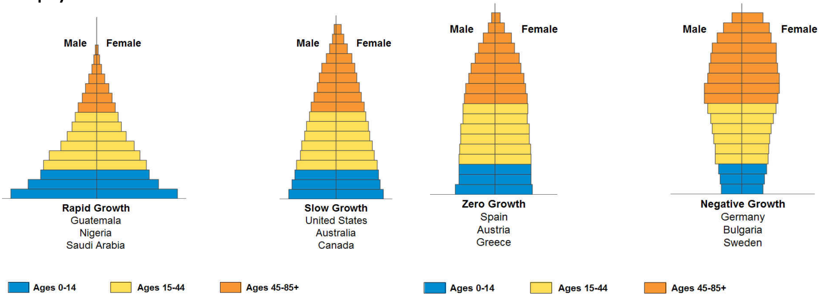
Outline

Age structure

- In long-lived perennial organisms (humans, large mammals, birds, trees, some commercial fish stocks, etc.) – **age** is often an important structuring variable.
- Age is often associated with size (e.g., in fish or trees) or physiological/reproductive state (e.g., immature, mature, senescent).
- Body size and physiological state clearly affect mortality and fecundity rates (e.g., in many organisms, larger females are more fecund) → leading to age-dependent mortality and fecundity.
- **Stage** (i.e., developmental stage) is sometimes used instead of age, e.g., if stage is more convenient or logical to use, or in field studies where often exact age cannot be determined.

Age structure

- Age-structure is often described using a population pyramid.
- There are consistent patterns between growth of decline of populations and the shape of the population pyramid.

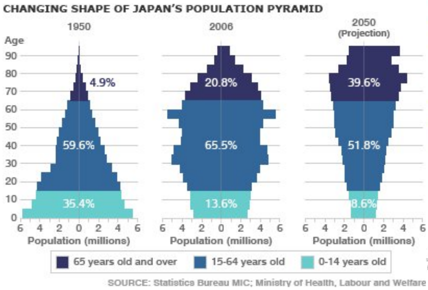


- More rapidly growing populations are younger on average, and have relatively larger young age-classes, (this is often strengthened by lower life expectancy; e.g., in developing countries).

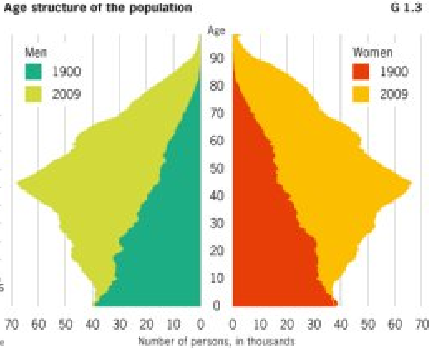
Age structure

- Transition from positive growth to stability and negative growth can be seen when comparing age structure in different years.

Japan (1950-2050)



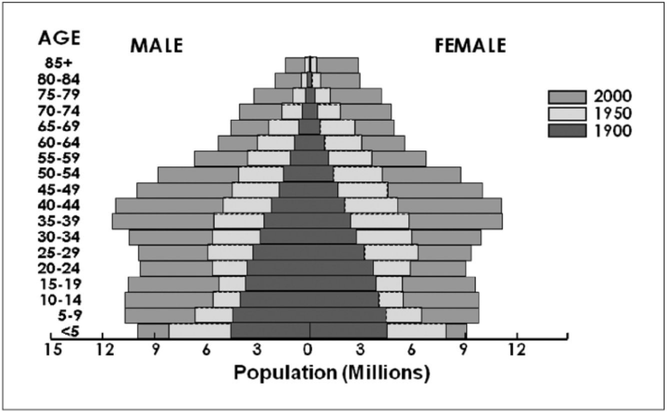
Switzerland (1900-2009)



Age structure

- Transition from positive growth to stability and negative growth can be seen when comparing age structure in different years.

USA (1900-2000)



Age structure

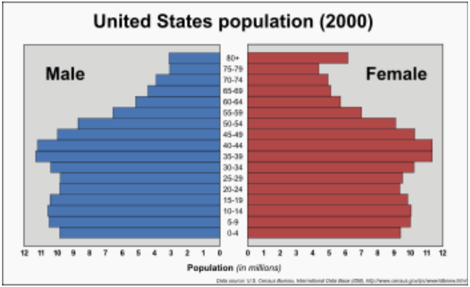
- Observe how historical events – years of significantly reduced or elevated birth rates – are recorded in the age structure, somewhat like tree rings.

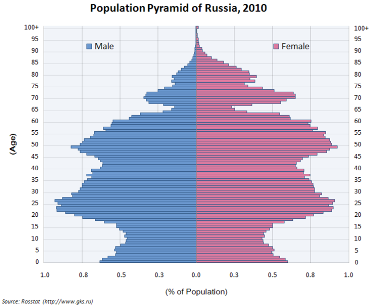
Finland (1917-2006)

Age structure

The "baby boom" of 50s and 60s, following WWII, is still apparent today in the age structure of many nations.

USA (2000) **Russia(2010)**

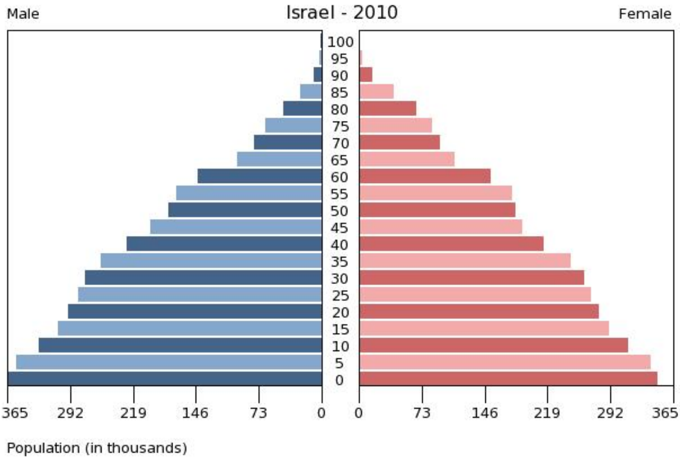




On the Russian side – we can still see effects of the great famines of 20s and 30s, as well as the greatly distorted sex-ratio caused by the heavy casualties of WWII. A steep fall in births is also apparent following the collapse of USSR in 1990s.

Age structure

Israel still has a rapidly growing population

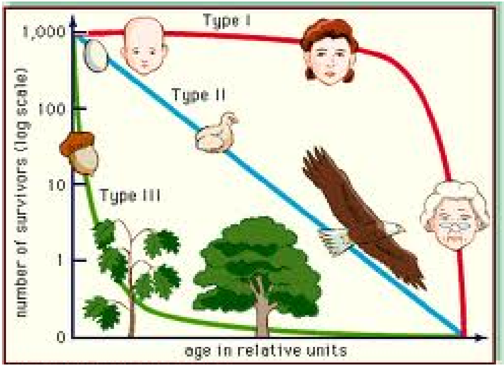


Age-dependent survival

- Obviously, age-classes do not mix – e.g., the number of individuals born in 1996 cannot increase (in a closed population); it can only decrease through mortality.
- The pattern of decrease in numbers within an age class is determined by age-dependent survival.
- l_a =the percentage of individuals surviving to age a, out of the original number of individuals in the age-group (when they were born).
- Alternatively (and equivalently), l_a is the probability to survive to age a.
- Obviously, if an individual survives to age a, it also survived to all ages upto a.
- Consequently, l_a decreases with age.

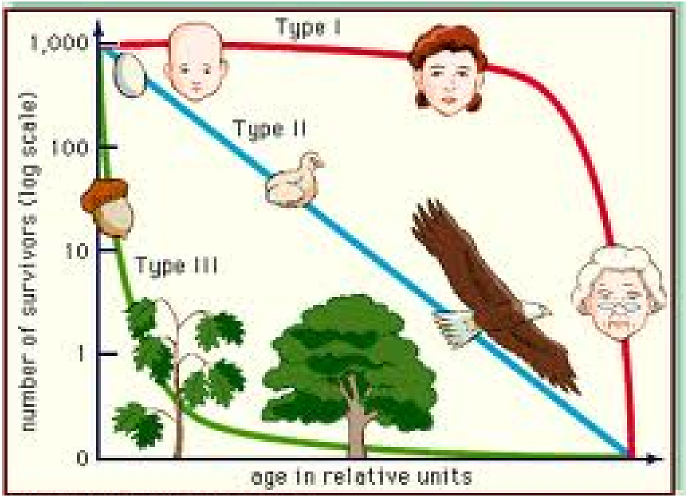
Age-dependent survival

- Survival probability is related to mortality rate.
- If mortality is constant (i.e., independent of age), we get Type II survivorship curve – a straight line in logarithmic scale
- If mortality is initially low and increases at old age, we get Type I.
- If mortality is high at young ages and decreases as the organism matures, we get Type III.



Age-dependent survival

- Some organisms or taxonomic groups may fit more or less to this simple classification of survival patterns.
- But usually, real survival curves are more complex.

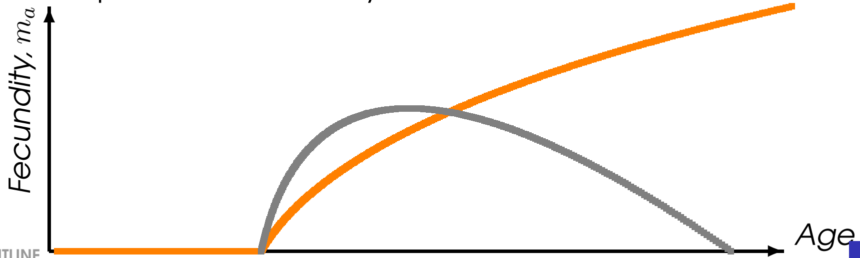


Age-dependent survival

- Human populations in developed countries may follow Type I curve nowadays.
- But even today, 5% of children do not survive to age 5.
- In some areas of Africa this figure is 20%.
- Moreover, throughout most of human history (also in Europe, upto 19th century) this figure was between 20% to 50%.
- Adult mortality was also higher, and life expectancy much lower than today.
- The "natural" human survivorship curve (at least since invenstion of agriculture) may look something like this:

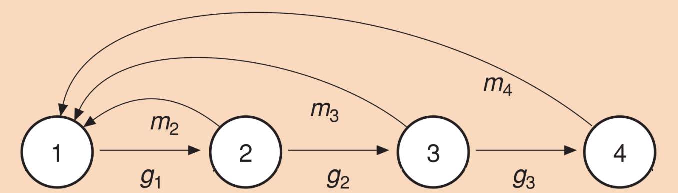
Age-dependent fecundity

- Similarly to survival, fecundity may also be described by an age-schedule.
- Age-dependent fecundity, m_a, is initially zero, while the individual is immature.
- Then, either increasing with age indefinitely (usually for organisms, such as fish an trees, that continue to grow also after reproduction commences).
- Or increasing to a maximum and then declining (e.g., in humans, other mammals, insects) – a "triangular" pattern of fecundity.



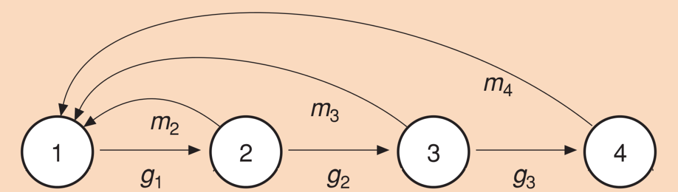
Outline

Population dynamics with age-structure



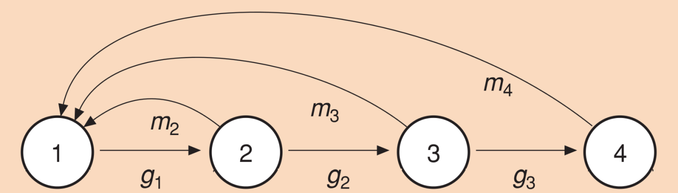
- Fecundity, m_a, summed over all age-classes is translated into the age-class of newborns (age 1 in the above diagram) for any given year.
- Survival from one age to the next is given by g_a.
- Such that $l_2 = g_1$, $l_3 = g_1 g_2$ and $l_4 = g_1 g_2 g_3$.
  If $g_a = 0.5$ for all ages, $l_2 = 0.5$, $l_3 = 0.25$, $l_4 = 0.125$, etc.
- Obviously, the population finite rate of increase or net reproductive rate will depend on the values of age-dependent survival and fecundity.

Population dynamics with age-structure



- For example, assume that reproduction occurs only in the fourth year ($m_2 = m_3 = 0$), and $l_4 = 0.1$, while $m_4 = 5$.
- Starting with 100 newborns (age 1) after 3 years only 10 will remain – i.e., only 10 successfully reached age 4.
- They then reproduce and die. leaving after them 50 newborns.
- Compared to the 100 individuals that started the parent generation, there are now only 50 individuals starting the second generation. $\Rightarrow R_0$ or λ in this case are 0.5.

Population dynamics with age-structure



- The general expression for R_0 given age-dependent survival and fecundity is

$$R_0 = \sum_a l_a m_a \ .$$

- This is a weighted sum where each age-dependent fecundity value (m_a) is weighted according to the probability (l_a) to reach that age alive.
- In the above diagram, given $l_1 = 1, l_2 = 0.5, l_3 = 0.25, l_4 = 0$ and $m_1 = 0, m_2 = 2, m_3 = 0.5$ and $m_4 = 1000$, we get $R_0 = 0 + 1 + 0.125 + 0 = 1.125$

Population dynamics with age-structure

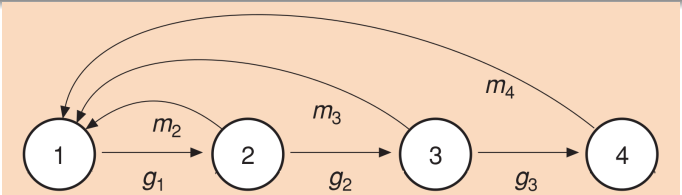
- There is a similar equation for r, which is given by the solution to

$$\sum_a e^{-ra} l_a m_a = 1 \ .$$

- Exponential growth with continuous deaths and births, $r = b - d$, $R_0 = b/d$; **or** the case of only a single lifetime reproductive event (semelparous lifecycle; e.g., unicellulars), $r = \frac{\log R_0}{T}$; are both special cases of the above general equations for r and R_0 (assuming specific patterns of l_a and m_a).
- Generation time is also found from age schedules of survival and fecundity.
- Generation time is often calculated as a weighted average of reproductive ages:

$$T = \frac{\sum_a a l_a m_a}{\sum_a l_a m_a} = \frac{\sum_a a l_a m_a}{R_0}$$

Population dynamics with age-structure



- In the above diagram, given $l_1 = 1$, $l_2 = 0.5$, $l_3 = 0.25$, $l_4 = 0$ and $m_1 = 0$, $m_2 = 2$, $m_3 = 0.5$ and $m_4 = 1000$, we get $R_0 = 0 + 1 + 0.125 + 0 = 1.125$
- The generation time in this example is

$$T = \frac{0 + 2 * 1 + 3 * 0.125 + 0}{1.125} = 2.1111 \text{ years}$$

- An approximate value of r is given by

$$r = \frac{\log R_0}{T} = 0.0558 \text{ year}^{-1}$$

Life Tables

- Calculations of R_0, T and r are often aided by constructing a life table.
- The simplest life table is a **cohort life table**, in which one follows the survival and fecundity schedules of a single age-group (cohort) throughout its existence from birth until (in theory) the last of them dies.
- For example, age-dependent survival and fecundity of a representative group of human females born 1900 in the USA.
- One records events of deaths and births and summarizes them in a table, e.g.,

age, x	no. survivors, a_x	l_x	m_x	$l_x m_x$	...
0	1000	1	0	0	
1	965	0.965	0	0	
...					
27	890	0.89	0.7	0.623	
...					

Life Tables

- After constructing the table, one can sum up the $l_x m_x$ column to get R_0.
- Or an $x l_x m_x$ column to get generation time, T.
- Or draw graphs of l_x or m_x or $l_x m_x$ to study the patterns of age-dependent survival, fecundity, or effective fecundity (respectively) in the population.
- Obviously, for long-lived organisms such as humans today, and given the tremendous technological and social changes occurring during a single lifetime, patterns of survival and fecundity will be different for different cohorts (year groups).
- But in natural populations, such patterns, obtained from a single cohort, may be representative of specific species or populations, and remain more or less the same for several generations.

Life Tables

- An example of a life table for a barnacle population

Age (years) x	a_x	l_x	m_x	$l_x m_x$	$x l_x m_x$
0	1,000,000	1.000	0	0	
1	62	0.0000620	4,600	0.285	0.285
2	34	0.0000340	8,700	0.296	0.592
3	20	0.0000200	11,600	0.232	0.696
4	15.5*	0.0000155	12,700	0.197	0.788
5	11	0.000110	12,700	0.140	0.700
6	6.5*	0.0000065	12,700	0.082	0.492
7	2	0.0000020	12,700	0.025	0.175
8	2	0.0000020	12,700	0.025	0.200
				1.282	3.928

$$R_0 = 1.282; \quad T_c = \frac{3.928}{1.282} = 3.1; \quad r \approx \frac{\ln R_0}{T_c} = 0.08014.$$

Life Tables

- A second type of life table is a **static life table**, in which one records deaths and births in all age-classes simultaneously during one year (or a similarly fixed period), and then constructs the relevant columns of l_x, m_x, etc.
- Nowadays, there are more modern statistical techniques to investigate schedules of mortality and reproductive events – this group of statistical methods is collectively known as **survival analysis** or **failure-time analysis** and is widely used in medicine, engineering, and also ecology.
- One can use survival analysis techniques to investigate not only events of mortality or reproduction, but also other vital rates, such as timing of developmental transitions (molts, pupation, emergence, metamorphosis, etc.).