Population Ecology II: Life tables

What is a Life Table?

- A more sophisticated method for examining population abundance is to construct a life table
- This table will have a schedule of all births and deaths in all, or more likely some portion, of our population

Two types of life table

- Cohort (or dynamic) life table: follow all offspring born at a given time (the cohort) from birth until the death of the last individual.
  - This is the preferred way to generate a life table
  - It works best for organisms that live for a relatively short time period
- Static (or time-specific) life table: count all individuals alive at a given time and record the age of each
  - This method is less preferred (we'll see why later…)
  - However, it is simpler to use for longer-lived organisms that the researcher may not be able to follow across the organism's entire lifetime

What information can you get from a life table?

- Population age structure—Are there lots of: young individuals? Old individuals? Reproductive age individuals?; and similar questions
- Population growth rate—How fast is the population size growing (or shrinking)?
- Population survivorship patterns—Does most mortality occur in the very young? The very old? Or equally across all ages?

Life table variables

- Life tables may vary in what information they contain, but we'll use the following variables:
- x = the age (ex: 0, 1, 2, 3 years old) or stage (ex: egg, larvae, nymph, adult) class
- n_x = the number of individuals in each age/stage x
- l_x = the percent of the original cohort that survives to age/stage x (= n_x / n_0)
- d_x = the probability of dying during age/stage x (= $l_x - l_{x+1}$)
- q_x = the percent of dying between age/stage x and age/stage x+1 (= d_x / l_x)
- b_x = the number of offspring produced per individual in age/stage x

A cohort life table example

(complete with fake data for the real spider *Apopyllus now*)

x (months)	n_x	l_x	d_x	q_x
0	250			
1	125			
2	86			
3	68			
4	53			
5	6			
6	0			

We get this by simply counting spiders alive at each age x (in this case, at the start of each month)

A cohort life table example
(complete with fake data for the real spider *Apopyllus now*)

x (months)	n_x	l_x	d_x	q_x
0	250	1.000		
1	125	0.500		
2	86	0.344		
3	68	0.272		
4	53	0.212		
5	6	0.024		
6	0	0.000		

We get this by dividing each n by n_0, or 250 (try it yourself!)

A cohort life table example
(complete with fake data for the real spider *Apopyllus now*)

x (months)	n_x	l_x	d_x	q_x
0	250	1.000	0.500	
1	125	0.500	0.156	
2	86	0.344	0.072	
3	68	0.272	0.060	
4	53	0.212	0.188	
5	6	0.024	0.024	
6	0	0.000	--	

We get this by taking each l and subtracting from it the l at the next older age

A cohort life table example
(complete with fake data for the real spider *Apopyllus now*)

x (months)	n_x	l_x	d_x	q_x
0	250	1.000	0.500	0.500
1	125	0.500	0.156	0.312
2	86	0.344	0.072	0.209
3	68	0.272	0.060	0.221
4	53	0.212	0.188	0.887
5	6	0.024	0.024	1.000
6	0	0.000	--	--

We get this by dividing each d value by the corresponding l value

A cohort life table example
(complete with fake data for the real spider *Apopyllus now*)

x (months)	n_x	l_x	b_x	l_xb_x
0	250	1.000	0	
1	125	0.500	0	
2	86	0.344	0	
3	68	0.272	0	
4	53	0.212	17.1	
5	6	0.024	34.6	
6	0	0.000	0	

Now, let's assume these are the average # of offspring made by each female at each age

A cohort life table example
(complete with fake data for the real spider *Apopyllus now*)

x (months)	n_x	l_x	b_x	l_xb_x
0	250	1.000	0	0
1	125	0.500	0	0
2	86	0.344	0	0
3	68	0.272	0	0
4	53	0.212	17.1	3.63
5	6	0.024	34.6	0.83
6	0	0.000	0	0

These are then the values you get multiplying each b value by the corresponding l value

What does the *A. now* life table tell us?

- These spiders all die before they reach 6 months of age
- Lots of spiders die before reaching 1 month old
- After 1 month, survival rate is relatively constant until after spiders reach 4 months of age
- Maturity occurs at age 4 months
- 5 month old spiders have twice as many offspring as 4 month old spiders

Before talking about some information we can glean from a life table (and answer why that $l_x b_x$ column is in there), let's look at a sample static life table. Recall that this is obtained by simply going out and counting all individuals alive at a given time, sorting them by age or stage.

A static life table example

(with fake data for the real weevil *Notiocryptorrhynchus punctatocarinulatus*)

x	n_x	l_x	d_x	q_x
0	500	1.000	0.270	0.270
1	365	0.730	0.472	0.647
2	129	0.258	-0.058	-0.225
3	158	0.316	0.160	0.506
4	78	0.156	0.124	0.795
5	16	0.032	0.032	1.000
6	0	0.000	--	--

Problem 1: We have more age 3 individuals than age 2 individuals! This can't happen in a cohort table.

Problem 2: We have negative values for d_2 and q_2!

What does this weevil's life table tell us?

- A lot less than the cohort life table!! But…
- This weevil dies before reaching 6 months of age.
- Survival to age 1 month is relatively high; most mortality occurs between 1 and 3 months.
- We have no information on births, since we do not observe any (we essentially just take a "snapshot" of the population at a single point in time).

Stage (x)	Number observed at start of each stage n_x	Proportion of original cohort surviving to start of each stage l_x	Proportion of original cohort dying during each stage d_x	Mortality rate q_x	$\log_{10} a_x$	$\log_{10} l_x$	$\log_{10} a_x - \log_{10} a_{x+1} = k_x$	Eggs produced in each stage F_x	Eggs produced per surviving individual in each stage m_x	Eggs produced per original individual in each stage $l_x m_x$
Eggs (0)	44000	1.000	0.920	0.92	4.64	0.00	1.09	--	--	--
Instar I (1)	3513	0.080	0.022	0.28	3.55	−1.09	0.15	--	--	--
Instar II (2)	2529	0.058	0.014	0.24	3.40	−1.24	0.12	--	--	--
Instar III (3)	1922	0.044	0.011	0.25	3.28	−1.36	0.12	--	--	--
Instar IV (4)	1461	0.033	0.003	0.11	3.16	−1.48	0.05	--	--	--
Adults (5)	1300	0.030	--	--	3.11	−1.53	--	22617	17	0.51

$R_0 = \sum l_x m_x = \frac{\sum F_x}{a_0} = 0.51.$

A more detailed, actual cohort life table for the grasshopper *Chorthippus bruneus*

Age (years) x	Number of individuals observed of age x n_x	l_x	d_x	q_x	Smoothed l_x	Smoothed d_x	Smoothed q_x
1	129	1.000	0.116	0.116	1.000	0.137	0.137
2	114	0.884	0.008	0.009	0.863	0.085	0.097
3	113	0.876	0.251	0.287	0.778	0.084	0.108
4	81	0.625	0.020	0.032	0.694	0.084	0.121
5	78	0.605	0.148	0.245	0.610	0.084	0.137
6	59	0.457	−0.047	—	0.526	0.084	0.159
7	65	0.504	0.078	0.155	0.442	0.085	0.190
8	55	0.426	0.232	0.545	0.357	0.176	0.502
9	25	0.194	0.124	0.639	0.181	0.122	0.672
10	9	0.070	0.008	0.114	0.059	0.008	0.141
11	8	0.062	0.008	0.129	0.051	0.009	0.165
12	7	0.054	0.038	0.704	0.042	0.008	0.198
13	2	0.016	0.008	0.500	0.034	0.009	0.247
14	1	0.080	−0.023	—	0.025	0.008	0.329
15	4	0.031	0.015	0.484	0.017	0.008	0.492
16	2	0.016	—	—	0.009	0.009	1.000

A more detailed, actual static life table for the red deer *Cervus elaphus*

Summary information obtained from the cohort life table: R_0

- We can use the cohort LH data to measure several important population variables.
- The first is R_0, or net reproductive rate (a measure of the change in population size), where:

$$R_0 = \Sigma l_x b_x$$

- Note that Σ is the summation sign (that is, we add up all the $l_x b_x$ values across the entire table)
- For our spider, $R_0 = 0 + 0 + 0 + 0 + 3.63 + 0.83 + 0 = 4.46$
- Thus, on average, each spider in the initial cohort (the age 0 group of 250) has 4.46 offspring. Thus, the next cohort will start off with 1115 (=250 * 4.46) spiders!

Summary information obtained from the cohort life table: *T*

- The second important summary variable is *T*, the generation time (the time between the birth of one cohort and the birth of their offspring)
- It is calculated using the following formula:

$$T = (\Sigma x l_x b_x) / R_0$$

- So, for our spider, $T = (0 + 0 + 0 + 0 + [4*3.63] + [5*0.83] + 0) / 4.46 = 4.2$ months
- This tells us that, on average, cohort 1 begins producing offspring (cohort 2) 4.2 months after cohort 1 individuals are born

Summary information obtained from the cohort life table: *r*

- The third important summary variable is *r*, the per capita rate of increase (like R_0, a measure of the change in population size)
- It is calculated using the following formula:

$$r = \ln R_0 / T$$

- Note that "ln" is the shorthand for the natural log function
- For our spider, $r = \ln 4.46 / 4.2 = 0.36$
- *r* is more difficult to interpret than is R_0, at least for now. Suffice it to say that this tells us that our spider population is experiencing more births than deaths.

Some notes on interpreting R_0 and *r*

- First, note that R_0 and *r* do not give the same value!!
- R_0 has the following properties:
  - If $R_0 > 1$, the population is increasing in size
  - If $R_0 < 1$, the population is decreasing in size
  - If $R_0 = 1$, the population size is constant
- *r* has the following properties:
  - If $r > 0$, the population is increasing in size
  - If $r < 0$, the population is decreasing in size
  - If $r = 0$, the population size is constant

Stable Age Distribution

- The stable age distribution (SAD) is reached when each age group individually always increases by the exact same value each time period

Age (*x*)	Time 1	Time 2	Time 3	Time 4
0	100	200	400	800
1	75	150	300	600
2	50	100	200	400
3	40	80	160	320
4	20	40	80	160
5	10	20	40	80
6	2	4	8	16

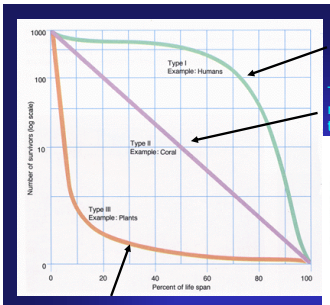
Stable Age Distribution II

- The population below would not be at an SAD

Age (*x*)	Time 1	Time 2	Time 3	Time 4
0	100	175	290	670
1	75	150	300	600
2	50	100	200	400
3	40	60	100	220
4	20	25	40	90
5	10	12	22	25
6	2	3	5	6

Survivorship Curves

- A survivorship curve plots the *x* values (the ages or stages) on the horizontal axis, and the l_x values on the vertical axis.
- Two biologists, Pearl and Deevey, categorized these curves into three main types: Type I, Type II, and Type III survivorship curves (not very original names, however).
- Type I curves are typical of many long-lived organisms (such as elephants, tigers, humans) with lots of parental care of young
- Type III curves are typical of short-lived organisms (such as insects) and many plants, where offspring mortality is high.
- Type II curves are fairly uncommon.



TYPE I: high survivorship for juveniles; most mortality late in life

TYPE II: survivorship (or mortality) is relatively constant throughout life

TYPE III: low survivorship for juveniles; survivorship high once older ages are reached

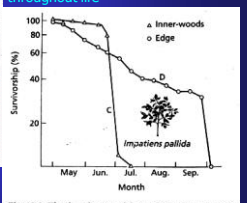
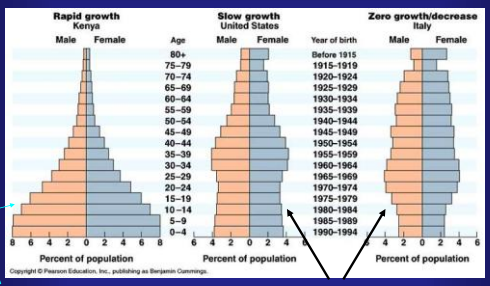


Fig. 10.3 The distribution of dates of first flowering in a greenhouse for *Impatiens pallida* collected from A, a site where it was attacked by a herbivore in July, and from B, a site where it was not attacked. C and D show survivorship of natural populations at the two sites (from Schemske 1984).

Population Age Structure

- A third bit of summary information we can obtain from the life table comes is an age structure diagram
- To obtain this, we plot the # of individuals in each of our age or stage classes (the *x* categories).
- These plots can be in the form of bar graphs (or histograms), or in the form of age pyramids.
- One thing we gain by looking at these is a prediction about how rapidly the population should grow (or shrink)
  - If the pyramid is "bottom-heavy" there are lots of young individuals = good chance of growth
  - If the pyramid is more equal across age groups there are fewer young individuals = lower chance of growth

Age pyramids for different human populations



Lots of young individuals, which means chance of rapid growth (= high r or R_0)

Fewer young individuals, which means less chance of rapid growth (= low r or R_0)