WORKSHEET — LIFE TABLES

Note: Many examples included herein refer to insects because those examples were available, but the techniques work for other organisms, too.

In nature, a number of factors determine the rate of increase (**r**) of a population of a given species. The maximal rate of increase under optimum conditions (the innate capacity for increase) is symbolized by $\mathbf{r_m}$. Birth and death rates are influencing factors. Note that the birth rate can be less than, equal to, or greater than the death rate. Some other symbols used in these calculations are:

- **x** = a given age group within the population
- $\mathbf{l_x}$ = the probability of being alive at age x; the proportion (as a decimal) of survivors at age x; the number of survivors at the beginning of x
- $\mathbf{M_x}$ = total eggs or young produced per female at age x
- $\mathbf{m_x}$ = the number of female births; the number of eggs or young which are female (in a species with a 1:1 sex ratio, this = $M_x/2$)
- **T** = the mean time from birth of parents to birth of offspring; the average length of time for one generation; average age of parents who had offspring
- $\mathbf{R_o}$ = the ratio of total female births in two successive generations OR the ratio of offspring to parents; the net reproductive rate
- $\mathbf{N_o}$ = the number of individuals at time zero; the number of females at the beginning of the experiment
- $\mathbf{N_t}$ = the number of individuals after time t; the number of females at time t; the number of females after one or more generations

The actual calculation of r_m involves a knowledge of both birth and death rates for each age group within the population. Since, for most organisms, one male can fertilize a number of females, the size of the population is more dependent on the number of females present, and the calculations are usually done using only females. The birth rate of the population is expressed as a table showing the number of offspring/eggs produced per given unit of time by a female of age x, and is symbolized by $\mathbf{m_x}$ (which is half of the total eggs/offspring produced in that age interval if the sex ratio is equal).

A **life table** gives the probability at birth of being alive at age x (designated as $\mathbf{l_x}$). At zero age, this is $\mathbf{l_o}$, which by definition, equals one. For example, in Table 1, where x = 4.5 weeks and l_x = 0.87, this means that from a sample of 100 newly-laid eggs, 87 will survive for 4.5 weeks.

The following formulae are used to determine r_m:

a) $l_x m_x$ = (prob. of reaching age x)(# of female eggs at age x) = # of births per female
$\Sigma l_x m_x$ = total female eggs produced over period of study

b) $$T = \frac{(\#\ of\ offspring) \times (age\ when\ had)}{total\ \#\ of\ births\ (= R_o)} = \frac{\Sigma l_x m_x x}{\Sigma l_x m_x} = \frac{\Sigma l_x m_x x}{R_o}$$

c) for

generation 1	generation 2	generation 3
# = N_o	births = $\Sigma l_x m_x$ per female	$\Sigma l_x m_x$ from gen. 2, etc. · total # of females, N_o = $N_o \Sigma l_x m_x$

thus, $$R_o = \frac{N_o \Sigma l_x m_x}{N_o} = \Sigma l_x m_x = \frac{N_t}{N_o}$$

d) If r_m = rate and T = time for one generation, then $r_m T$ = # of individuals at time T. By definition, $R_o = e^{r_m T}$ or $\ln(R_o) = r_m T$, thus $r_m = [\ln(R_o)]/T$

Problems:

1. Complete Table 1.

Table 1. Life Table and Age-Specific Fecundity Rate of Insects in a Laboratory Environment.

Age in Weeks (x)	l_x	$M_x/2=m_x$	$l_x m_x$	$l_x m_x x$
0.5 1.5 2.5 3.5	0.90	. . . Immature Stages . . .		
4.5	0.87	20.0		
5.5	0.83	23.0		
6.5	0.81	15.0		
7.5	0.80	12.5		
8.5	0.79	12.5		
9.5	0.77	14.0		
10.5	0.74	12.5		
11.5	0.66	14.5		
12.5	0.59	11.0		
13.5	0.52	9.5		
14.5	0.45	2.5		
15.5	0.36	2.5		
16.5	0.29	2.5		
17.5	0.25	4.0		
18.5	0.19	1.0		
			$\Sigma = R_o =$	$\Sigma =$
$T = \Sigma l_x m_x x / \Sigma l_x m_x = \Sigma l_x m_x x / R_o =$				
$r_m = \ln(R_o)/T =$				

2. Calculate T using formula b above.
3. Calculate r_m using formula d above.
4. Make a graph (actually two graphs in one) of the data in Table 1 as follows:
   a) On the horizontal (x) axis, place the age in weeks (**x**) using a scale of 0 to 19 or 20.
   b) On the vertical (y) axis on the LEFT side of the page, place the probability of survival ($\mathbf{l_x}$) using a scale of 0 to 1.
   c) On the vertical axis on the RIGHT side of the page, place the eggs per female per week ($\mathbf{M_x}$) using a scale of 0 to 46 or 50 (Note that the third column in Table 1 must be doubled).

Another type of life table can be constructed as follows. The following column headings are used:

x = age in appropriate interval group
l_x = the number surviving at the beginning of the age interval, x
d_x = the number dying within age interval, x
q_x = the rate of mortality, d_x/l_x (optionally x 100 = %)
d_xF = the factor that was cause of death (reason why)

Since several samples are often averaged together, l_x and d_x may not be whole numbers. Note also that $l_{x+1} = l_x - d_x$.

Table 2. Life Table for the Spruce Budworm in Experimental Plot A.

x	l_x	d_xF	d_x	$100(d_x/l_x) = 100(q_x)$
eggs	174.00	parasites, predators	18.00	
		other causes	1.00	
		TOTAL		
instar I (1st larval stage)	155.00	dispersion, etc.	74.40	
overwintering stage	80.60	winter	13.70	
instar II	66.90	dispersion, etc.	42.20	
instars III through VI	24.70	parasites	8.92	
		disease	0.54	
		birds	3.39	
		other causes	10.57	
		TOTAL		
pupae	1.28	parasites, predators	0.23	
		other causes	0.23	
		TOTAL		
# moths to adult	0.82	sex ratio 50:50--OK	0.00	0.00
# moths remaining	0.82	abnormal or small	0.00	0.00
# living to reproduce	0.82			
generation totals	174.00		173.18	
Since 0.82 moths lived to reproduce and 50% are females, that means 0.41 are females. The average female lays an average of 150 eggs, thus the expected number of eggs would be 0.41 × 150 = 62. The actual eggs counted = 575, so:				
		migration in	62 − 575 = −513	(−513/62)×100 = −827

The index of population trend is: expected = (62/174)·100 = 36% increase
observed = (575/174)·100 = 330% increase

Table 3. Life Table for the Spruce Budworm in Experimental Plot B.

x	l_x	d_xF	d_x	$100(d_x/l_x) = 100(q_x)$
eggs	2176.00	parasites, predators	175.00	
		other causes	21.00	
		TOTAL		
instar I (1st larval stage)	1980.00	dispersion, etc.	1148.00	
overwintering stage	832.00	winter	141.00	
instar II	691.00	dispersion, etc.	484.00	
instars III through VI	207.00	parasites	2.90	
		disease	0.30	
		birds	1.70	
		starvation	165.30	
		DDT	8.30	
		other causes	10.57	
		TOTAL		
pupae	1.80	parasites, predators	0.24	
		other causes	0.27	
		TOTAL		
# moths to adult	1.29	sex ratio 54:46--(abnormal)	0.10	0.00
# moths remaining	0.19	abnormal, small, weak	0.57	0.00
# living to reproduce	0.62			
generation totals	2176.00		2175.38	
Since 0.62 moths lived to reproduce and 46% are females, that means 0.29 are females. The average female lays an average of 150 eggs, thus the expected number of eggs would be 0.29 × 150 = 43. The actual eggs counted = 246, so:				
		migration in	43 − 246 = −203	(−203/43)×100 = −472

The index of population trend is: expected = (43/2176)·100 = 2% increase
observed = (246/2176)·100 = 11% increase

The comparison of life tables over a period of years/generations can help to reveal the influences of climate, parasites and predators, diseases, food supply, etc.

Tables 2 and 3 are each for one generation of an insect called a spruce budworm in an experimental plot consisting of 10 sq. ft. of branch surface on the spruce tree.

Problem:

Calculate the q_x values in Tables 2 and 3, then answer the following questions.

1. On the basis of the initial egg population, in which plot would you expect the most eggs in the next generation? Did this happen?
2. What was the major mortality factor for each age group/interval? Are the tables alike in this respect? Where are the weakest points in the insect's life cycle?
3. What explanation can you give for the difference between the expected and actual numbers of eggs and index of population trend for the next generation?

POPULATION AGE DISTRIBUTION AND GROWTH CURVES:

Four beetles of a species known as Confused Flour Beetles were introduced into a container holding 8 g of flour. For the next several months, the numbers of beetles in each stage of their life cycle (eggs-larvae-pupae-adults) were counted.

The following data were gathered:

Table 4. Numbers of Confused Flour Beetles in 8 gm of Flour.

days	eggs		larvae		pupae		adults		total
	#	%	#	%	#	%	#	%	
0	0		0		0		4		
15	62		17		0		4		
30	30		168		0		3		
50	47	17.9	75	28.5	51	19.4	90	34.2	263
64	107		47		12		144		
78	114		11		20		144		
101	185		30		0		156		
114	180		20		7		156		
134	257		3		0		159		
156	236		2		0		157		

Problem:

1. For each TIME:
   a. Add up all the beetles in all stages of the life cycle to determine how many beetles, total, were present (note completed example).
   b. Then, for each time, calculate what percentage of the beetles were in each stage of the life cycle.
2. Make a population growth curve. On the x-axis, place "Time in Days" (range 0 to 156), making sure to use proper spacing (156 does not immediately follow 134). On the y-axis, place actual "Number of Individuals." Plot curves for each of the four stages in the life cycle (one each for eggs, larvae, pupae, and adults) as well as for the whole population--a total of five lines on the graph.
3. Make a series of population age distribution graphs. Make one each for 30, 64, and 114 days (do other days as time and interest permit). The Y-axis represents the four age groups: Eggs, Larvae, Pupae, and Adults. The X-axis represents the percentage of the total population falling into each of those groups, divided by sex. Since we don't know which are males and which are females, we'll assume they are 50:50. Thus the x-axis will extend 50 percentage units to each side of a center line. For example, the graph for the 50 day sample would be based on the following numbers: 47 eggs = 17.87% (÷2 = 8.94% each of males and of females), 75 larvae = 28.52% (÷2 = 14.26% each), 51 pupae = 19.39% (÷2 = 9.70% each), 90 adults = 34.22% (÷2 = 17.11% each). Percentage of males in each age category are graphed to the left of the center line, and percentages of females are graphed to the right of the center line. The finished graph would look like Figure 1.

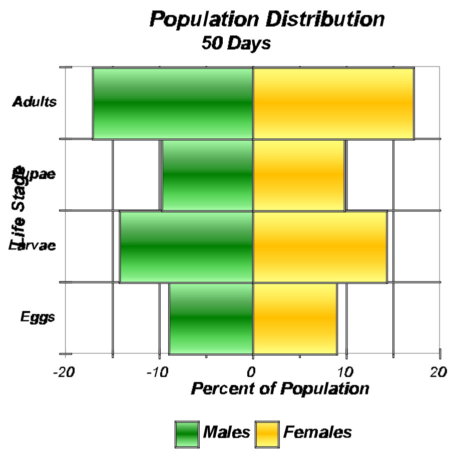

Figure 1. Population Age Distribution Curve for 50 Days

Similar curves can also be used where the numbers of males and females are known. Consider the data in Table 5:

Table 5. Census Data from Mid-1980's

Community	North Avondale				West Norwood				Active Members, Church in Norwood			
Age	#M	%M	#F	%F	#M	%M	#F	%F	#M	%M	#F	%F
0-5	173	2.6	162	2.4	367	3.7	318	3.2	4	2.2	8	4.4
5-10	136	2.0	176	2.6	349	3.5	379	3.8	6	3.3	8	4.4
10-15	229	3.4	192	2.8	347	3.5	319	3.3	7	3.9	3	1.7
15-20	514	7.6	449	6.6	465	4.7	482	4.9	0	0	7	3.9
20-25	482	7.1	492	7.3	536	5.4	535	5.4	3	1.7	4	2.2
25-30	260	3.8	300	4.4	334	3.4	411	4.1	5	2.8	8	4.4
30-35	231	3.4	229	3.4	321	3.2	265	2.7	7	3.9	7	3.9
35-45*	349	5.2	370	5.5	505	5.1	573	5.8	7	3.9	13	7.2
45-55*	302	4.5	397	5.9	478	4.8	598	6.0	3	1.7	4	2.2
55-60	157	2.3	185	2.7	252	2.5	305	3.1	3	1.7	7	3.9
60-65	160	2.4	150	2.2	223	2.3	246	2.5	7	3.9	7	3.9
65-75*	178	2.6	158	2.3	236	2.4	392	4.0	8	4.4	13	7.2
75+	102	1.5	229	3.4	217	2.2	452	4.6	8	4.4	23	12.8
Σ =	3273	48.4	3489	51.6	4630	46.7	5275	53.3	68	37.8	112	62.2
Σ =	6762				9905				180			

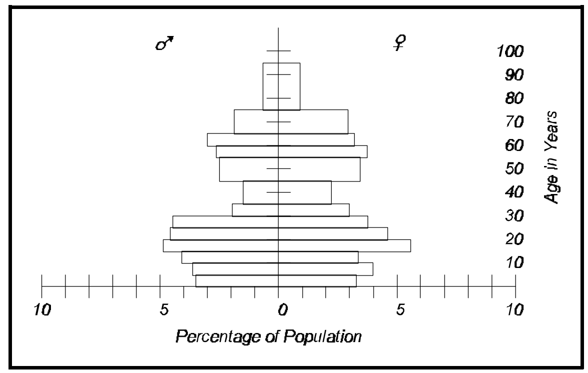

Figure 2. Graph of Census Data from Evanston

From these data, similar graphs can be constructed, again with percent on the x-axis--males left of center and females to the right of center. Age goes on the y-axis. A graph of data from the community of Evanston would look like Figure 2.

Problem: Make age distribution graphs for the three populations for which data are given in Table 5. Notice that where the time period is twice as long (35-45 years, for example) the percentage used on the graph should be half as much so the area of the rectangle is correct. For example, if 4.8% of the male population is between 35 and 45, that is equivalent to 2.4% between 35 and 40 and 2.4% between 40 and 45. Two possible ways to handle the 75+ category would be to treat it like a 75 to 95 category and divide the percentage by four, or to indicate half of the percentage on the 75 line, tapering to zero at 95 (or 100?).

1. Which of the populations has the most even age distribution?
2. In an "ideal" population, this sort of age distribution graph should form a triangle which is wider at the base, tapering to a point at the top. Do any of these populations come close to the "ideal?"
3. Can you generalize about which populations are growing, declining or stable?
4. In general, based on the age distribution curves, would the Norwood church be a place you could go to meet other people your own age? How does the age distribution graph support your answer?

ANSWERS

Table 1. Life Table and Age-Specific Fecundity Rate of Insects in a Laboratory Environment.

Age in Weeks (x)	l_x	$M_x/2=m_x$	l_xm_x	l_xm_xx
0.5 1.5 2.5 3.5	0.90	. . . Immature Stages . . .		
4.5	0.87	20.0	17.40	78.30
5.5	0.83	23.0	19.09	105.00
6.5	0.81	15.0	12.15	78.98
7.5	0.80	12.5	10.00	75.00
8.5	0.79	12.5	9.88	83.94
9.5	0.77	14.0	10.78	102.41
10.5	0.74	12.5	9.25	97.13
11.5	0.66	14.5	9.57	110.06
12.5	0.59	11.0	6.49	81.12
13.5	0.52	9.5	4.94	66.69
14.5	0.45	2.5	1.13	16.31
15.5	0.36	2.5	0.90	13.95
16.5	0.29	2.5	0.73	11.96
17.5	0.25	4.0	1.00	17.50
18.5	0.19	1.0	0.19	3.52
			$\Sigma = R_o = 113.48$	$\Sigma = 941.85$
$T = \Sigma l_xm_xx/\Sigma l_xm_x = \Sigma l_xm_xx/R_o = 8.30$				
$r_m = \ln(R_o)/T = 0.57$				

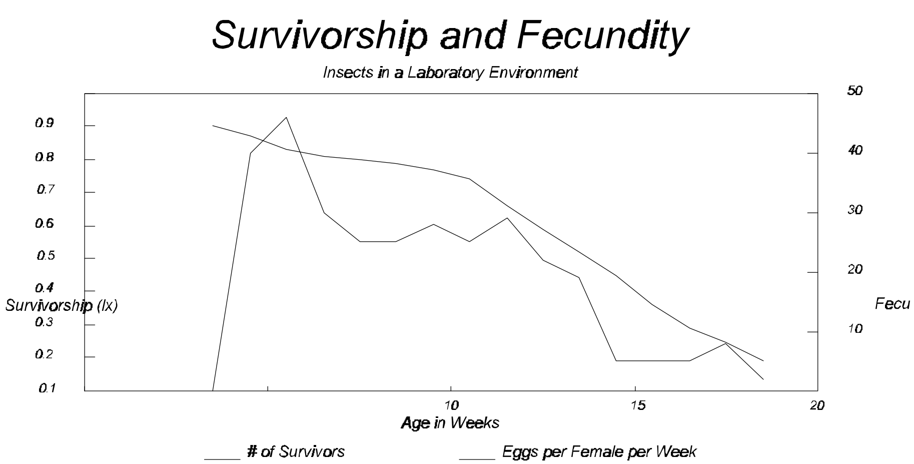

Table 2. Life Table for the Spruce Budworm in Experimental Plot A.

x	l_x	d_xF	d_x	$100(d_x/l_x)$ $=100(q_x)$
eggs	174.00	parasites, predators	18.00	10.34
		other causes	1.00	0.57
		TOTAL	19.00	10.92
instar I (1st larval stage)	155.00	dispersion, etc.	74.40	48.00
overwintering stage	80.60	winter	13.70	17.00
instar II	66.90	dispersion, etc.	42.20	63.08
instars III through VI	24.70	parasites	8.92	36.11
		disease	0.54	2.19
		birds	3.39	13.72
		other causes	10.57	42.79
		TOTAL	23.42	94.82
pupae	1.28	parasites, predators	0.23	17.97
		other causes	0.23	17.97
		TOTAL	0.46	35.94
# moths to adult	0.82	sex ratio 50:50--OK	0.00	0.00
# moths remaining	0.82	abnormal or small	0.00	0.00
# living to reproduce	0.82			
generation totals	174.00		173.18	99.53
Since 0.82 moths lived to reproduce and 50% are females, that means 0.41 are females. The average female lays an average of 150 eggs, thus the expected number of eggs would be 0.41 × 150 = 61.5. The actual eggs counted = 575, so:				
		migration in	61.5 − 575 = −513.5 †	(−513.5/61.5) ×100 = −834.96 *

The index of population trend is: expected = (61.5/174) × 100 = 35.34% increase[1]
observed = (575/174) × 100 = 330.46% increase[2]

† expected − observed = difference
* difference ÷ expected × 100 = %
[1] E = expected # eggs ÷ starting # eggs × 100
[2] O = actual # eggs ÷ starting # eggs × 100

Table 3. Life Table for the Spruce Budworm in Experimental Plot B.

x	l_x	d_xF	d_x	$100(d_x/l_x)$ $=100(q_x)$
eggs	2176.00	parasites, predators	175.00	8.04
		other causes	21.00	0.97
		TOTAL	196.00	9.01
instar I (1st larval stage)	1980.00	dispersion, etc.	1148.00	57.98
overwintering stage	832.00	winter	141.00	16.95
instar II	691.00	dispersion, etc.	484.00	70.04
instars III through VI	207.00	parasites	2.90	1.40
		disease	0.30	0.14
		birds	1.70	0.82
		starvation	165.30	79.86
		DDT	8.30	4.01
		other causes	26.70	12.90
		TOTAL	205.20	99.13
pupae	1.80	parasites, predators	0.24	13.33
		other causes	0.27	15.00
		TOTAL	0.51	28.33
# moths to adult	1.29	sex ratio 54:46--(abnormal)	0.10*	7.75
# moths remaining	1.19	abnormal, small, weak	0.57	47.90
# living to reproduce	0.62			
generation totals	2176.00		2175.38	99.97
Since 0.62 moths lived to reproduce and 46% are females, that means 0.29 are females. The average female lays an average of 150 eggs, thus the expected number of eggs would be 0.29 × 150 = 42.78. The actual eggs counted = 246, so:				
		migration in	44.78 − 246 = −203.22	(−203.22/42.78)×100 = −475.04

The index of population trend is: expected = (42.78/2176) × 100 = 1.97% increase
observed = (246/2176) × 100 = 11.31% increase

* 54 − 46 = 8 and 8/100 × 1.29 = 0.1032

1. Plot B had more eggs initially, so one might think there would be more eggs produced. However, plot A had higher numbers of both expected and observed eggs.
2. Look at the numbers--note starvation in plot B.
3. Immigration--numbers of moths coming in and laying eggs.

Table 4. Numbers of Confused Flour Beetles in 8 gm of Flour.

days	eggs		larvae		pupae		adults		total
	#	%	#	%	#	%	#	%	
0	0	0	0	0	0	0	4	100.00	4
15	62	74.70	17	20.48	0	0	4	2.92	83
30	30	14.93	168	83.58	0	0	3	1.49	201
50	47	17.87	75	28.52	51	19.39	90	34.22	263
64	107	34.52	47	15.16	12	3.87	144	46.45	310
78	114	39.45	11	3.81	20	6.92	144	49.83	289
101	185	49.87	30	8.09	0	0	156	42.05	371
114	180	49.59	20	5.51	7	1.93	156	42.98	363
134	257	61.34	3	0.72	0	0	159	37.95	419
156	236	59.75	2	0.51	0	0	157	39.75	395