Bio 21/51/120, Exercise #3
Due: 10 October 2006 Name:____

Mortality and natality data for a cohort of Belding's ground squirrel, *Citellus beldingi* (after Zammuto and Sherman 1986, Can. J. Zool. 64 602-605). Squirrels were censused once per year in mid-summer, shortly after weaning; m_x is the average number of female young just weaned by a female of age x.

Age class x	Number alive N_x	Annual Survival S_x	Cumulative survival l_x	Expected life e_x	Fecundity m_x	Realized fecundity $l_x m_x$	Reproductive value V_x	Cohort size at SAD C_x
0	238				0.0			
1	93				1.7			
2	49				2.1			
3	18				2.4			
4	12				3.0			
5	6				2.1			
6	0							

1. Fill in the life table.
2. What proportion of squirrels live to be 2 years old?
3. Of those squirrels that live to be 1 year old, what proportion survive to the 2nd year?
4. What is the expected future lifespan of a 1 year old squirrel?
5. Calculate R_0. Write it with the correct units. If there are 100 squirrels in mid-summer this year, how many would you expect to find in mid-summer next year? How many the year after?
6. Write the correct general equation for calculating reproductive value V_x for a post-breeding model.
7. If you were managing this population of squirrels and a users group wanted to harvest as many squirrels as possible on a sustained yield basis, which age class would you recommend that they exploit? Explain.

BIO 21/51/120: EXAMPLE OF LIFE TABLE CALCULATIONS

Cohort life table for little brown bat *Myotis lucifugus* (based on annual pre-breeding censuses*)

x	N_x	S_x	l_x	e_x	m_x	$l_x m_x$	V_x	C_x	$\lambda^{-x} l_x$	$l_x m_x x$	v_x	v_{x+1}	v_{x+2}	v_{x+3}	v_{x+4}
1*	320	0.4	1	0.82	0	0	1.1	0.563	0.968	0	0	0.4	0.42	0.28	0
2	128	0.7	0.4	1.05	1	0.4	2.75	0.218	0.375	0.80	1	1.05	0.7	0	
3	90	0.5	0.28	0.5	1.5	0.42	2.5	0.148	0.254	1.26	1.5	1	0		
4	45	0	0.14	0	2	0.28	2	0.071	0.123	1.12	2	0			
5	0		0			0		0	0	0					
$\sum$						1.10		1.000	1.718	3.18					

* The value of x in the first row of the table is the approximate age at the time of sampling of the youngest individuals that are recognized (with a pre-breeding census, the table starts with $x = 1$; with a post-breeding census, the table starts with $x = 0$).

N_x = **Number in cohort surviving to age x** (measured; e.g., from marked individuals).

S_x = **Annual probability of survival**
= Probability that an individual of age x will survive to age x+1.
= N_{x+1} / N_x eq. 1

0.40 = 128 / 320

l_x = **Cumulative Survivorship**
= Proportion of individuals in age class 0 that survive to age class x. Note that $l_0 = 1.0$ by definition.
= $l_{x-1} \bullet S_{x-1}$; eq. 2

0.4 = 1 • 0.4 i.e., $l_1 = l_0 \bullet P_0$
0.28 = 0.4 • 0.7

e_x = **Expected life**
= Expectation of future life given survival to age x.

$$= \left(\sum_{i=x+1}^{\infty} l_i \right) \bullet \frac{1}{l_x} \quad \text{eq. 3}$$

1.05 = (0.28 + 0.14) / 0.4

m_x = **Fecundity at age x** (average number of female offspring produced during the next year that survive to the time of the next census; e.g., average number of female bats produced last summer that survived to the next spring; measured in nature). Note that this is sometimes denoted as b_x in life table models. Note that we define m_x differently in a post-breeding model.

$l_x m_x$ = **Realized fecundity**
= $l_x \bullet m_x$ eq. 4
= Probability of survival to age x · Fecundity given survival.
= Female offspring in year x per initial female of age 1

0.42 = 0.28 • 1.5 females / female

R_0 = **Net reproductive rate (per capita progeny / lifetime, individuals • individual^{-1} • lifetime^{-1})**
= Average number of offspring produced by an average newborn offspring during its entire lifetime. Also equals the reproductive value for age class 0 (RV_0).

$$= \sum_{x=0}^{\infty} l_x m_x \quad \text{eq. 5}$$

= 1.10

G = **Generation time (units = time step of life table; in this case, years)**

= Average difference between the birth of an individual and the birth of its own progeny

$$\approx \left(\sum_{x=0}^{\infty} l_x m_x x \right) \ / \ R_0. \qquad \text{eq. 6}$$

2.89 = 3.18 / 1.10 .

r = **Intrinsic rate of increase (individuals • individual^{-1} • year^{-1})**

$\approx \ln R_0 \ / \ G.$ eq. 7 An exact solution requires iteration with Euler's equation.

0.033 $\approx$ ln1.10 / 2.89

λ = **Finite rate of increase. (pronounced lambda)**

= e^{r} eq. 8

1.034 = $e^{0.033}$

V_x = **Reproductive value**[a]

= Age-specific expectation of future offspring (females of age 1 / female of age x)

= Expected reproduction during the remainder of its life for an organism of age x

$$= m_x + \sum_{i=x+1}^{\infty} \left(\frac{l_i}{l_x} \bullet m_i \right) \qquad \text{eq. 9}$$

Note that columns in the table labelled v_0, v_1, etc., show values used in the summation for each V_x

2.75 = 1 + .28 / .4 • 1.5 + .14 / .4 • 2

= 1 + 1.05 + 0.7

[a] This equation can be different in alternative life table models. Derive it as Eq 10 for a post-breeding census model.

C_x = **Cohort size at stable age distribution**

= Proportion of total population of age x at stable age distribution

$$= \frac{\lambda^{-x} \bullet l_x}{\sum_{x=0}^{\infty} \left(\lambda^{-x} \bullet l_x \right)}. \qquad \text{eq. 11}$$

0.563 = 1 / 1.718

0.218 = 0.375 / 1.718

Given current population size, N_0, future population size at time t can be projected using r or λ assuming that (1) mortality and natality schedules remain the same and (2) the population is at a stable age distribution.

$$N_t = N_0 \bullet e^{r \bullet t} \qquad \text{eq. 12}$$

e.g., if N_0 = 100, and r = 0.033, N_{10} = 139

$$N_t = \lambda^t \bullet N_0 \qquad \text{eq. 13}$$

e.g., if N_0 = 100, and λ = 1.034, N_{10} = 139