



Life Tables, Darwin's Finches, and the Dynamics of Small Island Populations

by

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Part I – Life Tables Warm-up

Table 1. 1975 cohort of *G. scandens*.

Age Class (x)	Number Alive (N_x)	l_x	d_x	q_x
0	82	1.00		
1	42			
2	25			
3	17		X	X

1. Fill in the table above by calculating the following life tables values:

- a. Calculate l_x , the proportion of individuals surviving to each age class with respect to the initial number of individuals.

$$l_x = N_x / N_0 \quad (\text{where } N_0 \text{ is the number alive in age class "0"})$$

- b. Calculate d_x , the proportion of individuals dying between age classes x and $x + 1$.

$$d_x = l_x - l_{x+1}$$

- c. Calculate the mortality rate, q_x , or the proportion dying as compared to the proportion surviving.

$$q_x = d_x / l_x$$

- d. What information would you need to fill in the shaded boxes with Xs in them?

Part II – Survivorship Curves

In one of their numerous studies, Peter and Rosemary Grant (1992) tracked the births, deaths, and reproduction of two species of finch on the island Daphne Major in the Galapagos. From 1975 to 1991, the Grants collected nearly complete life table data for a 1975 and a 1978 cohort of both *Geospiza scandens* (common cactus finch) and *Geospiza fortis* (medium ground finch). Using the data below, fill in the rest of the life table (Table 3) for the *G. fortis* 1975 cohort. Values for the *G. scandens* 1975 cohort, which appeared in the “warm-up” that you just completed, have been filled in for you below (Table 2). Check your previous work with Table 2, complete Table 3, and then answer the questions below.

Table 2. 1975 cohort of *G. scandens*.

x	N_x	l_x	d_x	q_x
0	82	1.000	0.488	0.488
1	42	0.512	0.207	0.405
2	25	0.305	0.098	0.320
3	17	0.207	0.037	0.176
4	14	0.171	0.000	0.000
5	14	0.171	0.012	0.071
6	13	0.159	0.000	0.000
7	13	0.159	0.000	0.000
8	13	0.159	0.073	0.462
9	7	0.085	0.037	0.429
10	4	0.049	0.000	0.000
11	4	0.049	0.000	0.000
12	4	0.049	0.024	0.500
13	2	0.024	0.000	0.000
14	2	0.024	0.012	0.500
15	1	0.012	0.012	1.000
16	0	0.000

Table 3. 1975 cohort of *G. fortis*.

x	N_x	l_x	d_x	q_x
0	314	1.000		
1	198			
2	89			
3	39			
4	28			
5	27			
6	24			
7	23			
8	20			
9	8			
10	4			
11	4			
12	2			
13	2			
14	1			
15	0	

Life Table Formulas

x = Age Class

N_x = Number Alive Each Year

l_x = Proportion Surviving = N_x / N_0

d_x = Proportion Dying = $l_x - l_{x+1}$

q_x = Mortality Rate = d_x / l_x
(for each x)

Questions

1. The Grants mention in their paper that finches and other passerine birds often experience the highest mortality early in life. Is there support for this in your life table calculations above for each finch species? Explain.
2. You may have noticed that the mortality rate fluctuates when it might otherwise be expected to steadily decrease as the cohort ages. State a reasonable hypothesis for these fluctuations in mortality rate (q_x).

3. To visualize survivorship in a graph, it is often helpful to calculate the log of survivorship so that the graphed data are more reasonably scaled. Complete Table 4 to the right to log-transform the survivorship data for the 1975 cohort of *G. scandens* (round to the hundredths place).
4. Use your values from Table 4 and the grid below to create a survivorship curve for the 1975 cohort of *G. scandens*. Make sure to label the axes and provide appropriate scales. (*Note:* Values of N_x that are not log-transformed should not be used in this graph.) Once your graph is complete, indicate the points on the graph that represent the years 1978, 1983, and 1987 with arrows and label them “1978,” “1983,” and “1987.”
- Which type of survivorship curve best represents your graphed data? (Circle one):

I

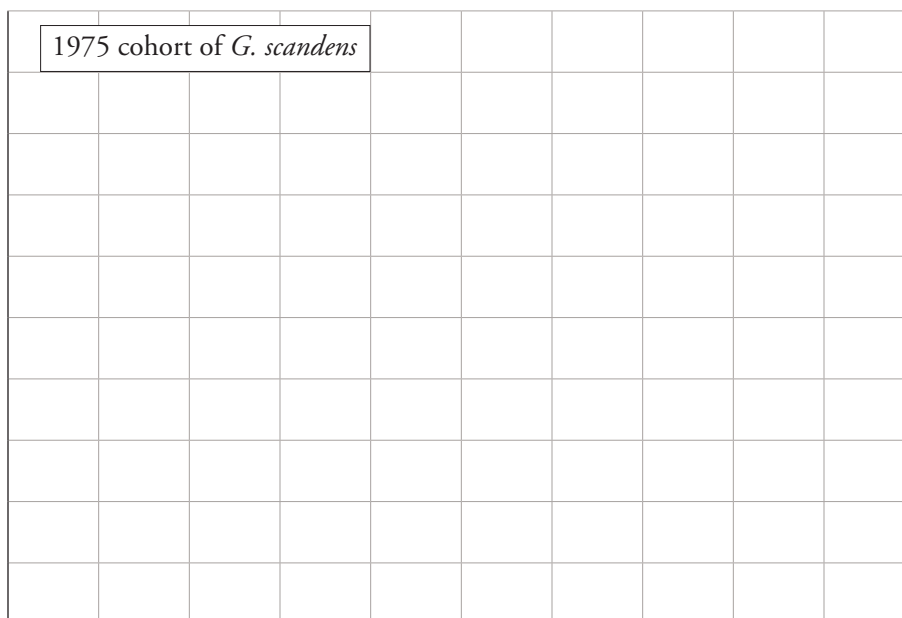
II

III

Provide a brief explanation for your choice:

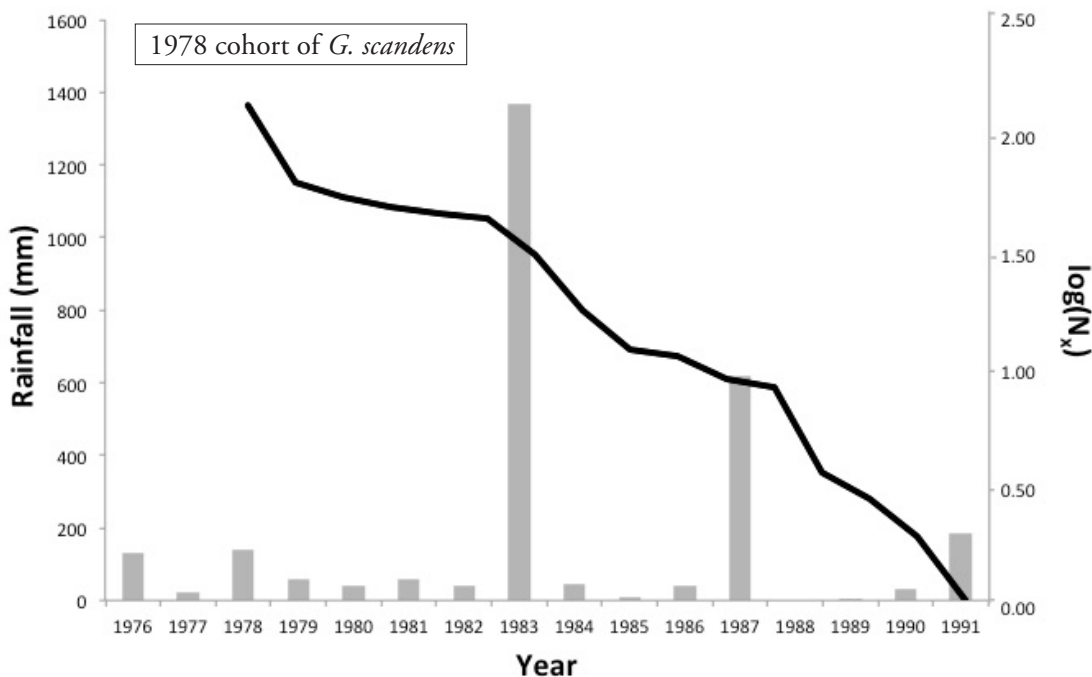
Table 4. 1975 cohort of *G. scandens*.

x	N_x	$\log(N_x)$
0	82	
1	42	
2	25	
3	17	
4	14	
5	14	
6	13	
7	13	
8	13	
9	7	
10	4	
11	4	
12	4	
13	2	
14	2	
15	1	
16	0	...



Part III – Survivorship in a Changing Environment

Island populations can be especially sensitive to environmental variation as they tend to be smaller and thus more susceptible to chance events. The ever-fluctuating climate of the Galapagos Islands is a driving selective force on the finch populations. In the Grant's long-term study, they tracked rainfall, which affects available resources for these birds. Finches are relatively well adapted to lower rainfall conditions, so any rainfall can often substantially and positively affect their fitness through an increase in resources. Additionally, different cohorts of the same species will experience climatic patterns at different life stages; experience at certain life stages may be more important to survival and reproduction. Below is a graph depicting rainfall over the course of the Grant's study (shown with bars) and the survivorship curve of the 1978 cohort of *G. scandens* (shown with a line). Use the graph below and the survivorship curve you made in Part II for the 1975 cohort to answer the following questions.



Questions

- During which time intervals/years is survival highest in each cohort of *G. scandens* (i.e., where is the slope of the survivorship curve closest to zero on the graph)?

<i>G. scandens</i> Cohort	Years of Highest Survival
1975	
1978	

- During which time intervals/years is survival lowest in each cohort of *G. scandens* (i.e., where is the slope of the survivorship steepest on the graph)?

<i>G. scandens</i> Cohort	Years of Lowest Survival
1975	
1978	

3. Is there evidence from the Grants' data that the environmental factor of rainfall (occurrence and/or consistency) is associated with survivorship in *G. scandens*? Explain the relationship (if any). (Consider that there may be time lags between environmental change and when changes in survivorship are realized.)
4. Why is no increase observed in the survivorship curves?



Illustration of female common cactus finch (*Geospiza scandens*), by John Gould (1804–1881), P.D., https://commons.wikimedia.org/wiki/File:Cactornis_assimilis.jpg.

Part IV – Reproductive Output

The Grants tracked the reproduction of a *subset* of the cohorts they were studying by counting the fledglings each year. m_x refers to the *average* expected reproductive output at age class x (some text books use the term b_x instead of m_x). For example, for the surviving 5 females from the 1975 *G. scandens* cohort in year $x = 2$, the average reproductive output is low (0.187) compared to other years, which indicates that few females reproduced that year and also had very few offspring. For the same cohort at age 3, the higher m_x reflects either that more females reproduced or that a few females had lots of offspring.

The quantity $l_x m_x$ ($l_x^* m_x$) considers the probability of an individual surviving to a certain age class (l_x) and achieving an observed reproductive output (m_x) together. If survival is low, it may follow that expected reproduction would then be lower, and $l_x m_x$ accounts for this. Fill in the tables below for the 1975 and 1978 cohorts of *G. scandens*. Then answer the questions.

Table 5. 1975 cohort of *G. scandens*, females.

x	N_x	l_x	m_x (or b_x)	$l_x m_x$
0	17	1.000	0.000	
1	9	0.529	0.364	
2	5	0.294	0.187	
3	5	0.294	1.438	
4	4	0.235	0.833	
5	4	0.235	0.500	
6	4	0.235	0.833	
7	4	0.235	0.250	
8	4	0.235	3.333	
9	2	0.118	0.125	
10	1	0.059	0.000	
11	1	0.059	0.000	
12	1	0.059	3.500	
13	0	0.000
14
15

Table 6. 1978 cohort of *G. scandens*, females.

x	N_x	l_x	m_x (or b_x)	$l_x m_x$
0	90		0.0	
1	39		0.051	
2	33		0.667	
3	30		1.500	
4	29		0.655	
5	27		5.500	
6	16		0.687	
7	8		0.0	
8	5		0.000	
9	5		2.200	
10	3		0.0	
11	2		0.0	
12	0	

x = Age Class

N_x = Number Alive Each Year

l_x = Proportion Surviving = N_x/N_0
(for each x)

Questions

- The sum of all $l_x m_x$ values is the net reproductive rate (R_0), which provides the mean number of offspring per individual over a life span. Calculate R_0 values for the two tables above.

<i>G. scandens</i> Cohort	R_0
1975	
1978	

2. Generation time is the amount of time from “egg to egg” or the age at first breeding. Generation time for a population with repeated breeding like the finches is given by:

$$T_c = \frac{\sum(l_x * m_x * x)}{\sum(l_x * m_x)} \quad (\text{for each } x)$$

- a. Use values from Tables 5 and 6 to calculate the generation time for each cohort of *G. scandens* females:

<i>G. scandens</i> Cohort	T_c
1975	
1978	

- b. Give a reasonable hypothesis for any difference in generation time between the 1975 and 1978 cohorts of *G. scandens* females. You can use observations provided throughout this case study in your rationale.

- c. On average, at what age does a female finch from the 1975 cohort reproduce?

3. Effective population size is the actual number of breeding individuals (contributing genes to the next generation) in a population. The small island populations of *G. scandens* and *G. fortis* had effective population sizes of 40% and 31%, respectively, in the Grants’ study (1992). Which evolutionary force is likely to be greater in small populations with very few breeders, and how might that impact survival?
4. Finches from other Galapagos Islands often land on Daphne Major. Additionally, *G. scandens* and *G. fortis* sometimes hybridize. Using this information and information presented throughout the case study as rationale, provide a reasonable hypothesis for the present-day persistence of Galapagos Island finches. Give the reasoning behind your hypotheses.