

Introduction to Life Tables



Life tables are used to describe age-specific mortality and survival rates for a population. When this information is combined with fecundity data, life-tables can be used to estimate rates of population change (e.g., r , λ , and R_0).

I. Types of Life Tables

1. **Cohort** or **age-specific** or **dynamic** life tables: data are collected by following a cohort throughout its life. This is rarely possible with natural populations of animals. Note: a cohort is a group of individuals all born during the same time interval.
2. **Static** or **time-specific** life tables: age-distribution data are collected from a cross-section of the population at one particular time or during a short *segment* of time, such as through mortality data. Resulting age-specific data are treated as *if* a cohort was followed through time (i.e., the number of animals alive in age class x must be less than alive in age class $x-1$). Because of variation caused by small samples, data-smoothing techniques may be required (see Caughley 1977).
3. **Composite** - data are gathered over a number of years and generations using cohort **or** time-specific techniques. This method allows the natural variability in rates of survival to be monitored and assessed (Begon and Mortimer 1986).

II. Semelparity and Iteroparity

- **Semelparity** - Individuals that have only a single, distinct period of reproductive output in their lives, prior to which they have largely ceased to grow, during which they invest little or nothing in survival to future reproductive events and after which they therefore die (Begon et al. 1996:147). For annual species, this results in nonoverlapping generations. Examples other than annual plants and some insects?
- **Iteroparity** - Individuals that normally experience several or many such reproductive events. During each period of reproductive activity the individual continues to invest in future survival and possibly growth, and beyond each it therefore has a reasonable chance of surviving to reproduce again (Begon et al. 1996:147). Results in overlapping generations.
 1. **Birth pulse** - reproductive activity is restricted to a specific breeding season. Begon et al. (1996) refer to this as "overlapping semelparity."
 2. **Birth flow** - reproductive events merge into a single extended

period.

III. Life-Table Notation (columns in a life table):

$x =$	age, measured in years or some other conventional unit. With longer-lived animals and plants this is often 1 year, but for voles it might be 1 week and for some insects 1 day. Often expressed as an interval, e.g., 0-1 years old.
$n_x = n_{x-1} - d_{x-1}$	the number of individuals surviving at the <i>start</i> of age interval x . Note: $n_0 = \text{sum}(d_x)$ if d_x expressed as numbers dying and the survival schedule is complete for all members of the cohort.
$d_x = n_x - n_{x+1} =$	the number of individuals of a cohort dying <i>during</i> the age interval x to $x+1$. Note: sometimes calculated as proportion dying.
$q_x = d_x / n_x =$	<i>finite rate of mortality</i> during the age interval x to $x + 1$. Note: this parameter is least affected by bias in the sample and gives the most direct projection of the mortality pattern in a population. It is often used to make comparisons within and between species.
$S_x = (n_x - d_x) / n_x$ or $1 - q_x$ $=$	<i>finite rate of survival</i> during the age interval x to $x + 1$. This parameter is used in harvest calculations and in population modeling. Note: <i>finite</i> rates cannot be added to get total survival rate for a longer period of time; however, finite survival rates are <i>multiplicative</i> (i.e., survival from age 0 to 3 = $S_0 \times S_1 \times S_2$).
$l_x = n_x / n_0 =$	the proportion (scaled from 0 to 1) of individuals surviving at the <i>start</i> of age interval x . You will also see l_x expressed per 1,000, i.e., $= (n_x / n_0)1000$. This parameter is used to plot survivorship curves (see comments below).
$k_x = \log_{10} n_x - \log_{10} n_{x+1} =$	<i>killing power</i> or a standardized measure of the intensity (rate) of mortality. Unlike q_x -values, k_x -values can be added to determine the mortality rate for a number of age classes. Note: because k_x -values are calculated using $\log_{10}$, you must take the antilog of the common log to convert back to finite survival (i.e., $S = 10^{-k}$).

IV. Extended or Expanded Life Tables = Survival + Fecundity Schedules

$m_x =$	fecundity rate (i.e., average number of female offspring produced <i>per female</i> in the population over some period of time, generally a year).
$l_x m_x =$	The mean number of female offspring produced by females in an age class. This information is used to calculate net reproductive rate (R_0) and the instantaneous rate of change (r).
$R_0 = [\text{sum } (l_x m_x)] / l_0 =$	the <i>net reproductive rate per generation</i> . Or in other words, the mean number of female offspring produced by a female during her lifetime (i.e., the replacement rate). Note: $R_0 < 1$ indicates the members of the population are <i>not</i> replacing themselves (i.e., the population is declining). $R_0 > 1$ denotes an increasing population. $R_0 = 1$ indicates a stationary or "stable" population.
$G = \text{Sum}(l_x m_x x) / R_0 =$	the mean length of a generation. Other definitions include (1) the time elapsing between birth of a female and mean time (age) of birth of her offspring and (2) the average age that adult females give birth.
λ (lambda) = $R_0^{1/G} = e^r =$	the <i>finite rate of population change</i> or the net reproductive rate over some time interval, which is a year in many cases. Lambda >1 indicates an increasing population, lambda=1 indicates a stationary population, and lambda<1 indicates a decreasing population. The use of this parameter is geared toward organisms that reproduce during a short breeding season (i.e., discrete growth or <i>birth-pulse fertility</i>). Note: your textbook uses "R" to denote lambda.
$r \sim = \ln(R_0)/G = \ln(\lambda) =$	<i>intrinsic or instantaneous rate of increase</i> (i.e., the change in population size per individual per unit of time). An r>0 indicates an increasing population, r=0 indicates a stationary pop'n, and an r<0 indicates a declining population. Note: the equations listed only give you an approximation of r . You need to solve <i>Euler's equation</i> for a precise estimate of r (see Begon et al. 1996:165).
$e_x = T_x / L_x =$ where $L_x = (l_x + l_{x+1}) / 2$ $T_x = (\text{Sum } (L_x)) - L_{x-1}$	mean expectation of further life for individuals alive at the start of age interval x . The mean expectation of further life can be used as one way of compressing an entire life table into one number. It has limited application for wildlife studies, but is commonly used in the insurance business.

$$C_x = \frac{\lambda^{-x} \ell_x}{\sum_{x=0}^{\infty} \lambda^{-x} \ell_x}$$

= stable age distribution (i.e., where the proportion of the population in each age class remains constant over time). This is only achieved if the observed survival and fecundity schedules remain constant over a long period of time. **Note:** population projections from simple deterministic growth models (e.g., the exponential and logistic growth models) are based on the assumption that the population has a stable age distribution.



NOTE: Population ecologists do not all use the same life-table notation. For example, Begon et al. (1996) use different symbols to denote the finite rate of increase and mean generation length. Nevertheless, data and calculations in the respective columns have the same meaning.

V. Methods of Collecting Life-Table Data:

1. **Age at Death Recorded Directly** - the number of individuals dying in successive intervals of time is recorded for a group of individuals born at the same time. This is the most precise type of data available because it is based on a single cohort followed through time. The observed data are the d_x column of the life table.
2. **Cohort Size Recorded Directly** - The number of individuals alive in successive intervals of time is recorded for a cohort of individuals. These data are similar to those obtained with Method 1, except that those *surviving* are tallied, not those dying. These data are also precise and specific to the cohort studied. Observed data are entered into the n_x column of the life table.
3. **Age at Death Recorded for Several Cohorts** - Individuals are marked at birth and their death recorded, as in Method 1, but several cohorts are pooled from different years or seasons. These data are usually treated as if the individuals were members of one cohort and the analysis of Method 1 is applied.
4. **Age Structure Recorded Directly** - The number of individuals aged x in a population is compared with the number of these that died before reaching age $x+1$. The number of deaths in that age interval, divided by the number alive at the start of the age interval, gives an estimate of q_x directly.
5. **Ages at Death Recorded with a Stable Age Distribution and Known Rate of Increase** - Often it is possible to find skulls or other remains that give the age at death of an individual. These data can be tallied into a frequency distribution of deaths and thus give d_x directly.
6. **Age Distribution Recorded for a Population with a Stable Age Distribution and Known Rate of Increase** - In this case, the age

distribution is measured directly by sampling. The number of individuals born is calculated from fertility rates.



Note: Methods 5 and 6 are based on the *critical* assumption that the rate of population change is known (or the population is stationary, i.e., $r=0$) and the age distribution is stable. Although methods 5 and 6 appear more realistic in terms of data collection, there are numerous ways in which time-specific life tables have been calculated incorrectly, e.g., from hunter kills (see Caughley 1977).

VI. Sample size, Precision, and Accuracy of Life tables

Caughley (1977) recommended that the cohort consist of at least 150 individuals when basing survival estimates on the stable-age assumption. However, age determination is difficult for many species, and if age is not measured carefully the resulting life table may be very inaccurate.

VII. Value of Life Tables

The main value of a life table lies in what it tells us about the population's strategy for survival, i.e., life tables help us to understand the dynamics of populations. For example, time-specific life tables, although often not meeting the assumptions necessary to estimate survival rates, are valuable to a manager of exploited populations because they show the existence of strong year classes or help identify weak age classes.

Although we have used age-structured schedules, for some organisms age is not the best life history variable on which to develop analyses of population change. For example, the stage of development (egg, larval, pupal, adult stages) of some insects may be a more important life history variable. If predation on fish is size-dependent, then size rather than age would be the appropriate stage-variable.

VIII. Limitations of Life Tables

Opportunities to follow cohorts for long periods of time are rare, which precludes cohort analysis, and the critical assumption of a stable-age distribution is so difficult to meet that it makes the use of time-specific life tables (Johnson 1994).

IX. Survivorship and Mortality Curves

- **Survivorship curves** are usually created by plotting l_x on the y-axis and

age on the x -axis. Occasionally you may see n_x plotted on the y -axis. The y -axis is usually logarithmic, i.e., $\log_{10}(l_x)$, to allow comparisons among different studies and species. In other words, log transformations standardize the survivorship curve.

- **Mortality curves** are created by plotting q_x or k_x against age.
- Compare your survivorship/mortality curves to those described in Begon and Mortimer (1996:153-154) and Johnson (1992:433).

X. In-class Exercise

XI. Selected References

- **Begon, M., J. L. Harper and C. R. Townsend.** 1996. Ecology: Individuals, populations and communities. 3rd ed. Blackwell Scientific Ltd., Cambridge, Mass. 1068pp.
- **Begon, M., and M. Mortimer.** 1986. Population ecology: a unified study of animals and plants, 2nd edition. Blackwell Sci. Publ., Boston, Mass.
- **Caughley, G.** 1977. Analysis of vertebrate populations. John Wiley & Sons, New York. 234pp.
- **Johnson, D.** 1994. Population analysis. Pages 419- 444 *in* T. Bookhout, ed. Research and management techniques for wildlife and habitats. Fifth ed. The Wildl. Soc., Bethesda, Md.
- **Krebs, C. J.** 1989. Ecological methodology. Harper & Row, Publ., New York. 654pp.