1

Introduction

All biological populations obey the immutable rule that, migration withstanding, the difference between their birth and death rates determines the direction and size of their growth rate. This relationship provides the foundation for demography—the study of populations and the processes that shape them (Pressat, 1985).

Demography began as the study of *human* populations and literally means "description of the people." The word is derived from the Greek root *demos*, meaning "the people," and was coined by a Belgian, Achille Guillard, in 1855 as *demographie* (*Elements of Human Statistics or Comparative Demography*). He defined demography as the natural and social history of the human species or the mathematical knowledge of populations, of their general changes, and of their physical, civil, intellectual, and moral condition (Shryock et al., 1976).

Although demography is a distinct discipline in its own right, only a few academic departments or graduate groups exist worldwide that are devoted exclusively to demography. Aside from census bureau personnel, the vast majority of researchers or practitioners who use demographic methods are part of more broadly defined disciplines such as sociology, psychology, business, and medicine for human populations or ecology, fisheries, wildlife, forestry, and entomology for plant and animal populations. In principle both demography as a field and population as an entity can be defined in the abstract and thus encompass the social as well as the biological sciences. However, in practice this is not the case. Every field creates definitions that fits its needs. Social scientists tend to refine versions of Guillard's original definition of demography. Hence populations that represent their center of relevance are almost always human and are typically defined in geopolitical terms.

Biologists typically define *population* in Mendelian terms such as "a group of interbreeding organisms belonging to the same species and occupying a clearly delimited space at the same time" (Wilson, 1975) or "...a cluster of individuals with a high probability of mating with each other compared to their probability of mating with a member of some other population" (Pianka, 1978). In many applied areas of biology the term *population* often refers to an entity about which statistical information is desired. For example, sampling leaves for insect infestation levels is viewed in statistics as sampling

from a population (i.e., the totality of elements about which information is desired). Samples from this target "population" will generate a mean and variance and in turn enable one to test statistical hypotheses. Population in this sense may be relevant to demographers though it may have little to do with an interbreeding group of individuals in the biological sense. Thus it is often necessary to move back and forth between the concept of a population as a material aggregate and population as a biologically reproducing entity. *Population* is defined here in general terms simply as "a group of individuals coexisting at a given moment" (Pressat, 1985).

Classical demography is concerned basically with four aspects of populations (Shryock et al., 1976): (1) *size*—the number of units (organisms) in the population; (2) *distribution*—the arrangement of the population in space at a given time; (3) *structure*—the distribution of the population among its sex and age groupings; and (4) *change*—the growth or decline of the total population or one of its structural units. The first three—size, distribution, and structure—are referred to as population statics, while the last—change—is referred to as the population dynamics. Hauser and Duncan (1959) regard the field of demography as consisting of two parts: i) *formal demography*—a narrow scope confined to the study of components of population variation and change (i.e., births, deaths, and migration); and ii) *population studies*—a broader scope concerned with population variables as well as other variables. In a biological context these other variables may include genetics, behavior, and other aspects of an organism's biology. The methodology of demographic studies includes data collection, demographic analysis, and data interpretation.

In biology it is often difficult to determine where one field leaves off and the other begins. But many apply demographic methods or use the concepts in some way. *Ecology* is concerned with the interrelationship of organisms and their surroundings; *population biology* is often used interchangeably with ecology but usually implies an emphasis on evolutionary relations; *population ecology* is distinct from *community ecology* in that the former is usually concerned with the interactions of a few species, while the latter with the interactions of many; *population dynamics* implies the study of the mechanisms and consequences of population change (usually numbers); *population genetics* is less concerned with numbers of individuals in a population and more concerned with gene frequencies and their rate of change, and *applied ecology* is a rubric for areas such as forestry, fisheries, and pest management.

Demographers conceive the population as the singular object for scientific analysis and research. However, as Pressat (1970) notes, population is everywhere and nowhere in the sense that many aspects of demography can be studied simply as component parts of the disciplines considered. He states, "But to bring together all the theories on population considered as a collection of individuals subject to process of evolution, has the advantage of throwing into relief the many interactions which activate a population and the varied characteristics of that population."

FORMALIZATION

Demographic Levels and Traits

The basic unit and starting point for demographic analysis is the *individual*, which, according to Willekens (1986), is defined simply as "a single organism that is a carrier of demographic attributes." The individual is a natural unit and need not be contrived like "power" or "community." The basic attributes of individuals include a development rate, an age-specific level of reproduction, and a time of death.

The next demographic level for which traits are considered is that of the *cohort*, defined as "a group of same-aged individuals" or, more generally, "a group who experience the same significant event in a particular time period, and who can thus be identified as a group for subsequent analysis" (Pressat, 1985). Cohort attributes are to be distinguished from individual traits in that they possess a mean and variance and therefore are statistical. These traits are often expressed in the form of an age schedule.

The age schedule of events in cohorts determines their *population traits*—the third demographic level. These traits result from the interplay of cohort attributes that are, in turn, set by the individuals within the cohort.

The Life Course

A universal constant for all life is chronological age, which is the exact difference between the time on which the calculation is made and the time of the individual's birth. This difference is typically termed *exact age* and is to be contrasted with *age class*, which groups exact ages into periods. The passage from one stage to another is formally termed an *event*. The sequence of events and the duration of intervening stages throughout the life of the organism is termed its *life course*.

It is clear that age is an important dimension of life and grouping individuals into age classes or at least distinguishing between young and old is useful. Therefore I denote the age of egg hatch as η (eta), age of pupation as π (pi), age of eclosion (first day of adulthood) as ε (epsilon), age of first reproduction as α (alpha), age of last reproduction as β (beta), and oldest possible age as ω (omega), Several key intervals can then be defined using this notion and are summarized in Table 1-1.

This scheme is depicted graphically in Figure 1-1. The notation for adult traits, particularly α, β, and ω, is a convention in demography, while the notation for the preadult is not. In general, age is the characteristic, central variable in almost all demographic analysis and serves as a surrogate for more fundamental measures (e.g., physiological state) and duration of exposure to risk.

Demographic Rates

Demographic rates can be grouped into five categories according either to the kind of population counted in the denominator or to the kind of events

Table 1-1. Summary of Key Intervals in an Insect Life Course

Interval	Notation
Preadult	
Egg incubation	0–η
Nymphal or larval period	η–π
Pupal period	π–ε
Adult	
Preovipositional period	ε–α
Reproductive period	α–β
Postreproductive period	β–ω
Adult life span	ε–ω
Total life span	0–ω

counted in the numerator (Ross, 1982). These include—

1. *Crude rates.* This category uses the total population as the denominator. Thus we may consider crude birth rate (number of births per number in the population), crude death rate (number of deaths per number in population), and crude rate of natural increase (difference between crude birth and death rates). The results are "crude" in that they consider all individuals rather than by age or sex groupings.
2. *Age-specific rates.* These are the same as crude rates except with age restrictions for both numerator and denominator. For example, age-specific fecundity for an insect 20 days old counts only offspring produced by females in that age group and counts only females of that age in the denominator. Thus a *schedule* of rates is created.
3. *Restricted rates.* These rates apply to any special sub-group. For example, in human demography the number of births to married women (rather than to all women) is termed "marital age-specific fertility rate." In insects a restricted rate of this sort could be fecundity rates of females that produce at least one offspring. This would therefore exclude all steriles.
4. *Rates by topic.* These rates apply to each specialized topic in demo-

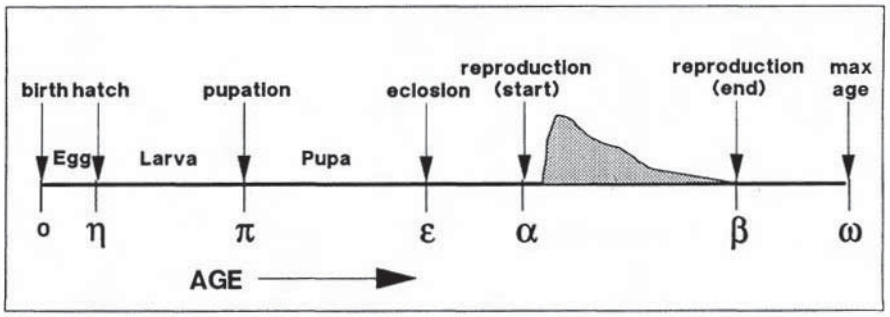

Figure 1-1. Generic diagram of an insect life course.

graphy. For example, reproductive rates may include total fertility rate, gross reproductive rate, or net reproductive rate.

5. *Intrinsic rates.* The rates that prevail in a stable population are referred to as intrinsic rates in that they cannot reflect any accidental or transient short-term feature of the age distribution. Thus they are considered "intrinsic" or "true" rates.

ELEMENTARY CHARACTERISTICS OF POPULATIONS

Information on populations is obtained either through a census or through a survey, the distinction which is far from clear-cut. A census is typically thought of as a complete canvass of an area; the intent is to enumerate every individual in the population by direct counting and further, to cross-classify by age (stage), sex, and so forth. The intent of a survey is to estimate population characteristics on a sample basis.

Population Size

In concept, the notion of population size is extremely simple since it means the total number of individuals in the population. However, human demographers make a distinction between *de facto* enumeration, which records where each individual is at the time of the census (i.e., includes military or migrant workers), and *de jure* enumeration, which records usual residence (i.e., only records military personnel at place of residence).

Population Distribution

There are basically three broad spatial measures that characterize a particular distribution. These are—

1. *Number by spatial subdivision.* Statistics in this case can be given as i) percentage of the total by subdivision, or ii) a rank order from the subdivision with the highest count to the spatial unit with the lowest. Depending upon which method is used, comparisons of two census times will reveal the change in percentage or the change in rank by spatial location.
2. *Measures of central location.* The center of a population or the mean point of the population distributed over an area is defined as the center of population gravity or of population mass. The formula for the coordinates of the population center is given by

$$x = \sum_{i=1}^{k} p_i x_i / \sum_{i=1}^{k} p_i \qquad (1\text{-}1a)$$

$$y = \sum_{i=1}^{k} p_i y_i / \sum_{i=1}^{k} p_i \qquad (1\text{-}1b)$$

where p_i is the number in the population at point i and x_i and y_i are its horizontal and vertical coordinates, respectively. Population center can also be defined in three-dimensional space (e.g., vertical distribution on plants) by adding the z-coordinate and computing z.

3. *Measures of concentration and spacing.* The simplest measure of the degree of dispersion of a population in the xy-plane is known as the *standard distance.* This measure bears the same kind of relationship to the center of the population that the standard deviation of any frequency distribution bears to the arithmetic mean. If x and y are the coordinates of the population center, then the standard distance, D, is given by

$$D = \left[\frac{\sum_{i=1}^{k} \{f_i(x_i - x)^2\}}{n} + \frac{\sum_{i=1}^{k} \{f_i(y_i - y)^2\}}{n} \right]^{1/2} \tag{1-2}$$

where f_i is the number of organisms in a particular area and $n = \sum_{i=1}^{k} f_i$.

Population Structure

The structure of a population is the relative frequency of any enumerable or measurable characteristic, quality, trait, attribute, or variable observed for individuals (Ryder, 1964). These items could include age, sex, genetic constitution, weight, length, shape, color, biotype, birth origin, and spatial distribution. Only age and sex will be covered here since they are the most common traits by which individuals in populations are decomposed.

Sex ratio (SR) is the principal measure of sex composition and is usually defined as the number of males per female or

$$SR = n_m/n_f \tag{1-3}$$

where n_m and n_f represent the number of males and the number of females, respectively. The proportion of males (PM) in a population is given by

$$PM = n_m/n_T \tag{1-4}$$

where $n_T = n_m + n_f$. This measure expresses males as a fraction of the total and not as a ratio in the conventional sense. Additional measures of sex composition in ecology include the *primary sex ratio* (sex ratio at conception or birth) and the *secondary sex ratio* (sex ratio at adulthood or at the end of parental care).

The simplest kind of analysis of age or stage data is the frequency distribution of the total population by age or

$$f_x = n_x/N \tag{1-5}$$

where f_x is the frequency of individual aged x, n_x is the number in the population at age x, and N is the total number in the population. An *age*

pyramid is often used to illustrate the age-by-sex distribution of a population.

Population Change (in Size)

If a population numbers N_t and N_{t+1} at times t and $t+1$, respectively, then the *amount* of change equals

$$N_t - N_{t+1} = \text{amount of change} \tag{1-6a}$$

which is simply the difference in the population number at the two time periods. However, the *rate* of change is given by

$$N_{t+1}/N_t = \text{total rate of change} \tag{1-6b}$$

which gives the *factor* by which the population changed over one time period relative to the number at time *t* and

$$(N_{t+1} - N_t)/N_t = \text{fractional rate of change} \tag{1-6c}$$

which gives the *fraction* by which the population changes over one time period relative to the number at time *t*.

Population Change (in Space)

Population change occurs when *migrants* move from one area to another (Shryock and Siegel 1976). Every move is an out-migration with respect to the area of ogirin and an in-migration with respect to area of destination. The balance between in-migration and out-migration is termed *net migration.* The sum total of migrants moving in one direction or the other is termed *gross in-migration* or *gross out-migration.* The sum total of both in- and out-migrations is termed *turnover.* A group of migrants having a common origin and destination is termed a *migration stream.* The difference between a stream and its counterstream is the *net stream* or *net interchange* between two areas. The sum of the stream and the counterstream is called the *gross interchange* between the two areas.

Various rates can be expressed arithmetically as

$$\text{mobility rate} = M/P \tag{1-7}$$

where M denotes the number of movers and P denotes the population at risk of moving. Other formulae for movement include

$$\text{in-migration rate} = M_i = I/P \tag{1-8a}$$

$$\text{out-migration rate} = M_0 = O/P \tag{1-8b}$$

$$\text{net migration rate} = (I - O)/P \tag{1-8c}$$

where I and O denote the number of in-migrants and out-migrants, respectively.

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2

Life Tables

GENERAL CONCEPTS

A life table is a detailed description of the mortality of a population giving the probability of dying and various other statistics at each age (Pressat, 1985). There are two general forms of the life table. The first is the *cohort life table*, which provides a longitudinal perspective in that it includes the mortality experience of a particular cohort from the moment of birth through consecutive ages until no individuals remain in the original cohort. The second basic form is the *current life table*, which is cross-sectional. This table assumes a hypothetical cohort subject throughout its lifetime to the age-specific mortality rates prevailing for the actual population over a specified period. These are often referred to in ecology as time-specific life tables and are used to construct a *synthetic* cohort.

Both cohort and current life tables may be either *complete* or *abridged*. In a complete life table the functions are computed for each day of life. An abridged life table deals with age intervals greater than one day, such as over a complete stage (e.g., larval period), where precise determination of daily survival is difficult. The distinction between complete and abridged has to do with the length of the age interval considered. Both forms of the life table may be either *single decrement* or *multiple decrement*. The first of these lumps all forms of death into one and the second disaggregates death by cause.

My objective in this chapter is to introduce the basic concepts, notation, and methods of life table analysis, including complete and abridged tables; special properties of the life table, such as sensitivity analysis; and the multiple decrement life table. More advanced treatments of life tables include the works by Brass (1971), Keyfitz and Frauenthal (1975), Schoen (1975), Batten (1978), Elandt-Johnson and Johnson (1980), Chiang (1984), Manton and Stallard (1984), Hakkert (1987), and Pollard (1988).

THE SINGLE DECREMENT LIFE TABLE

Life Table Radix

A radix in mathematics is a number that is arbitrarily made the fundamental number of a system of numbers. In the life table the radix is the number of

births at the start of the life table against which the survivors at each age are compared. More generally it is the initial size of any cohort subjected to a particular chance of experiencing an event (Pressat, 1985).

In human demography a typical radix is assigned a number such as 100,000. Thus any number remaining at successive ages can be conveniently expressed as the number of survivors out of 100,000. In population biology the life table radix is usually assigned the value of unity, so that subsequent survivors are expressed as a fraction of the original number. The radix is associated with the survival column of the life table, denoted l_x. This gives the number of individuals surviving to age x. Historically the radix index is zero (i.e., newborns are aged zero days at the beginning of the interval).

Life Table Functions

The proportion of a cohort surviving from birth to exact age x is designated l_x. The difference in number of survivors for successive ages x and x + 1 is designated d_x:

$$d_x = l_x - l_{x+1} \tag{2-1a}$$

and the difference in survivorship for ages n days apart is

$$_nd_x = l_x - l_{x+n} \tag{2-1b}$$

Thus the d_x and $_nd_x$ schedules give the frequency distribution of deaths in the cohort.

The probability of surviving from age x to x + 1 is designated p_x, where

$$p_x = l_{x+1}/l_x \tag{2-2a}$$

and more generally the probability of surviving from age x the age x + n is designated $_np_x$, where

$$_np_x = l_{x+n}/l_x \tag{2-2b}$$

Both p_x and $_np_x$ are termed *period survivorship.*

The complements of these survival probabilities, designated $q_x (= 1 - p_x)$ and $_nq_x (= 1 - {}_np_x)$ are termed *period mortality* and represent the probability of dying over these respective periods. Note that

$$\begin{aligned} q_x &= \frac{d_x}{l_x} & {}_nq_x &= \frac{{}_nd_x}{l_x} \\ &= \frac{l_x - l_{x+1}}{l_x} & &= \frac{l_x - l_{x+n}}{l_x} \\ &= 1 - \frac{l_{x+1}}{l_x} & &= 1 - \frac{l_{x+n}}{l_x} \\ &= 1 - p_x & &= 1 - {}_np_x \end{aligned}$$

A concept fundamental to life table analysis is the number of days lived

in an age interval. If we assume that individuals that die in an interval do so at the midpoint of the interval, then the number of days lived by the average individual in the cohort from x to x + 1, denoted L_x, is given by the formula

$$\begin{aligned} L_x &= (l_x - d_x) + \tfrac{1}{2}d_x \\ &= (l_x - (d_x/2)) \\ &= \frac{(l_x + l_{x+1})}{2} \end{aligned} \tag{2-3a}$$

and for the age interval n-days apart is given as

$$\begin{aligned} {}_nL_x &= n(l_x - \tfrac{1}{2}{}_nd_x) \\ &= .5n(l_x + l_{x+n}) \end{aligned} \tag{2-3b}$$

If L_x gives the number of days lived by the average individual within a cohort in the interval x to x + 1, then the total number of days to be lived by the average individual within a cohort from age x to the last day of possible life is

$$T_x = \sum_{y=x}^{\omega} L_y \tag{2-4}$$

where T_x denotes this total. Since there are l_x individuals that survive to age x in the cohort and a total of T_x insect-days remaining to these l_x individuals, the number of per capita days of life remaining to the average individual living at age x is

$$e_x = T_x/l_x \tag{2-5}$$

The term e_x denotes the expectation of life at age x. The average age of death of an individual age x is simply its current age plus the expectation of life at that age ($= x + e_x$).

Complete Cohort Life Table

A complete cohort life table is constructed by recording the number of deaths in an initial cohort of identically aged individuals at each point in time until all have died. The information is placed in columns according to the number alive at the beginning of each age interval, denoted K_x, and the number of deaths in the interval, denoted D_x. This information is then arranged by age class in eight columns representing the life table functions. An example of the data needed for life table construction and the complete cohort life table are given in Tables 2-1 and 2-2 for the human louse, *Pediculus humanus* (data from Evans and Smith, 1952).

The complete life table (Table 2-2) consists of eight columns:

Column 1

Age class. This is the age index and designates the exact age at which the interval begins *relative to the initial cohort*. Age class x includes the interval

Table 2-1. Life Table Construction for the Human Louse, *Pediculus humanus*, Using Data from Evans and Smith (1952) and a Hypothetical Cohort of 1000 Newborns

Stage	Age Class (Days), x	Age Interval (Days), x to x + 1	Number Alive at Beginning of Interval, K_x	Number of Deaths in Age Interval, D_x
Egg	0	0–1	1000	14
Egg	1	1–2	986	13
Egg	2	2–3	973	14
Egg	3	3–4	959	14
Egg	4	4–5	945	13
Egg	5	5–6	932	14
Egg	6	6–7	918	14
Egg	7	7–8	904	13
Egg	8	8–9	891	14
1st instar	9	9–10	877	7
1st instar	10	10–11	870	6
1st instar	11	11–12	864	7
1st instar	12	12–13	857	6
1st instar	13	13–14	851	7
2nd instar	14	14–15	844	6
2nd instar	15	15–16	838	6
2nd instar	16	16–17	832	5
2nd instar	17	17–18	827	4
3rd instar	18	18–19	823	8
3rd instar	19	19–20	815	8
3rd instar	20	20–21	807	7
3rd instar	21	21–22	800	7
Adult	22	22–23	793	8
Adult	23	23–24	785	2
Adult	24	24–25	783	20
Adult	25	25–26	763	12
Adult	26	26–27	751	17
Adult	27	27–28	734	24
Adult	28	28–29	710	14
Adult	29	29–30	696	26
Adult	30	30–31	670	32
Adult	31	31–32	638	31
Adult	32	32–33	607	28
Adult	33	33–34	579	44
Adult	34	34–35	535	43
Adult	35	35–36	492	32
Adult	36	36–37	460	44
Adult	37	37–38	416	43
Adult	38	38–39	373	30
Adult	39	39–40	343	30
Adult	40	40–41	313	33
Adult	41	41–42	280	6
Adult	42	42–43	274	28
Adult	43	43–44	246	20
Adult	44	44–45	226	28
Adult	45	45–46	198	28
Adult	46	46–47	170	23
Adult	47	47–48	147	18

Table 2-1. *(Contd.)*

Stage	Age Class (Days), x	Age Interval (Days), x to x + 1	Number Alive at Beginning of Interval, K_x	Number of Deaths in Age Interval, D_x
Adult	48	48–49	129	20
Adult	49	49–50	109	26
Adult	50	50–51	83	18
Adult	51	51–52	65	21
Adult	52	52–53	44	8
Adult	53	53–54	36	14
Adult	54	54–55	22	12
Adult	55	55–56	10	1
Adult	56	56–57	9	1
Adult	57	57–58	8	1
Adult	58	58–59	7	1
Adult	59	59–60	6	1
Adult	60	60–61	5	1
Adult	61	61–62	4	1
Adult	62	62–63	3	1
Adult	63	63–64	2	1
Adult	64	64–65	1	1
Adult	65	65–66	0	–

Table 2-2. Complete Life Table for *Pediculus humanus*

Age Class, x (1)	Fraction Living at Age x, l_x (2)	Fraction Surviving from x to x + 1, p_x (3)	Fraction Dying from x to x + 1, q_x (4)	Fraction Dying in Interval x to x + 1, d_x (5)	Days Lived in Interval, L_x (6)	Number Days Lived Beyond Age x, T_x (7)	Expectation of Life, e_x (8)
0	1.000	.986	.014	.014	.993	32.438	32.438
1	.986	.987	.013	.013	.980	31.445	31.891
2	.973	.986	.014	.014	.966	30.465	31.311
3	.959	.985	.015	.014	.952	29.499	30.761
4	.945	.986	.014	.013	.939	28.548	30.209
5	.932	.985	.015	.014	.925	27.609	29.623
6	.918	.985	.015	.014	.911	26.684	29.068
7	.904	.986	.014	.013	.898	25.773	28.510
8	.891	.984	.016	.014	.884	24.876	27.919
9	.877	.992	.008	.007	.874	23.992	27.356
10	.870	.993	.007	.006	.867	23.118	26.572
11	.864	.992	.008	.007	.861	22.251	25.753
12	.857	.993	.007	.006	.854	21.391	24.960
13	.851	.992	.008	.007	.847	20.537	24.132
14	.844	.993	.007	.006	.841	19.689	24.328
15	.838	.993	.007	.006	.835	18.848	22.492
16	.832	.994	.006	.005	.830	18.013	21.650
17	.827	.995	.005	.004	.825	17.184	20.778
18	.823	.990	.010	.008	.819	16.359	19.877
19	.815	.990	.010	.008	.811	15.540	19.067
20	.807	.991	.009	.007	.803	14.729	18.251

Table 2-2. (*Contd.*)

Age Class, x (1)	Fraction Living at Age x, l_x (2)	Fraction Surviving from x to x + 1, p_x (3)	Fraction Dying from x to x + 1, q_x (4)	Fraction Dying in Interval x to x + 1, d_x (5)	Days Lived in Interval, L_x (6)	Number Days Lived Beyond Age x, T_x (7)	Expectation of Life, e_x (8)
21	.800	.991	.009	.007	.796	13.925	17.406
22	.793	.990	.010	.008	.789	13.128	16.555
23	.785	.997	.003	.002	.784	12.340	15.719
24	.783	.974	.026	.020	.773	11.555	14.758
25	.763	.984	.016	.012	.757	10.783	14.132
26	.751	.977	.023	.017	.742	10.026	13.350
27	.734	.967	.033	.024	.722	9.283	12.647
28	.710	.980	.020	.014	.703	8.561	12.058
29	.696	.963	.037	.026	.683	7.858	11.290
30	.670	.952	.048	.032	.654	7.175	10.709
31	.638	.951	.049	.031	.623	6.521	10.221
32	.607	.954	.046	.028	.593	5.899	9.717
33	.579	.924	.076	.044	.557	5.306	9.163
34	.535	.920	.080	.043	.514	4.749	8.876
35	.492	.935	.065	.032	.476	4.235	8.608
36	.460	.904	.096	.044	.438	3.759	8.172
37	.416	.897	.103	.043	.395	3.321	7.983
38	.373	.920	.080	.030	.358	2.927	7.846
39	.343	.913	.087	.030	.328	2.568	7.488
40	.313	.895	.105	.033	.297	2.241	7.158
41	.280	.979	.021	.006	.277	1.944	6.943
42	.274	.898	.102	.028	.260	1.667	6.084
43	.246	.919	.081	.020	.236	1.407	5.720
44	.226	.876	.124	.028	.212	1.171	5.181
45	.198	.859	.141	.028	.184	0.959	4.843
46	.170	.865	.135	.023	.159	0.775	4.559
47	.147	.878	.122	.018	.138	0.616	4.194
48	.129	.845	.155	.020	.119	0.479	3.709
49	.109	.761	.239	.026	.096	0.360	3.298
50	.083	.783	.217	.018	.074	0.264	3.175
51	.065	.677	.323	.021	.055	0.189	2.915
52	.044	.818	.182	.008	.040	0.135	3.068
53	.036	.611	.389	.014	.029	0.095	2.639
54	.022	.455	.545	.012	.016	0.066	3.000
55	.010	.900	.100	.001	.010	0.050	5.000
56	.009	.889	.111	.001	.008	0.041	4.500
57	.008	.875	.125	.001	.008	0.032	4.000
58	.007	.857	.143	.001	.007	0.024	3.500
59	.006	.833	.167	.001	.006	0.018	3.000
60	.005	.800	.200	.001	.005	0.012	2.500
61	.004	.750	.250	.001	.004	0.008	2.000
62	.003	.667	.333	.001	.003	0.005	1.500
63	.002	.500	.500	.001	.002	0.002	1.000
64	.001	.000	1.000	.001	.001	0.001	0.500
65	.000	—	—	.000			
				1.000			

from exact age x to exact age $x + 1$. For example, age class 0 specifies the interval from age 0 to age 1.

Column 2

Fraction of the original cohort alive at age x, l_x. The first fraction in this column, l_0, is the radix, and each successive number represents the fraction of survivors at the exact age x from the cohort of size l_0 (normalized to 1.0). For example, 807 individuals in the cohort survived to age 20. Thus .807 of the original cohort survived to this age since the cohort stated with 1,000 newborn.

Column 3

Proportion of those alive at age x that survive through the interval x to $x + 1$, p_x. For example,

$$\begin{aligned} p_0 &= l_1/l_0 & p_1 &= l_2/l_1 \\ &= .986/1.000 & &= .973/.986 \\ &= .986 & &= .987 \\ p_{50} &= l_{51}/l_{50} & p_{51} &= l_{52}/l_{51} \\ &= .065/.083 & &= .044/.065 \\ &= .783 & &= .677 \end{aligned}$$

Column 4

Proportion of those alive at age x that die in the interval x to $x + 1$, q_x, For example,

$$\begin{aligned} q_0 &= 1.000 - p_1 & q_1 &= 1.000 - p_2 \\ &= 1.000 - .986 & &= 1.000 - .987 \\ &= .014 & &= .013 \\ q_{50} &= 1.000 - p_{51} & q_{51} &= 1.000 - p_{52} \\ &= 1.000 - .783 & &= 1.000 - .677 \\ &= .217 & &= .323 \end{aligned}$$

Column 5

Fraction of the original cohort, l_0, that die in the age interval x to $x + 1$, d_x. Therefore, the d_x column represents the frequency distribution of deaths in the cohort and its sum is unity.

$$\begin{aligned} d_0 &= l_0 - l_1 & d_1 &= l_1 - l_2 \\ &= 1.000 - .986 & &= .986 - .973 \\ &= .014 & &= .013 \\ d_{50} &= l_{50} - l_{51} & d_{51} &= l_{51} - l_{52} \\ &= .083 - .065 & &= .065 - .044 \\ &= .018 & &= .021 \end{aligned}$$

Column 6

Per capita fraction of interval lived in the age interval x to x + 1, L_x. For example,

$$\begin{aligned} L_0 &= l_0 - (1/2)d_0 \\ &= 1.000 - (1/2)(.014) \\ &= .993 \end{aligned} \qquad \begin{aligned} L_1 &= l_1 - (1/2)d_1 \\ &= .986 - (1/2)(.013) \\ &= .980 \end{aligned}$$

$$\begin{aligned} L_{50} &= l_{50} - (1/2)d_{50} \\ &= .083 - (1/2)(.018) \\ &= .074 \end{aligned} \qquad \begin{aligned} L_{51} &= l_{51} - (1/2)d_{51} \\ &= .065 - (1/2)(.021) \\ &= .055 \end{aligned}$$

Column 7

Total number of days lived beyond age x, T_x. This total is essential to the computation of life expectancy since it gives the number of insect-days lived by the cohort after age x uncorrected for the total beginning at age x. For example,

$$\begin{aligned} T_0 &= \sum_{x=0}^{\omega} L_x \\ &= L_0 + L_1 + \cdots + L_{63} + L_{64} \\ &= .993 + .980 + \cdots + .002 + .001 \\ &= 32.438 \end{aligned} \qquad \begin{aligned} T_1 &= \sum_{x=1}^{\omega} L_x \\ &= L_1 + L_2 + \cdots + L_{63} + L_{64} \\ &= .980 + .966 + \cdots + .022 + .001 \\ &= 31.445 \end{aligned}$$

$$\begin{aligned} T_{50} &= \sum_{x=50}^{\omega} L_x \\ &= L_{50} + L_{51} + \cdots + L_{63} + L_{64} \\ &= .074 + .055 + \cdots + .002 + .001 \\ &= .264 \end{aligned} \qquad \begin{aligned} T_{51} &= \sum_{x=51}^{\omega} L_x \\ &= L_{51} + L_{52} + \cdots + L_{63} + L_{64} \\ &= .055 + .040 + \cdots + .022 + .001 \\ &= .189 \end{aligned}$$

Column 8

Expectation of life at age x, e_x. This gives the average remaining lifetime for an individual who survives to the beginning of the indicated age interval. For example,

$$\begin{aligned} e_0 &= T_0/l_0 \\ &= 32.438/1.000 \\ &= 32.438 \end{aligned} \qquad \begin{aligned} e_1 &= T_1/l_1 \\ &= 31.445/.986 \\ &= 31.891 \end{aligned}$$

$$\begin{aligned} e_{50} &= T_{50}/l_{50} \\ &= .264/.083 \\ &= 3.175 \end{aligned} \qquad \begin{aligned} e_{51} &= T_{51}/l_{51} \\ &= .189/.065 \\ &= 2.915 \end{aligned}$$

A number of relationships emerge from this life table analysis that merit comment. *First*, the expectation of life for a newborn louse is over one month. A louse that survives to one month is expected to live an average of 10 days more. A two-month-old (60 days) louse lives an average of only 2 more days.

Second, around a third of all deaths occur in the first 30 days, but another third of all deaths occur in the following 10 days (i.e., 30 to 40 days). The last third of all deaths occur over the last 3 weeks of possible life. *Third*, the probability of surviving from age 0 to 35 days is around .50. However, of all those alive at age 36 the probability of surviving for the next 8 days is also .50. *Fourth*, the probability of dying from age x to $x + 1$ when lice are under 10 days old is up to 50-fold less than when they are over 50 days old. For example, the probability of an individual's dying from age 54 to 55 days is 54-fold greater than the probability of the same individual's dying from age 19 to 20 days.

THE ABRIDGED LIFE TABLE

The complete life table has two disadvantages that can be removed by constructing an abridged table. *First*, it is sometimes not possible to monitor daily mortality of individuals in a cohort over their entire life course. For example, it is extremely difficult to determine the precise time of death for eggs and pupae for most insects. Thus the practical solution for determining cohort mortality for these stages is to note the number entering and the number surviving through the stage, which will yield period (stage) survival. Because the duration of each stage is typically greater than one day and two stages seldom have the same duration, the methodology for constructing the complete life table is not appropriate. *Second*, a table of 50 to 100 age groups with 5 to 7 life table functions (columns) is difficult to fully comprehend and contains details that are often not of concern. By grouping deaths into larger intervals it is possible to summarize the information concisely while still retaining the basic life table format and concepts.

The abridged life table generally contains the same functions as the complete table. In addition, the duration of each stage is given as n to specify the age interval over which mortality is assessed. An example of an abridged life table is given in Table 2-3 for worker honey bees, *Apis mellifera*.

Column 1

Stage and duration (n). This gives the stage over which mortality is measured and the duration of the stage. Preadult stages can be further subdivided into instars, and adults can be divided into various physiological divisions such as preovipositional and ovipositional or into arbitrary age groupings as given for the honey bee.

Column 2

Age index, x. This column gives the age associated with each stage. For example, the egg stage lasts 3 days, beginning at age $x = 0$ and extending to age $x + n = 0 + 3 = 3$. This is the starting age index for the unsealed brood.

Table 2-3. Abridged Life Table for Worker Honey Bees (Data from Sakagami and Fukuda, 1986)

STAGE (n = duration in days) (1)	Age Interval, x (2)	Parameter						
		l_x (3)	${}_nP_x$ (4)	${}_nq_x$ (5)	${}_nd_x$ (6)	${}_nL_x$ (7)	T_x (8)	e_x (9)
Egg (n = 3)	0–3	1.000	.958	.042	.042	2.937	40.482	40.482
Unsealed brood (n = 5)	3–8	.958	.857	.143	.137	4.448	37.545	39.191
Sealed brood (n = 12)	8–20	.821	.988	.012	.010	9.792	33.097	40.313
Adult (n = 10)	20–30	.811	.945	.055	.031	7.955	23.305	28.736
Adult (n = 10)	30–40	.780	.947	.053	.041	7.595	15.350	19.679
Adult (n = 10)	40–50	.739	.499	.501	.370	5.540	7.755	10.494
Adult (n = 10)	50–60	.369	.100	.900	.332	2.030	2.215	6.003
Adult (n = 10)	>60	.037	.000	1.00	.037	.185	.185	5.000
					1.000	40.482		

The unsealed brood lasts 5 days (n = 5) beginning at age x = 3 and extending to age x + n = 3 + 5 = 8. The adult stage is divided into 10-day increments beginning at age 20 days when the average preadult matures.

Column 3

Fraction of the original cohort alive at the beginning of the designated age interval, x to x + n, l_x. This measure corresponds exactly to the l_x column in the complete life table. For example, the fraction that survives to the unsealed brood is .958, and to the adult stage it is .811.

Column 4

Proportion of those alive at age x that survive through the interval x to x + n, ${}_nP_x$. For example,

$$\begin{aligned} {}_3P_0 &= l_3/l_0 (= \text{egg survival}) \\ &= .958/1.000 \\ &= .958 \\ {}_{12}P_8 &= l_{20}/l_8 (= \text{sealed brood survival}) \\ &= .811/.821 \\ &= .988 \end{aligned}$$

Column 5

Proportion of those alive at age x that die in the interval x to x + n, ${}_nq_x$. For example,

$$\begin{aligned} {}_3q_0 &= 1 - {}_3P_0 (= \text{egg mortality}) \\ &= 1 - .958 \\ &= .042 \end{aligned}$$

$$
\begin{aligned}
{}_{12}q_8 &= 1 - {}_{12}p_8 (= \text{sealed brood mortality}) \\
&= 1 - .988 \\
&= .012
\end{aligned}
$$

Column 6

Fraction of the original cohort, l_0, that die in the age interval x to $x + n$, ${}_nd_x$. For example,

$$
\begin{aligned}
{}_3d_0 &= l_0 - l_3 \text{ (fraction of all deaths in egg)} \\
&= 1.000 - .958 \\
&= .042 \\
{}_{12}d_8 &= l_8 - l_{20} \text{(fraction of all deaths in sealed brood)} \\
&= .821 - .811 \\
&= .010
\end{aligned}
$$

Column 7

Per capita fraction of interval lived in the age interval x to $x + n$, ${}_nL_x$. For example

$$
\begin{aligned}
{}_3L_0 &= 3[l_0 - (1/2){}_3d_0] \\
&= 3[1.000 - (1/2).042] \\
&= (3)(.979) \\
&= 2.937 \\
{}_{12}L_8 &= 12[l_8 - (1/2){}_{12}d_8] \\
&= 12[.821 - (1/2).010] \\
&= (12)(.816) \\
&= 9.792
\end{aligned}
$$

Column 8

Total number of days lived beyond age x, T_x. For example,

$$
\begin{aligned}
T_0 &= {}_3L_0 + {}_5L_3 + {}_{12}L_8 + {}_{10}L_{20} + \cdots + {}_{10}L_{60} \\
&= 2.937 + 4.448 + 9.792 + 7.955 + \cdots + .185 \\
&= 40.482 \\
T_8 &= {}_{12}L_8 + {}_{10}L_{20} + \cdots + {}_{10}L_{60} \\
&= 9.792 + 7.955 + \cdots + .185 \\
&= 33.097
\end{aligned}
$$

Column 9

Expected number of additional days the average individual age x will live, e_x. For example,

$$e_0 = T_0/l_0$$

$$= 40.482/1.000$$
$$= 40.482$$
$$e_8 = T_8/l_8$$
$$= 33.097/.821$$
$$= 40.313$$

Several aspects of the mortality and survival of worker bees are noteworthy (i) over 80% of all newborn survive to adulthood and over one-third survive to age 50 days (from l_x schedule); (ii) the probability of dying from age 20 to 30 (first 10 days of adulthood) is around 10-fold less than in the interval from 40 to 50 days old (i.e., when adults are 20 to 30 days old); and (iii) the expectation of life of a newly enclosed adult worker beee is nearly one month.

THE MULTIPLE DECREMENT LIFE TABLE

The multiple decrement life table is used widely in human actuarial studies to address questions concerning the frequency of occurrence for causes of death and how life expectancy might change if certain causes were eliminated. The conventional single decrement life table shows the probability of survivorship of an individual subject to the one undifferentiated hazard of death. In multiple decrement tables the individual is subject to a number of mutually exclusive hazards, such as disease, predators, or parasites, and is followed in the table only to its exit, as in the ordinary life table. But in the multiple decrement table there is now more than one way of exiting (Anon., 1962; Preston et al., 1972; Carey, 1989).

Two probabilities and hence two kinds of tables are commonly recognized in the study of cause of death. One is the probability of dying of a certain cause in the presence of other causes; the other is the probability of dying of a certain cause in the absence of other causes (Preston et al., 1972). The first gives rise to the multiple decrement table proper. The second gives rise to an associated single decrement table and is applied to find the probability of dying if one or more factors were to disappear as a cause of death.

The assumption of the multiple decrement life table is that multiple causes of death act independently. It is concerned with the probability that an individual will die of a certain cause in the presence of other causes. The concept itself stems from reliability theory in operations research. Keyfitz (1982, 1985) uses an example of a watch that can operate only as long as all its parts are functioning: each part has its own life table. The probability that an individual (i.e., the watch) will survive to a given age is the product of the independent probabilities that each of its components will "survive" to that age. The same notion of probabilities applied to internal components causing the death of a system can also be applied to external components such as disease and accidents in humans or predation and parasitism in insects. The concept here is that the probability of an insect's surviving to a certain age (or stage) is the product of all independent risk probabilities.

In general, multiple decrement theory is basically concerned with three questions (Elandt-Johnson and Johnson, 1980): i) What is the age (stage) distribution of deaths from different causes acting simultaneously in a given population? ii) What is the probability that a newborn individual will die after a given age or stage from a specified cause? iii) How might the mortality pattern or expectation of life change if certain causes were eliminated? The first two questions are concerned with evaluating patterns and rates of mortality, while the last question is concerned with what is termed "competing risk analysis." In both cases the analyses are based on three assumptions: i) each death is due to a single cause; ii) each individual in a population has exactly the same probability of dying from any of the causes operating in the population (see Moriyama, 1956; Vaupel and Yashin, 1984); and iii) the probability of dying from any given cause is independent of the probability of dying from any other source.

Data and Data Organization

A hypothetical data set for analyzing mortality in a synthetic cohort was derived using average stage-by-cause mortality from 25 life tables given in Cameron and Morrison (1977) for the apple maggot, *Rhagoletis pomonella.* The original data were divided into death due to 11 factors—one for egg, four for larval, and six for pupal and adult emergence. These sources of mortality are here lumped into four categories: predation, parasitism, disease, and other causes. The group within which a cause of death was placed was arbitrary in several cases.

The hypothetical mortality data for the four categories (causes) of death in preadult *R. pomonella* are given in Table 2-4, where K_x is the number in the cohort aged x, D_x is the total number of deaths in stage x, and D_{ix} is the number of deaths due to cause i in stage x. Note that $D_x = D_{1x} + D_{2x} + D_{3x} + D_{4x}$ and also that the K_x column does not represent the non-normalized survival column. That is, the K_x column gives the number of insects at the

Table 2-4. Deaths from Four Causes in *Rhagoletis pomonella* Populations Using a Hypothetical Data Set[1].

Stage (index), x	Number Beginning Stage, K_x	Total Deaths, D_x	Number Deaths from—			
			Predators, D_{1x}	Parasites, D_{2x}	Disease, D_{3x}	Other causes, D_{4x}
Egg (1)	977	14	0	0	0	14
Early larvae (2)	963	810	0	224	0	586
Late larvae (3)	153	112	100	12	0	0
Early pupae (4)	435	98	88	0	10	0
Late pupae (5)	351	206	133	0	19	54
Adult (6)	—	—	—	—	—	—

[1]The data presented in Cameron and Morrison (1977) were used as guidelines for the relative numbers of deaths by cause.

beginning of the stage that were exposed to risk through the stage. This is not the same as the number that would be exposed to risk in a true cohort where the numbers would decrease from stage to stage.

General Framework and Notation

The notation for all functions in the multiple decrement table corresponds to the single decrement cases except i) the prefix *a* is added to denote "in presence of all causes"; and ii) the symbol *x* is used to denote the stage index rather than the age interval. Therefore, let

al_{ix} = fraction of original cohort living at age x that ultimately die from cause i

al_x = fraction of survivors at age x out of original cohort of al_1 (start index at x = 1)

ad_{ix} = fraction of deaths in stage x from cause i among al_x living at stage x

ad_x = fraction of deaths in stage x from all causes $(= ad_{1x} + ad_{2x} + \cdots + ad_{kx})$

aq_{ix} = fraction of deaths from cause i in stage x in the presence of all other causes, given that the individual is alive at beginning of stage x

aq_x = fraction of deaths from all causes in stage x, given that individual is alive at stage x $(= aq_{1x} + aq_{2x} + \cdots + aq_{kx})$

The fraction dying in the interval designated aq_x is

$$aq_x = D_x/K_x \tag{2-6}$$

The fraction of the cohort age x dying in stage x due to cause i is given by

$$aq_{ix} = D_{ix}/K_x \tag{2-7}$$

For example, no deaths occurred in the egg stage due to predators, parasites, or disease. Thus

$$aq_{1,1} = aq_{2,1} = aq_{3,1} = 0.0$$

However, 14 of 977 eggs died of "other causes", therefore

$$\begin{aligned} aq_{4,1} &= D_{4,1}/K_1 \\ &= 14/977 \\ &= .01433 \end{aligned}$$

and

$$aq_1 = aq_{4,1} = .01433$$

since "other causes" was the only source of death. The complete table of death probabilities based on the mortality data of Table 2-4 is given in Table 2-5. The computation of these rates is necessary for completing the full

Table 2-5. Cause-Specific Probability of Death from Specified Causes in the Presence of All Causes for *Rhagoletis pomonella* using Hypothetical Data Presented in Table 2-4

Stage (Index), x	Total, aq_x	Cause of Death			
		Predators, aq_{1x}	Parasites, aq_{2x}	Disease, aq_{3x}	Other, aq_{ux}
Egg (1)	.01433	.00000	.00000	.00000	.01433
Early larvae (2)	.84112	.00000	.23261	.000000	.60851
Late larvae (3)	.73203	.65359	.07842	.00000	.00000
Early pupae (4)	.22529	.20230	.00000	.02299	.00000
Late pupae (5)	.58690	.37892	.00000	.05413	.15385
Adult (6)	1.00000	—	—	—	—

multiple decrement analysis. Note in Table 2-5 that the stage- and cause-specific mortality rates derived from the data are now expressed as per capita probabilities. Two aspects of this table may be noted: i) the highest death rate is due to late larval predation; and ii) the highest stage-specific mortality occurs in early larvae and is due to both predation and other causes.

Table Construction

The main multiple decrement table uses the aq_{ix} value in Table 2-5 to determine schedules for the fraction of the starting cohort dying in stage x from cause i ($ad_{i,x}$), the total fraction dying in stage x from all causes (ad_x), and the fraction of newborn surviving to stage x (al_x). These are computed as follows:

Step 1. Compute survival to stage x subject to all causes. We use an index of $x = 1$ for the first stage (i.e., egg), set $al_1 = 1.0$, and compute progressively

$$al_{x+1} = al_x(1.0 - aq_x)$$

For example,

$$\begin{aligned} al_2 &= al_1(1.0 - aq_1) \\ &= 1.0(1.0 - .0143) \\ &= .9857 \\ al_3 &= .9857(1.0 - .8411) \\ &= .1566 \end{aligned}$$

Step 2. Compute the fraction of newborns dying in stage x from all causes. This is computed as

$$ad_x = al_x - al_{x+1}$$

For example,

$$\begin{aligned} ad_1 &= al_1 - al_2 \\ &= 1.0 - .9857 \\ &= .0143 \end{aligned}$$

Step 3. Compute the fraction of newborns dying in stage x from cause i. We use the formula

$$ad_{i,x} = al_x(aq_{i,x})$$

For example,

$$\begin{aligned} ad_{4,1} &= al_1(aq_{4,1}) \\ &= 1.0(.0143) \\ &= .0143 \\ ad_{1,3} &= al_3(aq_{1,3}) \\ &= .1566(.65359) \\ &= .1024 \end{aligned}$$

Values for the various relationships are given in Table 2-6. This table reveals relations that were not evident from Table 2-4. For example, nearly 83% of all deaths occurred in the early larval stage, only about 4% of all newborn survived to the pupal stage, nearly 62% of all deaths were a result of other causes, and disease accounted for less than 1% of all deaths.

Elimination of Cause—Concept

Farr (1875) apparently was the first to ask the question, what would be the effect on life expectancy if a certain disease were eliminated as a cause of death? This question is particularly germane to management questions since if it is possible to gain an understanding of the effect on life expectancy of eliminating a particular source of death, it follows that the same methods could be used to determine the impact of adding a source of death.

The only definitive method for determining the effect on expectation of life in arthropod populations of eliminating a certain cause of death is through experiment (DeBach and Huffacker, 1971; Royama, 1984; Luck et al., 1988). However, experimentation is sometimes either not possible or the only data available is natural history. Therefore it is necessary mathematically to approximate the effect of eliminating a certain cause. One such approach is described as follows. Suppose the probability of surviving factor A alone is p_A and the probability of surviving factor B alone is p_B. Then the probability of surviving both independent causes together, denoted p_{AB}, is given as

$$p_{AB} = p_A p_B \tag{2-8a}$$

or

$$p_{AB} = (1 - q_A)(1 - q_B) \tag{2-8b}$$

where q_A and q_B are complements of p_A and p_B, respectively. If D_A and D_B denote the fraction of all individuals observed that died of cause A and B, respectively, then

$$p_{AB} = 1 - (D_A + D_B) \tag{2-9a}$$

and

$$1 - (D_A + D_B) = (1 - q_A)(1 - q_B) \tag{2-9b}$$

Table 2-6. The Multiple Decrement Life Table for Life Table Deaths from Specified Causes at Given Stage of *R. pomonella*

Stage (Index), x	Probability of Death, aq_x	Fraction Living at Beginning of Interval, al_x	Fraction of All Deaths, ad_x	Fraction Deaths from —			
				Predator, ad_{1x}	Parasites, ad_{2x}	Disease, ad_{3x}	Other Causes, ad_{4x}
Egg (1)	.0143	1.0000	.0143	.0000	.0000	.0000	.0143
Early larvae (2)	.8411	.9857	.8291	.0000	.2293	.0000	.5998
Late larvae (3)	.7320	.1566	.1146	.1024	.0122	.0000	.0000
Early pupae (4)	.2253	.0420	.0095	.0085	.0000	.0010	.0000
Late pupae (5)	.5869	.0325	.0191	.0123	.0000	.0018	.0050
Adult (6)	—	.0134	—	—	—	—	—
Total[1]	—	—	.9866	.1232	.2415	.0028	.6191

[1] Apply only to the total mortality to the adult stage (i.e., ad_x) and the totals for each of the four mortality causes (i.e., ad_{ix}'s)

The objective is to obtain values for q_A and q_B since we would like to determine mortality in the absence of one or the other factor. It is necessary to specify a second equation since Equation 2-9b has two unknowns. By assuming that the ratio of numbers dying from factor A to the numbers dying from factor B equals the ratio of the probability of dying from factor A to the probability of dying from factor B, we can obtain the second equation:

$$\frac{q_A}{q_B} = \frac{D_A}{D_B} \tag{2-10}$$

Therefore Equations 2-9b and 2-10 represent two simultaneous equations in two unknows (q_A and q_B). Expressing q_A in Equation 2-10 in terms of q_B, D_A, and D_B and then substituting this expression in Equation 2-9b yields the quadratic equation

$$aq_B^2 + bq_B + c = 0 \tag{2-11}$$

where $a = D_A$; $b = -(D_A + D_B)$; $c = D_B(D_A + D_B)$.

The value of q_B is found by substituting a, b, and c into the quadratic formula

$$q_B = \frac{-b - \sqrt{b^2 - 4ac}}{2a} \tag{2-12}$$

Elandt-Johnson and Johnson (1980), Namboordiri and Suchindran (1987), and Preston et al. (1972) present alternative approaches for finding the solutions to the independent risk probabilities.

As an example, suppose that of 1000 individuals observed over their preadult lifetime, 20 remained alive (i.e., 2%), 370 died as a result of natural enemies and 610 died of other causes. Therefore set $D_A = .37$ and $D_B = .61$. Substituting these values into Equation 2-12 yields $a = .37$, $b = -.98$, and $c = .598$. Therefore,

$$q_B = \frac{[.98 - \sqrt{(.98)^2 - 4(.37)(.598)}]}{2(.37)}$$
$$= .953$$

and

$$q_A = q_B D_A / D_B$$
$$= (.953)(.37)/.61$$
$$= .578$$

A graphical interpretation of the analysis is presented in Figure 2-1. The results state that if factor A were completely eliminated as a source of mortality, factor B alone would still kill 95.3% of the original cohort. This is a substantial increase from the 61% mortality owing to this factor in the presence of factor A. On the other hand, 57.8% would die if factor A alone accounted for deaths. In short, adding factor A as a cause of mortality when B is already present would increase mortality from 95.3% to 98%, or less than 3%. However, adding factor B as a cause of mortality when factor A

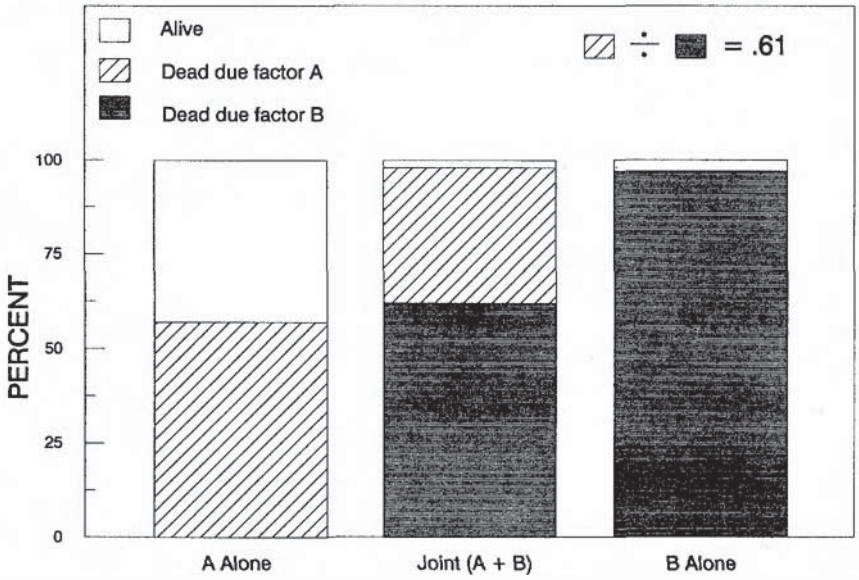

Figure 2-1. Illustration of the concept of competing risk in hypothetical cohorts subject to mortality factors A alone, B alone, and A and B jointly. Note that the ratio of those dead owing to A alone (q_A) and B alone (q_B) equals the ratio of the cause-specific mortalities when the two factors act jointly (i.e., D_A & D_B). That is, $q_A/q_B = D_A/D_B = .61$ (redrawn from Carey, 1989).

is already present would increase mortality from 57.8% to 98% or by over 40%. These differences are referred to in the ecological literature as indispensable (or irreplaceable) mortality (Huffaker and Kennet, 1965; Southwood, 1971).

Note that computationally the concept of double decrement given here embraces all the issues of multiple decrement (Preston et al., 1972). That is, no matter how many causes are considered, the probability of dying from each can be computed by considering the one in question versus "all others".

Elimination of Cause—Application

The data presented in Table 2-4 are used to compute the independent stage-by-cause probabilities of dying, q_{ix}'s. Note from this table that the egg stage has a single risk ("Other Causes"); early larvae, late larvae, and early pupae have two competing risks each, and late pupae have three competing risks each. Thus for the egg stage we have

$$q_{11} = q_{21} = q_{31} = 0$$

and

$$q_{41} = 1 - (963/977)$$
$$= .0143$$

The independent probabilities for the two competing risks in each of the next three stages can be computed using the same relationships described in the earlier example with the quadratic equation. For example, 224 of 963 individuals were parasitized in stage 2 (early larvae) and 586 died of other causes. Therefore, let D_A denote the fraction of the total that died of parasites,

$$D_A = 224/963 = .2326$$

and let D_B denote the fraction that died of other causes,

$$D_B = 586/963 = .6085$$

Substituting these values in Equation 2-12 yields values for $q_{22} = .296$ and $q_{42} = .775$. Probabilities for the three causes in stage 5 (i.e., predators, disease, & other causes) are determined by applying the quadratic to three 2-cause cases: i) predators vs. (disease + other causes); ii) disease vs. (predators + other causes); and iii) other causes vs. (predators + disease).

The results of this analysis are given in Table 2-7, where the q_{ix}'s denote the probability of dying in stage x of cause i in the absence of all other causes of death. These relations show that if a single cause of death were retained in the population, predation alone would reduce the cohort by over 87%, while other causes would reduce it by around 76%. This ranking of importance differs from the mortality data in the presence of all causes given in Table 2-5. From this perspective, predators appear to be less important in the presence of all causes since they attack later stages. Thus earlier causes of death reduced the number at risk in the stages susceptable to predation.

The q_{xi} values in Table 2-7 were used to compute the effect of various combinations of factors on total mortality. For example, the effect of predators + parasites on total mortality was computed by i) determining the probability of surviving each source in the absence of other sources over all stages—i.e., $(1 - q_{1x})$ and $(1 - q_{2x})$; ii) obtaining the product of the two survival probabilities within each stage; and iii) computing the product of these products over all stages. Since this gives total survival, 1 minus this value yields total mortality. The computations for this two-cause case are $[(1 - 0)(1 - 0)] \times [(1 - 0)(1 - .296)] \times [(1 - .708)(1 - .085)] \times$

Table 2-7. Stage- and Cause-Specific Probability of Death for *R. pomonella* in the Absence of All Other Causes (Totals computed prior to rounding)

		Cause of Death			
Stage (Index), x	Total, q_x	Predators, q_{1x}	Parasites, q_{2x}	Disease, q_{3x}	Other, q_{4x}
Egg (1)	.014	.000	.000	.000	.014
Early larvae (2)	.842	.000	.296	.000	.775
Late larvae (3)	.733	.708	.085	.000	.000
Early pupae (4)	.225	.207	.000	.023	.000
Late pupae (5)	.587	.458	.000	.065	.186
Egg to adult	.987	.874	.356	.087	.762

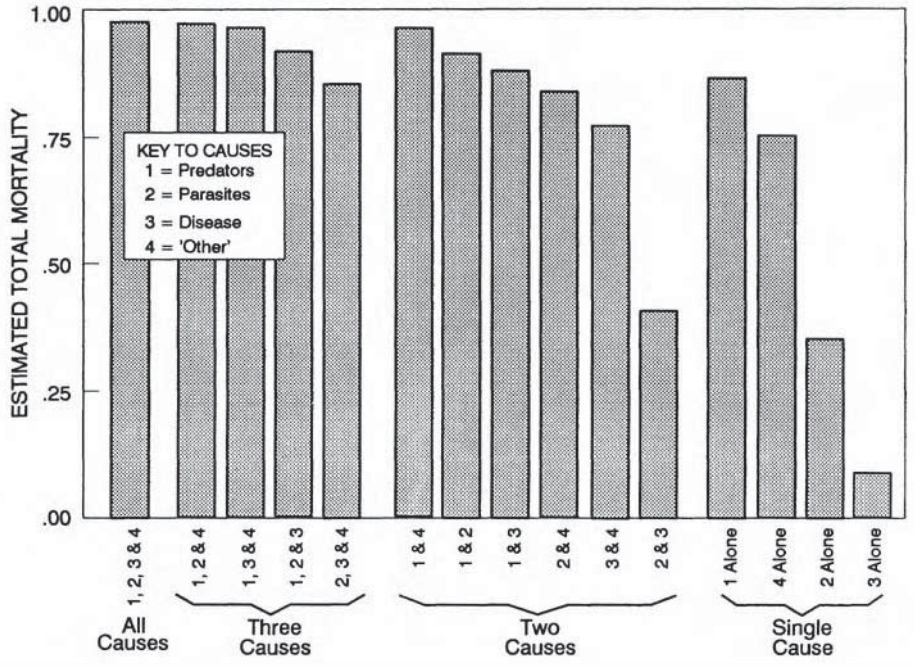

Figure 2-2. Estimated total mortality in *R. pomonella* cohorts for different cause-specific combinations.

$[(1-.207)(1-0)] \times [(1-.458)(1-0)] = .081$. This represents the fraction surviving to adulthood. Thus $(1-.081) = .919$ gives the total preadult mortality.

The results of the complete analysis are given in Figure 2-2. Several aspects of these results merit comment. *First*, the effect of simultaneously eliminating multiple cause-of-death agents from the population cannot be inferred from observing the effect of eliminating each individually. The total contribution to mortality exceeds the sum of the individual components of total mortality (Preston et al., 1972). *Second*, while predators alone would kill 87% of an original cohort, predators plus other causes would reduce the population by nearly 98%. Thus the effect of adding parasites and disease to the system in the presence of the other two factors is negligible. *Third*, any pairwise combination of parasites, disease, and other causes, as well as all three causes combined, would reduce the population less than would predation alone. Conversely, adding or subtracting predation as a source of mortality affects total mortality much greater than adding or subtracting any other single source.

General Concepts

Multiple decrement theory embraces most of the major concepts and techniques currently used in insect mortality analysis, including the conventional

life table (Deevey, 1947), Abbott's correction (Abbott, 1925), key factor analysis (Varley, 1947; Morris, 1965; Harcourt, 1969), tests for joint chemical toxicity (e.g., Hewlett and Plackett, 1959), and probit analysis (Finney, 1964). The interconnections of these tools and multiple decrement theory are described as follows:

1. The independent variable for each is time, age, stage, or dose. And for chemical tests such as probit analysis, dose and age are interchangeable in that age can be viewed as a dose of time. Thus probit analysis and life table analysis are conceptually and statistically identical (see Carey, 1986). Abbott's correction is simply a double decrement, single-time-step life table and tests of joint toxicity are essentially multiple decrement, one-time-step life tables. Key factor analysis orders events by stage as well as causes of death within a stage and is therefore a type of sequential risk life table.
2. All of the techniques either explicitly or implicitly rely on the assumption of competing risk. That is, the removal of one of several mortality factors within a stage or prior to the stage will change the number of individuals exposed to the risk of the cause in question. Thompson (1955) labeled these contemporaneous mortality factors, and Huffaker and Kennett (1966) referred to the non-additive changes in mortality on removal of one of several competing risks as compensatory mortality. In the conventional single decrement life table, death at early stages is "competing" against death at later stages. That is, a small fraction of the total deaths occur at older ages simply because most individuals die before attaining old age. This is a form of sequential competing risk.
3. Most of the techniques are based on the assumption of independence. In conventional life table analysis it is assumed that the probability of surviving from age x to age $x + 1$ is independent of the probability of surviving from age $x - 1$ to age x and also independent of density. This assumption is explicit in Abbott's correction or in the tests for joint toxicity where one chemical does not change the biological effect in the presence of another chemical. Likewise, in multiple decrement life tables it is assumed, for example, that if an insect is infected with a pathogen it is no more susceptible to predation than if it were not infected and that the associated probabilities of dying of either are density independent. Although it is commonly understood that few mortality factors are totally independent of the presence of other factors or of density, efforts at measuring and modeling these aspects have been less than satisfactory.

Despite the fact that demographers concerned with humans originated the life table that was introduced to the ecological literature by Deevey (1947) and is now viewed as convention, ecologists have subsequently resisted drawing from the human demographic and actuarial literature for analytical techniques concerned with survival. The reason most frequently given for this provincialism concerns differences in the quality of the data. While the data on causes of death and death rates in plant and animal populations

may be less accurate than human vital statistics, concepts for data evaluation are identical in both cases. Even the concepts involved in cause of death in humans (e.g., Moriyama, 1956; Anon, 1962; Kitagawa, 1977) or differences in susceptibility to death (e.g., Vaupel and Yashin, 1985) have direct bearing on coding, classifying, and interpreting mortality patterns in insect populations. Distinguishing between the underlying cause of death and contributory causes of death is often as difficult in humans as it is in animals. In short, multiple decrement theory is as relevant to insects and populations of other non-human species as it is to humans.

SELECTED PROPERTIES OF MODEL LIFE TABLES

The life table is often thought of more as an organizational framework than as a model, but it is both. In this section I present three examples of the use of the life table in the context of a model: i) a statistical model; ii) sensitivity analysis, which relates the effect of a small change in mortality at a particular age to expectation of life; and iii) entropy, which characterizes the broad pattern of mortality over the entire life course.

Life Table Statistics

The pioneers of life table techniques were actuaries who had little need for application of probability theory or statistical methods. Actuaries typically use the weight of large numbers on which to base their arguments. On the other hand, biologists often use life tables as a bioassay tool where the number of individuals is less than 50. For these cases a statistical perspective for analysis of mortality is needed.

The life table is similar to statistical reliability theory in that life is a random experiment; its outcomes, survival and death, are subject to chance (Chiang, 1984). The period mortality correspond to failure rate. A statistical perspective on life table analysis is important for several reasons. *First*, demographic techniques given earlier provide specific methodologies for collecting, compiling, organizing, and analyzing demographic data in more of a deterministic context (e.g., l_x = fraction of a cohort surviving to age x). However, this fraction also represents a probability. *Second*, hypothesis testing is fundamental to science. A statistical perspective for life table analysis provides an epistemological link to other experimental and theoretical sciences. *Third*, many arithmetic and statistical techniques used in ecology and bioassay are related to those in demographic analysis. Therefore, the formal statistical bases of demography must be established before these ties can be fully understood. Two statistical perspectives on the life table will be introduced in this section—i) probability and ii) mean and variance. More detailed aspects of life table statistics can be obtained in Chiang (1984).

Probability

Probability is defined as the number of favorable outcomes in a series of experiments divided by the total number of possible outcomes. Consider an

Table 2-8. Summary of Two-Spotted Spider Mite Sex-Specific Survival and Mortality by Sex to Age 21 Days (Data from Hamilton, 1984)

Sex	Alive (A)	Dead (A′)	Total
Female (F)	13 n(FA)	12 n(FA′)	25 n(F)
Male (F′)	42 n(F′A)	11 n(F′A′)	53 n(F′)
Total	55 n(A)	23 n(A′)	78 n

adult cohort of the two-spotted spider mite, *Tetranychus urticae*, consisting of 53 males and 25 females held at 27°C. After 21 days, it is observed that 12 of the females and 11 of the males have died (data from A. Hamilton, M. S. Thesis, UCD, 1984). These data are summarized in the Table 2-8, where F = female, F′ = not female (= male), A = alive, and A′ = not alive (= dead) and n = number observed in the specified category.

The probability of a mite's dying in this experiment, denoted Pr(A′), is equal to the number of dead mites at the end of 21 days divided by the total number subject to death over the period:

$$\begin{aligned} \Pr(A') &= n(A')/n \\ &= 23/78 \\ &= .29 \end{aligned}$$

This is called *a posteriori probability* or frequency as distinct from classical, or *a priori probability*. The later type of probability is associated with coin tosses or dice rolling in basic statistical theory. For example, given a well-balanced coin, one would expect that the coin is just as likely to fall heads as tails; hence, the probability of the event of a head is given the value of $\frac{1}{2}$. There is no need to flip a coin several hundred times to determine this probability. Examples of classical probability used in biology include Hardy-Weinberg or Mendelian proportions in genetics and the normal distribution. Typically a test is conducted to tell whether an observed distribution departs from the classical, or "expected", distribution.

Mortality data is a form of a frequency or *a posteriori probability* since it is necessary to first observe death rates before we can make statements regarding how other groups of mites might react (survive) under similar conditions. The probability of a mite's being alive is

$$\begin{aligned} \Pr(A) &= n(A)/n \\ &= 55/78 \\ &= .71 \end{aligned} \qquad (2\text{-}13a)$$

or of a mite's being a female is

$$\begin{aligned} \Pr(F) &= n(F)/n \\ &= 25/78 \\ &= .32 \end{aligned} \tag{2-13b}$$

The complements of two of these probabilities can be given as

$$\begin{aligned} \Pr(F) &= 1 - \Pr(F) \\ &= 1 - (25/78) \\ &= .68 \end{aligned} \tag{2-13c}$$

$$\begin{aligned} \Pr(A') &= 1 - \Pr(A) \\ &= 1 - (55/78) \\ &= .29 \end{aligned} \tag{2-13d}$$

The probability of not being a female (i.e., being a male) is 1 minus the probability of being a female, and the probability of not being alive (i.e., being dead) is 1 minus the probability of being alive.

Mean and variance

There are three different types of arithmetic means: i) expectation of a sample proportion; ii) expectation of a sample sum; and iii) expectation of a random variable. The distinction among these three types of means may best be explained by considering the following. Suppose the length of life of each individual adult fly in a large group was determined by an experimenter who rolled a fair die as each one eclosed. The number of days the individual was "allowed" to live would correspond to the number that turned up. Thus each fly would have an equal probability of living 1, 2, 3, 4, 5, or 6 days. The *expectation of a sample proportion* will be the proportion of flies expected to live for, say, 3 days. This is expressed as

$$E(p) = p \tag{2-14}$$

and equals $\frac{1}{6}$ in this case. This probability is identical with all of the others since each number is equally likely to be rolled.

The *expectation of a sample sum* is equal to the number of times a particular number will appear out of n trials (flies). This is expressed as

$$E(x_1 + x_2 + \cdots + x_n) = np \tag{2-15}$$

and equals 17 flies out of 100 trials for the current case (i.e., one-sixth of 100). This represents the expected number of times the number 3 appeared out of the 100 rolls of the die. This is the number of flies that would be allowed to live 3 days.

The expectation of a random variable equals the sum of the product of the probabilities (frequencies) and the values and is expressed as

$$E(x) = \sum_{k} k \Pr(x = k) \tag{2-16}$$

where k is the number of possible outcomes. The value of k weights proba-

bility (i.e., proportion) by the number of days. In the current case for the die throws determining longevity gives an average life expectancy of

1 day $(k = 1) \times$ frequency of occurrence $(\Pr[x = 1]) = 1 \times 1/6 = .167$
2 days $(k = 2) \times$ frequency of occurrence $(\Pr[x = 2]) = 2 \times 1/6 = .333$
3 days $(k = 3) \times$ frequency of occurrence $(\Pr[x = 3]) = 3 \times 1/6 = .500$
4 days $(k = 4) \times$ frequency of occurrence $(\Pr[x = 4]) = 4 \times 1/6 = .667$
5 days $(k = 5) \times$ frequency of occurrence $(\Pr[x = 5]) = 5 \times 1/6 = .833$
6 days $(k = 6) \times$ frequency of occurrence $(\Pr[x = 6]) = 6 \times 1/6 = 1.000$

Thus

$$E(x) = \sum_k k \Pr[x = k]/k \qquad (k = 1, 2, \ldots, 6)$$
$$= .167 + .333 + .500 + .667 + .833 + 1.000$$
$$= 3.5 \text{ days}$$

Therefore the average fly lives 3.5 days.

In summary, the three averages in the demographic context are—

1. *Expectation of a sample proportion*—the *proportion* of all individuals that lived over the specified period.
2. *Expectation of a sample sum*—the *number* of individuals which are likely to live over the specified period.
3. *Expectation of a random variable*—the average number of individuals that experienced all events averaged.

The variance of each of these means is defined as

$$\text{variance of a sample proportion} = \text{Var}(p) = pq/n$$
$$\text{variance of sample sum} = \text{Var}(x_1 + \cdots x_n) = npq$$
$$\text{variance of random variable} = \sigma^2 = \sum_k [k - E(x)]^2 \Pr(x = k)$$

The standard deviation (SD) of each is the square root of their variance.

In order to illustrate each of these statistical measures, suppose that a group of 100 insects exhibited the life table characteristics shown in Table 2-9.

Table 2-9. Hypothetical Life Table for 100 Insects

x	l_x	d_x
0	100	26
1	74	18
2	56	14
3	42	24
4	18	18
5	0	0

The expectation of sample proportion living to age class 3 and the variance is

$$\begin{aligned} E(2) &= p = 56/100 = .56 \\ Var(p) &= np(1-p) \\ &= 100(.56)(.44) \\ &= .0025 \\ SD &= \sqrt{.0025} \\ &= .05 \end{aligned}$$

Thus the interrelation between the expectation of the sample proportion and the expectation of the sample sum in this example is as follows. Assuming that the hundred individuals in the hypothetical study are typical of all other groups of one hundred, 67% of the time the fraction of the cohort surviving to age class 3 should be within 1 SD of $p = 0.56$: i.e., between $p = 0.51$ (i.e., $p = .56 - .05$) and $p = .61$ (i.e., $p = .56 + .05$). Likewise, the number of individuals surviving to age 3 should be within 1 SD of the mean number out of 100 or between 51 and 61 individuals.

The random variable in a life table is death, and its probability distribution is the d_x schedule. Hence the mean age of death at birth is the life table parameter e_0. That is,

$$\begin{aligned} \text{mean age of death} &= e_0 \\ &= \sum_{x=0}^{\omega} x d_x \\ &= 0(.26) + 1(.18) + 2(.14) + 3(.24) + 4(.18) \\ &= 1.9 \end{aligned}$$

Thus x in the equation is the age interval in which death may occur and d_x is the probability that death of a newborn will occur in the interval x to $x + 1$. The variance of deaths around this mean age is

$$\begin{aligned} \text{Variance} &= \sum_{x=0}^{\omega} (x - e_0)^2 d_x \\ &= (0 - 1.9)^2(.26) + (1 - 1.9)^2(.18) + (2 - 1.9)^2(.14) \\ &\quad + (3 - 1.9)^2(.24) + (4 - 1.9)^2(.18) \\ \sigma^2 &= 2.17 \end{aligned}$$

As an example problem, suppose the death rate of a group of insects is normally distributed with $\mu = 20$ days and $\sigma = 6$: i) What fraction of all deaths occur before 10 days? Before 35 days? ii) What fraction of deaths occur between ages 15 and 25 days?

The first question calls for the probabilities

$$Pr(x < 10) \text{ and } Pr(x < 35)$$

Converting x to standard normal random variables yields

$$Pr(Z < [10 - 20]/6) \text{ and } Pr(Z < [35 - 20]/6)$$

or

$$\Pr(Z < -1.67) \text{ and } \Pr(Z < 2.5)$$

Consulting a normal distribution table reveals that

$$\Pr(Z < -1.67) = .05$$

and

$$\Pr(Z < 2.50) = .995$$

Thus 5% of all deaths occur before age 10 days and 99.5% of all deaths are expected to have occurred by age 35 days.

The second question calls for the probability

$$\Pr(15 < x < 25)$$

Converting to the Z scale yields

$$\Pr(Z < [15 - 20]/6) \text{ and } \Pr(Z < [25 - 20]/6)$$
$$\Pr(-0.83 < Z < 0.83)$$

The normal distribution table shows that the area up to $Z = -.83$ is .197. Since the distribution is symmetrical, this will also equal the area greater than 0.83. Therefore

$$\Pr[-.83 < Z < .83] = 1.0 - 2(.197)$$
$$= .61$$

Thus 61% of all deaths would be expected to occur between the ages of 15 and 25 days.

Sensitivity Analysis

A question of importance in the analysis of survivorship involves the extent to which a slight change in survival at a specified age changes the expectation of life at birth, e_0. Assuming that the age interval is short, we can examine this in terms of l_x's.

$$e_0 = \sum_{x=0}^{\omega} l_x$$
$$= \sum_{x=0}^{\omega} l_0 \prod_{y=0}^{x-1} p_y$$
$$= 1 + p_0 + p_0p_1 + p_0p_1p_2 + \cdots \qquad (2\text{-}14)$$

To determine the effect of a small change in, for example, p_1 of a four-age-class cohort, we set

$$e_0 = 1 + p_0 + p_0p_1 + p_0p_1p_2$$

and

$$de_0/dp_1 = p_0 + p_0p_2$$

The derivative can also be expressed as

$$de_0/dp_1 = (1/p_1) \sum_{x=2}^{3} l_x$$

since

$$p_0 + p_0p_2 = (p_0p_1/p_1) + (p_0p_1p_2)/p_1$$

The term $(1/p_1)$ can be factored out of the right-hand side, yielding

$$(1/p_1)(p_0p_1 + p_0p_1p_2)$$

or

$$(1/p_1)(l_2 + l_3)$$

Therefore the general form is

$$de_0/dp_x = (1/p_x) \sum_{y=x+1}^{\omega} l_y \qquad (2\text{-}15)$$

This expression illustrates two important aspects of the sensitivity of e_0 to changes in period survival. *First*, as x increases, the sum of the l_x's from x to ω continually decreases. Therefore the effect of a change in period survival on e_0 will always be greater at young ages than at older ages, all else being equal. *Second*, e_0 will be most greatly affected by changes in period survivorships (p_x's) that are low rather than those that are high. This is evident by noting that the term outside the summation is an inverse of a fraction. For example, if $p_x = .9$ the factor by which the sum of l_x's will be multiplied is 1.1 ($= 1/.9$). On the other hand if $p_x = .5$, the sum will be multiplied by 2.0 ($= 1/.5$). The reason for this is that a "small" change is a greater proportion of p_x when p_x is small than when it is large. In short, small changes in survival at young ages when mortality is high will most greatly affect the expectation of life at age 0.

Life Table Entropy

If all individuals die at exactly the same age, the shape of the l_x schedule is "rectangular," whereas if all individuals have exactly the same probability of dying at each age (i.e., all p_x's are identical), the l_x schedule decreases geometrically. The distribution of deaths by age varies greatly between the two patterns. A measure of this heterogeneity is referred to as entropy (H). Demitrius (1978, 1979) is recognized as originating this concept as applied to demographic heterogeneity. Goldman and Lord (1986) provided more intuitive interpretations of the measure. The formula for this measure using life table notation is

$$H = \left\{ \sum_{x=0}^{\omega} e_x d_x \right\} \Big/ e_0 \qquad (2\text{-}16)$$

The numerator (i.e., sum of products e_xd_x) can be interpreted in three different ways: i) the weighted average of life expectancies at age x; ii) the average days of future life that are lost by the observed deaths; or iii) the average

number of days an individual could expect to live, given a second chance on life. The denominator is the expectation of life at birth, e_0, and thus converts the absolute effect to a relative effect.

Vaupel (1986) provided three different interpretations of entropy, H: i) the proportional increase in life expectancy at birth if every individual's first death were averted; ii) percentage change in life expectancy produced by a reduction of 1% in the force of mortality at all ages; and iii) the number of days lost owing to death per number of days lived. In general, entropy serves as a quantitative characterization of survival pattern. If $H = 0$, then all deaths occur at exactly the same age, and if $H = 1$, then the l_x schedule is exponentially declining. The intermediate value, $H = 0.5$, indicates a linear l_x schedule.

As an example, consider entropy for the human louse life table given in Table 2-2:

$$\begin{aligned} H &= (e_0d_0 + e_1d_1 + \cdots + e_{64}d_{64} + e_{65}d_{65})/e_0 \\ &= [32.438(.014) + 31.891(.013) + \cdots + 1.000(.001) + .500(.001)]/32.438 \\ &= 11.794/32.438 \\ &= .364(= \text{entropy}) \end{aligned}$$

The louse survival schedule and various entropy values are presented in Figure 2-3. Note that for reference when $H = 0$ all individuals die at once, thus heterogeneity in the death rate is nil. When $H = 1$ the number of days

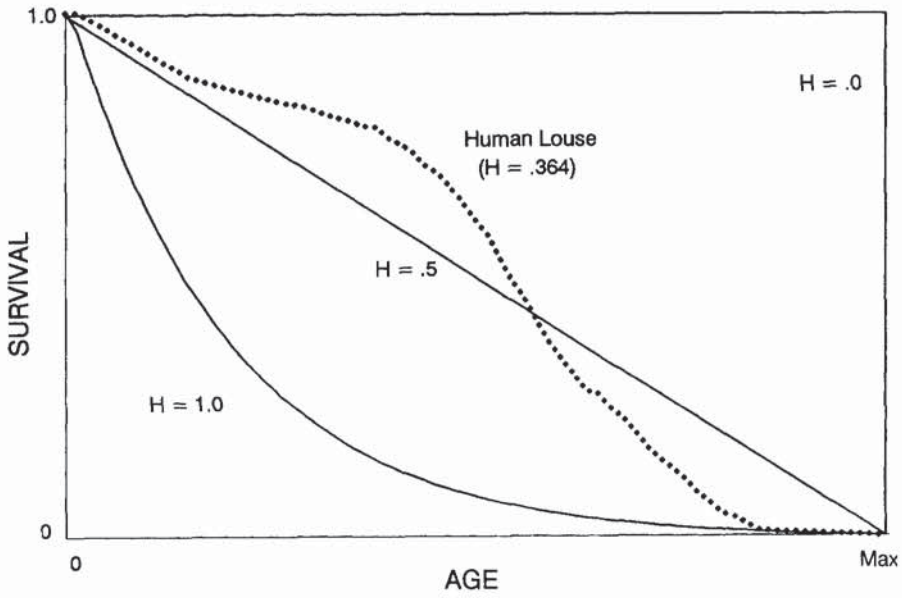

Figure 2-3. Shapes of three hypothetical life table survival schedules and associated entropy values, H. Life table of human louse taken from survival schedule given in Table 2-2.

lost in the cohort owing to death equals the average number of days lived by a newborn. The case of H = .5 is intermediate between the two extremes. The entropy value for the louse life table states that .36 days would be gained by the average individual if every first death were averted.

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