A Manual for
DEMOGRAPHIC ANALYSIS
of
WILD POPULATIONS

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Preface

Acknowledgements

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Chapter 1

The Population as a Biological Entity

Demography, the study of vital statistics of populations, is a sub-discipline of the field of Population Ecology, which in turn is a sub-discipline of Biology. In the material that follows, I deal with the treatment of vital statistics as they contribute to the understanding of wild populations of both higher plants and animals. Demography is more than simply compiling data on births and deaths. Taken broadly, demographic analyses, with associated projections and interpretations, comprise the essence of the study of population dynamics.

Populations take their place in the hierarchy of biological organization between the individual level and the community level. Groups of individuals make up a population, while groups of populations (perhaps with trophic structure and mutual adjustment) make up a community. Specifying the characteristics of individuals in a population give rise to the many definitions of population.

In statistics, a population is a defined unit from which samples are taken, and about which inferences are made. Individuals may be washers or light bulbs, as well as biological organisms. Biologically, population has been accorded several meanings, all being useful in specific instances, and in general requiring a modifying adjective for precise communication. Thus, population has been used to refer to:

1. a group of individuals comprising several species with a particular impact on a defined area (*e.g.* herbivore population or predator population);

2. a group of individuals from a common upper level taxon inhabiting a specified area (e.g. ungulate or raptor population, grass population);

3. a group of individuals belonging to a specified taxon inhabiting an area that is politically defined (state, county, management area, *etc.*);

4. a group of individuals of the same species, located such that individual actions may affect others occurring in a common area ("metapopulation"); and

5. members of a randomly interbreeding group (Mendelian or panmictic population, commonly called a deme).

As a general working rule in Ecology, "population" refers to definition 4 above, however, this is by no means always the case. In this manual, I use "population" in the context of definition 4, referring to a group of individuals of the same species in a particular area at a particular time. Further, the size of this area should be such that the potential exists for each individual to somehow affect other individuals, either by direct or by indirect means. The size of this particular area is thus arbitrary and will be determined, among other factors, by mobility, behavioral, and reproductive, characteristics of that species. Basically, this means that a population is a collection of individuals about which it is meaningful to speak of density-dependent mechanisms. In practice this definition encompasses the statisticians' use of population by adding these biological considerations.

It is justifiable to speak of a population as a biological entity because populations possess characteristics that individuals lack. For this reason, it is not meaningful to compute estimates of vital statistics for a group of individuals that do not comprise a population in the sense of definition 4 above. Group characteristics are what is being estimated, and thus the group must be a functional biological entity. These group characteristics are of three general types.

1. A population has abundance or density. We will not be concerned here with techniques involved in the determination of density, but rather with the question: "What do we need to know about a population in order to be able to predict its' abundance (or some other response) at some specified future time?" There are two ways of treating abundance that makes the term not strictly synonymous with density. The special case of zero density may be treated as "no abundance", and forms the basis for the study of determinants of distributional patterns within a species. Consideration of changes in relative numbers through time is another way of looking at abundance, and is the interpretation to which the above question is directed.

2. The second type of general population characteristics are the primary determinants of population size; natality, mortality, immigration, and emigration. Any factor that affects population size is ultimately expressed as one of these 4 parameters. Some factors that affect population size are external, and are not to be considered as characteristics of a population (*e.g.* catastrophic weather that causes unusual mortality) while other factors may affect the primary population parameters in a more general sense. It is these latter affects that demographic analyses could profitably be designed to discover.

3. Finally, characteristics such as age structure, gene frequencies, dispersion and spacing of individuals, behavioral responses such as population agression levels, physiological attributes such as Oxygen demand reductions because of group denning or huddling, comprise the remainder of population level attributes.

Population characteristics are statistical reductions and reformations of various measurements taken from individual members of the population. Thus, an individual may contribute to the birth of a given clutch but a population has a birth rate; an individual has age, but a population has age structure; an individual houses its respective genome, but a population has genetic structure in the form of gene frequencies. Emergent

properties of populations occur as a result of interactions among individuals that are often density-dependant. While there is yet no evidence that populations are intrinsically regulated as a matter of course, the general effects of intraspecific competition and various mutualisms are generally acknowledged.

Aside from the problems of obtaining and interpreting demographic data, a real challenge exists in the determination of boundaries within which a valid, density-dependent, interacting group of individuals is functioning. Such a decision poses little problem with closed populations, where all members of that species that are present can be thought of as participating in various population processes. The other extreme is evidenced by extensive homogenous expanses inhabited by members of a species, where discrete populations are not found; rather, some kind of a continuum with dynamic population edges must exist. In both cases, immigration and emigration are of varying, and often unknowable, intensities. These problems cannot be solved by any typical analysis, and are pointed out to emphasize the need for interpretive abstractions that remain aware of the dynamic nature of boundaries that delimit populations.

All too often, a "population" is treated as a group of individuals within some artificially defined political boundaries. Demographic analyses are directed to the biological characteristics of a population; it is senseless to analyze political units as if they had some relevancy to biologic function. The procedures described in this manual assume that the abstract nature of population boundaries are understood; they assume that a demographic unit is an interacting group of individuals of the same species, functioning together with demographic awareness and in a potentially density-dependent manner. Failure to take cognizance of this fact will get you wrong answers more often than not.

Chapter 2

Natality

Information on natality is typically presented as an age-specific column that represents the expected number of female offspring produced per female of age x to $x + 1$. The natality schedule is denoted by m_x. Prior to describing the mathematical decomposition of of m_x, it is necessary to take a brief aside and provide some definitions.

Birth: To give rise to, to originate. Restricted to mammals. (see parturition).

Birthrate: Births *per capita* per unit time. Restricted to mammals. See natality.

Breed, Breeding: To produce offspring by hatching or parturition. Restricted to emergence of offspring from egg or uterus. "Breeding season" is that period of time during which offspring are being produced. "Breeding" does not refer refer to copulation behavior.

Copulation: Act of engaging in sexual intercourse.

Fecundity: Number of offspring, either in the form of eggs laid or live births produced, per breeding female per effort. Denoted F_x.

Fertility: Capable of producing offspring (presence of viable sperm in male, or ovulation in female).

Gestation: Act of producing offspring "*in utero*;" period of time between fertilization and parturition. Restricted to mammals.

Incubation: Period of time between egg-laying and hatching. Analogous to gestation, applied to to Fishes, Amphibians, Reptiles, and Birds, and other animals that lay eggs.

Hatch: To emerge from an egg. Analogous to parturition in mammals. Applied to fishes, amphibians, reptiles, birds, monotreme mammals, and other animals that lay eggs.

Mate, Mating: See Copulation.

Natality: Number of female offspring produced per female per unit time. Applies to all organisms. See *Birthrate*. Denoted as m_x.

Parturition: Act of giving birth. Restricted to mammals. See *Birth*.

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Proportion Breeding: Proportion of females in the x to $x + 1$ age class actually producing offspring at time t. Denoted as β_x.

Proportion Males: See *Sex Ratio At Fertilization* (or birth, hatching, germination, *etc.*).

Reproduction: To make a representation of ..., to produce offspring. The process of offspring actually emerging from egg or uterus. See *Breed*.

Sex Ratio At Fertilization: Expressed as proportion males or ratio of males to total clutch. Denoted ρ_x. $\rho_x = males/(males + females)$. Therefore, the proportion of females at fertilization is $1 - \rho_x$. In this manner, *Sex Ratio At Birth* is bounded by 0 (all females) and 1 (all males). This approach standardizes raw sex ratios, which otherwise lack bounds, and is thus a statistic that provides generality across various populations.

Depending on the species being examined, natality data range from relatively simple to almost impossible to obtain. In order to simplify data collection, to facilitate interpretation, to better reflect the complex biology involved, and indeed, to promote clear thinking about reproductive attributes, natality, m_x, is decomposed into a function containing 3 elements

$$m_x = F_x(1 - \rho_x)\beta_x \qquad (2.1)$$

The first right hand term is Fecundity, denoted by F_x. Fecundity is defined as the number of offspring (both male and female), either in the form of eggs laid or live births, produced by a breeding female per reproductive effort. Fecundity is thus an age-specific value that reflects "clutch size."

The second term describing natality is sex ratio at birth, denoted ρ_x. Again, sex ratios will be expressed as proportion males; *i.e.* $\rho_x = males/(females + males)$. The proportion of females per clutch per event is $1 - \rho_x$. Since natality strictly refers to female offspring, only the proportion of the clutch that is female is represented.

The third term describing natality is Proportion Breeding, denoted β_x. Proportion breeding is an age-specific value referring to the proportion of females in an age class that actually produce offspring during any specified breeding season.

Natality, as defined here, is a more complex function than that usually found in the demographic literature; the final result, however, is similar. The decomposition and detailed specification of the biological factors that proximally define m_x provide interesting insight into population processes.

The inclusion of natal sex ratio is a straight-forward method of relaxing the implicit assumption of equal sex ratios at birth contained in most population models. Even though there is compelling theoretical argument for why natal proportions of males to females should be equal, there are significant deviations of this pattern in a variety of well-studied species that warrant the inclusion of natal sex ratios as a definitive part of any discussion of natality. Some of the theoretical foundations for a tendency toward sex ratios of 0.5 are considered in an appendix to this chapter.

Decomposing m_x into the 3 terms F_x, ρ_x, and β_x, confounds distinctly different biological processes affecting the demographic character of the population. First, given that a female will produce offspring, how many daughter offspring she will produce (expected clutch size and expected sex ratio) is determined primarily by a long

evolutionary history and adaptation to large *vs.* small clutches and life history strategy that results in even *vs.* uneven sex ratios. These ultimate factors are offset in any specific breeding period by the ecologically proximate question of whether or not a given female produces offspring at all.

The number of offspring a female can or will produce in any given reproductive event is, to a large extent, a consequence of the evolutionary history ("reproductive strategy") of the species. Thus, expected clutch size for equids is 1; for bighorn sheep usually 1 occasionally 2; for white-tail deer 1, or 2, or occasionally 3; kangaroo rats 2 or 3; ground squirrels 6 to 8; mourning doves 2, most gallinacious birds 10 to 14; the same for many species of lizards and snakes; and among the fishes a range of from 10 to 14 up to as much as 1 million (codfish). These expected clutch sizes are subject to modification by proximate factors such as nutrition, but in general, one expects a species to produce clutch sizes that are statistically "standard" for that species. Consider, for example, what physiological and morphological changes would have to occur if horses were to begin to successfully produce clutch sizes of 8 to 10. Or the behavioral changes (*e.g.* protection of offspring) that would be required for non-extinction if codfish were to shift to clutch sizes of around 4 or 5. In this context, clutch sizes are clearly fixed genetically within certain limits. Similar arguments apply for sex ratios.

The evolutionary consequences that set the boundaries on clutch size for a species are the ultimate determinates, and may produce clutch sizes that are essentially without variance (*e.g.* horses = 1, doves = 2), or larger clutches where variances on the expected values may be relatively high.

Optimum (in some sense) values of clutch size can be modified by a variety of proximate ecological factors, among which for example, nutrition induced stress often plays an important role. Nutrition mediated clutch sizes often reflect severe resource shortages, and are often demonstrated by poor body condition, particularly among gravid females.

While nutrition mediated clutch sizes can be a significant factor, a generally more important demographic question is whether or not an average female will breed at all in any given season. Proportion breeding is a highly variable demographic component, determined, apparently, by a host of ecologically relevant, proximate attributes of the ecological environment. Such factors include nutrition, behavior, competition, and abiotic resources, to mention just a few. As will be demonstrated in later chapters of this manual, the proportion of females breeding in any given season is a more influential demographic attribute than are clutch size differences that represent only a small percentage of the expected production of offspring. The relative influence of changes in proportion breeding is dependent on the size of the original F_x values; other things being equal, proportion breeding has greater effect if F_x is high and less effect when F_x is 1 or perhaps 2. The demographic attributes F_x, ρ_x, and β_x have been treated as if they were fixed, parametric values for a given population. A moment of reflection will indicate that because these are expected values, higher moment statistics are available and worthy of estimation. While it is true, for example, when $F_x = 1$ that variances are relatively uninteresting, as clutch sizes increase the distributional properties of variance, skewness, and kurtosis become interpretive aids to understanding a species' reproductive responses to variable environments. Such stochastic attributes of population models will be described in a subsequent chapter.

Clutch Size = # a horse can produce in a given event

Chapter 3

Analysis of Survival Data

3.1 Basic Life Tables

Strictly speaking, a life table is a schedule of survivors over time. Other useful information may be derived from a survival schedule and such data, taken together, comprise an "expanded" life table. Columns in an expanded life table that are derived from a survival schedule may be similarly computed for males or females; several additional columns that require natality data are specific to females, and allow estimations of such attributes as rates of increase, reproductive values, and generation times.

A life table is a method for logically arranging much of the descriptive demographic data for population analysis. Good life table data are difficult to obtain and subject to considerable misinterpretation. The basic assumptions involved in life table construction are described in Chapter 7. While these assumptions are critical to interpreting results of a demographic analysis, mechanical aspects of computing various elements in an expanded life table do not require an explicit statement of critical assumptions at this time. I first cover the mechanics, and will return to the assumptions and interpretations in later chapters.

A cohort is a group of individuals of the same age at the same time within a population. Occasionally the term cohort is used to refer to size classes in plants. This is not an entirely suitable use of the term; the general effect of doing so will be covered in Chapters 10 and 11.

At any time t, there are $n_{x,t}$ individuals in the cohort (x refers to the age of individuals, and t to time). Time and age are described in arbitrary units of time depending upon the intent of the investigator. For example, time and age in a deer or wild horse population are typically expressed in terms of single year intervals because these animals have only a single breeding season each year. In small mammal populations gestation times are on the order of several weeks to only a few months, and demographic projections can make best use of such time intervals. Pooling reproductive time intervals is reasonably done provided you are willing to sacrifice the some resolution in your analyses resulting from the use of stacked expectations (means of means). Such pooling is frequently done over 5 yr intervals (as in studies in human demography or other long lived species), or perhaps over generation times.

Arithmetically, obtaining a survival schedule is a simple operation. The age of a new cohort at $t = 0$ is $x = 0$. Starting with a cohort of 100 females $n_0 = 100$ at $t = 0$, and

$x = age$
$t = time$

x	n_x	D_x	l_x	m_x	$l_x m_x$
0	100.00	40.00	1.000	0.0	0.000
1	60.00	24.00	0.600	0.75	0.450
2	36.00	14.40	0.360	0.75	0.270
3	21.60	8.64	0.216	0.75	0.162
4	12.96	5.19	0.129	0.75	0.096
5	7.77	3.11	0.077	0.75	0.057
6	4.66	4.66	0.046	0.75	0.034

Table 3.1: A Simple Expanded Life Table

Sample data show calculations based on an initial cohort of 100 females, 60% per year survival, and expected production of female offspring. All numbers are truncated at accuracy level shown to avoid "rounding rules."

applying a constant survival rate of 60% per time period, the cohort will decrease in size so that at $t = 1$, $n_1 = 60$ (60% of the initial 100 individuals survive to enter the next age class). At $t = 2$, $n_2 = 36$; at $t = 3$, $n_3 = 21.6$ and so on. Note that as time increases by unit intervals, the individuals age by one unit, but that there are always 40% fewer than the previous time unit contained. These results can be seen in Table 3.1.

Notationally, n_x refers to the number of individuals in a cohort that are alive at the beginning of the age interval x to $x + 1$. The number that die during this interval is D_x. Columns of n_x and D_x express information in terms of numbers of individuals in the cohort. A more general procedure is to convert this information to proportions (probabilities), thus allowing comparisons among cohorts of different initial sizes. The n_x column provides a simple probability of survival by dividing the number that enter a given age x by the number that started the cohort, n_0. This result is denoted by l_x, and is given by

$$l_x = \frac{n_x}{n_o} \tag{3.1}$$

This new value, l_x, is the probability that an individual of age zero will survive to enter some subsequent x^{th} age class. The various values of $l_0, l_1, \ldots, l_\omega$, where ω represents the final age class, may be graphed against age resulting in a "survival curve" or "survival schedule;" several examples of l_x curves are shown in Figure 3.1. Table 3.1 shows an expanded life table with 6 columns.

In this manner, for a cohort of any initial size, standardized curves are produced for comparison with other populations or species. It is a common practice in some disciplines (although by no means necessary or desirable) to express survival schedules as numbers surviving per thousand. This is readily accomplished by multiplying each l_x by 10^3. Base cohorts to any power of 10 are obtained in a similar fashion. Two columns in the expanded life table, L_x and T_x, are best understood when cohorts are treated as individuals rather than probabilities; for wild populations, it is common to use a base of 1,000 for these columns. Demographers studying human populations typically use a base cohort of 10,000.
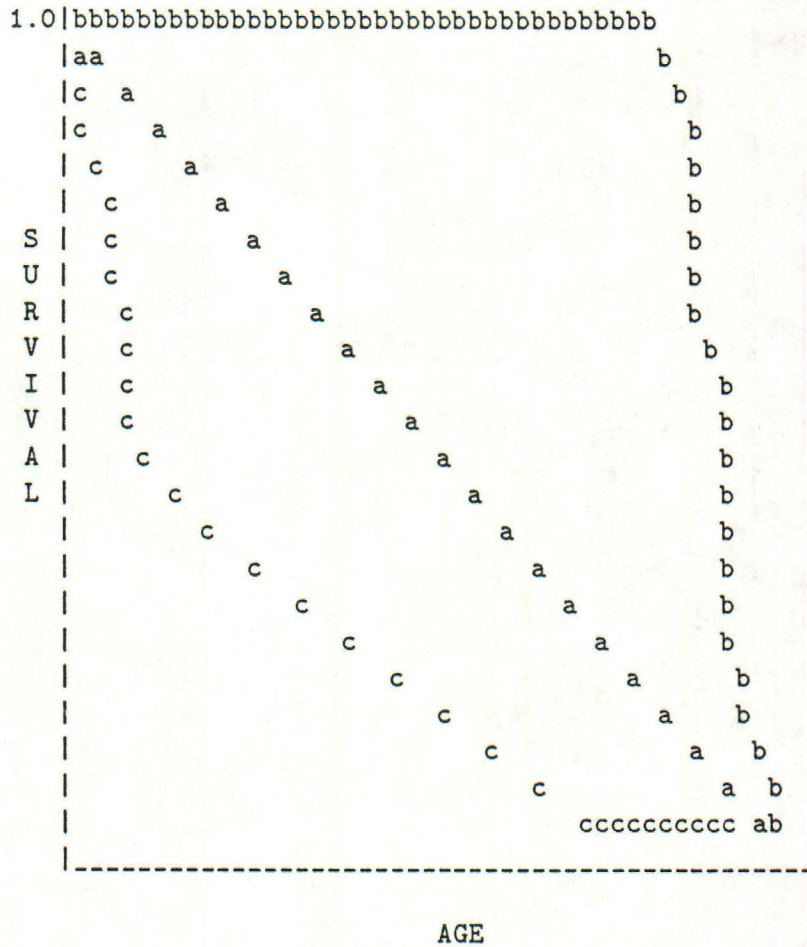
```
  1.0|bbbbbbbbbbbbbbbbbbbbbbbbbbbbbbbbbbbbb
     |aa                                    b
     |c   a                                 b
     |c     a                               b
     |  c     a                             b
     |   c      a                           b
  S  |   c        a                         b
  U  |   c          a                       b
  R  |    c           a                     b
  V  |    c             a                   b
  I  |    c               a                 b
  V  |    c                 a               b
  A  |     c                  a             b
  L  |       c                  a           b
     |         c                  a         b
     |           c                  a       b
     |             c                  a     b
     |               c                  a   b
     |                 c                  a b
     |                   c                a   b
     |                     c             a  b
     |                       c          a  b
     |                         c       a  b
     |                           cccccccccc ab
     |
     |_____

                        AGE
```

Figure 3.1: Three Typical Survival Schedules

*Survival curves representing three possible life history strategies. Curve **a** represents a species with a relatively constant mortality such as bird species. Curve **b** might be indicative of large mammal species that has low early mortality and a higher old age mortality. Curve **c** represents a species with high infant mortality such as many fishes.*

3.2 Expanded Life Tables

Given schedules of l_x and m_x, a variety of informative columns may be generated to form an "expanded" life table. Most of these columns may be calculated by starting with the l_x schedules described above. It is important to recognize that there is no new information in these derived columns; they simply represent different ways of expressing the original survival data to facilitate various interpretations.

As mentioned, l_x is the probability that an individual of age zero will survive to enter the xth age class. Once an individual reaches the xth age class, the probability that it will survive to enter the $x + 1$ age class is denoted by p_x. Age-specific survival, p_x, is obtained by dividing the number of individuals that survived the xth age class (those entering the $x + 1$ age class) by the total number of individuals that entered the xth age class,

$$p_x = \frac{n_{x+1}}{n_x} \tag{3.2}$$

Because age-specific survival rate is independent between age classes, the probability at $x = 0$ of surviving to enter the x_{th} age class, l_x, is equal to the product of the successive age-specific survival rates. This is

$$l_x = \prod_{i=0}^{x-1} p_i \tag{3.3}$$

$$= p_0 p_1 p_2 \cdots p_{x-2} p_{x-1} \tag{3.4}$$

$$= \left(\frac{n_1}{n_0}\right)\left(\frac{n_2}{n_1}\right) \cdots \left(\frac{n_{x-1}}{n_{x-2}}\right)\left(\frac{n_x}{n_{x-1}}\right) \tag{3.5}$$

$$= \frac{n_x}{n_0} \tag{3.6}$$

$$\tag{3.7}$$

The inverse of l_x is the death schedule, d_x, the probability at $x = 0$ of an individual dying during the age interval x to $x + 1$, and is obtained by

$$d_x = l_x - l_{x+1} \tag{3.8}$$

$$= \frac{n_x - n_{x+1}}{n_0} \tag{3.9}$$

$$= \frac{D_x}{n_0} \tag{3.10}$$

$$\tag{3.11}$$

Age-specific death rate, q_x, is the probability that an individual that enters the xth age class will die before entering the $x + 1$ age class. Thus, q_x is the compliment of p_x, and is obtained by

$$q_x = \frac{d_x}{l_x} \tag{3.12}$$

$$= \frac{\frac{n_x - n_{x+1}}{n_0}}{\frac{n_x}{n_0}} \tag{3.13}$$

$$= \frac{n_x - n_{x+1}}{n_x} \tag{3.14}$$

$$= 1 - \frac{n_{x+1}}{n_x} \tag{3.15}$$

$$= 1 - p_x \tag{3.16}$$

$$\tag{3.17}$$

The number of animal time units to be lived in the x to $x + 1$ age class, L_x, is obtained by integrating the l_x curve,

$$L(x) = \int_{x=x}^{x+1} l_x dx \tag{3.18}$$

Values of L_x are reasonably approximated by

$$L_x = \frac{l_x + l_{x+1}}{2.0} \tag{3.19}$$

under the assumption that l_x is linear between x and $x + 1$. Values of L_x are more readily interpreted when put into a base cohort of 1,000 (or whatever you prefer), thus, $L_x(10^3)$ represents the number of individual "time units" to be lived by that cohort during the age x to $x + 1$. The concept is analogous to "man hours" or "man years."

The estimated total number of animal time units remaining to be lived from age x is

$$T_x = \int_{x=x}^{\omega} l_x dx \tag{3.20}$$

where ω is the last age class that contains individuals. Contrasting to L_x, the values of T_x are the area under the l_x curve from age x until no individuals remain from the cohort. T_x is reasonably approximated by summing appropriate values of L_x

$$T_x = \sum_{x=x}^{\omega} L_x \tag{3.21}$$

Life expectancy, e_x, or mean length of life remaining to an individual entering age x, is

$$e_x = \frac{\int_{x=x}^{\omega} l_x dx}{l_x} \tag{3.22}$$

Values of e_x are reasonably approximated by

$$e_x = \frac{T_x}{l_x} \tag{3.23}$$

The $l_x m_x$ column is an age-specific, expected-reproduction column, with expectations based on an individual of age $x = 0$. If all females were to live to the maximum age, and breed at the expected rate throughout, the Gross Reproductive Rate (GRR) would be achieved. Thus GRR is the sum of the m_x values

$$GRR = \sum_{x=0}^{\omega} m_x \tag{3.24}$$

However, since the average individual dies somewhere between $x = 0$ and maximum age, ω, the GRR represents a maximum potential reproductive rate, that will rarely be achieved.

Summing the $l_x m_x$ column provides the Net Reproductive Rate, R_o, and is the average number of female offspring (or in an extended case to be discussed later, males) that will be produced by the average female in the population.

$$R_o = \sum_{x=0}^{\omega} l_x m_x \tag{3.25}$$

A complete equation structure for an expanded life table is shown in Table 3.2, and examples of the calculations are provided in Tables 3.3 and 3.4. Each of these columns have useful information, subject to restrictive assumptions concerning the validity of the data involved. Although the calculations for an expanded life table are relatively simple, several implicit constraints can make the results less than useful. Chapter 7, Assumptions, details pitfalls in life table construction and interpretation. For the time being, and for the purpose of building a foundation for such interpretations, I assume that these qualifications are met.

3.3 A Gross Estimate of Survival

A time-specific column of number of individuals per age class (denoted n'_x to distinguish from a true cohort, or diagonal column of n_x) while not adequate for most purposes, can none-the-less provide a careful analyst with relevant information. One procedure for extracting a pooled (population level) survival estimate is as follows.

Given a time-specific column of individuals per age class, n'_x, straighten out the curve by natural log transform

$$n_x = \ln(n'_x + 1.0). \tag{3.34}$$

Denote the age class vector as $\mathbf{x}$ and the vector of n'_x as $\mathbf{n}'$. Then conduct a linear least-squares unreplicated fit of $\ln \mathbf{n}'$ against $\mathbf{x}$ as follows:

$$\omega = number of age classes \tag{3.35}$$

the mean of $\mathbf{x}$ is

$$\overline{\mathbf{x}} = \frac{1}{\omega} \sum_{x=0}^{\omega} \mathbf{x}_x \tag{3.36}$$

the mean of $\mathbf{n}'$ is

$$\overline{\mathbf{n}'} = \frac{1}{\omega} \sum_{x=0}^{\omega} \mathbf{n}_x \tag{3.37}$$

the sum of squares of $\mathbf{x}$ is

$$\sum \mathbf{x}^2 = \sum_{x=0}^{\omega} \mathbf{x}^2{}_x \tag{3.38}$$

the sum of squares of $\mathbf{n}'$ is

$$\sum \mathbf{n}'^2 = \sum_{x=0}^{\omega} \mathbf{n}'^2{}_x \tag{3.39}$$

x	n_x	D_x	l_x	d_x	q_x
0	n_0	$n_0 - n_1$	n_0/n_0	$l_0 - l_1$	d_0/l_0
1	n_1	$n_1 - n_2$	n_1/n_0	$l_1 - l_2$	d_1/l_1
2	n_2	$n_2 - n_3$	n_2/n_0	$l_2 - l_3$	d_2/l_2
.	.	.	.	.	.
.	.	.	.	.	.
.	.	.	.	.	.
x	n_x	$n_x - n_{x+1}$	n_x/n_0	$l_x - l_{x+1}$	d_x/l_x

x	p_x	L_x	T_x	e_x	P_x
0	$1 - q_0$	$(l_0 + l_1)/2$	$L_0 + L_1 + \cdots + L_\omega$	T_0/l_0	L_1/L_0
1	$1 - q_1$	$(l_1 + l_2)/2$	$L_1 + L_2 + \cdots + L_\omega$	T_1/l_1	L_2/L_1
2	$1 - q_2$	$(l_2 + l_3)/2$	$L_2 + L_3 + \cdots + L_\omega$	T_2/l_2	L_3/L_2
.	.	.	.	.	.
.	.	.	.	.	.
.	.	.	.	.	.
x	$1 - q_x$	$(l_x + l_{x+1})/2$	$\sum_{x=x}^{\omega} L_x$	T_x/l_x	L_{x+1}/L_x

x	F_x	$1 - \rho_x$	β_x	$l_x m_x$	v_x	c_x
0	F_0	$1 - \rho_0$	β_0	$l_0 m_0$	.	.
1	F_1	$1 - \rho_1$	β_1	$l_1 m_1$	.	.
2	F_2	$1 - \rho_2$	β_2	$l_2 m_2$	.	.
.	.	.	.	.	.	.
.	.	.	.	.	.	.
.	.	.	.	.	.	.
x	F_x	$1 - \rho_x$	β_x	$l_x m_x$	see below	see below

$$v_x = \frac{\lambda^x}{l_x} \sum_{y=x}^{\omega} \lambda^{-y} l_y m_y \qquad (3.26)$$

formal calculation

$$c_x = \frac{\lambda^{-x} l_x}{\sum_{y=0}^{\omega} \lambda^{-y} l_y} \qquad (3.27)$$

stable age

$$T_c = \frac{1}{R_o} \sum_{x=0}^{\omega} x l_x m_x \qquad (3.28)$$

$$\overline{T} = \sum_{x=0}^{\omega} x \lambda^{-x} l_x m_x \qquad (3.29)$$

$$R_o = \sum_{x=0}^{\omega} l_x m_x \qquad (3.30)$$

net rate of increase

$$1 = \sum_{x=1}^{\omega} \lambda^{-x} l_x m_x \qquad (3.31)$$

landa

$$r = \ln \lambda \qquad (3.32)$$

$$(3.33)$$

Table 3.2: Equation Structure for an Expanded Life Table

x	n_x	D_x	l_x	d_x	q_x	p_x	L_x	T_x	e_x
0	475.82	235.94	1.000	0.495	0.495	0.504	752.0	1500.0	1.500
1	239.88	118.95	0.504	0.249	0.495	0.504	379.1	747.9	1.483
2	120.93	59.96	0.254	0.126	0.495	0.504	191.1	368.8	1.451
3	60.97	30.24	0.128	0.063	0.495	0.504	96.3	177.6	1.386
4	30.73	15.24	0.064	0.032	0.495	0.504	48.5	81.3	1.258
5	15.49	7.68	0.032	0.016	0.495	0.504	24.4	32.7	1.004
6	7.81	7.81	0.016	0.016	1.000	0.0	8.2	8.2	0.500

x	m_x	$l_x m_x$
0	0.0	0.0
1	1.0	0.504
2	1.0	0.254
3	1.0	0.128
4	1.0	0.064
5	1.0	0.032
6	1.0	0.016
$\sum$	6.0	0.999

Table 3.3: An Expanded Life Table

Table 3.3A. Expanded life tables from data presented in Table 6.1. All numbers are truncated at accuracy level shown. Table 3.3A. A time-specific analysis taken from Year 9, Table 4.8. See also Table 6.2 for further extensions.

x	n_x	D_x	l_x	d_x	q_x	p_x	L_x	T_x	e_x
0	167.40	66.96	1.000	0.400	0.400	0.600	800.0	1929.9	1.929
1	100.44	40.18	0.600	0.240	0.400	0.599	479.9	1129.9	1.883
2	60.26	24.11	0.359	0.144	0.400	0.599	287.9	649.9	1.805
3	36.15	14.46	0.215	0.086	0.400	0.600	172.7	361.9	1.675
4	21.69	8.68	0.129	0.051	0.400	0.599	103.6	189.2	1.459
5	13.01	5.20	0.077	0.031	0.399	0.600	62.1	85.5	1.100
6	7.81	7.81	0.046	0.046	1.000	0.0	23.3	23.3	0.500

x	m_x	$l_x m_x$
0	0.0	0.0
1	1.0	0.600
2	1.0	0.359
3	1.0	0.215
4	1.0	0.129
5	1.0	0.077
6	1.0	0.046
$\sum$	6.0	1.4298

Table 3.4: table3.3B

Table 3.3B. A cohort analysis that starts in Year 3 and ends in Year 9 of Table 4.8. See also Table 6.2 for further extensions.

Diagonal is the true cohort

the sum of the cross products is

$$\sum \mathbf{xn'}^2 = \sum_{x=0}^{\omega} \mathbf{x}_x \mathbf{n'}_x \frac{(\sum_{x=0}^{\omega} \mathbf{x}_x)(\sum_{x=0}^{\omega} \mathbf{n'}_x)}{\omega} \tag{3.40}$$

the slope of the regression line is an instantaneous survival rate across all members of the sample population, and is given by

$$s_{\mathbf{x},\mathbf{n'}} = \frac{\sum \mathbf{xn'}^2}{\sum \mathbf{x}^2} \tag{3.41}$$

which can be converted to an annual survival rate by

$$S_{\mathbf{x},\mathbf{n'}} = e^s \tag{3.42}$$

and annual mortality rate, Q, is

$$Q = 1 - S. \tag{3.43}$$

For some purposes, it is worthwhile to back-calculate a "smoothed" column of number of individuals per age class, based on the regression equation obtained as above. This is done by obtaining the intercept, a, by

$$a = \overline{\mathbf{n'}} - (s * \overline{\mathbf{x}}) \tag{3.44}$$

then,

$$\mathbf{n'}_0 = e^a \tag{3.45}$$

estimates the zero age class, and

$$\mathbf{n'}_x = e^a + s(\mathbf{x}_x); x = 1, 2, \cdots, \omega \tag{3.46}$$

gives the remaining numbers of individuals per age class. The smoothed column of $\mathbf{n'}$ obtained in this manner can be used in various population projections, under the assumption that the annual survival rate, S, obtained in this manner is what you have chosen to evaluate in your modelling exercises. You must be aware that massaging the data in this manner is a bit extreme, and that the questions that you pose of the model must be carefully evaluated.

Appropriate confidence limits can be computed for the instantaneous survival rate, and the estimated $\mathbf{n'}_x$ values; see any introductory text in regression statistics for these calculations. A test of significance on the slope of the regression line is not relevant, and should not be computed. Given a data set that contained many samples $\mathbf{n'}$ from a range of real populations, *i.e.* a sample of time-specific age structures from a variety of populations and/or times, it is interesting to compare such populations in the above manner.

Chapter 4

Elementary Population Projections

Assuming for the moment that new individuals in the population are produced during the same brief time interval, the number of females that enter the population at time t is obtained by multiplying the number of females in each age class by the expected production of female offspring for that age class. These products are then summed across the age classes.

For example, in Table 4.2 the number of new individuals entering the population at year 3, the top entry, $n_{x=0,t=3}$, in year 3 is obtained by summing the products of the number of females in a given age class and their expected production of female offspring. This is

$$n_{0,3} = n_{1,3}m_1 + n_{2,3}m_2 + n_{3,3}m_3 + \cdots + n_{\omega,3}m_\omega \tag{4.1}$$

or more specifically,

$$317.0 = 82.0(1.25) + 41.0(1.5) + \cdots + 32.4(1.5) + 21.6(1.5) \tag{4.2}$$

In general, the number of age-zero females that enter the population during the tth time interval is expressed as:

$$n_{o,t} = \sum_{x=1}^{\omega} n_{x,t}m_x 4.1 \tag{4.3}$$

Although portions of individuals typically do not survive in real populations, several decimal places should be carried in these calculations to avoid accumulating excessive rounding errors.

Individuals in any given age class at time t that survive until time $t + 1$ will appear in the next age class. The diagonal transitions in the projection table are obtained by multiplying the number of individuals in an age class at time t by the age-specific survival rate, p_x. In Table 4.2 individuals in the year 3 column move to year 4 as shown in the sequence given in Table 4.1. In general, individuals move from one age class to the next according to

$$n_{x+1,t+1} = n_{x,t}p_x 4.2 \tag{4.4}$$

which projects age classes along the diagonals in the projection table.

AGE	Year 3		Year 4	AGE
0	317.0(.2)	=	63.4	1
1	82.0(.4)	=	32.8	2
2	41.0(.6)	=	24.6	3
3	19.2(.6)	=	11.5	4
4	28.8(.6)	=	17.3	5
5	32.4(.6)	=	19.4	6
6	21.6(.0)	=	0	-

Table 4.1: Survival Transitions

See text for discussion. Note that individuals in age class 6 have no chance of surviving to another time interval.

A diagonal such as one in Table 4.2 starting at year 3 with $n_0 = 317.0$ and ending at year 9 with $n_6 = 3.3$ consists of all same-age individuals, and represents the fate of a cohort. Such a cohort may be analyzed by means of an expanded life table as described in Chapter 3 and a true rate of increase can be derived for the population. Tables 4.2, 4.3, and 4.4 are life history projections that demonstrate effects of varying probabilities of age specific survival, resulting in decreasing, stable, and increasing populations. Natality is the same for each projection. All populations have reached stable age distribution by year 12. Population projections such as those shown in Table 4.2 and 4.3 assume that age-specific survival rates remain constant over time. Because environments within which populations exist are dynamic, this assumption almost never holds true for wild populations. Thus elementary population projections contain some particularly restrictive assumptions, and while they may indicate possible population trends, cannot be considered as a prediction of population growth. In spite of these restrictions, age schedules can provide information on certain population potentials; in later chapters I consider the effects of failed assumptions, and some methods for examining population data in spite of the problems.

Examine the life history projections shown in Tables 4.1 A through C, and 4.2 A through C, and convince yourself that the equations actually provide a projection of the population through time. These simple examples were contrived to emphasize specific points; however, conducting projections with more complex survival and fertility schedules is similar.

The proportion of the total population contained in the x to x+1 age class at time t is obtained by dividing the total number of individuals in the age class $n_{x,t}$ by the total number of individuals in the population N_t (see Table 4.5). From Table 4.3, Year 9, the proportions (*i.e.* age structure) in the age classes are shown in the rightmost column of Table 4.5.

A column of proportions as in Table 4.5 indicates the age structure of the population at time t. Understanding age structure patterns is a fundamental challenge in analyses of wild populations. Often the biologist has only age structure data with which to work, and must estimate the various population parameters from such data. Raw age structure, denoted C_x, is the proportion of the population in the x to $x + 1$ age class at time t. Successive elements of the age structure column are given by

$$C_{x,t} = \frac{n_{x,t}}{N_t}.$$

(4.5)

Age	p_x	m_x	Year 0	Year 1	Year 2	Year 3	Year 4	Year 5
0	.2	0.00	400.0	512.5	410.1	317.0	237.7	175.1
1	.4	1.25	200.0	80.0	102.5	82.0	63.4	47.5
2	.6	1.50	150.0	80.0	32.0	41.0	32.8	25.4
3	.6	1.50	100.0	90.0	48.0	19.2	24.6	19.7
4	.6	1.50	50.0	60.0	54.0	28.8	11.5	14.8
5	.6	1.50	25.0	30.0	36.0	32.4	17.3	6.9
6	0	1.50	10.0	15.0	18.0	21.6	19.4	10.4
Σ			935.0	867.5	700.6	542.1	406.8	299.7

Age	Year 6	Year 7	Year 8	Year 9	Year 10	Year 11	Year 12
0	132.3	103.5	79.2	60.4	46.0	35.1	26.8
1	35.0	26.5	20.7	15.8	12.1	9.2	7.0
2	19.0	14.0	10.6	8.3	6.3	4.8	3.7
3	15.2	11.4	8.4	6.4	5.0	3.8	2.9
4	11.8	9.1	6.8	5.0	3.8	3.0	2.3
5	8.9	7.1	5.5	4.1	3.0	2.3	1.8
6	4.1	5.3	4.3	3.3	2.5	1.8	1.4
Σ	226.4	176.9	135.5	103.3	78.8	60.0	45.8

Table 4.2: Table 4.1A

A. Decreasing population with p_x and m_x as shown, $\lambda = 0.763$.

Age	p_x	m_x	Year 0	Year 1	Year 2	Year 3	Year 4	Year 5
0	.3	0.00	400.0	641.2	656.0	655.4	643.9	629.8
1	.5	1.25	200.0	120.0	192.4	196.8	196.6	193.2
2	.7	1.50	150.0	100.0	60.0	96.2	98.4	98.3
3	.7	1.50	100.0	105.0	70.0	42.0	67.3	68.9
4	.7	1.50	50.0	70.0	73.5	49.0	29.4	47.1
5	.7	1.50	25.0	35.0	49.0	51.4	34.3	20.6
6	0	1.50	10.0	17.5	24.5	34.3	36.0	24.0
Σ			935.0	1088.7	1125.3	1125.1	1106.0	1081.9

Age	Year 6	Year 7	Year 8	Year 9	Year 10	Year 11	Year 12
0	627.7	636.0	636.0	635.0	634.0	633.4	633.3
1	189.0	188.3	190.8	190.8	190.5	190.2	190.0
2	96.6	94.5	94.2	95.4	95.4	95.3	95.1
3	68.8	67.6	66.1	65.9	66.8	66.8	66.7
4	48.2	48.2	47.3	46.3	46.1	46.7	46.7
5	33.0	33.7	33.7	33.1	32.4	32.3	32.7
6	14.4	23.1	23.6	23.6	23.2	22.7	22.6
Σ	1077.7	1091.5	1091.7	1090.1	1088.4	1087.3	1087.2

Table 4.3: Table 4.1B

B. Stationary population with p_x and m_x as shown, $\lambda = 0.999$.

Age	p_x	m_x	Year 0	Year 1	Year 2	Year 3	Year 4	Year 5
0	.4	0	400.0	770.0	961.0	1180.1	1434.2	1743.6
1	.6	1.25	200.0	160.0	308.0	384.4	472.0	573.7
2	.8	1.50	150.0	120.0	96.0	184.8	230.6	283.2
3	.8	1.50	100.0	120.0	96.0	76.8	147.8	184.5
4	.8	1.50	50.0	80.0	96.0	76.8	61.4	118.3
5	.8	1.50	25.0	40.0	64.0	76.8	61.4	49.2
6	0	1.50	10.0	20.0	32.0	51.2	61.4	49.2
$\sum$			935.0	1310.0	1653.0	2030.9	2469.1	3001.6

Age	Year 6	Year 7	Year 8	Year 9	Year 10	Year 11	Year 12
0	2150.3	2678.5	3305.2	4076.2	5027.6	6203.7	7658.0
1	697.4	860.1	1071.4	1322.1	1630.5	2011.1	2481.5
2	344.2	418.5	516.1	642.8	793.2	978.3	1206.6
3	226.6	275.4	334.8	412.9	514.3	634.6	782.6
4	147.6	181.3	220.3	267.8	330.3	411.4	507.7
5	94.6	118.1	145.0	176.2	214.3	264.2	329.1
6	39.3	75.7	94.5	116.0	141.0	171.4	211.4
$\sum$	3700.1	4607.5	5687.2	7014.0	8651.2	10674.7	13176.9

Table 4.4: Table 4.1C

C. Increasing population with p_x and m_x as shown, $\lambda = 1.234$.

AGE	n_x/N_t		proportion
0	635.0/1090.1	=	0.583
1	190.8/1090.1	=	0.175
2	95.4/1090.1	=	0.088
3	65.9/1090.1	=	0.060
4	46.3/1090.1	=	0.042
5	33.1/1090.1	=	0.030
6	23.6/1090.1	=	0.022

Table 4.5: Calculations of Age Structure

The n_x data were taken from Year 9, Table 4.3.

Age	Year 0	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
0	100.00	78.75	62.50	49.60	39.36	31.23	24.78
1	50.00	40.00	31.25	25.00	19.84	15.74	12.49
2	25.00	20.00	16.00	12.60	10.00	7.93	6.29
3	12.50	10.00	8.00	6.40	5.04	4.00	3.17
4	6.25	5.00	4.00	3.20	2.56	2.01	1.60
5	3.12	2.50	2.00	1.60	1.28	1.02	0.80
6	1.56	1.25	1.00	0.80	0.64	0.51	0.40
$\sum$	198.43	157.50	125.00	99.20	78.72	62.46	49.53

Age	year 7	Year 8	Year 9
0	19.66	15.60	12.37
1	9.91	7.86	6.23
2	4.99	3.96	3.14
3	2.51	1.99	1.58
4	1.25	1.00	0.79
5	0.64	0.50	0.40
6	0.32	0.25	0.20
$\sum$	39.39	31.26	24.71

Table 4.6: A Decreasing Population

A. Age-specific survival 40% for all age classes. Production of 1 female offspring per year beginning at age 1. Finite rate of increase, $\lambda = 0.79343$.

A fundamental law of demographic mechanics is that although populations may have shifting age distributions at certain stages of growth, given constant survival, l_x, and natality, m_x, they tend toward, and will ultimately reach an unchanging or "stable" age distribution. A stable age distribution is where the proportions of individuals in each age class remains constant through successive time iterations. While stable age distributions never seem to be found in wild populations, the concept is of major theoretical importance. Populations may be increasing, not changing, or decreasing, and still be at stable age distribution. A special case of stable age distribution, called "stationary" age distribution, exists when the population abundance as well as age structure is unchanging. Tables 4.6, 4.7 and 4.8 illustrate decreasing, stationary, and increasing populations that have reached stable age distribution. Note that stable age distribution is determined by the relative values of l_x and m_x, not by the initial age structure.

Tables 4.6, 4.7, and 4.8 show 3 life history projections that demonstrate effects of varying probabilities of survival across age classes. Note that even though each population has identical initial numerical and age structures, all have different stable age distributions as a consequence of differing l_x schedules. All populations shown are at stable age distribution by Year 9. All numbers have been truncated at accuracy level shown.

Tables 4.9, 4.10, and 4.11 show life history projections that demonstrate the effects of varying initial age composition. For these tables, all $p_x = 0.6$, $m_o = 0.0$, and all other m_x entries are 1.0. The population in Table 4.9 was started with 100 age zero individuals; Table 4.10 was started with 100 age 1 individuals; and Table 4.11 was started with 100 age 4 individuals. Note that the age zero offspring in Tables 4.10 and 4.11 are produced

Age	Year 0	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
0	100.00	98.43	97.65	96.87	96.09	95.31	94.53
1	50.00	50.00	49.21	48.82	48.43	48.04	47.65
2	25.00	25.00	25.00	24.60	24.41	24.21	24.02
3	12.50	12.50	12.50	12.50	12.30	12.20	12.10
4	6.25	6.25	6.25	6.25	6.25	6.15	6.10
5	3.12	3.12	3.12	3.12	3.12	3.12	3.07
6	1.56	1.56	1.56	1.56	1.56	1.56	1.53
$\sum$	198.43	196.76	195.29	193.72	192.16	190.59	189.03

Age	Year 7	Year 8	Year 9
0	93.75	92.28	92.21
1	47.26	46.87	46.49
2	23.82	23.63	23.43
3	12.01	11.91	11.81
4	6.05	6.00	5.95
5	3.05	3.02	3.00
6	1.53	1.52	1.51
$\sum$	187.47	185.93	184.40

Table 4.7: A Stationary Population

B. Age-specific survival 50% for all age classes. Production of 1 female offspring per year beginning at age 1. Finite rate of increase, $\lambda = 0.99179$.

by the 100 females in age classes 1 (Table 4.10) and 4 (Table 4.11). All populations are at stable age distribution at $t = 9$. All numbers have been truncated at accuracy level shown. The finite rate of increase, $\lambda = 1.19014$ for each of these 3 projections.

Age	Year 0	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
0	100.00	118.12	140.62	167.40	199.26	237.17	282.27
1	50.00	60.00	70.87	84.37	100.44	119.56	142.30
2	25.00	30.00	36.00	42.52	50.62	60.26	71.73
3	12.50	15.00	18.00	21.60	25.51	30.37	36.15
4	6.25	7.50	9.00	10.80	12.96	15.30	18.22
5	3.12	3.75	4.50	5.40	6.48	7.77	9.18
6	1.56	1.87	2.25	2.70	3.24	3.88	4.66
$\sum$	198.43	236.24	281.24	334.79	398.51	474.31	564.51

Age	Year 7	Year 8	Year 9
0	335.92	399.80	475.82
1	169.36	201.55	239.88
2	85.38	101.62	120.93
3	43.04	51.22	60.97
4	21.69	25.82	30.73
5	10.93	13.01	15.49
6	5.51	6.56	7.81
$\sum$	671.83	799.58	951.63

Table 4.8: An Increasing Population

C. Age-specific survival 60% for all age classes. Production of 1 female offspring per year beginning at age 1. Finite rate of increase, lambda = 1.19014.

Age	Year 0	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
0	100.00	60.00	72.00	86.40	103.68	124.42	149.30
1		60.00	36.00	43.20	51.84	62.20	74.64
2			36.00	21.60	25.92	31.10	37.32
3				21.60	12.96	15.55	18.66
4					12.96	7.77	9.33
5						7.77	4.66
6							4.66
$\sum$	100.0	120.00	144.00	172.80	207.36	248.83	298.52

Age	Year 7	Year 8	Year9
0	176.36	209.95	249.93
1	89.57	105.82	125.97
2	44.79	53.74	63.48
3	22.39	26.87	32.24
4	11.19	13.43	16.12
5	5.59	6.71	8.06
6	2.79	3.35	4.03
$\sum$	352.71	419.90	499.85

Table 4.9: table4.3A

Age	Year 0	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
0	100.00	120.00	144.00	172.80	207.36	248.83	293.93
1	100.00	60.00	72.00	86.40	103.68	124.42	149.28
2		60.00	36.00	43.20	51.84	62.20	74.64
3			36.00	21.60	25.92	31.10	37.32
4				21.60	12.96	15.55	18.66
5					12.96	7.77	9.33
6							4.66
$\sum$	200.00	240.00	288.00	345.60	414.71	497.60	587.86

Age	Year 7	Year 8	Year 9
0	349.92	416.54	495.82
1	176.36	209.95	249.93
2	89.57	105.82	125.97
3	44.79	53.74	63.48
4	22.39	26.87	32.24
5	11.19	13.43	16.12
6	5.59	6.71	8.06
$\sum$	699.83	833.08	991.64

Table 4.10: table4.3B

Age	Year 0	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
0	100.00	120.00	144.00	151.20	181.44	217.73	261.27
1		60.00	72.00	86.40	90.72	108.86	130.64
2			36.00	43.20	51.84	54.43	65.31
3				21.60	25.92	31.10	32.65
4	100.00				12.96	15.55	18.66
5		60.00				7.77	9.33
6			36.00				4.66
$\sum$	200.00	240.00	288.00	302.39	362.87	435.45	522.45

Age	Year 7	Year 8	Year 9
0	310.73	369.51	439.39
1	156.76	186.44	221.71
2	78.38	94.05	111.86
3	39.19	47.02	56.43
4	19.59	23.51	28.21
5	11.19	11.75	14.10
6	5.59	6.71	7.05
$\sum$	621.45	739.02	878.77

Table 4.11:

Life history projections showing effects of varying initial age composition. For these tables, all p_x values are 0.6. For the m_x vector, $m_1 = 0.0$ and m_1 through m_6 are set to 1.0. Population 4.9 was started with $n_0 = 100.0$ individuals. Population 4.10 was started with $n_1 = 100.0$, and population 4.11 was initialized with $n_4 = 100.0$ individuals. Note that in the Tables 4.10 and 4.11 the 100 n_0 individuals in Year 0 are offspring of the initializing 100 individuals in ages 1 and 4 respectively.

Chapter 5

Contents of this Chapter are pending.

Chapter 6

Derivable Population Attributes

Given fixed schedules of l_x and m_x and sufficient time, populations tend toward and finally reach a "stable age distribution."

Once stable age distribution is reached, population growth with respect to time is

$$\frac{dN_t}{dt} = rN_t \tag{6.1}$$

In integrated form this is

$$N_t = N_0 e^{rt} \tag{6.2}$$

Taking natural logs of both sides of Equation 6.2 gives

$$\ln N_t = \ln N_0 + rt \tag{6.3}$$

from which a graph of Log_e of population size against time is a straight line of slope r. Replacing t with 1 in Equation 6.2 defines the finite rate of increase, lambda,

$$
\begin{aligned}
N_1 &= N_0 e^r \tag{6.4}\\
&= N_0 \lambda \tag{6.5}\\
\ln \lambda &= r, \tag{6.6}\\
\lambda &= e^r \tag{6.7}
\end{aligned}
$$

$$\tag{6.8}$$

Given a population that has attained a stable age distribution and is increasing at the finite rate λ per unit time, the ratio of total population size at $t-1$ divided into the population size at t is the finite rate of increase. This fact is expressed as

$$\lambda = \frac{N_t}{N_{t-1}} \tag{6.9}$$

Solving for N_t gives

$$N_t = \lambda N_{t-1} \tag{6.10}$$

and, continuing backward 1 time step gives

$$N_{t-1} = \lambda N_{t-2} \tag{6.11}$$

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and reaching backward for k time periods gives

$$N_t = \lambda^k N^{t-k} \tag{6.12}$$

Here again is the geometric growth series, with the difference that Equation 6.12 is reaching back into time for values of N_{t-k} and computing successive steps results in population size for time t.

Given a sequence where it may be assumed that all members entered the population at age n_0 (for example, starting about Year 6 in Table 4.8), then the number of individuals in any given age x to $x + 1$ at t is

$$n_{x,t} = n_{0,t-x} l_x \tag{6.13}$$

In Equation 6.13, the number of individuals in the x to $x + 1$ age class at time t is the total number that began that cohort at $t - x$, (that is $n_{0,t-x}$) multiplied by the probability of survival from age 0 to age x (l_x).

As discribed in Chapter 4, the number of new n_0 individuals entering the population at t is produced by the number of reproducing females in the various age classes at time t. This relationship was

$$n_{0,t} = \sum_{1,w}^{\omega} n_{x,t} m_x \tag{6.14}$$

Then, utilizing Equation 6.14, to express the number of age zero individuals entering the population, but substituting, $n_{0,t-x} l_x$, from Equation 6.13 for $n_{x,t}$ in the right hand side gives

$$n_{0,t} = \sum_{x=1}^{\omega} n_{0,t-x} l_x m_x \tag{6.15}$$

Dividing both sides by $n_{0,t}$ gives

$$1 = \sum_{x=1}^{\omega} \frac{n_{x,t-x} l_x m_x}{n_{0,t}} \tag{6.16}$$

As previously discussed, the rate of increase of total population size once stable age has been attained is, from Equation 6.12, for k seasons of population growth

$$\frac{N_t}{N_{t-k}} = \lambda^k \tag{6.17}$$

Since the proportion in any given age class does not change in a stable age distribution, this result will hold for any age class. Thus, the number of age zero individuals entering the population at time t (that is $n_{0,t}$) has a similar relationship to the number of new individuals at $t - 1$. The rate of increase of the zero age class is given by

$$\frac{n_{0,t}}{n_{0,t-x}} = \lambda^x. \tag{6.18}$$

Taking reciprocals, this becomes

$$\frac{n_{0,t-x}}{n_{0,t}} = \lambda^{-x}. \tag{6.19}$$

Substituting this result in Equation 6.16, we obtain

$$1 = \sum_{x=1}^{\omega} \lambda^{-x} l_x m_x \qquad (6.20)$$

Equation 6.20 is a solution for the finite rate of increase, λ, in a seasonally breeding population with overlapping generations. It is a discrete version of

$$1 = \int_{x=0}^{\omega} e^{-rx} l_x m_x dx \qquad (6.21)$$

which is appropriate for continuously breeding populations.

6.1 Rates of Increase

Equation 6.20 is a polynomial in lambda and, given constancy in l_x and m_x, can be solved by inserting trial-and-error values of λ. A simple first approximation of lambda can be obtained by applying Equation 6.9 to total population, N_t, sizes from population projections such as those in Tables 4.2 and 4.3, and 4.8. Thus, the finite rate of increase can be obtained for any set of l_x and m_x schedules in 2 ways: (i) iterate through a life history projection as in Table 4.2; or (ii) solve Equation 6.20 by inserting trial-and-error values of lambda.

An instantaneous rate of increase, r, is obtained by taking the natural log of lambda (see Equation 6.2). Considerable confusion exists as to what this rate of increase really implies. Various instantaneous rates of increase exist according to the restrictions, or assumptions, placed on the l_x and m_x schedules in Equations 6.20 or Equation 6.21. If environmental conditions are optimal in all respects for the growth of a population, the rate of increase is appropriately called "biotic-potential," and can be denoted by r_p. Under specified conditions of temperature, humidity and other abiotic factors, and with biotic factors (such as competitors, predators, etc.) being optimal for population growth, the intrinsic rate of increase, r_m is obtained. Specifying the abiotic and biotic environments — both of which are presumably sub-optimal for population growth — produces a rate of increase denoted by r_s.

Each of the 3 rates of increase (r_p, r_m, and r_s), are computed in identical ways as described above. The differences between them lie in the assumptions placed on the respective l_x and m_x schedules. Additionally, each of these 3 rates of increase contains the implicit assumption that the population is at a stable age distribution; thus, each rate of increase is to be considered as a constant under specified conditions.

A fourth rate of increase, denoted r, can be obtained (see Equation 6.2). Here only density estimates over time are required. By conducting a regression analysis of lnN_t against t, a straight line of slope r is obtained. This rate of increase, r, under conditions of specified assumptions described above, can estimate any of the 3 rates of increase: r_p, r_m or r_s. Conversely, r may not be an estimate of any of these 3 rates of increase, because the restrictive assumptions are not met. It will most often be the case that wild populations are not at stable age distribution, and that estimating the rate of increase as described in this chapter is often simply not worth trying.

These instantaneous rates of increase may be either negative, zero or positive. Finite rates of increase such as λ or R_o may be either zero or positive.

6.2 Stable Age Distribution

It may be seen, from Tables 4.2, 4.3, and 4.4, that an iterative solution for stable age distribution is obtained from the life history projections. By having an estimate of λ for a population, several additional demographic parameters become available.

The equation for stable age distribution can be derived by starting with the equation for age structure (see Chapter 3). In this equation, C_x was used to denote simple age distribution. Stable age distribution will be denoted by c_x. By utilizing concepts developed above in the derivation of λ, we can obtain the derivation for stable age distribution. As previously indicated, the equation for computing age structure, which was written as (now substituting c for C)

$$c_{x,t} = \frac{n_{x,t}}{\sum_{y=0}^{\omega} n_{y,t}} \tag{6.22}$$

is modified using the relationship

$$n_{x,t} = n_{0,t-x} l_x \tag{6.23}$$

to obtain

$$c_{x,t} = \frac{n_{0,t-x} l_x}{\sum_{y=0}^{\omega} n_{0,t-y} l_y} \tag{6.24}$$

Dividing the numerator and denominator of the right hand side by $n_{0,t}$ gives

$$c_{x,t} = \frac{n_{0,t-x} l_x / n_{0,t}}{\sum_{y=0}^{\omega} n_{0,t-y} l_y / n_{0,t}} \tag{6.25}$$

and by applying the fact that

$$\lambda^{-x} = \frac{n_{0,t-x}}{n_{0,t}}, \tag{6.26}$$

the result is

$$c_{x,t} = \frac{\lambda^{-x} l_x}{\sum_{y=0}^{\omega} \lambda^{-y} l_y} \tag{6.27}$$

Using Equation 6.27, stable age distribution can be obtained as shown in Tables 6.1 and 6.2. The stable age distribution obtained in Table 6.1 is the same as the age distribution for Table 4.8 Year 9. This shows that stable age distributions also may be obtained by iterating through a life history projection, or by utilizing Equation 6.27 if an estimate of λ is available.

6.3 Generation Time

It has been shown previously (Chapter 3) that Net Reproductive Rate, R_o, of a population starting with an n_0 cohort at stable age distribution is the sum of the products of the expected age-specific production of females and the respective age-specific probabilities of survival. This value is the net reproductive rate of the population over the time an average female is expected to remain in the population, and is expressed as

$$R_o = \int_{x=0}^{\omega} l_x m_x dx \tag{6.28}$$

x	n_x	l_x	m_x	λ^{-x}	$\lambda^{-x}l_x$	c_x
0	475.82	1.000	0.0	1.000000	1.000000	0.500002
1	239.88	0.504	1.0	1.000012	0.504146	0.252974
2	120.93	0.254	1.0	1.000024	0.254156	0.127078
3	60.97	0.128	1.0	1.000036	0.128145	0.064073
4	30.73	0.064	1.0	1.000048	0.064583	0.032036
5	15.49	0.032	1.0	1.000060	0.032552	0.016276
6	7.81	0.016	1.0	1.000072	0.016411	0.008206
$\sum$					1.999993	0.999745

Table 6.1: Stable Age Distribution from Time-Specific Data

Calculation of Stable Age Distribution with n_x data from time-specific column in Table 4.8 Year 9. Value of λ used was 0.999988.

x	n_x	l_x	m_x	λ^{-x}	$\lambda^{-x}l_x$	c_x
0	167.40	1.000	0.0	1.000000	1.000000	0.499999
1	100.44	0.600	1.0	0.840231	0.504139	0.252069
2	60.26	0.360	1.0	0.705988	0.254156	0.127078
3	36.15	0.215	1.0	0.593193	0.128130	0.064065
4	21.69	0.129	1.0	0.498419	0.064595	0.032297
5	13.01	0.077	1.0	0.418787	0.032565	0.016282
6	7.81	0.046	1.0	0.351878	0.016419	0.008209
$\sum$					2.000104	0.99999

Table 6.2: Stable Age Distribution from Cohort Data

Calculated stable age distribution from cohort (time-dynamic) analysis. Cohort is taken from Table 4.8 beginning in Year 3 and ending Year 9. Value of λ used was 1.190149.

or approximately as

$$R_o = \sum_{x=0}^{\omega} l_x m_x \qquad (6.29)$$

If, in its lifetime, a female is expected to produce R_o female offspring, and generation time is defined as the time it takes a population at a stable age distribution to grow by the factor R_o, one notion of generation time may be derived as follows. Given that a population is growing according to

$$N_t = N_0 e^{rt}, \qquad (6.30)$$

let T be generation time, and substitute T for t as follows

$$N_T = N_0 e^{rT}. \qquad (6.31)$$

Dividing both sides by N_0 gives

$$\frac{N_T}{N_0} = e^{rT}, \qquad (6.32)$$

but since N_T/N_0 is the rate that the population will grow during the time T, then

$$\frac{N_T}{N_0} = R_o = e^{rT}. \qquad (6.33)$$

Taking

$$\ln R_o = \ln e^{rT} = rT \qquad (6.34)$$

and dividing both sides by r, an expression is obtained for generation time, T, as

$$T = \frac{\ln R_o}{r} \qquad (6.35)$$

While this expression may seem to make sense for some situations, it is undefined for the case of a stationary age distribution where $r = 0$, thus making the solution unsatisfactory as a general property of populations.

Other derivations for generation time follow from the notion that equations of the form

$$E_x = \sum_{x=0}^{\omega} x f_x \qquad (6.36)$$

are a general solution for the first moment of f_x; that is, the mean of the discrete probability density function f_x. One such measure is "cohort generation time," T_c, which is expressed as

$$T_c = \frac{1}{R_o} \int_{x=0}^{\omega} x l_x m_x dx \qquad (6.37)$$

or approximately

$$T_c = \frac{1}{R_o} \sum_{x=0}^{\omega} x l_x m_x \qquad (6.38)$$

Here we have the mean of the $l_x m_x$ schedules divided by the net reproductive rate. This equation for T_c represents the mean age of mature females at the birth of all of their female offspring. It is scaled externally (outside the integral) by the fact that the population may not be at a stationary age distribution.

A slightly different interpretation of generation time can be obtained as

$$\overline{T} = \int_{x=0}^{\omega} x e^{-rx} l_x m_x dx \tag{6.39}$$

or approximately as

$$\overline{T} = \sum_{x=0}^{\omega} x \lambda^{-x} l_x m_x \tag{6.40}$$

In this case, $\overline{T}$ represents the mean age of mature females at the birth of their first female offspring. Thus, $\overline{T}$ is the expected value (mean) of the density function

$$e^{-rx} l_x m_x. \tag{6.41}$$

Only in the case where the population is at a stationary age distribution ($\lambda = 1, R_o = 1, r = 0$) will T_c and $\overline{T}$ provide the same result. The value $\overline{T}$ "corrects" for the fact that the population may not be at a stationary age distribution (note, however, that the population must still be at stable age distribution). However, these corrections appear within the integral; that is, $l_x m_x$ for each x is being scaled by e^{-rx} while T_c scales the summed products of the $l_x m_x$ schedule.

Thus, T_c and $\overline{T}$ present rather different biological interpretations, with T_c being an estimate of the mean age of mature females at the birth of all offspring, and $\overline{T}$ being an estimate of the mean age of mature females at birth of their first offspring. In a growing population where younger age classes are heavily represented, $\overline{T}$ will be smaller than T_c, since the probability that any given age zero individual will survive to reproduce is proportionally high. In a declining population the reverse is true, and $\overline{T}$ will be greater than T_c. The important point to recognize is that neither of these values, T_c or $\overline{T}$, is necessarily preferable, and that both provide somewhat different information about population mechanisms. Taken together, they provide a better understanding of the population than either presented alone. A sample computation of these two generation times is shown in Table 6.3.

6.4 Reproductive Value

If a female is removed from a population, its yet-to-be-born offspring (and their offspring, etc.) also are removed. Some age classes have the potential to contribute more future offspring than others. Thus, a female past reproductive age can be removed without any depressant effect on population growth rate, while a female just entering breeding age might have quite a strong effect, particularly in a small population. This concept can be observed in Chapter 4 Tables 4.9 and Table 4.10.

Each population in Tables 4.9 and 4.10 starts with 100 individuals and, once stable age distribution is reached, will grow at the same rate because the $l_x m_x$ schedules are the same. It can be seen, however, that the population in Table 4.10 contains roughly twice as many individuals in Year 9 as does the population in Table 4.9. Since both of these populations were started with the same number of females, one might guess that in this example a one-year old female is worth about $991.42/499.64 = 1.98$ times as much as a zero-year old female.

x	l_x	m_x	λ^{-x}	$x l_x m_x$	$\lambda^{-x} x l_x m_x$
0	1.0000	0.0	1.0000	0.0	0.0
1	0.6000	1.0	0.8402	0.6000	0.5041
2	0.3600	1.0	0.7059	0.7200	0.5083
3	0.2160	1.0	0.5932	0.6300	0.3737
4	0.1296	1.0	0.4984	0.5184	0.2583
5	0.0777	1.0	0.4188	0.3885	0.1627
6	0.0466	1.0	0.3518	0.2796	0.0983
$\sum$				3.1365	1.9056

$$R_o = \sum_{x=0}^{\omega} l_x m_x \tag{6.42}$$

$$= 1.4299 \tag{6.43}$$

$$\tag{6.44}$$

$$T_c = \frac{1}{R_o} \sum_{x=0}^{\omega} x l_x m_x \tag{6.45}$$

$$= 0.6993(3.1365) \tag{6.46}$$

$$= 2.19 \tag{6.47}$$

$$\tag{6.48}$$

$$\overline{T} = \sum_{x=0}^{\omega} \lambda^{-x} x l_x m_x \tag{6.49}$$

$$= 1.90 \tag{6.50}$$

$$\tag{6.51}$$

Table 6.3: Calculating Generation Times

Calculation of 2 different generation times, T_c and $\overline{T}$. Data taken from the Cohort schedule in Table 3.4. The value of λ used is 1.19014.

x	l_x	m_x	λ^x	λ^x/l_x
0	1.000	0.0	1.000000	1.000000
1	0.600	1.0	1.190140	1.983567
2	0.360	1.0	1.416433	3.934537
3	0.215	1.0	1.685754	7.840715
4	0.129	1.0	2.006283	15.552582
5	0.077	1.0	2.387758	31.009841
6	0.046	1.0	2.841766	61.777210

x	λ^{-y}	$\lambda^{-y}l_y m_y$	$\sum_{x=y}^{\omega} \lambda^{-y}l_y m_y$	v_x
0	1.000000	0.0	0.998574	0.998574
1	0.840237	0.504142	0.998574	1.980738
2	0.705999	0.254160	0.494432	1.945361
3	0.593206	0.127539	0.240272	1.883904
4	0.498434	0.064298	0.112733	1.753289
5	0.418803	0.032248	0.048435	1.501962
6	0.351894	0.016187	0.016187	0.999993

Table 6.4: Calculating Fisher's Reproductive Value

Data taken from cohort schedule in Table 3.4. The value of λ used is 1.19014. All numbers were truncated at accuracy level shown.

One procedure for estimating reproductive value is to set the value of a zero year old at 1. Then, for seasonal breeders, reproductive values for the remainder of the age classes are relative to 1, and are given by

$$v_x = \frac{\lambda_x}{l_x} \sum_{y=x}^{\omega} \lambda_{-y} l_y m_y \qquad (6.52)$$

where v_x is the reproductive value of an x year old, relative to $v_0 = 1$. The procedure for calculating reproductive values is shown in Table 6.4. Subject to some rounding errors, the v_x column in Table 6.4 shows a reproductive value of about 1 for the zero age group, 1.98 for the one year olds and so on.

Knowledge of reproductive value can have important applications. If a goal is to control overpopulation, females of higher reproductive values might be removed. Conversely, one should leave such females if goals involve optimizing or maximizing production. In restocking or introduction programs where population success is the goal, females of high reproductive value should be well-represented in the translocated population. Similar applications of reproductive value to plant populations do not work as well, since older age classes of perennial plants do not translocate very well.

Chapter 7

Assumptions and Population Projections

The chapters on Natality, Survival, and Elementary Population Projections (Chapters 2, 3, and 4) were presumptuous enough to show the algebraic manipulation of natality and survival data without specific reference to the quality of the data or to the explicit assumptions that restrict the scope of inference available. The principal purpose for constructing a life schedule is to estimate patterns of mortality in study populations. Given natality data, it is further possible to develop projections of population responses such as growth, demographic transition patterns, or responses to hypothetical perturbations. If the data are collected properly and meet the required assumptions this goal is attainable. The opposite conclusion is equally true; if the data are not appropriate, then no amount of manipulation will retrieve the "truth" in the sense of proper estimations of parametric values. In the absence of a stationary age distribution, the *only* way to obtain a true estimate of survival is to analyze time-dynamic (*i.e.* Cohort) data. Given only a single sample from a population, it is not possible to detect a stationary age distribution even if such an unlikely event were to occur. In spite of the fact that life-table analyses are commonly produced on age-structure data taken from a time-specific sample of a population, this procedure is subject to particularly restrictive assumptions, and it is easily demonstrated that the resultant estimates may well be grossly erroneous.

For example, note the considerable differences between the expanded life tables shown in Tables 3.3 and 3.4 . The true picture of what occurs in the population projection in Table 4.8 is reflected by the Cohort analysis shown in Table 3.4. That is, the survival values from which Table 4.8 was generated are retrieved only by the Cohort analysis conducted and shown in Table 3.4. The time-specific analysis of Table 4.8 is shown in Table 3.3. Clearly, these are different versions of the same population. The time-dynamic vs. time-specific analyses produce different results. The same thing would be true if such a comparative analysis were to be conducted on the declining population shown in Table 4.6.

In a growing population, for example Table 4.8 a time-specific analysis will underestimate true survival. In a declining population, for example Table 4.6, a time-specific analysis will overestimate true survival. Only in the case where the population is at Stationary Age Distribution will a time-specific analysis retrieve the true survival schedule, as properly revealed by a time-dynamic analysis. In a time-specific

analysis, the extent to which survival schedules are underestimated (in a growing population), or overestimated (in a declining population) depends on the distance these growth rates are from Stationary Age Distribution. As λ diverges from 1 in either direction, the amount of bias in survival estimates increases accordingly. A time-dynamic (or diagonal or cohort) analysis will always estimate the true survival rates of the population.

The message is a simple one: if you require accurate estimates of survival, design the experimental procedures such that a full cohort may be followed. Note however, that the worth of the survival estimates also depends on sampling design and intensity. Simply following individuals in the population through time is necessary but not sufficient for good estimates. If you are able to follow all individuals in a population through time, and thus obtain survival data without sampling error, these equations will work for estimating survival schedules. However, if as will more typically be the case, you are sampling from a population, estimating survival is even more difficult, and you will want to use one of the capture-recapture algorithms (such as those modified from the Jolly methods) for estimating population parameters.

If you cannot, or choose not to follow the dictates of this assumption of Stationary Age Distribution, you must be particularly cautious in interpreting the results. In Chapter 10, I have described a modelling approach that amounts to a statistical reconstruction of the population history. The approach is clearly not entirely adequate. However, in cases where the gaining of some understanding is essential, you may well be left with little choice. The object then, is to make the best use of what data you do have, with full recognition of the pitfalls involved.

The basic population projection algorithm described in Chapter 4 reduces to the commonly seen exponential growth equation

$$\frac{dN}{dt} = rN \tag{7.1}$$

as described in Chapter 6.

The simple addition of a density-dependent "damping" function, to the right hand side produces the familiar Lotka-Volterra equation for population growth

$$\frac{dN}{dt} = rN \left(\frac{K - N}{K} \right) \tag{7.2}$$

This equation, typically referred to as the "logistic equation," is further discussed in Chapter 12.

The basic equation shown in Chapter 6 and again as Equation 7.1 above can be converted to an iterative form by integrating to give

$$N_t = N_0 e^{rt} \tag{7.3}$$

The expansion of Equation 7.3 to include age structure then led to an additional series of equations shown in Chapter 4. These were the natality projection (leaving aside the decomposition of m_x for the moment)

$$n_{0,t} = \sum_{x=1}^{\omega} n_{x,t} m_x \tag{7.4}$$

and the survival projection

$$n_{x+1,t+1} = n_{x,t}p_x \qquad (7.5)$$

Equations 7.4 and 7.5 thus form an elementary population projection model that has relatively low sophistication, but is useful as a pedagogical tool and for its' ability to be expanded into a real population projection algorithm. This elementary population model also provides a focal point for discussions concerning assumptions in population models.

One reasonable approach to the craft of model building is to start with a basic model structure, detail the various assumptions, (explicit ones are easy, implicit ones may be subtle and difficult), and then construct a model structure that allows relaxation of those assumptions you are interested in evaluating.

As described in Chapter 1, there are 4 primary population parameters, natality, mortality, immigration, and emigration. In Equation 7.1 the population model is about as fundamental as such things can get, and only abundance (N) and an instantaneous rate of increase (r) are included as parameters. The rate of increase can be any of the several described in Chapter 4, and you must know which in order to make proper use of the model for interpreting population mechanisms. In Equations 7.4 and 7.5, the addition of age structure leads to the basic projection model that includes only natality, survival, age, and time. Biologically these are necessary parameters for describing population processes. However, these attributes are not sufficient to describe the complex demographic patterns that species exhibit. The following assumptions limit the applicability of this basic model, and detract from the biological inferences and realism of resulting simulations.

1. The population is closed with respect to immigration and emigration; therefore abundance can only be changed through natality and mortality.

2. Natality (m_x) and survival rates (p_x) are constant across time, and are therefore independent of changes in population abundance or in the environment.

3. The inclusion of only females in the population model implies that there is no shortage of males for mating, that production of felmales and males is equal (*i.e.* the proportion of males across all age classes is 0.5 and constant), and and survival rates are equal for both sexes across all age classes.

4. The size of the age classes x to $x+1$ must be equal for all x, and must also be equal to the time intervals t to $t+1$. This imposes a restriction on the number of age classes used to describe the population since the age classes must be small enough to permit a transition into a subsequent age class (*e.g.* 5 year intervals for a species with a 5 day life expectancy will not work). Also, in general, time intervals must be large enough to permit only one reproductive effort. (In this instance, it is possible to pool across multiple reproductive periods, with subsequent loss of resolution).

5. All individuals within an age class are qualitatively identical; this means that they are behaviorally, genetically, and physiologically the same.

6. All females in the population reproduce according to the m_x schedule during each time interval; further, the m_x schedule is constant.

7. Response of the population structure is instantaneous; there are no time lags and no asymptotic limits.

8. Population parameters are constant over time and independent of abundance and environment (assumption No. 2 above); population growth is therefore deterministic and exponential.

One goal in writing a population model might be to develop a model structure that incorporates functional relationships such as those in the above list of assumptions. The model thus becomes more able to reflect real population biology. Adding such detail has the concommitant effect of requiring ever more data from the real population, and such data are quite difficult to obtain. Thus the trade-off is between abstraction and reality, with the deciding factor being availabiltiy of information on the real population, and your intent in conducting the modelling exercise in the first place.

Chapter 8

Modelling Complex Population Dynamics

Making a population model more realistic, therefore more complex, involves envisioning the biological phenomena to be described, and writing mathematical structures that produce the desired results. The basic model described in Chapter 4 serves as a foundation. By successive relaxation of assumptions of interest (see Chapter 7), and by incorporating such other phenomena as you wish to study, a model for computing population projections emerges. The computational model is no more than a complex calculator conducting its' work according to a specified "algorithm." An algorithm is simply a computational solution to a particular mathematical structure. The model is a computing device that reflects your perception of how the demographic machinery of a population operates.

A philosophy for appropriate use of computer simulation models is discussed more fully in Chapter 10. The purpose of this chapter is to describe the mathematical structure of a particular algorithm as an example of how such models are developed. This algorithm follows a mathematical model that calculates population projections as described in Chapter 4, with consideration of many of the assumptions as described in Chapter 7.

This algorithm was designed and written to provide insight into the demographic machinery of exploited populations. The program deals with populations that:

1. are bisexual (therefore have sex-specific attributes);

2. have extended life spans with overlapping generations (therefore have age-specific attributes);

3. are iteroparous (therefore have complex reproductive attributes);

4. are wholly exploitable (therefore have complex mortality attributes); and

5. are variable through time (therefore possessing complex temporal functions related to 1) through 4) above.

Assumptions that currently constrain the model are:

1. it is independent of abundance and environmental specifics;

2. the size of the age classes x to $x + 1$ must be equally divisible into a reproductive "season" and a non-reproductive season;

3. the additive mortality prescribed influences only the non-reproductive season (this corresponds to "winter" mortality, hunting, etc.);

4. the span of time, t to $t + 1$ must be equally divisible into two "seasons," and t to $t + 1$ is equal to x to $x + 1$;

5. the model is deterministic;

6. the model lacks specific time lags (hypothesized time lags may be incorporated).

The coded version of this model is modular, with the practical result that constraint assumptions 1, 5, and 6 above can be readily relaxed by writing specific functional relations. Doing so requires species- and site-specific data (especially for assumptions 1 and 6), as well as uniquely hypothesized functional relations for attributes of concern. (SUBROUTINE DRIVE2, called by SUBROUTINE DRIVE1 is provided for these purposes).

Hunt[1] categories are age- and sex-specific; the maximum complexity possible is for each sex and age cell to equal 1 hunt category. Conversely, hunt categories can be pooled across ages. Sexes cannot be pooled (although they can be harvested similarly if one so chooses). Within a hunt category that contains pooled ages, individuals are removed proportional to their abundance in each age class.

Sex ratios at birth are obtained from clutch size data F'_x and sex ratio at birth data, $SEXRAT_x$, thus producing age-specific expectations for both females and males (females only are assumed to do the "producing," males contribute sperm subject to constraints described below).

Thus, preliminarily

$$F(x, i) = F'(x)SEXRAT(x) \tag{8.1}$$

where $F_{x,i}$ is expected sex-specific clutch size, x is age, and $i = 1 =$ females, $i = 2 =$ males. Specifically,

$$F_{x,2} = F'_x SEXRAT_x \tag{8.2}$$

and

$$F_{x,1} = F'_x - F_{x,2} \tag{8.3}$$

Sex-specificity in a model implies copulation ratios as well as other attributes. The usual implicit assumption is that sufficient adequate males are available so that copulation intensity is not reduced as a function of lack of capable males. However, real populations may well experience depression in potential rates of increase because of too few males. Thus, given minimum ages for participation in copulation for both females and males, and given a Critical Breeding Sex Ratio, $CBSR$, that is, the minimum ratio of males required for full fertilization of females who choose to participate, it is possible to modify breeding

---

[1]It is to be reemphasized that this model can deal with any abstraction that involves additive mortality. Thus, "hunt" is simply a euphemism for any hypothesized mortality agent, and might include such processes as competition, predation, accidents, and so forth. The decision concerning whether these processes are actually additive requires further information from the population in question.

proportions, β_x, accordingly. Compare the Operating Sex Ratio, OSR (the sex ratio of copulating adults at the onset of the insemination period) to $CBSR$, and if

$$OSR < CBSR \tag{8.4}$$

then breeding populations of females is reduced by

$$\beta_x OSR \tag{8.5}$$

and per capita age specific expectation of offspring is given by

$$M_{x,i,t} = F_{x,i,t}\beta_{x,t}OSR \tag{8.6}$$

These preliminary computations are made prior to each inseminating period.

Given these results and a survival schedule (p_x) from previously available data, projections from "Fall" (the insemination period) to "Spring" (the period where reproduction is a demographic reality and offspring are actually produced) follow from

$$n_{0,i,t} = \sum_{1,i,t}^{\omega} n_{x,1,t}m_{x,i} \tag{8.7}$$

and

$$n_{x+.5,i,t+.5} = n_{x,i,t}\sqrt{p_x} \tag{8.8}$$

For Spring, and a preliminary mortality (i.e. "ambient" mortality - that without any added harvest), for projection into Fall we use:

$$n_{x+1,i,t+1} = n_{x+.5,i,t+.5}\sqrt{p_x} \tag{8.9}$$

Note that p_x is the probability of survival across a whole age class, and thus $\sqrt{p_x}$ gives probability of survival across a half age class. Natality and mortality occur in the Spring, mortality only occurs in the Fall.

Given a tentative Fall projection of population structure, a choice is available of whether or not to impose an additive mortality schedule, if not, the model proceeds to options of changing primary population attributes, F_x, ρ_x, β_x, p_x, and thence into further projections.

Harvesting is imposed on the Fall population, according to the Hunt Categories described above, and a stated level of additional mortality per sex and hunt category. Given the total number of individuals to be removed during a hunt sequence, the sum across ages within sex and hunt category, and the proportions by sex and hunt category that are to be removed, a loop is generated across ages within sex and hunt categories and an appropriate number of individuals is removed from the previously generated Tentative Fall Population. This manipulation is:

$$n_{x,i}\prime = n_{x,i} - ((n_{x,i}/S)(PROP_{x,i}TOTKIL)) \tag{8.10}$$

The element $n_{x,i}/S$, S being the sum mentioned above, is the proportion of each age class within the hunt category to which the age class was assigned. $PROP_{x,i}$ is the specified proportion of individuals to be removed from a sex and hunt category. $PROP_{x,i}$ values are identical for all age classes within a single hunt category. The value

$PROP_{x,i} TOTKIL$ is the number of individuals to be removed from a hunt category. Multiplying this by the proportion of an age class within a hunt category, *i.e.* $n_{x,i}/S$, produces the number of individuals to be removed from an age class. This removal is thus scaled to the proportion of that age class within the hunt category.

A schematic of these relationships, natality plus mortality (Spring), ambient mortality only (Fall), additive mortality if requested (Fall), is shown in Figure 8.1. The mathematical structure of this model is relatively straightforward. Much of the complexity of the coded version stems from input/output requirements and staging of program integrity and fail-safe mechanisms.

It is instructive to conduct comparative analyses on data from a simulation model where you know the answers (in the sense of the parameters that were used to initialize and drive the simulation). Ths program computes life history and survival analyses following Chapter '3 on any of the Fall population structures. The internal mechanism for these analyses is a `History` matrix within the model that stores population structure for each spring and fall population. This matrix is of such a size that a full diagonal cohort occupies the cells, and thus, once this matrix is filled, cohort (the principle diagonal on the history matrix) analyses are available.

These life-history analyses are conducted on females, males, and both sexes. There are several obvious theoretical problems in so doing, nonetheless, the results are intriguing, and worth contemplating. Interpreting these results is described further in Chapter 10.

Chapter 9

Complex Dynamics: II

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Chapter 10

A Philosophy of Model Use

10.1 A Philosophy of Using What You Have

Good data are never very easy to obtain. In the case of demographic analyses of wild populations this is particularly true. If, however, one were to wait for totally proper and adequate data before attempting a demographic analysis, none would ever get done. Further, managing wild populations (in contrast to simply writing scholarly papers about them) often times requires that decisions be made whether or not adequate data exist. In such cases, you must make the best with what is available.

The objective, then, might well be framed in the context of conducting the most rigorous analysis that your data allow, and then proceed into an interpretative analysis that is fully cognizant of the consequences of the failure of the data to meet various mathematical assumptions in the analysis and modelling of the population. This Chapter describes an approach to demographic analysis and interpretation that represents an attempt to get the best from what you have, while at the same time, incorporating relevant amounts of caution.

Life history patterns of species differ in various ways, however, the basic theoretical considerations are common to all. Often, being interested in a particular phenomenon rather than a particular species, a researcher can choose life history patterns that provide relevant examples and relative ease with which certain attributes may be measured.

For example, clutch sizes and factors affecting them are well known for many birds (one has "only" to locate the nests and count eggs), and for many mammals (placental scars, embryo counts, etc.). In contrast, clutch sizes are poorly known for many species reptiles, and for fish and amphibians that scatter their eggs. As a result, an intensive study on the phenomenon of clutch sizes as a function of environment would be easier (not necessarily better) on such species as birds and mammals.

Conversely, much is known regarding survival patterns of birds from hatching to fledgling, and almost nothing from fledgling through adult life. Banding returns are notoriously low in such species, and relevant statistical inferences, while indicative of trends, are complex, difficult, and produce generally large variances. For the same reasons, survival in bats is poorly understood. Animals that can be marked and trapped again and again provide excellent subject for survival studies. Here, small mammals excel, and large mammals with long life spans have tended to be generally poor subjects. Lizards, too, are amenable to survival studies (in some species clutch size analyses as well, while results

with most species of fish, amphibians, and snakes have been disappointing at best.

The pattern is clear, logically and mathematically correct survival analysis requires cohort data. That means data collected over time domains that include a large portion (minimally) of the maximum life span of the individuals being studied. This is, for economic reasons as well as biological, a generally difficult task that for many species, has produced less than satisfactory results. Either it is technically or logistically impossible to obtain the needed data (*e.g.* many species of waterfowl), or the life-spans are such that the duration of the average research project is simply too short to produce good data.

Management disciplines have extended age-structure analysis by examining harvested animals as they are brought through "check stations." These data thus represent time-specific images of population age structure (problems of biased sampling and poor aging techniques aside). Because they represent data that superficially resemble cohort data, *i.e.* they both describe numbers of individuals per age class, they have long been utilized in life history analyses. Although the practice of gathering of this kind of data is quite common, proper analyses of such data are not common.

Under the argument that being able to determine the age of individuals from any given population is important, a large and diverse literature has developed over the past 100 or so years. The premise goes like this: age structure analysis will reveal survival patterns (using the algebraic procedures described in Chapter 3), therefore, it is important to know how to age animal species, and it is important to collect such data as ages of individuals in selected populations. Thus has grown what can only be called the "aging industry" in population ecology. This effort is particularly true in applied ecology, but no less important in non-management oriented research.

Various expressions of concern and advice to use caution on this matter have been produced in the past. However, the use and mis-use of aging data continues, often under a cloak of ignorance, and if not that, then under the contention that "it's better than nothing," or "we've got to do something..."

Careful examination of the projection tables shown in Chapter 4, the discussion of assumptions in Chapter 7, and the examples of survival schedule construction for time-specific vs. time-dynamic samples (Tables 3.3 and 3.4), show the effect of the critical assumption involved: *populations must be at stationary age distribution for an accurate revelation of truth from time-specific data.*

As previously indicated, Stationary Age Distribution is a special case of Stable Age Distribution, and the only way population structure will reach a Stable Age Distribution is for survival, l_x, and natality, m_x, to remain constant. The time span required for these schedules to remain constant is at least as many years as the maximum life span of the species, and then a few more. The length of time required depends upon the accuracy of the estimate for Stable Age Distribution desired.

For example, a simple functional definition of Stable Age Distribution can be devised through specification of an acceptable percentage deviation through time of

$$\lambda_t = \lambda_{t-1} = \lambda(t-2), = ... = \lambda_{t-k} \qquad (10.1)$$

for $k =$ perhaps one-fourth of the years involved in maximum age of the species being considered. This is not as good as checking for percentage deviation across each age and sex class proportion, $C_{x,i,t}$ *vs.* $C_{x,i,t-1}$, etc., since any given constant λ does not uniquely define a given Stable Age Distribution. It does, however, serve as a test value for most

purposes. It is possible on a computer to require 6 or more decimal place accuracy, which would take a population many annual iterations to reach Stable Age Distribution; conversely, one might specify agreement at the 5% level and thus be working with a much more "loose" Stable Age Distribution. The requirements here depend upon the purpose the analysis is intended to serve.

What then should one do? The answer seems to depend on the relative importance to be attached to any predictions or recommendations derived from a demographic analysis, and the urgency attached to the "we have to do something now" problem.

An experienced demographer can extract useful information out of poor data. Various techniques exist for manipulating survival data so that some information can be retrieved. The goal might well be one of *excluding certain potentials* rather than seeking a single truth. It is in the establishment and definition of population response potentials that the models described in this manual are designed to help.

Conducting a demographic analysis in this manner allows a careful researcher to seek plausible scenarios within the available data. Extremes in population response potentials may thus be accorded low probabilities of occurrence, or excluded entirely. Plausible events may be defined and further evaluated, including information that is relevant but generally external (e.g. abundance or shortage, good year-bad year sequences, etc.) to demographic analyses as described in this manual.

Given a suitably imaginative approach, and well seasoned with caution and responsibility, considerable understanding can be gained that can change a wild ass guess into an informed decision. It is the goal and approach of this manual to demonstrate this philosophy.

10.2   Reconstructing a Population History

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Appendix A

Life Table Calculations

A.1 Columns in an Expanded Life Table

Program lifehist computes an expanded life table as described in the discussion on analysis of survival data (Chapter 3). Columns produced are as follows.

If natality data, m_x, are provided, the program produces columns that are described in Chapter 6. The notation for these columns is as follows.

Additional derived attributes are denoted as follows:

A.2 Computing an Expanded Life Table

To begin execution of program lifehist enter

```
lifehist
```

The program will prompt for information as follows:

```
enter title of lifetable
```

which is a request for up to 72 columns of alphameric characters that identify the data set. This is followed by:

x	Age class
n_x	Number of individuals in the x to $x + 1$ age class
l_x	Probability of survival from age 0 to age x
d_x	Probability at age 0 of death during the interval x to $x + 1$
q_x	Age-specific mortality
p_x	Age-specific survival
L_x	Animal units to be lived during the interval x to $x + 1$
T_x	Animal units to be lived during the interval x to ω
e_x	Life expectancy from age x
P_x	Age specific survival following Leslie (1945)

Table A.1: Expanded Life Table for Survival Data

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m_x	Natality (Sex-specific expected production of offspring)
$l_x m_x$	Age-specific expected reproduction value
v_x	Fisher's reproductive value
c_x	Stable age distribution

Table A.2: Expanded Life Table for Natality Data

GRR	Gross Reproductive Rate
R_o	Net rate of increase
T	Generation time according to Lotka and Sharpe
T_C	Generation time according to Laughlin
$\overline{T}$	Generation time according to Leslie
λ	Finite rate of increase
r	Instantaneous rate of increase

Table A.3: Derived Variables in an Expanded Life Table

```
enter number of age classes
```

enter an integer that is less than or equal to 60 age classes.

Survival data may be entered in either of 2 forms: *(i)* an age structure column, n_x; or *(i)* as an already computed survival schedule, l_x. Survival schedules are equally applicable to either males or females, and if survival analysis is what is required, either of these forms of input are appropriate.

If, in addition, computation of the attributes that require natality are desired, two data forms are available: *(i)* survival data as n_x with natality data m_x; or *(i)* survival data as l_x with natality data m_x. If these latter 2 options are used, the n_x or l_x data typically refers to females. (Note that it is possible to conduct such calculations on males with an interesting twist in interpretation of life history attributes.) The program prompt is:

```
WRITE FORM OF DATA
  1 = NX  W/O  MX
  2 = LX  W/O  MX
  3 = NX  W/   MX
  4 = LX  W/   MX
```

Enter the number, 1 through 4, that corresponds to the form of data to be used.

Program lifehist can conduct some internal comutations in various ways. Several of the columns in the expanded life table require that some estimate of areas under the l_x curve be obtained. As shown in Chapter 3, these can either be approximated by assuming linearity between points, or be conducting a numerical integration of the l_x curve to obtaining the data elements in L_x (which are subsequently used in other columns). This computation involves a "spline fit;" that is, it fits a cubic equation to each interval between data points on l_x under the restriction that the derivatives at the data points are zero. This procedure works very well for complex l(x) schedules. For more simple survival schedules, *i.e.* "smoother" curves that appear to be straight across adjacent points, the linear approximation for L_x is preferred. lifehist prompts for your choice as follows:

```
enter 1 for linear approximation
      2 for numerical integration by cubic spline fit
```

Enter either a 1 or a 2 for this request.

Subsequent prompts depend upon the form of data requested previously. lifehist will prompt:

```
enter n(x) data
```

or

```
enter l(x) data
```

and if you have natality data as indicated by previous entry of data form 3 or 4:

```
write m(x) data
```

The program is designed so that you can enter data in "free format." You may enter data with elements separated by at least 1 space, or you may enter your data elements separately, entering a RET after each one. In the latter case, the program will continue to read these data elements until you have entered the entire schedule.

Following successful entry of the survival data and natality data if you requested this option, the program will compute and print an expanded life table as described above, and in Chapter 3, including the list of derived variables if you entered some natality data. If you requested the numerical integration the program will print some internal variables for the cubic equations from the spline fit so that you may check the fit.

Following the printing of the expanded life table, you will have the opportunity to recycle and enter another data set, or leave the program. The prompt is:

```
do you want another lifetable (yes or no)
```

Entering a yes will take you to the top of the program as described above. Entering a no will initiate program termination.

The results from your computations are written to a file in your working directory called lifehist.rslt. If you requested multiple tables, each is successively appended to this file, and each will be identified by the title of the data set requested when you began data entry for a particular run.

An actual report from program lifehist looks like this:

```
Summary of Life History Information for test
 JOB NUMBER  1
 x    n(x)     l(x)      d(x)      q(x)      p(x)      L(x)     T(x)
  0 100.000  1.00000  0.10000  0.10000  0.90000  0.95000  2.9000
  1  90.000  0.90000  0.10000  0.11111  0.88889  0.85000  1.9500
  2  80.000  0.80000  0.10000  0.12500  0.87500  0.75000  1.1000
  3  70.000  0.70000  0.70000  1.00000  0.00000  0.35000  0.3500
 x    e(x)     P(x)      m(x)    l(x)m(x)    v(x)      c(x)
  0  2.9000  0.89474  2.00000  2.00000  1.00000  0.76104
  1  2.1667  0.88235  3.00000  2.70000  4.12654  0.18442
  2  1.3750  0.46667  4.00000  3.20000  4.70681  0.04414
```

```
 3   0.5000 0.00000 3.00000 2.10000 3.00000 0.01040
    GRR         Ro          T          Tc         Tbar        lambda       r

    12.00000    10.00000    1.75491    1.54000    1.31399    3.71388    1.31207
```

```
Summary of Life History Information for test2
JOB NUMBER  2
SPLINE DUMP FOR test2
Y(I) =    1.000000  0.900000  0.800000  0.700000  0.600000  0.000000
X(I) =    1.000000  2.000000  3.000000  4.000000  5.000000  6.000000
DERIVATIVES AT THE KNOTS ARE
  -0.102392 -0.095215 -0.116746 -0.037799 -0.332057 -0.733971
CUBICS ON INTERVALS ARE
 I= 1XCUBE* 0.23923e-02+ XSQR*-0.71774e-02+ X*-0.95214e-01+  0.11000e+01
 I= 2XCUBE*-0.11966e-01+ XSQR* 0.78947e-01+ X*-0.26746e+00+  0.12148e+01
 I= 3XCUBE* 0.45454e-01+ XSQR*-0.43780e+00+ X* 0.12827e+01+ -0.33540e+00
 I= 4XCUBE*-0.16985e+00+ XSQR* 0.21459e+01+ X*-0.90521e+01+  0.13444e+02
 I= 5XCUBE* 0.13397e+00+ XSQR*-0.24114e+01+ X* 0.13734e+02+ -0.24533e+02
                0.9494        1.0506        2.0000
                0.8518        2.0574        2.9092
                0.7434        1.7465        2.4899
                0.6745       16.2699       16.9444
                0.3335      -30.5287      -30.1952
```

```
 x   n(x)    l(x)     d(x)     q(x)     p(x)     L(x)     T(x)
 0   0.000  1.00000  0.10000  0.10000  0.90000  0.94940  3.5526
 1   0.000  0.90000  0.10000  0.11111  0.88889  0.85179  2.6032
 2   0.000  0.80000  0.10000  0.12500  0.87500  0.74342  1.7515
 3   0.000  0.70000  0.10000  0.14286  0.85714  0.67454  1.0080
 4   0.000  0.60000  0.60000  1.00000  0.00000  0.33350  0.3335
 x    e(x)    P(x)     m(x)    l(x)m(x)   v(x)      c(x)
 0   3.5526  0.89718  2.00000  2.00000  1.00000  0.76584
 1   2.8925  0.87278  3.00000  2.70000  4.24493  0.18041
 2   2.1893  0.90735  4.00000  3.20000  5.35070  0.04198
 3   1.4400  0.49441  5.00000  3.50000  5.89743  0.00961
 4   0.5558  0.00000  4.00000  2.40000  4.00000  0.00216
 GRR         Ro          T          Tc         Tbar        lambda       r
 18.00000    13.79999    1.95817    2.11594    1.37857    3.8204343  1.34036
```

Appendix B

Survival Estimates from Regression Analysis

Program **survive** computes a log_e transformed n_x against x linear regression analysis and provides estimates of instantaneous and annual survival rates as described in Chapter 3. The program produces about a half-page of printout for each analysis.

Initiate execution of program **survive** by entering;

survive

You will be prompted for the following information:

enter identification for current data set

This is a request for up to 72 columns of alphameric characters that identify the data set you are about to enter.

enter maximum age of Fall individuals

is the next request. Note that the request is for Fall aged individuals, for most vertebrate species where production of offspring occurs in the Spring or Summer, Fall ages are fractional, such as 4.5. Program **survive** responds by printing an echo of your Fall age, and a computation of total number of age classes as follows:

maximum age = n   no. age classes = mmm:

where nnn and mmm are ages corresponding to the above discussion.

Program **survive** next prints a request for the fall n_x data:

enter n(x) vector for Fall individuals

The program reads data in "free format" and you need only to put a space between data elements for separation. Alternatively, you may enter a single data element at a time and the program will iterate until you have entered the last value.

After entering these data, Program Survive echos your input, runs the computations, and reports the results. This information is written to the screen, and also into a file in your working directory named **survive.rslt**.

Various intermediate statistics are reported to facilitate further statistical analyses (comparison of two survival estimates, for example).

Following the analysis report, Program Survive will prompt you with:

```
enter ''yes'' for another run, or ''exit'':
```

Entering an exit here will terminate program execution, a yes response will recycle the program, and you may proceed with data entry as described above. If you request more than a single run, successive results are appended to the file named survive.rslt.

An actual report from program survive looks like this:

```
Enter identification for current data set:

test

Enter maximum age for fall individuals:
Maximum age =  3.5:  No. age classes =     4:

Enter n(x) vector for Fall individuals:
n(x) =    100.0    80.0    60.0    40.0
x(x) =      0.5     1.5     2.5     3.5


xmean                           =    2.0000
ymean                           =    4.1926
sum of x squared                =    5.0000
sum of y squared                =    0.4695
sum of cross products           =   -1.5183

Explained mean square           =    0.4610
Unexplained mean square         =    0.0085
Mean square error               =    0.0291


Attribute estimates and 95% confidence limits:

Instantaneous survival rate = -0.30  (-0.18 -   -0.43)
Annual survival rate        =  0.74  ( 0.65 -    0.84)
Annual mortality rate       =  0.26  ( 0.16 -    0.35)

F at 1 and  2 df = 108.894  for test on slope.

Estimated n(x) vector back-calculated to age 0:

    x       n(x)
   ----   --------
    0      121.5
    1       89.7
    2       66.2
    3       48.9


Enter "yes" for another run, or "exit":
```

Reply = n

Appendix C

Computing Elementary Population Projections

PROGRAM DUMPOP requires entry of basic population information. As execution begins, you will see

```
Population Projection Model: Ver. 2.2, 15 Sep 88
An NMSU Science Workbench Program

Enter identification for current data set:
```

The identification line is 72 columns of information that will be used to label your reports for each simulation. Note that the program will echo all of your entered data. Everything you see on the screen is also being written to a file in your working directory called `dumpop.rslt` which you can save and look at when you choose.

The program than requests initializing information beginning with:

```
  enter number of age classes
```

This value contains the zero age class through the oldest age class, inclusive. For example, if the oldest animals are 9 years of age, the number of age classes is 10 (0 - 9). The program handles up to 24 age classes.

You will then be requested to enter the initial number of individuals per age class. This set of input begins with

```
  enter NX
```

to which you enter your age structure data. Enter each age class with a space between age classes (you do not need to worry about specific columns or formats).

The next program request is for selection of the type of survival data you wish to enter. The program will print

```
  survival form?  enter <lx> or <px>
```

Enter one or the other of these alternatives (either lx or px). Depending on your choice, the next prompt will request that you enter the survival data and looks like this:

```
  enter lx vector
```

(or px if you chose to enter age-specific survival). Enter the decimal point just as if you were writing the number on a sheet of paper, and put a blank space between the age classes.

After entering the survival data, you will be prompted to enter the fertility data. This looks like this:

```
enter mx vector
```

to which you enter the age-specific expection of daughter offspring as described in Chapter 2.

When the fertility data have been entered, the program produces an initializing summary of the population at `time = 0`, that is, the program will produce the state of the population following the initial information that you have entered. This summary lists the age class (left column), number of animals in each age class (middle column), and the proportion represented by each age class relative to the total population (right column).

Below these columns is a summary statement,

```
total population size at t = 0 is     xxxxx
```

followed by a query concerning whether you want to continue the population projection to the next time step:

```
iterate to t+1?   enter <yes> or <no>
```

If no is entered, the program will print a summary of population density and then quit. If you enter a yes the program will project the population to the next time step, and report the state of the population at that point. In addition, the program will report a finite (annual) growth rate, and an instantaneous growth rate, following the statement of total population size. Following this, the program will ask you if you want to "iterate to t+1" once again.

You may iterate the projections up to 100 time steps.

An actual report from a population simulation looks like this:

```
Population Projection Model: Ver. 2.2, 15 sep 88
 An NMSU Science Workbench Program


Enter identification for current data set:

test

enter number of age classes
reply:      4
enter NX
reply: 100.00 90.00 80.00 70.00
survival form?  enter <lx> or <px>
reply: lx
enter lx vector
reply:   0.80  0.70  0.60  0.50
```

```
enter mx vector
reply:   0.00  2.00  3.00  2.00
-----------------------------------------------------

summary for time =   0
```

age class	number	proportion
0	100.0000	0.294118
1	90.0000	0.264706
2	80.0000	0.235294
3	70.0000	0.205882

```
total population size at t =   0 is              340.0000

iterate to t+1?  enter <yes> or <no>
reply: y
-----------------------------------------------------

summary for time =   1
```

age class	number	proportion
0	539.7619	0.700015
1	87.5000	0.113478
2	77.1429	0.100046
3	66.6667	0.086460

```
total population size at t =   1 is              771.0715

growth is      2.26785731  r is       0.81883550


iterate to t+1?  enter <yes> or <no>
reply: ye
-----------------------------------------------------

summary for time =   2
```

```
    age class            number            proportion

        0               1298.1548           0.679758
        1                472.2917           0.247308
        2                 75.0000           0.039273
        3                 64.2857           0.033662
total population size at t =    2 is                  1909.7322

growth is      2.47672534  r is       0.90693724


iterate to t+1?  enter <yes> or <no>
reply: no
----------------------------------------------------

summary for time =    3



    age class            number            proportion

        0               3611.2354           0.692545
        1               1135.8855           0.217835
        2                404.8214           0.077635
        3                 62.5000           0.011986
total population size at t =    3 is                  5214.4424

growth is      2.73045731  r is       1.00446916


iterate to t+1?  enter <yes> or <no>
reply: n
-----------------------------------------


summary of projections

    t               popsize   lambda

    1                 771.1   2.2678573
    2                1909.7   2.4767253
    3                5214.4   2.7304573
```

Appendix D

Computing Complex Population Projections

Program popmod computes population projections according to the mathematical framework described in Chapter 4, with extensions that include 2–sexes, seasonality, and selective mortality, as described in Chapter 8.

This particular version of popmod simulates populations that have life-history attributes as follows in that they are:

- relatively long lived and contain overlapping generations;

- bisexual;

- definable in the form of age-specific attributes;

- seasonal in the sense that they breed during one definable period, and are reproductively inactive during a second, equal length period;

- age definable such that these 2 periods are of equal length age intervals;

- definable such that the 2 seasonal periods, thus the 2 age intervals, combine to form an analog to an "annual cycle" (note that "annual" need not be 1 year in real time, even though the program labels the listing according to Spring, Fall, and YEAR), the requirement here is repeatability of potential breeding followed by reproductive quiescence followed by potential breeding,... *etc.*;

- definable in the non-breeding, *i.e.* "Fall" period.

All initialization occurs on "Fall" age individuals. That is, individuals that were produced in one of the previous "Spring" periods. Thus, Fall age structure contains individuals of half year ages while Spring contains only even year-old individuals. Details of program operation are as follows.

The model begins with an initial request for basic information

```
Program popmod: Version 3.1, May 87:

Enter identification for this simulation run:
```

and after you enter your identification data the program will echo your data as follows:

`Simulation run identification header:`

`Up to 72 columns of your identification information goes here...`

Note that program popmod echos all of your replies back to the screen. The program also writes 2 additional reports of your simulation run. These reports are written into your working directory. The first of these is labeled `popmod.rslt`[1] and is identical to the information that was written to your screen as you proceeded through the simulation run. The second report produced is named `popmod.dump`. The dump file contains all of the information written to the screen, as well as a large amount of internal data. These internal data consist of listings that either provide additional demographic information (of more detail than you will typically want to know), or listings of internal calculations that can be used to verify that the program is calculating the values properly. Note that these 2 files are opened at the beginning of each simulation run. If you want to save either file, you must rename it to prevent your previous simulation information from being destroyed.

The files `popmod.rslt` and particularly `popmod.dump` can get very large. The `popmod.rslt` file can be used to reinitialize the program if you interrupt a simulation run. This allows you to continue on from where you quit the program earlier. Another use of the `popmod.rslt` file is that you can edit this file (*carefully!!*), changing only certain of the demographic attributes that you want to vary. In this manner, you can conduct a series of "what if" simulations by manipulating individual values without having to go through the bother of keying the entire simulation again. Note that these changes are limited to the replies that you previously entered during a simulation run. Finally, this iteration scheme allows you to carefully work a simulation run to match up with analyses of real data that you have conducted independently of the simulation runs. This process, called "history reconstruction" is discussed further in Chapter 10.

In order to make use of the results file, the program will question you as follows:

`Data from results file? answer (y/n):`

to which a `yes` answer will produce a prompt that requests the name of the file that is to be read. Note that you must rename your previous `popmod.rslt` file, thus eliminating the possibly that you will destroy your data unintentionally. Reading this file is treated exactly as if you were answering the questions from the keyboard, and you will see all of the results move across your screen as the simulation proceeds automatically. When you get to the end of the file, the program switches back to the keyboard queries as if you had entered all of that data by hand.

If you do not want to read data derived from a previous simulation, a no answer causes the program to proceed to obtain the initializing information as described below.

First popmod requests the age of the oldest animals in the population based upon Fall observations. Since animals are born in the Spring, Fall ages will always be 0.5, 1.5, 2.5, ..., thus the age entered must follow this pattern. The value chosen may be taken from results of a previous hunt (*i.e.* the oldest animal harvested) or other available information. Note that the greatest age value accepted by the model is 19.5. This query takes the form:

---

[1]Note that on MS-DOS systems the suffixes are truncated to 3 characters because of the naming conventions imposed.

```
Enter the maximum age of animals (in the Fall)
  <= 19.5, Fall ages are X.5 years
```

The next set of requests seeks specification of hunt categories [2] — which are groups of age classes that will be harvested according to specified groupings. These are most appropriately based upon the general groups of age classes which can be identified by the mortality agent (hunter, predator, disease agent, *etc.*) in the field — for example, young (0.5), immature (1.5), and mature (2.5-9.5).

Since hunt categories are sex and age specific, in this case there would be 6 hunt categories: young females, young males, immature females, immature males, mature females, and mature males. A hunt category can contain only a single age class. Use this if it is anticipated that a particular age class could be harvested at a level different from its representation in the population. If harvesting is to be relatively random with little or no age discrimination by the hunter, then two hunt categories might be specified: females (0.5–9.5) and males (0.5–9.5). In this case, when removal levels are specified later in the program, animals will be removed in relation to their proportional representation by age class in the population. You are asked to enter the youngest age and oldest age (by sex) for each hunt category. Since hunting is conducted in the **Fall** (*i.e.* the non-breeding season), the ages entered must reflect Fall ages (0.5, 1.5, 2.5, ...). The two ages entered for each hunt category must be separated by a blank. Female hunt categories are established first with:

```
In the following query, if a hunt category is to
  contain animals of only 1 age, enter that age twice

  Enter the youngest age and the oldest age for
  females hunt category  1
```

If the request was for more than one hunt category in the females, the program repeats:

```
Enter the youngest age and the oldest age for
  females hunt category  2
```

Continue to specify ages until you have reached the oldest age previously defined. When the oldest age class entered for a hunt category is equal to that specified as maximum age in the population, the query repeats for male categories,

```
Enter the youngest age and the oldest age for
  males   hunt category  1
```

and if the request was for more than 1 hunt category in the males,

```
Enter the youngest age and the oldest age for
  males hunt category  2
```

---

[2]Note that throughout, "hunt" and "harvest", are used to label any form of additive mortality, and thus, includes "predation", "disease", "sport hunting", "commercial hunting", "competition dictated mortality", *etc.*

and continues until the oldest age class has been reached for males. Note that there is no requirement that female and male hunt categories be defined similarly.

This feature of the model has wide flexibility; male hunt categories can be specified with different age class groupings than those set for females. Any number of categories may be specified per sex, up to maximum specified age $+0.5$. For example, if maximum age is 5.5, up to 6 hunt categories can be specified for each or either sex, with each category containing a single age class. This might be used if each age class were in fact distinguishable to the hunter and thus could be harvested at an age-specific level.

In order to be able to calculate minimum breeding sex ratios, the program requires entry of the maximum number of females which can be inseminated by a single male under natural conditions. Thus, under some mortality conditions, the number of mature males could be reduced to a level such that there would not be enough males to inseminate all of the mature females in the population. At this point, the population growth would be reduced because of a decrease in the β_x, the percent of females breeding. The value entered in response to this request establishes a critical male:female breeding ratio threshold. When the number of males Falls below this level, an adjustment is automatically made in the β_x values and a report is issued that describes the new, reduced, β_x and thus m_x values. The program request is,

```
Enter the number of females that can be bred by a male
```

Next, the program requests specification of the youngest age at which animals can successfully copulate. Enter a value for females, followed by a blank, then a value for males.

```
Enter age at first copulation for females, then
    for males (breeding occurs in the Fall)
```

Copulation behavior occurs in the Fall, thus these values must reflect Fall ages (0.5, 1.5, ...). For example, a 0.5 entered for females indicates that it is possible for females born in the Spring to copulate sometime during the Fall or early winter, and to bear young as yearlings. Note that this parameter only sets up the potential for breeding. The actual frequency of this reproductive activity is determined by the β_x parameters (entered later) so enter the youngest ages for which there is any evidence for such reproductive behavior.

The program then requests 7 sets of age-specific data. All values for a given sex may be entered on a single line (separated by spaces), or individually; in which case, the program will prompt with a "?". The number of age-specific values required is the maximum age $+0.5$. For example, if maximum Fall age is 5.5, there are 6 age classes in the population (0.5–5.5) and 6 values are required for each set of age-specific attributes. If more than 6 values are entered, the program ignores the additional values; if fewer than 6 values are entered, a system prompt will appear to indicate a need for entry of the additional values. Again, the program provides a "data echo" so that you can check for proper entry.

The first request in this set is,

```
Enter initial n(x,1) for females
```

following your entries for the females, the request repeats for males,

```
Enter initial n(x,2) for males
```

These n_x values serve only to initialize the model population, and are not used to calculate survival information. They should reflect the initial **Fall**, post-hunt population.

Age-specific clutch size is requested next. As described in Chapter 2 on natality, this refers to the expected number of young (total males and females) per breeding female in each age class.

```
Enter age-specific clutch sizes, F(x)
```

which will be modified by the expected proportion of males per clutch, R_x), entered as follows:

```
Enter Age-Specific Proportion Males Per Clutch, r(x)
```

The program then combines expected clutch size with the expected proportion of males per clutch, and reports sex- and age-specific clutch sizes.

```
Expected sex-specific clutch sizes, f(x,i), for:
Females   ...   ...
Males     ...   ...
```

For most organisms, the theoretical expectation for proportion of males produced per clutch is 0.5 for all age classes. In real populations, however, this is often not true. This procedure allows evidence for skewed sex ratios among newborn animals to be incorporated in the simulation. As in the preceeding example, with 6 age classes, 6 values must be entered. This question appears only once, since only females produce offspring. Zero values should be entered for pre-copulation age females (as determined by specified age at first breeding) to facilitate clear thinking, although any values entered in these age classes are automatically ignored by the program.

The next request in the primary population attributes section provides for entry of proportion breeding, β_x, the proportion of females in each age class that will actually produce offspring during the upcoming breeding season. This query is:

```
Enter proportion breeding, b(x)
```

Age-specific survival is requested first for females;

```
Enter survival, p(x,1), for Females
```

and then, the request repeats for males;

```
Enter survival, p(x,1), for Males
```

Following entry of the survival data, the program enters a generating phase and the previous information is used to project the initial population through to the first Spring and Fall seasons. The Spring projection appears first, and shows ages, numbers, and proportions per age class for females, males, and combined sexes. Total numbers of females, males, and combined sexes are also reported. Note that ages reflect the Spring reproductive season; the 0 age class contains newborn animals and the older age classes contain those animals surviving from the initializing **Fall** through the **Spring**

reproductive period. All individuals are at this time at even year age intervals. The tentative Fall population projection follows immediately, appearing in a form identical to the Spring report. Fall age classes represent Fall ages, *i.e.* all are on half-year intervals, with the animals in each class being those surviving from the previous Spring.

The report looks like this:

```
Population statistics for Spring, year = 1
AGE           FEMALES              MALES              BOTH SEXES
        nx   proportion     nx   proportion     nx    proportion
0.0
1.0
2.0
  .
  .
  .
TOTALS
Tentative population statistics for Fall, year = 1
AGE           FEMALES              MALES              BOTH SEXES
        nx   proportion     nx   proportion     nx    proportion
0.5
1.5
2.5
  .
  .
  .
TOTALS
```

The projection through Spring (natality plus mortality) and into an unhunted Fall (mortality only) population utilizes the population attributes of clutch size, $F_{x,i}$, proportion males in clutch, ρ_x, proportion females breeding, β_x, and survival probabilities, $p_{x,i}$. The model assumes that the population is "closed," that is, there is no immigration or emigration (or that these immigration and emigration are somehow factored into the natality and mortality functions respectively). Given this consideration, the model provides a "trials and errors" service. It is possible to set up a projection, run the model one time step, examine the results, and then either continue on or back up 1 step, revise the above primary data, and re-project the population. These iterative revisions may continue until the desired result is obtained, whereupon the model is instructed to save the results, and proceed to the next stage.

These "try and try again" iterations logically occur:

1. after a projection from the `Fall` post-hunt population through `SRING` and into the `Fall` pre-hunt population; and

2. after harvesting the `Fall` population.

Thus, you as the operator have complete control over the population processes as dictated by the demographic mechanics, and you can attempt to match estimates from a real population with similar estimates from a hypothetical population. This procedure constitutes an attempt to reconstruct the history of the real world population. Surprisingly good results can be obtained if sufficiently long term data are available.

Program popmod will complete a projection through Spring and into Fall, and then print:

```
Satisfactory projection to Fall?
(yes-no-exit)
```

Entering an exit in response to this query and subsequent requests will cause immediate program termination. A no response will set the clock back to the previous Fall, and provide an opportunity to enter new primary values for clutch size, proportion males, proportion females breeding, and survival. The sequence is exactly as described above, and need not be repeated here. A yes response to this query leads to the hunt sequences.

As described in Chapter 8, the program displays a "tentative" Fall population. This tentative population is projected without any effects of additive mortality. This is what the population age and sex structure will be if no additional mortality is imposed.

Assuming, for the moment, that no additive mortality is to be imposed a NO response is entered to the question,

```
Hunt the tentative Fall population? (yes-no-exit)
```

If there is to be no hunt (or following a harvest cycle), there is an opportunity within each annual cycle, to change the previously established primary population attributes. Again, for the moment, assume that a no is entered in response to the question,

```
Update primary population attributes? (yes-no-exit)
```

in which case the program will produce the second iteration of projected population structure in the same form previously described, with the addition of sex-specific annual growth rates.

```
Population statistics for Spring, year = 2
AGE          FEMALES              MALES               BOTH SEXES
        nx    proportion     nx    proportion     nx    proportion
0.0
1.0
2.0
  .

  .
TOTALS
Tentative population statistics for Fall, year = 2
AGE          FEMALES              MALES               BOTH SEXES
        nx    proportion     nx    proportion     nx    proportion
0.5
1.5
2.5
  .

  .
TOTALS
Annual growth rates
Females =          Males =              Both sex =
```

Following each Fall projection, the program provides an opportunity to go back to the previous Fall and change the primary population attributes. In this example, we want to move on, and so have entered a yes to the question:

```
Satisfactory projection to Fall? (yes-no-exit)
```

The program will next request an answer to the previously shown hunting query.

```
Hunt the tentative Fall population?  (yes-no-exit)
```

A yes response will generate the request:

```
Enter total number of animals to be removed
    from the Fall population
```

This additional mortality will be applied to the tentative Fall population which was shown just previously to provide guidance. Entry of more individuals than the population contains will generate a request to re-enter an appropriate value. The program next requests information on which sexes are to be harvested:

```
Which sex or sexes are to be hunted?
(enter: 1 = Females only, 2 = Males only,
or 3 = both sexes)
```

followed by a sequence of sex-specific questions where-by percentages of each sex and hunt category to be removed are specified along with a cumulative total of these percentages. Enter integer values here, the program will do the conversions to proportions. The following example shows this sequence of questions with respect to 2 hunt categories for the females (ages 0.5 to 1.5, and 2.5 to maximum age of 4.5), being harvested at 20 and 30 percent respectively. (Note that the question mark shown is a system-specific prompt):

```
What percent of total kill is to be removed
from Females ages 0.5 thru 1.5?
(sum of percentages now equals  0 percent)
?
Reply:
    20
What percent of total kill is to be removed
from Females ages 2.5 thru 4.5?
(sum of percentages now equals 20 percent)
?
Reply:
    30
```

If similiar example values are applied to the males, the program will respond:

```
What percent of total kill is to be removed
from Males ages 0.5 thru 1.5?
(sum of percentages now equals 50 percent)
?
Reply:
```

```
      20
   What percent of total kill is to be removed
   from Males ages 2.5 thru 4.5?
   (sum of percentages now equals 70 percent)
   ?
Reply:
      30
```

Each of these hunt requests, for females, then males, automatically ceases when the number of hunt categories, and thereby maximum age, has been exhausted. The program will check to make sure that your total percentage does not exceed 100, and that your proportions and numbers make sense. Given that everything does make sense, the program will project a new Fall population — this one will have the additive mortality that you have just specified imposed.

```
   Population statistics for Fall, year = ...
   AGE        FEMALES            MALES            BOTH SEXES
         nx   proportion    nx   proportion    nx   proportion
   0.5
   1.5
   2.5
    .

    .

    .

   TOTALS
   Annual growth rates
   Females =              Males =              Both sex =
```

Followed by the query:

```
 Satisfactory hunt?  (yes-no-exit)
```

A yes response will lead forward toward a population projection for the next year, while a no steps back toward the previously unhunted Tentative Fall population.

In either case, there is an opportunity to modify the previously established primary population attributes thus allowing the important aspects of "tuning and searching" described in Chapter 10. The re-specification of primary population attributes follows in the same manner as previously described, except that the program will echo existing attribute vectors so that you can know the current status of all attributes.

These queries proceed as follows.

```
   Update primary population attributes? (yes-no-exit)
```

If you enter yes the program will step through each of the attribute vectors

```
   Current clutch sizes, F(x) =
   (the FX vector)
   input new data?  (yes-no-exit)
```

If yes the program prompts with

```
Enter age-specific clutch sizes, F(x)
```

if no, or following the above entry, the progam continues with

```
Current proportion males/clutch, r(x) =
(the r(x) vector)
input new data?  (yes-no-exit)
```

If yes the program prompts with

```
Enter proportion males per clutch, r(x)
```

If no, or following the above entry, the program continues with

```
Current proportion breeding, b(x) =
(the b(x) vector)
input new data? (yes-no-exit)
```

If yes the program prompts with

```
Enter proportion breeding, b(x)
```

If no, or following the above entry, the program continues with

```
Current survival,  p(x,i) =
Females:
(the p(x) vector for females)
Males:
(the p(x) vector for males)
input new data? (yes-no-exit)
```

If yes, the program prompts with

```
Enter survival p(x) for Females
```

and after you enter these data,

```
Enter survival p(x) for Males
```

Following the entry of these primary attributes, the program projects the population through Spring to the next Fall.

Successive annual iterations proceed as described with the program producing a Tentative Fall population, an opportunity to update primary population attributes, an opportunity to hunt this population, and again, an opportunity to update primary population attributes.

When the annual iterations have accumulated to the point where they equal the number of age classes specified, the programs' history matrix contains a full time-dynamic cohort. Beginning at this point and continuing after each accepted Fall population, the program will produce the request:

```
Compute life-history analyses on Females ? (yes-no)
```

Entry of a `no` will produce a similar question for `males`, while a `yes` will generate time-specific and cohort life history analyses for females as described in Chapters 2 and 3.

The first of these life-history analyses follows the discussion in Appendix B. It consists of a linear regression analysis on $\ln n_x$ data, and reports survival statistics and a computed $n(x)*$ vector that is back calculated to age $x = 0$. The program then transfers this hypothetical $n(x)*$ vector to a life-table routine, and produces an expanded life-table as described in Chapter 3. These analyses are completed for a diagonal cohort, then for the column n_x, (*i.e.* a Time-Specific vector). The form of this report is:

```
Time-dynamic life-history analysis
Note that nx reported is a least-squares fit on diagonal nx
x mean = 000   nx mean = 000   sumsqx = 000
Slope = 000    CI = 000    intercept = 000
F at 1 and (maxage - 1) df = 000 for test on bb
Attribute estimates and 95% confidence  limits for females cohort 0
Instantaneous survival rate = 000 (000 - 000)
Annual survival rate  =     000 (000 - 000)
Annual mortality rate =     000 (000 - 000)
Estimated n(x) vector back-calculated to age 0
age = 0  n(x) =     000
age = 1  n(x) =     000
age = 2  n(x) =     000
    .
    .
    .
```

The program then produces an expanded life-table based on the age structures from either n_x or $n(x)*$, and the current F_x, ρ_x, and β_x vectors.

These analyses are keyed to Spring populations since the zero age class is required for complete analysis. Results will be produced at "half year" age steps. The `cohort` analysis is produced first:

```
Time-dynamic life-history analysis
Summary of life history information for "cohort"  "_ _ _" Females
x    nx      lx      dx      qx      px      Lx      tx      ex      Px
0.0
0.5
1.0
1.5
 .

 .

x     mx      lxmx    vx      cx
0.0
0.5
1.0
1.5
 .
```

```
     GRR    Ro    t    Tc    Tbar    lambda    r
```

Followed by a similar set of analyses on the time-specific, column n_x, and the associated survival and life table analysis.

```
Time-specific life-history analysis
Note that n(x) reported is a least-squares fit on column n(x)*
x mean = 000  nx mean = 000   sumsqx = 000
slope = 000   CI = 000   intercept = 000
F at 1 and (maxage - 1) df = 000 for test on bb
Attribute estimates and 95% confidence  limits for females cohort 0
Instantaneous survival rate = 000 (000 - 000)
Annual survival rate =        000 (000 - 000)
Annual mortality rate =       000 (000 - 000)
Estimates n(x) vector back calculated to age 0
age = 0  n(x) = 000
age = 1  n(x) = 000
age = 2  n(x) = 000
  .
  .
  .
```

followed by the expanded life-table based on the column NX data.

```
Summary of life history information for "cohort"  "___" Females
x    nx    lx    dx    qx    px    Lx    tx    ex    Px
0.0
0.5
1.0
 .
 .
 .
 .

x    mx    lxmx    vx    cx
0.0
0.5
1.0
 .
 .
 .

     GRR    Ro    t    Tc    Tbar    lambda  r
```

This life-history analysis on the females is followed by similar potential computations for males,

```
Compute life-history analyses on males ?  (yes-no)
```

then for both sex:

```
Compute life-history analyses on both sex?  (yes-no)
```

Certain liberties are taken with demographic theory in these analyses, however, it is instructive to compute such statistics for these 3 categories, *i.e.* females, males, and both sex, particularly when widely varying sex-specific parameters are specified. These analyses are available after each annual iteration. As the continuing entry of no will become boring, a short cut has been incorporated. In response to the successive queries

```
  Compute life-history analyses on females? (yes-no)
   no
 Reply:
n
  Compute life-history analyses on males  ?  (yes-no)
 Reply:
n
  Compute life-history analyses on both sex? (yes-no)
  Reply:
n
```

and responses indicated, the entry of any other character than y or n (*e.g.* a skip) will cause an exit from the life-history loop. Thus, each between year set of requests reduces to:

```
  Hunt the tentative Fall population? (yes-no-exit)
```

If the answer is n, then

```
  Compute life-history analyses on Females ? (yes-no)
```

if the answer is other than yes or no then:

```
  Update primary population attributes? (yes-no-exit)
```

The program will continue to cycle until termination is indicated by entry of an exit in response to one of the queries where this is permitted.

After you have run through a series of time steps in the projection, and then entered an exit in response to one of the queries, the program writes a final tt popmod.summ file. This file contains the density values for Females, then Males, and finally for Both sex. After writing this summary, the program closes all files and terminates.