POPULATION ECOLOGY

A Unified Study of Animals and Plants

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Preface

This book is intended primarily for students. It is designed to describe the present state of Population Ecology in terms which can be readily understood by undergraduates with little or no prior knowledge of the subject. We have, however, presented *our* view, rather than some definitive view of the subject, and, consequently, we have tried to provide sufficient information for everybody (student and expert alike) to disagree with us wherever they think fit.

Population Ecology is, to us, the study of the sizes (and to a lesser extent the distributions) of plant and animal populations, and of the processes — particularly the biological processes — which determine these sizes. As such, it must inevitably be a numerical and quantitative subject. Nevertheless, we have avoided complex mathematics, and we have, wherever possible, relegated the mathematical aspects of a topic to the final parts of the section in which that topic is examined. This will, we hope, make Population Ecology more generally accessible, and more palatable. But this is not to say that the mathematics have been played down. Rather, we have tried to play *up* the importance of real data from the real world: it is these, and not some mathematical abstraction, which must always be the major and ultimate concern of the population ecologist.

Developing the subject in this way, however, emphasizes that mathematical models *do* have an essential role to play. Time and again they crystallize our understanding of a topic, or actually tell us more about the real world than we can learn directly from the real world itself. Nature may be the ultimate concern of Population Ecology, but mathematical models, laboratory experiments and field experiments and observations can all help to further our understanding.

We have also tried to establish the point implied by the subtitle: that Population Ecology is a unified study of animals *and* plants. We are, of course, aware of the differences between the two; and aware, too, of the view pioneered by Professor J. L. Harper and his school, that the most important distinction is between simple, unitary organisms (most animals), and ramified organisms composed of sub-units (a few animals and most plants). We feel, however, that plant and animal populations have had their own, independent ecologists for too long, and that, since the same fundamental principles apply to both, there is most to be gained at present from a concentration on similarities rather than differences.

The book is set out in three parts. The first starts from the simplest first principles and examines the dynamics and interactions occurring within single-species populations. The second part, occupying approximately half of the book, is concerned with interspecific interactions: interspecific competition and predation. 'Predation', however, is defined very broadly, and includes the plant–herbivore, host–parasite, host–parasitoid and prey–predator interactions. The third part of the book synthesizes and expands upon the topics from the preceding chapters, and does so at three levels: individual life-history 'strategies', the regulation and determination of population size, and the importance of intra- and interpopulation interactions in determining community structure.

A number of people read all or most of this book in manuscript, and made generous and helpful suggestions, many of which we have now incorporated. We are deeply grateful to Professor Tony Bradshaw, Professor J. L. Harper, Professor Michael Hassell, Dr Richard Law, Professor Geoffrey Sagar, Dr Bryan Shorrocks, Dr David Thompson and, most especially, Dr John Lawton.

We also thank Mrs Barbara Cotgreave for drawing the figures, Mr Brian Lewis for his photography and Anita Callaghan, Susan Scott and Miss D. S. Paterson for typing the manuscript.

Population Ecology has come a long way since its inception, and the rate of progress has never been faster than at present. Nevertheless, there are few, if any, populations for which we can claim to fully comprehend the underlying causes of abundance. Much remains to be understood, and a great deal more remains to be done.

Michael Begon
Martin Mortimer

PART 1 SINGLE-SPECIES POPULATIONS

Chapter 1 Describing Populations

1.1 Introduction

Few would disagree with the proposition that nature is immensely complex. However, if we wish to understand this complexity, we will be well advised to abstract relatively simple facets from nature and examine these first. Species–habitat interrelations could be considered, or interactions between species within communities; but before they are, we must examine the basic components: single-species populations.

Even here there is a wealth of general questions: 'What causes species to be common or rare?', 'What underlies the fluctuations in their numbers?', 'Why do populations of the same species vary in their size and age-structure?', and so on. The dynamics of single-species populations, therefore, must be described in a way that allows such questions to be approached; for it is only when actual populations are encapsulated by the appropriate description that we can go on to consider underlying causes. This first chapter, then, is concerned with description, and with abstracting from populations the common properties that link them together.

1.2 Population processes

Although studies of animal and plant populations have developed quite separately, these two life forms have much in common when examined from a demographic viewpoint. At the simplest level, plants are born from seeds just as birds are born from eggs; and old animals exhibit signs of senility just as old oak trees bear dead branches. Moreover, if we were to catalogue the ages of every dandelion plant and every vole living in a field, we would probably find a range of ages in each; and, as time passed, individuals would either die, or survive to reach the next age-group; and in some age-groups, at certain times, individuals would produce offspring of their own. From the outset, therefore, it would seem sensible to suggest that, even though life forms and stages of development may differ substantially amongst species, certain basic *population processes* are common to all of them.

We can start considering these population processes by imagining a study of the numbers of voles inhabiting a meadow. Let us suppose that the vole numbers increase. We know that there has *either* been an influx of voles from adjoining meadows, *or* young voles have been born, *or* both of these events have occurred. We have, therefore, pin-pointed two very basic processes which affect the size of a population: *immigration* and *birth*. If, on the other hand, vole numbers decline, then our explanation would be that voles must have either died, or simply left the meadow, or both. These processes, which reduce population numbers, are *death* and *emigration*.

Of course, there is no reason to suggest that all four processes are not occurring simultaneously in the population. If the population declines, then the reason is simply that death and emigration together have *outweighed* birth and immigration, and vice versa if the population increases. We can certainly say that birth, death, immigration and emigration are the four fundamental demographic parameters in any study of population dynamics. Moreover, they can be combined in a simple algebraic equation describing the change in numbers in a population between two points in time:

$$N_{t+1} = N_t + B - D + I - E \qquad (1.1)$$

where N_t is the population size (number of individuals) at time t, N_{t+1} is the population size one time-period later, at time $t+1$, B is the number of new individuals born between t and $t+1$, D is the number of individuals which die between t and $t+1$, and I and E, respectively, are the numbers of immigrants and emigrants during the same period of time.

If the population is so large that our study cannot encompass the whole of it, then this equation must be constructed in terms of densities rather than absolute numbers. Thus, samples are taken, and N_t, for instance, becomes 'the number of plants per square metre at time t' or 'the number of insects per leaf'. Nevertheless, equation (1.1) indicates that, at its simplest, the task of the demographer is to measure these four parameters and account for their values — yet the translation of this into practice is rarely straightforward. Almost all species pass through a number of stages in the life cycle. Insects metamorphose from eggs to larvae to adults, and some have a pupal stage as well; plants pass from seeds to seedlings and then to photosynthesizing adult plants, and so on. In all such cases the different stages must be studied individually. Also, in reality, the four 'basic' parameters are themselves often compounded from several other component processes. Equation (1.1), therefore, cannot be considered as anything more than a basis upon which more realistic descriptions can be built.

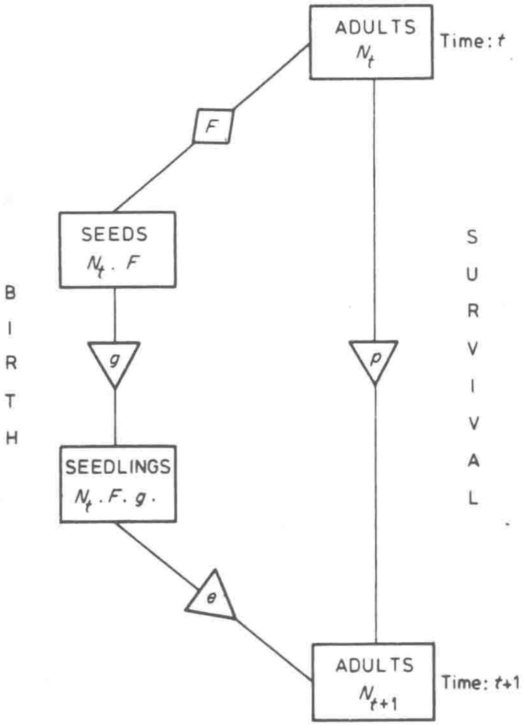

Fig. 1.1. A diagrammatic life-table for an idealized higher plant. F: number of seeds per plant; g: chance of a seed germinating ($0 \leqq g \leqq 1$); e: chance of a seedling establishing itself as an adult ($0 \leqq e \leqq 1$); p: chance of an adult surviving ($0 \leqq p \leqq 1$).

1.3 The diagrammatic life-table

1.3.1 General form

The description we require is one which retains the generality of equation (1.1), but can also reflect the complexities of most actual populations. One such description is the *diagrammatic life-table* (Sagar & Mortimer 1976), which is applied to an idealized higher plant in Fig. 1.1. The numbers at the *start* of each of the stages — seeds, seedlings and adults — are given in the square boxes. Thus, the N_{t+1} adults alive at time $t+1$ are derived from two sources. Some are the survivors of the N_t adults alive at time t. Their probability of survival (or, equivalently, the proportion of them that survive) is placed inside a triangle (or arrow) in Fig. 1.1, and denoted by p. So, for instance, if N_t is 100 and p, the survival-rate, is 0.9, then there are 100×0.9 or 90 survivors contributing to N_{t+1} at time $t+1$. (10 individuals have died; the mortality-rate $(1-p)$ between t and $t+1$ is clearly 0.1.)

The other source of the N_{t+1} adults is 'birth', which in the present case can be viewed as a multi-stage process involving seed production, seed germination and the growth and survival of seedlings. The average number of seeds produced per adult — the average *fecundity* of the plant population — is denoted by F in Fig. 1.1 and placed in a diamond. The total number of seeds produced is, therefore, $N_t \times F$. The proportion of these seeds that actually germinate on average is denoted by g, which, being essentially a survival-rate, is placed in an arrow in Fig. 1.1. Multiplying $N_t \times F$ by g gives us the number of seedlings which germinate successfully. The final part of the process is the physiological establishment of seedlings as independently photosynthesizing adults. The probability of surviving this very risky phase of plant growth is denoted by e (once again in an arrow), and the total number of 'births' is, therefore, $N_t \times F \times g \times e$. The number in the population at time $t+1$ is then the sum of this and the number of surviving adults, $N_t \times p$.

We can now substitute the terms from the life-table into our basic equation of population growth (equation

1.1) as follows:

$$N_{t+1} = \overbrace{N_t - \underbrace{N_t(1-p)}_{\text{Death}}}^{\text{Surviving}} + \underbrace{N_t \times F \times g \times e}_{\text{Birth}}. \qquad (1.2)$$

There are several points to note about this equation. The first is that both here and in Fig. 1.1 immigration and emigration have, for simplicity, been ignored, and our description of how a plant population may change in size is essentially incomplete. The second is that 'death' has been calculated as the product of N_t and the mortality-rate $(1-p)$ — survival and mortality are opposite sides of the same coin. The third point is that birth is quite clearly a complex product of 'birth-proper' and subsequent survival. This is frequently the case: even human 'birth'-rates are the product of the rate at which fertilized eggs implant in the womb and the rate of pre-natal survival.

1.3.2 *The common field grasshopper, an annual species*

In practice, careful and meticulous field-work is necessary to build a diagrammatic life-table of the type illustrated in Fig. 1.1. Reliable estimates of the transition probabilities (p, g and e in Fig. 1.1) are required, as well as measurements of the fecundity of adults. Such data for the common field grasshopper, *Chorthippus brunneus*, are illustrated in Fig. 1.2. These were obtained by a combination of field samples and back-up laboratory observations on a population near Ascot in Berkshire (Richards & Waloff 1954). The population was isolated so that immigration and emigration *could* be ignored.

The first point to note about Fig. 1.2 is that no adults survive from one year to the next ($p=0$). *Ch. brunneus* is, therefore, an 'annual' species; each generation lasts for just one year, and generations are discrete, i.e. they do not overlap. It is also clear that the 'birth' of adults is a complex process involving at least six stages. The first stage is the laying of egg-pods in the soil by adult females. On average, each female laid 7.3 pods, each containing 11 eggs. F is, therefore, 80.3. These eggs remain dormant over winter, and by early summer only 0.079 of them had survived to hatch into first-instar nymphs. Subsequently the transition probabilities between instars were fairly constant, taking a remorseless toll on the surviving population; less than a third of the first-instar nymphs survived to be 'born' into the adult population. Despite their apparently high fecundity, therefore, the adults of 1947 did little more than replace themselves with newly born adults in the following year.

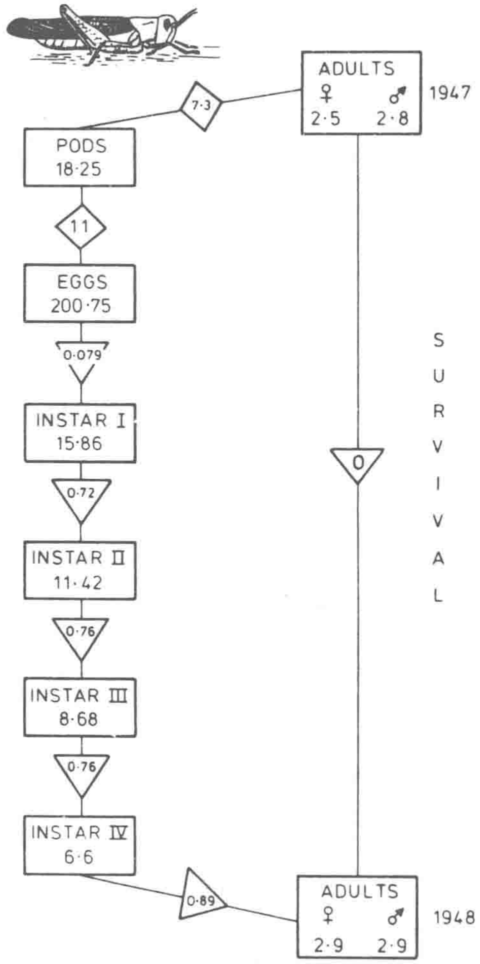

Fig. 1.2. Diagrammatic life-table of the field grasshopper, *Chorthippus brunneus*. (Population sizes are per 10 m^2; data from Richards & Waloff 1954.)

Ch. brunneus' diagrammatic life-table is illustrated in a simplified form in Fig. 1.3(a). This life-table is appropriate for all species which breed at a discrete period in their life cycle, and whose generations do not overlap. If

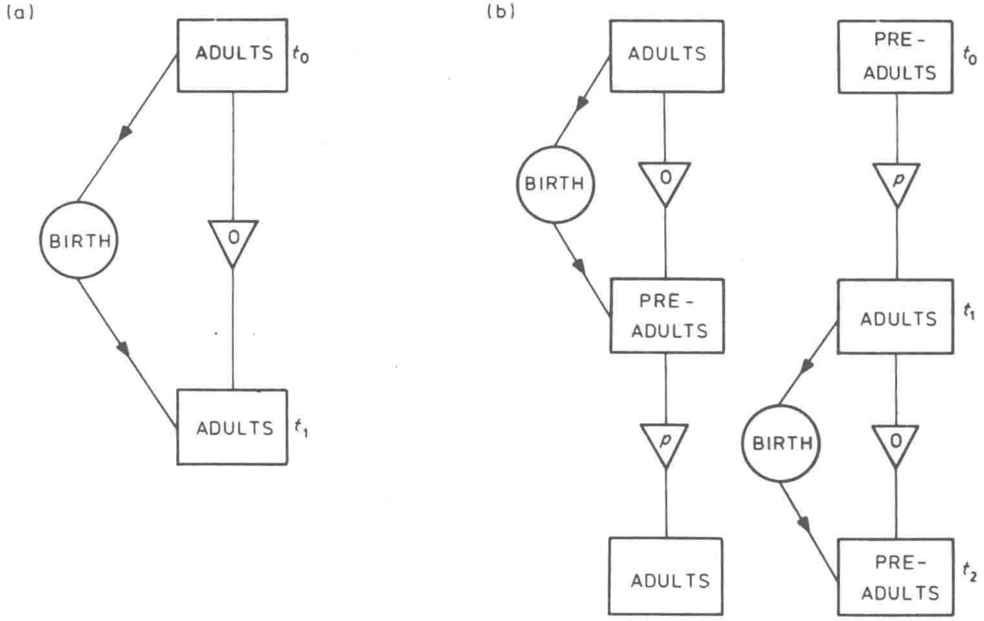

Fig. 1.3. Diagrammatic life-tables for species with discrete breeding seasons. (a) Generations do not overlap. (b) Generations overlap. (Birth processes are simplified.)

the time between t_0 and t_1 is one year, the life history is referred to as annual.

1.3.3 Ragwort, a biennial

An annual life history is only one of a number of possible patterns. If we consider species that live for two years rather than one, reproducing only in the final year, then we have a life history that involves breeding at one discrete time in the life cycle, but in which generations of adults may well overlap; this is illustrated in Fig. 1.3(b). If the time periods are years, then this life cycle is referred to as 'biennial'. During any one summer, the population contains both young adults which will not reproduce until the following year, and mature, reproducing adults.

Ragwort, *Senecio jacobaea*, is a biennial plant with a life cycle in which seeds germinate principally in the autumn. Then, during the next year, young plants form a rosette of leaves. In the second year a flowering stem is formed. A diagrammatic life-table for *S. jacobaea* is shown in Fig. 1.4, in which the birth-process has been expanded to include some extra stages which are specific to plants. The data come from measurements made on a population living in sand dune environments in the Netherlands (van der Meijden 1971). Of the 5040 seeds that are produced, 62% fall on to the ground; the other 38% are dispersed by the wind to other areas. By the same token there is quite a high chance that immigrants enter this population. This necessitates a further modification of our life-table, indicated in Fig. 1.4 by the inclusion of invading seeds, which may contribute either to the seed banks or to the incoming seed 'rain'.

Having arrived on the ground, various potential fates await ragwort seeds. They lie on the surface of the sand in the 'surface seed bank', where they may germinate, be eaten or just die. Alternatively, wind or insects, acting as migratory agents, may transport them to neighbouring areas; or they may become buried. The detailed fates of ragwort seeds in sand dune environments are not fully known, but only 11.4% stay in the surface seed bank; and of the 3124 seeds that rain on to the soil only 40

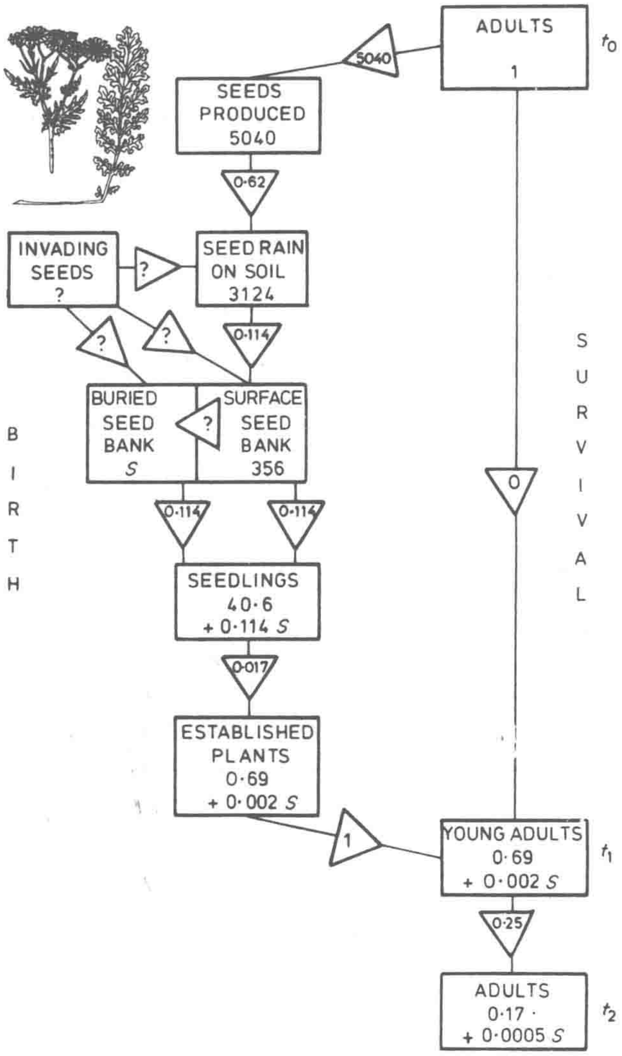

Fig. 1.4. Diagrammatic life-table of the biennial ragwort, *Senecio jacobaea*. (Population sizes are per 4 m^2; data from van der Meijden 1971.)

actually germinate successfully. However, seedlings can arise from an additional source: the buried seed bank. We do not know how many seeds are buried in the sand profile, but for many plant species, especially weeds, the numbers of buried seeds can be very high (up to 10 000 m^{-2}), and a proportion of each season's seed crop does become buried. To indicate that this is a birth route we have added to the 'seedling' and 'established plant' components a fraction of the buried seed bank, denoted by S. Finally, the transition from seedlings to young, established, photosynthetically independent adults in sand dune environments is also an exceedingly risky phase for ragwort: only 1.7% of the seedlings actually become established.

The life-table in Fig. 1.4, therefore, illustrates the importance of additional seed sources to the 4 m^2 area, since from t_0 to t_1 the original ragwort density of 1 becomes reduced to 0.69. Thus, to keep the number of young adults at t_1 up to exactly 1 we might argue that there are 155 seeds in the buried bank which germinate (since if $0.69+0.002S=1$, then $S=155$). Alternatively, some of these 155 might enter the 'birth process' as immigrants; and if we recall that 38% of the 5040 seeds were dispersed, we can see that there are ample numbers to rely upon. To complete this life-table, however, we should note that the chance of a young adult surviving to become a mature one *producing seed* is only 0.25. To ensure that the population size at t_2 is still 1, therefore, we will have to imagine a further input of seeds into the birth process.

Such data as these emphasize the extreme severity of the sand dune habitat to plant life, and the considerable mobility of seeds in the life cycle of ragwort: individual seeds may travel at least 15 m. Since sand dunes, by their very nature, offer shifting and temporarily suitable habitats for ragwort, we can infer that seed movement by dispersal on or above the sand is a very necessary feature in the life history of this plant.

1.3.4 More complex life cycles

Overlapping generations are not confined to biennials. Consider the population of great tits (*Parus major*) near Oxford studied by Perrins (1965) and illustrated in Fig. 1.5. Adult birds build their nests and lay eggs in the early summer, but of these eggs only a proportion (0.84 in this case) survive to hatch as nestlings. These nestlings are themselves subject to many dangers, and by the late summer only 71% of them survive to fledge — leaving the nest and fending for themselves. Of these fledglings, only a small proportion live through the winter to become breeding adults. However, a rather

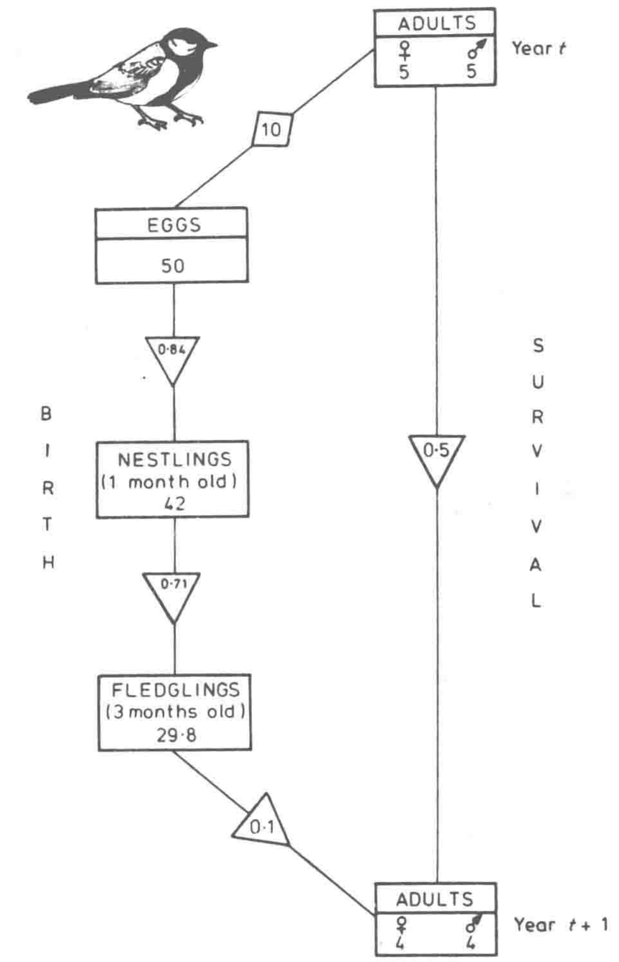

Fig. 1.5. Diagrammatic life-table of the perennial great tit, *Parus major*. (Population sizes are per hectare; data from Perrins 1965.)

larger proportion of the previous generation's adults have also survived. The population of breeding adults, therefore, consists of individuals of various ages, from one to five or more years old. As Fig. 1.5 shows, this situation is readily described by a variant of our diagrammatic life-table very similar to Fig. 1.1. We are dealing with a population in which breeding occurs at discrete time periods, but in which the individuals are potentially long-lived so that *many* generations overlap.

We have assumed with our great tits, however, that adults of different ages are equivalent and may be treated as equal members of a common pool. Yet there will be many instances in which their demographic characteristics will be 'age-dependent' or 'age-specific'. In such cases, a diagrammatic life-table of the type shown in Fig. 1.6 may be more appropriate. In Fig. 1.6, the population at any one time consists of individuals in a range of age-classes: a_0 individuals are in the youngest age-class, a_1 individuals in the next oldest, and so on. With the passage of one unit of time a proportion of the individuals in one age group survive to become individuals in the next oldest age group. Thus, p_{01} is the proportion of the a_0 individuals surviving to become a_1 individuals one time-

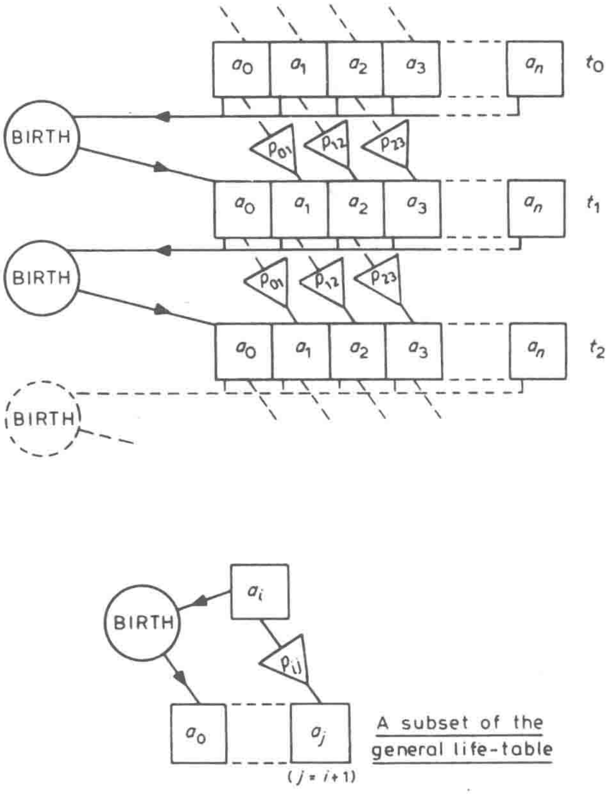

Fig. 1.6. A diagrammatic life-table for any species that breeds continuously with overlapping generations. a_0, a_1–a_n represent age-groups of individuals, a_n being the oldest group. p_{ij} is an age-specific probability of survival, where, for example, p_{01} is the probability of individuals in a_0 at one time surviving to reach a_1 by the next time period ($0 \leq p_{ij} \leq 1$). The inset shows a subset of the general life-table.

unit later, p_{12} is the proportion of the a_1 individuals surviving to become a_2 individuals, and so on (though in practice these p-values will, of course, vary with the changing circumstances of the population). Fig. 1.6 also shows that each age group has the potential to contribute to the youngest age-class via the birth process. For simplicity, birth from all age groups has been fused together; in reality, fecundity, like survival, would vary from age-class to age-class. Nevertheless, despite this increased sophistication, inspection of the life-table in Fig. 1.6 reveals that it is built up of units which are little more than the diagrammatic life-table with which we are already familiar. One such unit is illustrated in the inset in Fig. 1.6.

The implication in Fig. 1.6 is that breeding occurs at discrete periods, even though generations overlap and there are many age-classes each with their own birth- and survival-rate. In many species, however, birth (and death) occur continuously within a population. Fig. 1.6 is still appropriate in such cases, but time must be split arbitrarily into intervals, and the various terms take on slightly different meanings. Suppose, for instance, that we consider the numbers in a population at monthly intervals. At t_0, a_2 is the total number of individuals between two and three months old. One month later (at t_1), p_{23} of these will survive to become the a_3 individuals that are between three and four months old. Thus, even though birth and death are occurring continuously, they are considered 'one month at a time'.

1.4 Conventional life-tables

1.4.1 The cohort life-table

The most reliable method of determining age-specific mortality and fecundity for a continuously breeding population, or simply one in which generations are overlapping, is to follow the fate of a group of individuals, all born during the same time interval. Such a group is called a *cohort*. The process is essentially a journey from the top left-hand corner of Fig. 1.6 to its bottom right-hand corner, and, in many respects, it is similar to following the fate of an annual species throughout its yearly cycle. The difference in this case is that each individual has to be recognized and distinguished from those individuals belonging to other cohorts which are in the population at the same time. The situation is described diagrammatically in Fig. 1.7 in which individuals are represented by solid lines, ageing with time, and eventually dying (a 'spot' in Fig. 1.7). The cohort of four individuals (born at t_0) is observed again at t_1 (when there are two survivors), at t_2 (one survivor), and at t_3 (no survivors).

Plants are ideal subjects for such study, since they are generally sessile and can be tagged or mapped, enabling the fates of individuals to be precisely recorded and their reproductive output measured. Law (1975), for instance, followed the fate of a cohort of the annual meadow grass, *Poa annua*, from initial establishment to the ultimate death of the last individual. Recording the number alive at successive time periods and the number of offspring (seeds) produced per plant, he was able to compile a table of data showing survivorship and fecundity (Table 1.1). The first (left-hand) column gives the age at the beginning of each time interval. Thereafter, only the second and last columns (a_x and B_x) actually contain field data. All other columns are derived from the a_x column. We can see that this (conventional) life-table contains essentially the same information as the diagrammatic life-tables previously described.

The a_x column summarizes the raw data collected in the field by mapping the positions of 843 *Poa annua* plants that arose from naturally sown seeds in a number of metre-square quadrats. From this raw data 'l_x' values are calculated, by converting the numbers observed at the start of each time interval to the equivalent number that would have occurred had the starting density of the cohort been 1000; e.g. $l_3 = 316 \times 1000/843 = 375$. The value of this procedure is that l_x-values can be compared between populations, or between species, since they do not depend on the actual number of individuals considered in each study. In other words, an a_0 value of 843 is peculiar to *this* set of observations, whereas *all* studies have an l_0 value of 1000.

To consider mortality more explicitly, the standardized numbers dying in each time interval (d_x) must be computed, being simply the difference between l_x and l_{x+1}; e.g. $d_1 = 857 - 625 = 232$. q_x — the age-specific mortality-*rate* — has also been calculated. This relates

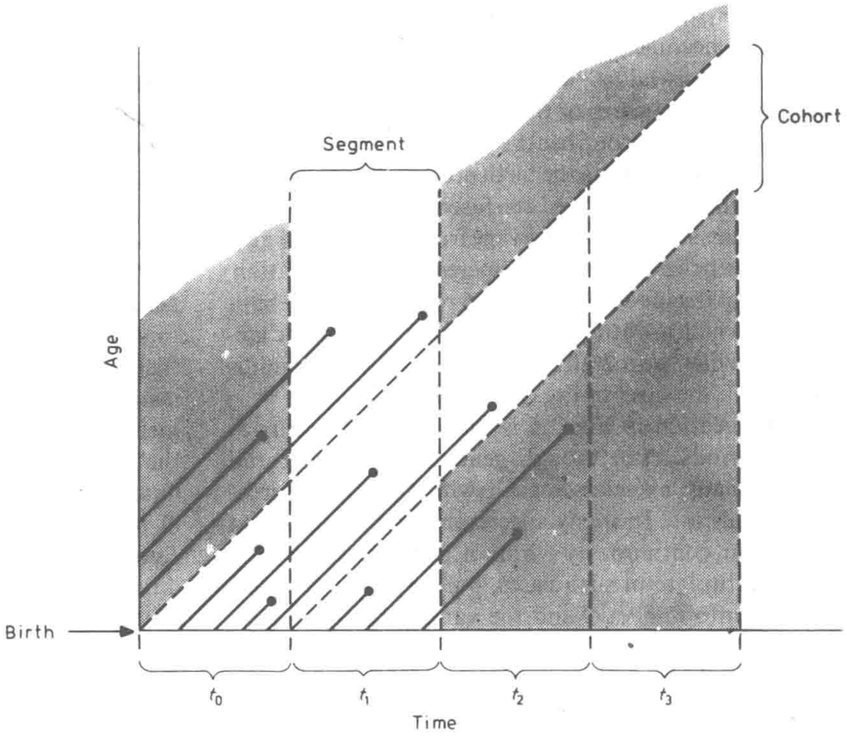

Fig. 1.7. A population portrayed as a set of diagonal lines, each line representing the life 'track' of an individual. As time progresses, each individual ages and eventually dies. Three individuals are born prior to t_0, four during t_0, and three during t_1. To construct a 'fixed cohort' life-table, a 'searchlight' is directed onto the cohort of individuals born during t_0 and the subsequent development of the cohort is monitored. Two of the four individuals have survived to the beginning of t_1; only one of these is alive at the beginning of t_2; and none survives to the start of t_3. To construct a 'static' life-table, the searchlight is directed onto the whole population during a single segment of time (t_1). The ages of the seven individuals alive at some time during t_1 may be taken as an indication of the age-specific survival-rates if we assume that the rates of birth and survival are constant. (After Skellam 1972.)

Table 1.1 A cohort life-table for *Poa annua*. (Adapted from Law 1975.)

Age (in three-month periods) x	Number observed alive at each quarter year a_x	Standardized number surviving at the start of age interval x l_x	Standardized number dying between x and $x+1$ d_x	Mortality-rate q_x	$\log_{10}a_x$	$\log_{10}l_x$	$\log_{10}a_x - \log_{10}a_{x+1}$ k_x	Average number of seeds per individual aged x B_x
0	843	1000	143	0.143	2.926	3.000	0.067	0
1	722	857	232	0.271	2.859	2.933	0.137	300
2	527	625	250	0.400	2.722	2.796	0.222	620
3	316	375	204	0.544	2.500	2.574	0.342	430
4	144	171	107	0.626	2.158	2.232	0.426	210
5	54	64	46.2	0.722	1.732	1.806	0.556	60
6	15	17.8	14.24	0.800	1.176	1.250	0.699	30
7	3	3.56	3.56	1.000	0.477	0.551		10
8	0	0	—					—

d_x to l_x in proportional terms, so that, for instance, q_2 — the proportion of the six-month-old individuals that die in the subsequent three-month period — is 250/625 or 0.4. q_x can also be thought of as the 'chance of death', and is equivalent to $(1-p_x)$, where 'p' refers to the survival-probability considered previously.

The advantage of the d_x-values is that they can be summed over a period time: the number dying in the first nine months is $d_0+d_1+d_2$ $(=625)$. The disadvantage is that the individual values give no real idea of the intensity or importance of mortality at a particular time. This is because the d_x-values are larger the more individuals there are to die. q_x-values, on the other hand, are a good measure of the intensity of mortality. Thus, in the present example, it is clear from the q_x column that the mortality-rate rose consistently with increasing age; this is not clear from the d_x column. The q_x-values, however, have the disadvantage of not being liable to summation: $q_0+q_1+q_2$ does *not* give us the overall mortality-rate for the first nine months. These advantages are combined, however, in the penultimate column of Table 1.1 in which 'k'-values (Haldane 1949, Varley & Gradwell 1970) are plotted. k_x is defined, simply, as $\log_{10}a_x-\log_{10}a_{x+1}$ (or, equivalently, $\log_{10}a_x/a_{x+1}$), and is sometimes referred to as 'killing-power'. Like the q_x's, k_x's reflect the intensity or rate of mortality, and, in the present case, they increase consistently with age. But, unlike the q_x's, summing the k_x's is a meaningful procedure. Thus the killing-power or k-value of the first nine months is $0.067+0.137+0.222=0.426$, which is also the value of $\log_{10}a_0-\log_{10}a_3$. Note, furthermore, that the k_x-values can be computed from the l_x-values as well as the a_x-values; and that, like the l_x's, the k_x's are standardized and are, therefore, appropriate for comparing quite separate studies. k-values will be of considerable use to us in later chapters.

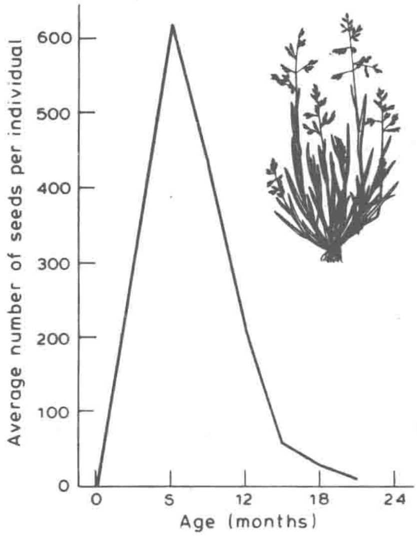

Fig. 1.8. Age-specific fecundity (B_x) for the annual meadow grass, *Poa annua*. (Data from Law 1975.)

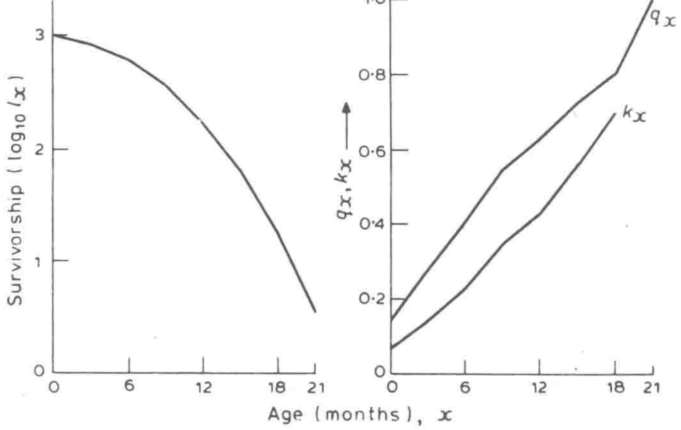

Fig. 1.9. (a) Age-specific survivorship ($\log_{10} l_x$), and (b) age-specific mortality-rates (q_x) and killing-powers (k_x) for the annual meadow grass, *Poa annua*. (Data from Law 1975.)

The age-specific patterns of fecundity and mortality have been plotted in Figs. 1.8 and 1.9. Fig. 1.8 indicates quite clearly an initial sharp rise in fecundity reaching a peak at six months, followed by a gradual decline until the death of the last individual after two years. Fig. 1.9 illustrates a single pattern in three different ways. Fig. 1.9(a) is a 'survivorship curve' — $\log_{10} l_x$ plotted against age — while Fig. 1.9(b) contains two mortality curves, q_x and k_x, plotted against age. All show a consistent rise in the rate of mortality, leading to an increasingly rapid decline in survivorship. Of the three, Fig. 1.9(a) — the survivorship curve — probably shows this most clearly.

The use of logarithms in the survivorship curve deserves further comment. Consider, for instance, the halving of a population over 1 unit of time, in one case from 100 to 50 individuals, and in another case from 10 to 5 individuals. In both cases there has been a reduction by half, i.e. the rate or probability of death *per individual* (usually referred to as the 'per capita rate') is the same. Nevertheless, the slope of an *arithmetic* survivorship curve would be -50 in the first case but -5 in the second. With logarithmic survivorship curves, however, the slopes in these two, equivalent cases are identical. In fact, equivalent advantages are gained by the use of k_x-values: being based on logarithms, they, too, allow recognition of cases in which per capita rates of mortality are the same. Moreover, logarithms also indicate when per capita rates of *increase* are identical. 'Log numbers' should therefore be used in preference to 'numbers' when numerical change is being plotted.

1.4.2 *The static life-table*

Unfortunately, it is not always possible to monitor the dynamics of a population by constructing a 'fixed cohort' life-table. It is, in fact, rarely possible with natural populations of animals, since the individuals are often highly mobile, highly cryptic or both. There is, however, a rather imperfect alternative, which is also illustrated diagrammatically in Fig. 1.7. It involves examining the age structure of the whole population at one particular time, or, since these things cannot be done instantaneously, during one short 'segment' of time.

As an example, we can consider the results, reported by Lowe (1969), of an extensive study of the red deer (*Cervus elaphus*) on the small island of Rhum, Scotland. Each year from 1957 onwards, Lowe and his co-workers examined every one of the deer that was shot under the rigorously controlled conditions of this Nature Conservancy Council reserve. They also made extensive searches for the carcasses of deer that had died from natural causes. Thus, they had access to a large proportion of the deer that died from 1957 onwards. Deer can be reliably aged by the examination of tooth replacement, eruption and wear, and Lowe and his co-workers carried out such examinations on all of the dead deer. If, for instance, they examined a six-year-old deer in 1961, they were able to conclude that, in 1957, this deer was alive and two years old. Thus, by examining carcasses, they were able to reconstruct the age structure of the 1957 population. (Their results did not represent the total numbers alive, because some carcasses must have decomposed before they could be discovered and examined.) Of course, the age structure of the 1957 population could have been ascertained by shooting and examining large numbers of deer in 1957; but, since the ultimate aim of the project was enlightened conservation of the deer, this method would have been somewhat inappropriate.

Lowe's raw data for red deer hinds are presented in column two of Table 1.2. As expected, there were many young deer and rather fewer old deer, but we can treat these raw data as the basis for a life-table *only* if we make a certain set of assumptions. We must assume that the 59 six-year-old deer alive in 1957 were the survivors of 78 five-year-old deer alive in 1956, which were themselves the survivors of 81 four-year-olds in 1955, and so on. In other words, we must assume that the numbers of births and age-specific survival-rates had remained the same from year to year, or, equivalently, that the a_x column of Table 1.2 is essentially the same as *would* have been obtained if we *had* followed a single cohort. Having made this assumption, l_x, d_x and q_x columns have been constructed. It is clear from Table 1.2, however, that our assumption is false. The 'cohort' actually increases in size from years 6 to 7 and 14 to 15, leading to 'negative' deaths and meaningless mortality-rates. The pitfalls of constructing such 'static' life-tables are, therefore, amply illustrated.