

maphroditic animals whose populations have different outcrossing rates (Johnston et al. 1998). Similarly, in wind-pollinated plants, where increased male gamete production may not be subject to diminishing fitness returns, the expected unusually high allocations to male functions are often observed, for example in some grasses (McKone et al. 1998).

9.5. AGE-STRUCTURED POPULATIONS AND THE EVOLUTION OF LIFE HISTORIES

9.5.i. Introduction

So far in this book, we have studied evolutionary processes in populations with discrete generations, in which the offspring are produced simultaneously by the adults, who then die. While this is characteristic of many species of annually breeding plants and insects, it applies to only a fraction of all species. In temperate regions, most species of birds, large mammals, and seed plants live for several years, reproducing in successive breeding seasons; reproduction, moreover, is often deferred for several years after birth. In the tropics, many species have no discrete breeding seasons, but reproduce more or less continuously throughout adult life. Familiar examples of this include *Drosophila melanogaster* and humans. Such populations are thus *age-structured*, with overlapping generations: individuals of different ages have different sizes, mortality rates, and rates of reproduction, and can reproduce with one another.

Are the population genetic results derived earlier still valid for age-structured populations, or do some of our major conclusions have to be revised for such populations? In the next sections, we extend the models of selection developed in **Chapters 2, 3, and 8** to age-structured populations, and show how most of the old results still apply, at least as approximations, while some new ones emerge. In addition, we show how understanding selection in age-structured populations sheds light on how selection shapes life histories, and, in particular, why aging evolves.

9.5.ii. Demographic models

9.5.ii.a. Basic concepts and notation

The theory of selection in age-structured populations rests on standard concepts from demography, e.g., Stearns (1992, Chapter 2), Charlesworth (1994b, Chapter 1), Caswell (2000, Chapter 1), and Roff (2002, Chapter 2), and so we start by introducing these. The science of demography relates the growth over time in the size of a population to the age-specific survival and reproductive rates of its constituent individuals—their *demographic parameters*. The popu-

lation is assumed to be sufficiently large that its behavior can be treated deterministically. For simplicity, we initially ignore sex differences in the case of a species with separate sexes, and consider only the female component of the population. The justification for this is that female fertility is rarely limited by the number of males in the population, so that population growth can be realistically modeled by considering females only. Similarly, for a cosexual population of animals or plants, we consider only the output of eggs or seeds, respectively.

We assume initially that the life history can be partitioned into discrete time intervals, e.g., the years separating successive annual breeding seasons of temperate zone species. Ignoring differences between genotypes for the moment, the state of the population at a given time t can be described by the number of individuals in each *age class* (**Figure 9.13**), such that $n(x, t)$ is the number of individuals of age class x at time t ; in an organism with an annual breeding season, these would be counted at the time of breeding. It is convenient to assign new zygotes to age 0. $n(0, t)$ is then the number of zygotes produced at time t , $n(1, t)$ is the number of surviving individuals that were in age class 0 at time $t - 1$, and so on. Individuals of a given age x have an age-dependent probability, $P(x, t)$, of survival to the next time interval, $t + 1$, when they will be aged $x + 1$ (**Figure 9.13**). The value of x has an upper limit, d , above which there are no surviving individuals in the population, so we can represent the state of the population by a vector $\mathbf{n}(t)$, with components $n(1, t), \dots, n(d, t)$.

Female fecundity at age x , $m(x, t)$, is defined as the expected number of daughters produced by a female aged x at time t . The age at which individuals start breeding (the age of reproductive maturity) is denoted by b , which is ≥ 1 (**Figure 9.13**). The chance of survival of a newborn to the next time interval, when they are aged 1, is $P(0, t)$. The effective fecundity of females aged x at time t , in terms of daughters contributed to the population at time $t + 1$, is thus $f(x, t) = m(x, t)P(0, t)$.

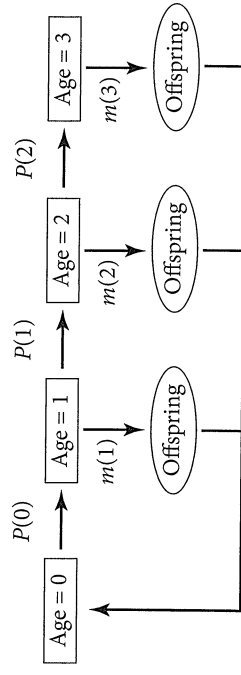


FIGURE 9.13 Number of individuals in each age class of a population with age structure (overlapping generations). In this example, individuals survive to a maximum age of three and start reproducing when they reach age one. The transitions between different age classes caused by survival and fecundity are indicated by the P and m values, respectively.

We initially assume that the demographic parameters are constant over time, so that the dependence on t of P and m can be dropped. The probability of survival from age x to $x + 1$ can then be related to an underlying rate of mortality, $\mu(x)$, per unit time over this interval, so that we can write $P(x) = \exp -\mu(x)$, applying the argument used in **Section 6.1.ii.b**. It follows that $\ln P(x) = -\mu(x)$.

The net probability of surviving from conception to age x is given by the *survival function*: $l(x) = P(0)P(1) \dots P(x-1)$. Because there is always some mortality at each age, $l(x)$ declines with age. Aging implies an increase in the rate of decline of $l(x)$ with age, but this is often detectable only when organisms are raised in sheltered conditions, because high rates of age-independent causes of death in the wild (caused by predation, disease, or starvation) conceal the underlying tendency for $P(x)$ for adult individuals to decline with age (Finch 1990, Chapter 1). An example is shown in **Figure 9.14**.

The life history can be summed up by the compound *reproductive function*: $k(x) = l(x)m(x)$, which is the expected number of daughters produced at age x by a newly formed female individual aged 0. The reproductive function, $k(x)$, is 0 for pre-reproductive ages ($x < b$), and rises after the start of reproduction. Because $l(x)$ declines with age, $k(x)$ may also start to decline, unless the decline in $l(x)$ is compensated for by an increase in $m(x)$. Such an increase happens in species that continue to grow after reaching reproductive maturity, and where fecundity is related to body size, as in trees and many cold-blooded vertebrates.

9.5.ii.b. Predicting population growth

With constant demographic parameters, the population rapidly approaches a constant exponential rate of growth in size, corresponding to a constant *age structure* [i.e., subject to some mild restrictions on the $k(x)$ function, the proportions of individuals in the different age classes remain unchanged over time]. The argument is outlined in **Box 9.8***. This growth rate, r , is the *intrinsic rate of increase* or *Malthusian parameter* (Fisher 1930b, p. 25), and is the unique real number that satisfies the *Euler-Lotka* equation, named after the eighteenth-century mathematician and the twentieth-century mathematical biologist who independently discovered it (Euler 1760; Sharpe and Lotka 1911). We have the following relation:

$$\sum_{x=b}^d \exp(-rx)k(x) = 1 \quad (9.3)$$

This representation is exact for species that reproduce at discrete time intervals. It is an approximation for species where reproduction occurs continuously in time, but it can be made arbitrarily close by increasing the number of age classes into which the life history is divided. Integration over a continuous range of ages then replaces summation (**Appendix A1.iii**). Given the values of

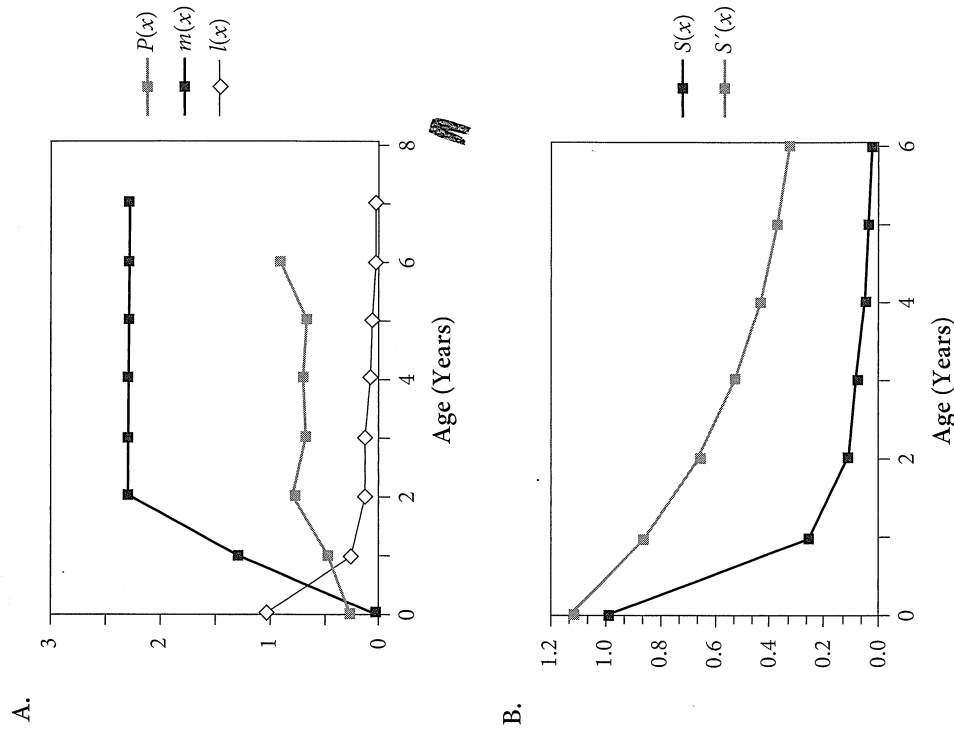


FIGURE 9.14 **A.** Demographic parameters for a wild population of gray squirrels (*Sciurus carolinensis*) in North Carolina. **B.** The corresponding sensitivities of fitness to changes in $\ln P(x)$ and $m(x)$, $S(x)$ and $S'(x)$, respectively, from **Equations B9.13.3b** and **B9.13.4** in **Section 9.5.v.a**. [Data from Barkalow et al. (1970).]

$k(x)$ for each x , r can be determined numerically from **Equation 9.3** by Newton's method (**Appendix A1.ii.b**).

Demographic theory shows that the state of constant growth rate and age structure is approached quickly for biologically realistic life histories. Once this state is reached, some important quantities can be derived, which are described in **Box 9.9**; as we show in **Sections 9.5.iii** and **9.5.v** below, these are very useful for analyzing the effects of selection on life histories. But we first deal with some population genetics that includes age structure.

Box 9.8* PREDICTING CHANGES IN AN AGE-STRUCTURED POPULATION OVER TIME

B9.8.i. The population projection matrix

The state of the population at time t can be represented by a column vector $\mathbf{n}(t)$, whose components are the numbers of individuals in age classes $1, 2, \dots, d$ at time t , i.e., $n(1, t), n(2, t), \dots, n(d, t)$. The numbers of individuals in age classes other than 1 at time $t + 1$ represent the survivors over one time interval, among individuals aged one unit less at time t , i.e.,

$$n(x + 1, t + 1) = n(x, t)P(x) \quad (x = 1, 2, \dots, d) \quad (\text{B9.8.1})$$

The individuals in age class 1 at time $t + 1$ are the survivors of the zygotes produced by the population at time t , whose number is denoted by $n(0, t)$.

This number is given by the sum over age classes b to d of $n(x, t)m(x)$; the number of survivors to stage 1 at time $t + 1$, $n(1, t + 1)$, is the product of this sum and $P(0)$. If we write $f(x) = m(x)P(0)$, we have:

$$n(1, t + 1) = \sum_{x=b}^d n(x, t)f(x) \quad (\text{B9.8.2})$$

This relation can be expressed in matrix notation (Appendix A1.iv.a) as:

$$\mathbf{n}(t + 1) = \mathbf{A}\mathbf{n}(t) \quad (\text{B9.8.3})$$

where \mathbf{A} is the *population projection* or *Leslie matrix* (P. H. Leslie was one of the ecologists who introduced this representation into population biology; see Leslie 1945).

B9.8.ii. The asymptotic rate of change in population size

Based on these equations, \mathbf{A} is a matrix whose elements are all 0, except (potentially) the members of the first row from column b onward, and for the sub-diagonal elements: $a_{i,i} = f(i)$ ($i = b, \dots, d$) and $a_{i,i+1} = P(i)$. It is thus a *non-negative* matrix, because its elements are positive or 0 in value. It is known from the general theory of non-negative matrices that the largest eigenvalue, λ_1 , of \mathbf{A} (Appendix A1.iv.c) is unique and real, unless the fecundities $f(x)$ are periodic, i.e., all the $f(x)$ are 0 except for x values that

are fixed multiples of an integer greater than 1 (Charlesworth 1994b, p. 23).

In all other cases, the population will reach a state in which $\mathbf{n}(t + 1) = \lambda_1 \mathbf{n}(t)$ (Appendix A1.iv.d), so that $n(x, t + 1) = \lambda_1 n(x, t + 1)$ for all x . If we take natural logarithms, the asymptotic rate of change in $\ln n(x, t)$ for all x is equal to $\ln \lambda_1$, which we can write as r , the *intrinsic rate of increase* of the population.

The *characteristic equation* that determines λ and r can be derived very easily by the following argument. Let $B(t)$ be the number of new zygotes formed at time t ; the number of females aged x at time t is then $B(t - x)l(x)$, each of which produces $m(x)$ daughters. For $t \geq d$, so that no individuals alive at time 0 contribute to the population, we have:

$$B(t) = \sum_{x=b}^d B(t - x)k(x) \quad (\text{B9.8.4})$$

If the population has reached the asymptotic rate of growth, we have:

$$B(t - x)/B(t) = \lambda_1^{-x} = \exp(-rx) \quad (\text{B9.8.5})$$

Dividing both sides of Equation B9.8.4 by $B(t)$ and using Equation B9.8.5, we obtain Equation 9.3 of the main text. This corresponds to the characteristic equation of \mathbf{A} , as can be confirmed by a direct evaluation.

Box 9.9 PROPERTIES OF A POPULATION WITH A CONSTANT AGE STRUCTURE

B9.9.i. The stable age distribution

The ratio of the number of individuals in two age classes (x and y) at time t is $n(x, t)/n(y, t)$. This represents the *age distribution* of the population, i.e., the relative frequencies of individuals in different age classes. We have $n(x, t) = B(t - x)l(x)$, so that $n(x, t)/n(y, t) = B(t - x)l(x)/B(t - y)l(y)$. If the population has reached its asymptotic rate of growth, Equation B9.8.5 implies that:

$$\frac{n(x, t)}{n(y, t)} = \frac{\exp(-rx)l(x)}{\exp(-ry)l(y)} \quad (\text{B9.9.1})$$

i.e., the age distribution is constant over time. This equilibrium age distribution is often referred to as the *stable age distribution*. Other things being equal, **Equation B9.9.1** implies that a high intrinsic rate of population growth causes the stable age distribution to be weighted towards a high frequency of young individuals.

B9.9.ii. Reproductive value

Fisher (1930b, pp. 27–28) introduced the concept of the *reproductive value* of age x , $v(x)$. This measures the expected net contribution of zygotes to the population from a female aged x , counting both the offspring she contributes at age x and the number she is expected to contribute from all future ages. Because the population increases by a factor of $\lambda_1 = \exp(r)$ each time interval, her fecundity at age $y = x + z$ is discounted by $\exp(-rz)$, multiplied by her probability of survival to age y , $l(y)/l(x)$. Summing over all ages from x on, this gives the following expression:

$$v(x) = \frac{\exp(rx)}{l(x)} \sum_{y=x}^d \exp(-ry)k(y) \quad (\text{B9.9.2})$$

As discussed in **Section 9.5.v**, reproductive value plays an important role in the theory of life history evolution. If this equation is applied to a new zygote, for which $x = 0$, its reproductive value is $v(0) = 1$.

B9.9.iii.* Mathematical interpretation of reproductive value and stable age distribution

It can be shown that the $v(x)$ values correspond to the components of the leading left eigenvector, \mathbf{v}_1 , of \mathbf{A} (**Appendices A1.iv.c** and **A1.iv.d**). **Equations B9.8.1–B9.8.3** give:

$$\lambda_1 \mathbf{v}(x) = f(x)v(1) + P(x)v(x+1) \quad (\text{B9.9.3})$$

(See **Problem 9.6.i***.) As is always the case with an eigenvector, only the relative values of the $v(x)$ are defined by this relation. Some simple algebra shows that this expression is equivalent to **Equation B9.9.2 (Problem 9.6.ii*)**.

Similarly, the relative values of the components of $\mathbf{n}(t)$ for large t are given by μ_1 , the leading right eigenvector of \mathbf{A} . **Equation B9.9.1** thus implies that the x th component of μ_1 is proportional to $\exp(-rx)l(x)$, i.e.,

the components of the leading right eigenvector are proportional to the relative numbers of individuals in the different age classes.

B9.9.iv. Generation time

Formally, there is no such thing as a generation in an age-structured population. However, for purposes of comparison with discrete generation models, it is useful to define a generation time. The most appropriate definition is the mean age of mothers of a set of zygotes at a given time t . In general, this is given by:

$$\frac{\sum_x x n(x, t) m(x)}{B(t)} = \frac{\sum_x x B(t-x)k(x)}{B(t)}$$

Because $B(t-x)/B(t) = \exp(-rx)$ for a population at the stable age distribution, this allows us to write the generation time for such a population as:

$$T = \sum_x x \exp(-rx)k(x) \quad (\text{B9.9.4})$$

This formula brings out clearly that a high rate of population growth is associated with a short generation time, because a large value of r causes $\exp(-rx)$ to be weighted towards low values of x .

B9.9.v. Net reproduction rate

Another quantity that plays an important role in demography is the *net reproduction rate* or *lifetime reproductive success*, R . This is simply the sum over all ages (x) of fecundity at age x , discounted by the probability of surviving to age x :

$$R = \sum_x k(x) \quad (\text{B9.9.5})$$

If the population is stationary in size (i.e., $r = 0$), this is equivalent to $v(0)$. An increase in population size requires $R > 1$, and a decrease corresponds to $R < 1$.

9.5.ii.c. Population genetics for age-structured populations

Consider a single autosomal locus with two alleles A_1 and A_2 . A given genotype $A_i A_j$ (i and $j = 1$ or 2) has its own set of demographic parameters for females, i.e., a set of values of $k_{ij}(x) = l_{ij}(x)m_{ij}(x)$. We can apply the Euler-Lotka equation to a hypothetical population exclusively of genotype $A_i A_j$, and define an intrinsic rate of increase r_{ij} for this genotype. This is often used as a measure of fitness, equivalent to the Malthusian parameter used for microbial populations in **Section 3.1.iii.d**.

If the population reproduces asexually, so that females produce only daughters, each genotype constitutes a separate sub-population that reproduces independently of the other genotypes. The genotype with the highest value of r_{ij} will thus eventually replace all of the others; similar principles apply to completely self-fertilizing populations of cosexuals (Pollak and Kempthorne 1970). This result has often been used by evolutionary ecologists to justify the use of r as a measure of fitness, initially by Cole (1954). The result applies to a population of any ploidy level.

For a sexually reproducing population, however, it is by no means obvious whether such a result is valid. Consider a population with separate sexes, where males and females contribute equally to the new zygotes. Both male and female demographic parameters must then appear in a selection model. The reproductive success of males (the number of offspring that they father) must in general depend on the age structure and the genotypic composition of the female population, because the number of offspring produced by a male depends on the ages and genotypes of the females with whom he mates. If some simplifying assumptions are made, however, a set of recursion relations for allele frequencies can be derived (**Box 9.10**). These assumptions include random mating with respect to age and genotype, progeny sex ratio independent of age and genotype, and the same ratios of male and female $k(x)$ values for a given genotype at each age x . For details, see Charlesworth (1994b, pp. 108–109).

9.5.iii. Selection equations

9.5.iii.a. The general recursion relations with no sex differences

The assumptions just mentioned mean that allele frequencies will be the same for the male and female gametes produced by the population at time t . As shown in **Box 9.10**, this yields a set of recursion equations that resemble those for selection at a single locus with discrete generations (**Section 2.1.ii**). This is the special case for a single age class with reproduction starting at age 1.

These results do not, however, immediately help us find a fitness measure analogous to that used in discrete generation models, because we have an intractable set of high-dimensional equations with no simple exact solution.

Box 9.10 THE SELECTION EQUATIONS FOR A RANDOMLY MATING AGE-STRUCTURED POPULATION

Let $p(t)$ and $q(t)$ be the frequencies of alleles A_1 and A_2 among the gametes produced at time t , where $q(t) = 1 - p(t)$. The simplifying assumptions described in the text mean that the frequencies of $A_1 A_1$ and $A_2 A_2$ individuals among the new zygotes produced at time t are $p(t)^2$ and $q(t)^2$, respectively, and the frequency of heterozygotes is $2p(t)q(t)$. This implies that the number of $A_1 A_1$ individuals aged x at time t is equal to $B(t-x)p_1(t-x)^2 l_{11}(x)$; the total number of offspring that they contribute to the population at time t is $m_{11}(x)/(1-c)$, where c is the proportion of males among the zygotes (the primary sex ratio of **Section 9.4.i**). Homozygotes $A_1 A_1$ aged x thus contribute $2B(t-x)p(t-x)^2 l_{11}(x)m_{11}(x)/(1-c)$ to the number of A_1 alleles among the zygotes produced at time t . Similarly, heterozygotes $A_1 A_2$ contribute $B(t-x)p(t-x)q(t-x)l_{12}(x)m_{12}(x)/(1-c)$.

The total number of A_1 alleles among the zygotes produced at time t , $B_1(t)$, is obtained by adding these terms and summing over x . A similar expression can be written for the total number of A_2 alleles, $B_2(t)$, substituting subscript 2 for 1. The total number of alleles entering the population at time t is $2B(t) = B_1(t) + B_2(t)$.

The frequency of A_1 among the zygotes at time t is thus $p(t) = B_1(t)/2B(t)$. The term $(1-c)$ cancels from the top and bottom of this expression, and we can replace $l_{ij}(x)m_{ij}(x)$ by $k_{ij}(x)$. This yields the following expressions:

$$p(t) = \frac{\sum_x B(t-x) [p(t-x)k_{11}(x) + q(t-x)k_{12}(x)]}{B(t)} \quad (\text{B9.10.1a})$$

$$q(t) = \frac{\sum_x B(t-x) [p(t-x)k_{21}(x) + q(t-x)k_{22}(x)]}{B(t)} \quad (\text{B9.10.1b})$$

$$B(t) = \sum_x B(t-x) [p(t-x)^2 k_{11}(x) + 2p(t-x)q(t-x)k_{12}(x) + q(t-x)^2 k_{22}(x)] \quad (\text{B9.10.1c})$$

9.5.iii.b. *Equilibrium conditions*

Several approaches have been used to solve this difficulty. A simple one is to consider the conditions for a polymorphic equilibrium, such that $p(t)$ and $q(t)$ have reached constant values, p^* and $q^* = 1 - p^*$, respectively. **Box 9.11** shows that the following expression determines p^* and q^* in the same way as the fitness w_{ij} with discrete generations:

$$w_{ij}(\tau) = \sum_x \exp(-rx)k_{ij}(x) \quad (9.4)$$

where r is the intrinsic rate of increase of the population as a whole.

To determine the genotypic composition of an equilibrium population with overlapping generations, we can use $w_{ij}(\tau)$ instead of the corresponding discrete generation fitness. This result applies quite generally, including equilibria under mutation–selection balance and multi-locus systems (Charlesworth

1994b, Chapter 3). It is worth noting that $w_{ij}(\tau)$ is the reproductive value at age 0 for genotype ij (**Box 9.9**).

A difficulty, however, is that the equation that determines r (i.e., **Equation B9.11.1**) itself involves the allele frequencies that are to be found. One solution to this problem is to regard r as a quantity that can be determined empirically. The other is to solve the set of simultaneous equations (**Equations B9.11.2a** and **B9.11.2b**), or their equivalents for more complex genetic models. There is a known solution for two alleles (Charlesworth 1994b, p. 122). For mutation–selection balance at a single site with two variants, r is well approximated by the value for a population homozygous for wild type (Charlesworth 1994b, p. 126). In general, however, the equations must be solved numerically.

A reasonable assumption for many natural populations is that the population growth rate is close to 0, due to density-dependent mortality or fertility (Begon et al. 2006, Chapter 5). **Equation 9.4** then reduces to the lifetime reproductive success or net reproduction rate R (**Box 9.9.v** of **Section 9.5.ii.b**) of genotype ij , which is often used by evolutionary ecologists as a fitness measure (e.g., Clutton-Brock 1988).

9.5.iii.c. *Stability and invasion conditions*

The second approach is to consider the conditions for the stability of equilibria, either global or local. The most complete treatment is that of Norton (1928) for the continuous-time version of **Equations B9.10.1a–B9.10.1c**. (Norton was the mathematician who also first investigated the speed of change of allele frequencies under selection for the discrete generation model; see **Section 3.1.iii.b**.) By a complicated argument, he showed that the ultimate outcome of selection is determined entirely by the relations between the r_{ij} . Allele A_2 tends to fixation if r_{22} is the largest of the set $\{r_{11}, r_{12}, r_{22}\}$. If there is heterozygote superiority in the r_{ij} , the allele frequencies tend to the neighborhood of the equilibrium discussed above; with heterozygote inferiority, the allele whose initial frequency lies between the equilibrium value and 1 tends to fixation. A local stability analysis of the polymorphic equilibrium can also be carried out for the discrete time interval model (Charlesworth 1994b, pp. 162–166) and gives corresponding results.

The local stability method can also be applied to the case of the invasion of a population that is fixed for allele A_1 by a rare, nonrecessive variant A_2 (Charlesworth 1973). The argument is displayed in **Box 9.12** and shows that the rate of increase in frequency of A_2 is determined by the difference between the intrinsic rate of increase of its heterozygous carriers, and that of the predominant homozygous genotype, A_1A_1 .

This type of analysis can be extended to the case of an initial population held at a stationary population size by density dependence (Charlesworth 1973); in this case, the demographic parameters for the invading mutant heterozygote

Box 9.11 CONDITIONS FOR A POLYMORPHIC EQUILIBRIUM

An equilibrium population can be treated as genetically homogeneous as far as its demography is concerned. It will thus achieve a constant growth rate, r , given by the equivalent of **Equation 9.3** of **Section 9.5.ii.b**. This means that $B(t-x)/B(t) = \exp(-rx)$, and so **Equation B9.10.1c** of **Section 9.5.iii.a** gives an Euler–Lotka equation:

$$\sum_x \exp(-rx) [p^{*2}k_{11}(x) + 2p^*q^*k_{12}(x) + q^{*2}k_{22}(x)] = 1 \quad (\text{B9.11.1})$$

Equations B9.10.1a and **B9.10.1b** become the following:

$$\sum_x \exp(-rx) [p^*k_{11}(x) + q^*k_{12}(x)] = 1 \quad (\text{B9.11.2a})$$

$$\sum_x \exp(-rx) [p^*k_{12}(x) + q^*k_{22}(x)] = 1 \quad (\text{B9.11.2b})$$

Comparison with the equivalent equations for the discrete generation case (**Section 2.1.ii.c**) shows that the discrete generation fitness w_{ij} for genotype ij plays the same role in determining p^* as the quantity $w_{ij}(\tau)$ defined by **Equation 9.4** of the main text.

Box 9.12 CONDITIONS FOR INITIAL INCREASE OF A RARE ALLELE

We use the same approach as for the initial increase of a rare allele in the discrete generation case, i.e., we ignore second-order terms in its frequency (Section 3.1.iii.c). Equation B9.10.1b of Section 9.5.iii.a then yields the following relation:

$$q(t) \approx \sum_x q(t-x) \exp(-r_{11}x) k_2(x) \quad (\text{B9.12.1})$$

This leads to an Euler-Lotka equation (Section 9.5.ii.b), which gives the asymptotic rate of change of the natural logarithm of $q(t)$ as the real root of the equation:

$$\sum_x \exp[-(r_{11} + r)x] k_2(x) = 1 \quad (\text{B9.12.2})$$

This implies that the rate of change is $r_{12} - r_{11}$, which provides a measure of the selective advantage of A_2 when rare. A_2 will thus invade a population fixed for A_1 when $r_{12} > r_{11}$. By symmetry, A_1 will invade a population fixed for A_2 when $r_{12} > r_{22}$, consistent with the results on heterozygote superiority described above.

The case of invasion by a recessive mutant allele A_2 is harder to analyze, because second-order terms in mutant allele frequency can no longer be neglected (see Section 3.1.iii.c), but it can be shown that A_2 will invade an A_1 population if $r_{22} > r_{11}$. Its selective advantage, however, is not equal to $r_{22} - r_{11}$, except as an approximation when selection is weak (Charlesworth 1994b, p. 152).

are evaluated under the conditions for the stationary initial population. The predominant homozygote necessarily has an intrinsic rate of 0, so that the variant will invade only if the heterozygote has a positive growth rate under the prevailing intensity of density-dependent factors.

9.5.iii.d. Weak selection approximations

The final method is to assume weak selection and to seek approximations for rates of change of allele frequencies. This was first done by Haldane (1927a, 1962) and was later generalized by Charlesworth (1994b, Chapter 4). We can select an arbitrary genotype as a standard, with life-history parameters $k_s(x)$.

Weak selection implies that any other genotype ij has a $k_{ij}(x)$ function differing from $k_s(x)$ by an amount that is smaller in magnitude than a measure of the strength of selection, ε , where ε is sufficiently small that second-order terms can be neglected.

Under these conditions, the rate of change per time interval in the frequency of allele A_2 in Equations B9.10.1b–B9.10.1c rapidly approaches:

$$\Delta q \approx pq(r_2 - r_1) \quad (9.5)$$

where $r_1 = pr_{11} + qr_{12}$, $r_2 = pr_{12} + qr_{22}$, and the error is on the order of ε^2 .

This is identical in form to the corresponding discrete generation equation with weak selection (Section 3.1.iii.b), except that the rate of change is per time interval, not per generation. This approach can also be extended to the case of density-dependent populations, yielding results similar to those for the discrete generation case (Charlesworth 1994b, pp. 147–149).

9.5.iii.e. Relationships between different fitness measures

The results of the exact analysis of equilibrium populations give one possible interpretation of what is meant by fitness in an age-structured population. The analyses of conditions for local and global stability give a somewhat different one, but suggest that we can use differences in intrinsic rates of increase among genotypes to predict rates of change of allele frequencies, at least as a first-order approximation when selection is weak or when a rare allele is invading a population. However, the equilibrium fitness expression of Equation 9.4 in Section 9.5.iii.b is not obviously related to the intrinsic rate of increase.

These discrepancies disappear, however, with sufficiently weak selection, as can be seen as follows. As noted above, the weak selection Equation 9.5 gives a rate of change per time interval, not per generation. To make it comparable to the discrete generation case, we need to convert to a time scale of generations. This can be done using the formula for the generation time with age structure, T (Box 9.9.iv of Section 9.5.ii.b). When the genotypes have different life-history parameters, we can again select a standard genotype and use its generation time T_s as an approximate measure for the population as a whole. If Equation 9.5 is multiplied by T_s , we obtain an expression for the rate of change of allele frequency that is on the same order of accuracy as the original equation, but expressed as a rate per generation. This shows that we can use $T_s'_{ij}$ as a measure of the fitness of genotype ij that is approximately equivalent to the familiar discrete generation measure w_{ij} .

This is confirmed by the fact that, with weak selection, genotypic differences in the equilibrium fitness function $w_{ij}(r)$ are approximately proportional to the corresponding differences in the intrinsic rates of increase, with a proportionality constant equal to the generation time for a standard genotype (Problem 9.7*).