CHAPTER 7

Effective Population Size

Medium ground finch, Example 7.2

Effective population size (N_e) is one of the most fundamental evolutionary parameters of biological systems, and it affects many processes that are relevant to biological conservation.

(Robin S. Waples 2002, p. 148)

Use of genomic SNP data could improve N_e estimation precision substantially, but could also cause a bias due to marker linkage (i.e. limited genome size).

(Mark Beaumont & Jinliang Wang 2019, p. 462)

We saw in the previous chapter that we expect heterozygosity to be lost at a rate of $1/2N$ per generation in ideal populations (Equation 6.5). However, this expectation holds only under conditions that rarely apply to real populations. For example, such factors as the number of individuals of reproductive age rather than the total of all ages, the sex ratio, and differences in reproductive success among individuals must be considered. Thus, the actual number of adult individuals in a natural population (census size, N_C) is not sufficient for predicting the rate of genetic drift. We will use the concept of effective population size to deal with the discrepancy between the demographic size and population size relevant to the rate of genetic drift in natural populations.

Perhaps the most important assumption of our model of genetic drift has been the absence of natural selection. That is, we have assumed that the genotypes under consideration do not affect the fitness (survival and reproductive success) of individuals. We would not be concerned with the retention of genetic variation in small populations if the assumption of genetic neutrality were true for all loci in the genome. However, the assumption of neutrality and the use of neutral loci allow us to predict the effects of finite population size with great generality. In Chapter 8, we will consider the effects of incorporating natural selection into our basic models of genetic drift.

7.1 Concept of effective population size

Our consideration in the previous chapter of genetic drift dealt only with "ideal" populations. **Effective population size** (N_e) is the size of the **ideal** (Wright–Fisher) **population** (N) that will result in the same amount of genetic drift as in the actual population being considered. The basic ideal population consists of "N diploid individuals reconstituted each generation from a random sample of $2N$ gametes" (Wright 1939, p. 298). In an ideal population, individuals produce both female and male gametes (**monoecy**) and self-fertilization is possible. Under these conditions, heterozygosity will decrease by exactly $1/2N$ per generation.

Conservation and the Genomics of Populations, Third Edition. Fred W. Allendorf, *et al.*, Oxford University Press.

We can see this by considering an ideal population of N individuals (say 10) in which each individual is heterozygous for two unique alleles for a total of 20 alleles (Figure 7.1). All of these 10 individuals will contribute equally to the gamete pool, which is sampled to create each individual in the next generation. Thus, each allele will be at a frequency of $1/2N = 0.05$ in the gamete pool. A new individual will only be homozygous if the same allele is present in both gametes. For the purposes of our calculations, it does not matter which allele is sampled first because all alleles are equally frequent. Let us say the first gamete chosen is *A15*. This individual will be homozygous only if the next gamete sampled is also *A15*. What is the probability that the next gamete sampled is *A15*? This probability is simply the frequency of the *A15* allele in the gamete pool, which is $1/2N = 0.05$ because all 20 alleles (2×10) are at equal frequency in the gamete pool (Figure 7.1). Therefore, the expected homozygosity is $1/2N$, and the expected heterozygosity of each individual in the next generation is $1 - (1/2N) = 0.95$.

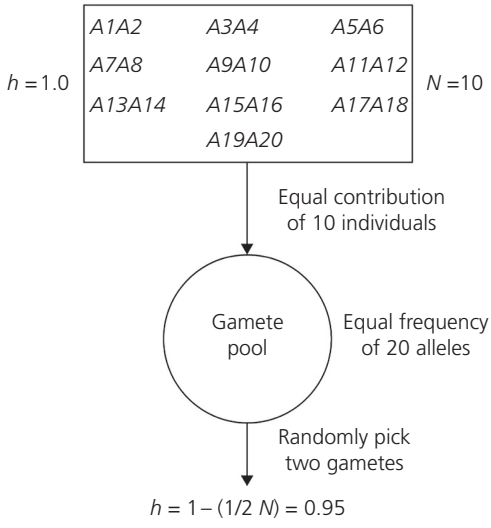

Figure 7.1 Diagram of reduction in heterozygosity (h) in an ideal population consisting of 10 individuals that are each heterozygous for two unique alleles ($h = 1$). Two gametes are picked from the gamete pool to create each individual in the next generation.

This conceptual model becomes more complicated if self-fertilization is prevented, or if the population is **dioecious**. In these two cases, the decrease in heterozygosity due to sampling individuals from the gamete pool will skip a generation because both gametes in an individual cannot come from the same parent. Nevertheless, the mean rate of loss per generation over many generations is similar in this case; heterozygosity is lost at a rate more closely approximated by $1/(2N+ 1)$ (Wright 1931; Crow and Denniston 1988). The difference between these two expectations, $1/2N$ and $1/(2N+ 1)$, is usually ignored because the difference is small except when N is very small (Luikart et al. 1999).

For our general purposes, the ideal population consists of a constant number of N diploid individuals ($N/2$ females and $N/2$ males) in which all parents have an equal probability of being the parent of any individual progeny. We will consider the following effects of violating the assumptions of such idealized populations on the rate of genetic drift:

1. Equal numbers of males and females.
2. All individuals have an equal probability of contributing an offspring to the next generation.
3. Constant population size.
4. Nonoverlapping (discrete) generations.

We have examined two expected effects of genetic drift: changes in allele frequency (Section 6.2) and a decrease in heterozygosity (Section 6.3). Thus, there are at least two possible measures of the effective population size. First, the "**variance effective number**" (N_{eV}) is whatever must be substituted in Equation 6.1 to predict the expected changes in allele frequency. Second, the "inbreeding effective number" (N_{eI}) is whatever must be substituted in Equation 6.2 to predict the expected reduction in heterozygosity (Example 7.1). See Ryman et al. (2019) for an extensive consideration of a variety of measures of effective population sizes. We will only consider the first two kinds of effective population size (N_{eV} and N_{eI}) because they have the most relevance for understanding the loss of genetic variation in populations.

Example 7.1 Effective population size of grizzly bears

Harris & Allendorf (1989) estimated the effective population size of grizzly bear populations using computer simulations based upon life history characteristics (survival, age at first reproduction, litter size, etc.). They estimated N_{el} by comparing the loss of heterozygosity in the simulated populations to that expected in an ideal population of $N = 100$ (Figure 7.2). Over a wide range of conditions, the effective population size was ~25% of the actual population size. However, this method, like others, does not account for all factors that might reduce N_e (e.g., high variance in reproductive success).

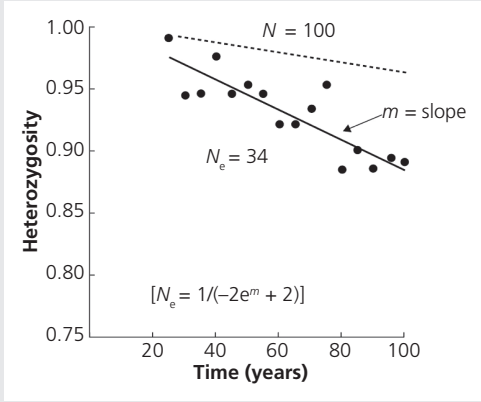

Figure 7.2 Estimation of effective size of grizzly bear populations ($N_C = 100$) by computer simulation. The dashed line shows the expected decline in heterozygosity over 10 generations (100 years) in an ideal population using Equation 6.7. The solid line shows the decline in heterozygosity in a simulated population. The decline in heterozygosity in the simulated population is equal to that expected in an ideal population of 34 bears; thus, $N_e = 34$ (m is the slope of the regression of the log of heterozygosity on time). From Harris & Allendorf (1989).

Crow & Denniston (1988) have clarified the distinction between these two measures of effective population size. In many cases, a population has nearly the same effective population size for either measure. Specifically, their values are identical in constant size populations in which the age and sex distributions are unchanging. We will first consider N_e to be the inbreeding effective population size under different circumstances because this number is most widely used, and we will then consider when these two numbers will differ.

7.2 Unequal sex ratio

Populations often have unequal numbers of males and females contributing to the next generation. The two sexes, however, contribute an equal number of autosomal genes to the next generation regardless of the total of males and females in the population. Therefore, the amount of genetic drift attributable to the two sexes must be considered separately. Consider the extreme case of one male mating with 100 females. In this case, all progeny will be half-sibs because they share the same father. In general, the rarer sex is going to have a much greater effect on genetic drift so that the effective population size will seldom be much greater than twice the size of the rarer sex.

What is the size of the ideal population that will lose heterozygosity at the same rate as the population we are considering which has different numbers of females and males? We saw in Section 6.3 that the increase in homozygosity due to genetic drift is caused by an individual being homozygous because its two gene copies were derived from a common ancestor in a previous generation. The inbreeding effective population size in a **monoecious** population in which selfing is permitted may be defined as the reciprocal of the probability that two uniting gametes come from the same parent. With separate sexes, or if selfing is not permitted, uniting gametes must come from different parents; thus, the effective population size is the probability that two uniting gametes come from the same grandparent.

The probability that the two uniting gametes in an individual came from a male grandparent is 1/4. (One-half of the time uniting gametes will come from a grandmother and a grandfather, and 1/4 of the time both gametes will come from a grandmother.) Given that both gametes come from a grandfather, the probability that both come from the same male is $1/N_m$, where N_m is the number of males in the grandparental generation. Thus, the combined probability that both uniting gametes come from the same grandfather is

$(1/4 \times 1/N_m) = 1/4N_m$. The same probabilities hold for grandmothers. Thus, the combined probability of uniting gametes coming from the same grandparent is then:

$$\frac{1}{N_e} = \frac{1}{4N_f} + \frac{1}{4N_m} \quad (7.1)$$

This is more commonly represented by solving for N_e with the following result:

$$N_e = \frac{4N_f N_m}{N_f + N_m} \quad (7.2)$$

As we expect, if there are equal numbers of males and females ($N_f = N_m = 0.5N$), then this expression reduces to $N_e = N$.

In general, a skewed sex ratio will not have a large effect on the N_e/N ratio unless there is a great excess of one sex or the other. Figure 7.3 shows this for a hypothetical population with a total of 100 individuals. N_e is maximum (100) when there is an equal number of males and females, but declines as the sex ratio departs from 50:50. However, small departures from 50:50 have little effect on N_e. The dashed lines in this figure show that the N_e/N ratio will only be reduced by half if the least common sex is less than 15% of the total population. In the most extreme case, the N_e will be approximately four times the rarer sex:

N_f	N_m	N_e
1,000	1	4.0
1,000	2	8.0
1,000	3	12.0
1,000	4	15.9
1,000	5	19.9

Some populations of ungulates in which males are more likely to be hunted can have highly skewed sex ratios. For example, males comprised less than 1% of all adult elk in the Elkhorn Mountains of Montana in 1985 (Lamb 2010). Several authors have suggested that only one male per 25–100 females is sufficient for maintaining population growth and demographic productivity in hunted ungulate populations (e.g., White et al. 2001).

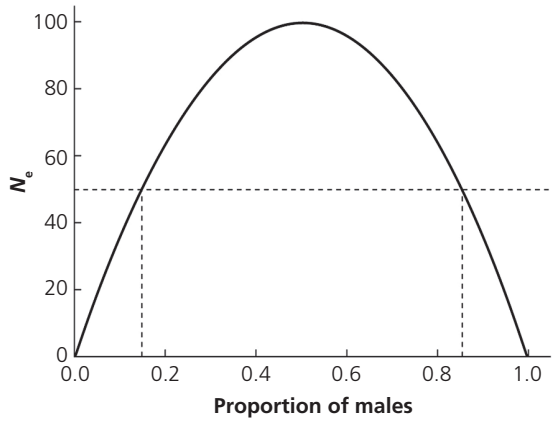

Figure 7.3 The effect of sex ratio on effective population size for a population with a total of 100 males and females using Equation 7.2. The dashed lines indicate the sex ratios at which N_e will be reduced by half because of a skewed sex ratio.

7.3 Nonrandom number of progeny

Our model of an ideal population assumes that all individuals have an equal probability of contributing progeny to the next generation. That is, a random sample of $2N$ gametes is drawn from a population of N diploid individuals. In real populations, parents seldom have an equal chance of contributing progeny because they differ in fertility and in the survival of their progeny. The variation among parents results in a greater proportion of the next generation coming from a smaller number of parents. Thus, the effective population size is reduced.

It is somewhat surprising just how much variation in reproductive success there is even when all individuals have equal probability of reproducing as in the ideal population. Figure 7.4 shows the expected frequency of progeny number in a very large stable population in which the mean number of progeny is two and all individuals have equal probability of reproducing. Take, for example, a stable population of 20 individuals (10 males and 10 females). On the average, each individual will have two progeny. However, ~12% of all individuals will not contribute any progeny! Consider that the probability of any male *not* fathering a particular progeny in this population is 0.90 (9/10). Therefore, the

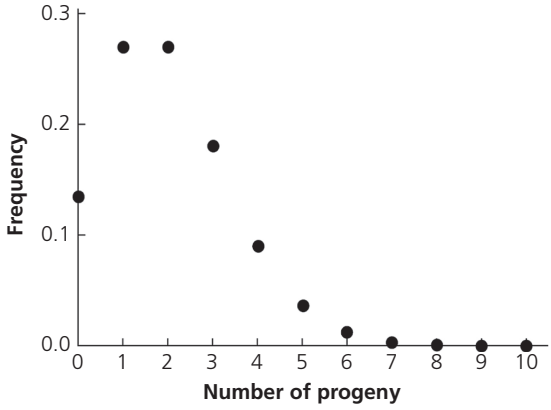

Figure 7.4 Expected frequency of number of progeny per individual in a large stable population in which the mean number of progeny per individual is two and all individuals have equal probability of reproducing.

probability of a male not contributing any of the 20 progeny is $(0.90)^{20}$, or ~12%. The same statistical reasoning applies for females as well. Thus, on average, two or three of the 20 individuals in this population are not expected to contribute any genes to the next generation, while one of the 20 individuals is expected to produce five or more progeny.

We can adjust for nonrandom progeny contribution following Wright (1939). Consider N individuals that contribute varying numbers of gametes (k) to the next generation of the same size (N) so that the mean number of gametes contributed per individual is $\bar{k} = 2$. The variance of the number of gametes contributed to the next generation is:

$$V_k = \frac{\sum_{i=1}^{N} (k_i - 2)^2}{N} \tag{7.3}$$

The proportion of cases in which two random gametes will come from the same parent is:

$$\frac{\sum_{i=1}^{N} k_i(k_i - 1)}{2N(2N - 1)} = \frac{2 + V_k}{4N - 2} \tag{7.4}$$

As we saw in the previous section, the effective population size may be defined as the reciprocal of the probability that two gametes come from the same parent. Thus, we may write the effective population size as:

$$N_e = \frac{4N - 2}{2 + V_k} \tag{7.5}$$

Random variation of k will produce a distribution that approximates a **Poisson distribution**. A Poisson distribution has a mean equal to the variance; thus, $V_k = \bar{k} = 2$ and $N_e = N$ for the idealized population (Section A3.3). However, as the variability in reproductive success among parents (V_k) increases, the effective population size decreases. An interesting result is that the effective population size will be larger than the actual population size if $V_k < 2$. In the extreme where each parent produces exactly two progeny, $N_e = 2N - 1$. Thus, in captive breeding where we can control reproduction, we may nearly double the effective population size by making sure that all individuals contribute equal numbers of progeny.

This potential near doubling of effective population size occurs because there are two sources of genetic drift: reproductive differences among individuals and Mendelian segregation in heterozygotes. These two sources contribute equally to genetic drift. Thus, eliminating differences in reproductive success will approximately double the effective population size. Unfortunately, there is no way to eliminate the second source of genetic drift (Mendelian segregation), except by nonsexual reproduction (cloning, etc.).

The following example considers three hypothetical populations of constant size $N = 10$ with extreme differences in individual reproductive success (Table 7.1). Each population consists of five pairs of mates. In Population A, only one pair of mates reproduces successfully. In Population B, each of the five pairs produces two offspring so that there is no variance in reproductive success. There is an intermediate amount of variability in reproductive success in Population C.

We can estimate N_e of each of these populations using Equations 7.3 and 7.5, as shown in Table 7.2. Thus, population B is expected to lose only ~3% ($1/2N_e = 0.026$) of its heterozygosity per generation, while populations A and C are expected to lose 24% and 5%, respectively. There are very few examples in natural populations where

Table 7.1 Estimation of effective population size in three hypothetical populations of constant size $N = 10$ with extreme differences in individual reproductive success. Each population consists of five pairs of mates. In Population A, only one pair of mates reproduces successfully. In Population B, each of the five pairs produces two offspring so that there is no variance in reproductive success. There is an intermediate amount of variability in reproductive success in Population C.

	A			B			C		
i	k_i	$k_i - \bar{k}$	$(k_i - \bar{k})^2$	k_i	$k_i - \bar{k}$	$(k_i - k)^2$	k_i	$k_i - \bar{k}$	$(k_i - \bar{k})^2$
1	10	8	64	2	0	0	0	−2	4
2	10	8	64	2	0	0	0	−2	4
3	0	−2	4	2	0	0	3	1	1
4	0	−2	4	2	0	0	3	1	1
5	0	−2	4	2	0	0	2	0	0
6	0	−2	4	2	0	0	2	0	0
7	0	−2	4	2	0	0	1	−1	1
8	0	−2	4	2	0	0	1	−1	1
9	0	−2	4	2	0	0	4	2	4
10	0	−2	4	2	0	0	4	2	4
			160			0			20

Table 7.2 Estimation of effective population size for three hypothetical populations in Table 7.1 with high, low, and intermediate variability in family size using Equation 7.5.

	$\Sigma(k_i - \bar{k})^2$	V_k	N_e	$1/2N_e$
Population A	160	16	2.11	0.237
Population B	0	0	19.00	0.026
Population C	20	2	9.50	0.053

the lifetime reproductive success of individuals is known so that N_e can be estimated using this approach (Example 7.2).

Equation 7.5 assumes that the variance in progeny number is the same in males and females. However, the variation in progeny number among parents is likely to be different for males and females. For many animal species, the variance of progeny number in males is expected to be larger than that for females. For example, according to the *Guinness Book of World Records*, the greatest number of children produced by a human mother is 69; in great contrast, the last Sharifian Emperor of Morocco is estimated to have fathered some 1,400 children! The current use of sperm donors can also result in males with many progeny. Some sperm donors have apparently fathered hundreds of progeny (Romm 2011).

We can take such differences between the sexes into account as shown:

$$N_e = \frac{8N - 4}{V_{km} + V_{kf} + 4} \tag{7.6}$$

The estimation of effective population size with nonrandom progeny number becomes much more complex if we relax our assumption of constant population size. In the case of separate sexes, the following expression may be used:

$$N_e = \frac{N_{t-2}\bar{k} - 2}{\bar{k} - 1 + \frac{V_k}{\bar{k}}} \tag{7.7}$$

where N_{t-2} is N in the grandparental generation (Crow & Denniston 1988).

7.4 Fluctuating population size

Natural populations sometimes fluctuate greatly in size. The rate of loss of heterozygosity ($1/2N$) is proportional to the reciprocal of population size ($1/N$). Thus, generations with small population sizes will dominate the effect on loss of heterozygosity. This is analogous to the sex with the smallest population size dominating the effect on loss of heterozygosity (Section 7.2). Therefore, the average population size over many generations is a poor metric for the loss of heterozygosity over many generations.

For example, consider three generations of a population that goes through a severe bottleneck, say $N_1 = 100$, $N_2 = 2$, and $N_3 = 100$. A very small proportion of the heterozygosity will be lost in generations 1 and 3 ($1/200 = 0.5\%$); however, 25% of the heterozygosity will be lost in the second generation. The exact heterozygosity remaining after these three generations can be found as shown:

$$h = \left(1 - \frac{1}{200}\right)\left(1 - \frac{1}{4}\right)\left(1 - \frac{1}{200}\right) = 0.743$$

The average population size over these three generations is $(100 + 2 + 100)/3 = 67.3$. Using Equation 6.7 we would expect to lose only ~2% of the heterozygosity over three generations with a population size of 67.3, rather than the 25.7% heterozygosity that is actually lost.

We can estimate the effective population size over these three generations by using the mean of the

Example 7.2 Effective population size of Darwin's finches

Grant & Grant (1992a) estimated the lifetime reproductive success of two species of Darwin's ground finches on Daphne Major, Galápagos: the cactus finch and the medium ground finch. They followed survival and lifetime reproductive success of four cohorts born in the years 1975–1978. Figure 7.5 shows the lifetime reproductive success of the 1975 cohort for both species. The variance in reproductive success for both species was much greater than expected in an ideal population (Figure 7.4). Over one-half of the birds in both species did not produce any recruits to the next generation, and several birds produced eight or more recruits. Eighteen cactus finches produced 33 recruits ($\bar{k}$ = 1.83) distributed with a variance (V_k) of 6.74; 65 medium ground finches produced 102 recruits ($\bar{k}$=1.57) distributed with a variance (V_k) of 7.12. The average number of breeding birds (census population sizes) for these years was ~94 cactus finches and 197 medium ground finches. The estimated N_e based on these data is 38 cactus finches and 60 medium ground finches. Thus, the N_e/N_C ratios for these two species are 38/94 = 0.40 and 60/197 = 0.30.

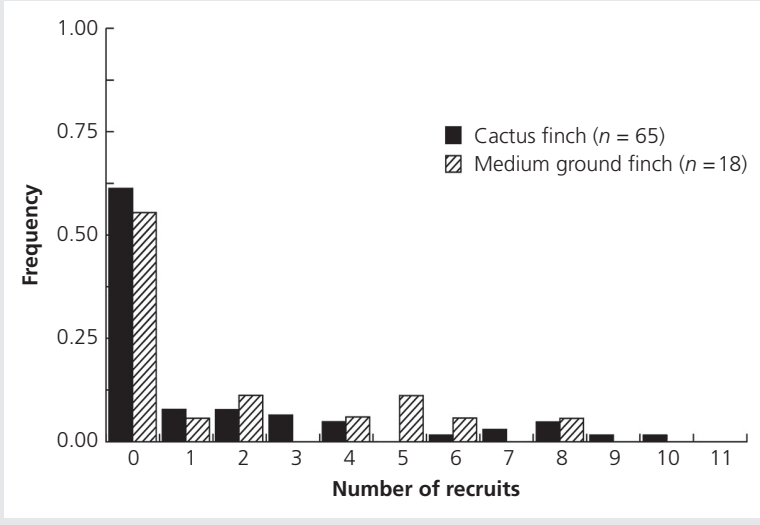

Figure 7.5 Lifetime reproductive success of the 1975 cohort of the cactus finch and medium ground finches on Isla Daphne Major, Galápagos. The *x*-axis shows the number of recruits (progeny that breed) produced. Thus, over 50% of the breeding birds for both species did not produce any progeny that lived to breed. From Grant & Grant (1992a).

reciprocal of population size ($1/N$) in successive generations, rather than the mean of N itself. This is known as the harmonic mean. Thus,

$$\frac{1}{N_e} = \frac{1}{t}\left(\frac{1}{N_1} + \frac{1}{N_2} + \frac{1}{N_3} + \ldots + \frac{1}{N_t}\right) \qquad (7.8)$$

After a little algebra, this becomes:

$$N_e = \frac{t}{\sum\left(\frac{1}{N_i}\right)} \qquad (7.9)$$

Generations with the smallest N have the greatest effect. A single generation of small population size may cause a large reduction in genetic variation. A rapid expansion in numbers does not affect the previous loss of genetic variation; it merely reduces the current rate of loss. This is known as the "bottleneck" effect as discussed in Section 6.5.

We can use Equation 7.9 to predict the expected loss of heterozygosity in the example that we began this section with:

$$N_e = \frac{3}{\left(\frac{1}{100} + \frac{1}{2} + \frac{1}{100}\right)} = 5.77$$

We expect to lose 23.8% of the heterozygosity in a population where N_e = 5.77 over three generations

(Equation 6.7). This is very close to the exact value of 25.7% that we calculated previously.

7.5 Overlapping generations

We so far have considered only populations with discrete generations. However, most species have overlapping generations. Hill (1979) has shown that the effective number in the case of overlapping generations is the same as that for discrete-generation populations having the same variance in lifetime progeny numbers and the same number of individuals entering the population each generation. Thus, the presence of overlapping generations itself does not have a major effect on N_e. However, this result assumes a constant population size and a stable age distribution. Crow & Denniston (1988) concluded that Hill's results are approximately correct for populations that are growing or contracting, as long as the age distribution is fairly stable. Waples et al. (2011) have provided a comprehensive consideration of this problem.

On the other hand, some biological aspects of overlapping generations can have a major effect on N_e (Nunney 2002). For example, N_e is likely to be reduced in polygamous species in which individuals reproduce over many years. In this case, the variance in reproductive success can be greatly increased if the same individuals tend to be relatively successful over many years (Chen et al. 2019; Example 7.3). In contrast, the presence of seed banks or diapausing eggs of freshwater crustaceans can greatly reduce the loss of heterozygosity over time, and thereby increase N_e (Nunney 2002).

Recent efforts to understand the N_e of species with overlapping generations have focused on estimating the effective number of breeders in one reproductive cycle (N_b), rather than on N_e per generation. Surprisingly, Waples et al. (2013) found that N_b for a single reproductive cycle is often larger than N_e per generation, and that an N_e larger than N_C is possible for species with delayed age at maturity. They also found that differences between species in the N_b/N_e ratio are explained largely by just two life history traits: age at sexual maturity and adult lifespan. These important results allow estimating and monitoring N_e per generation based on estimates of the number of breeders per reproductive cycle (N_b).

7.6 Variance versus inbreeding effective population size

The two primary measures of effective population size (N_{eI} and N_{eV}) differ when the population size is changing. In general, the inbreeding effective population size (N_{eI}) is more related to the number of parents since it is based on the probability of two gametes coming from the same parent. The variance effective population size (N_{eV}) is more related to the number of progeny since it is based on the number of gametes contributed rather than the number of parents (Crow & Kimura 1970, p. 361).

Consider the extreme of two parents that have a very large number of progeny. In this case, the allele frequencies in the progeny will be an accurate reflection of the allele frequencies in the parents; therefore, N_{eV} will be nearly infinite. However, all the progeny will be full sibs and thus their progeny will show the reduction in homozygosity expected in matings between full sibs; thus, N_{eI} is very small. In the other extreme, if each parent has exactly one offspring, then there will be no tendency for inbreeding in the populations, and, therefore, N_{eI} will be infinite. However, N_{eV} will be small.

Therefore, if a population is growing, the **inbreeding effective number** is usually less than the variance effective number (Waples 2002). If the population size is decreasing, the reverse is true. In the long run, these two effects will tend to cancel each other and the two effective numbers will be roughly the same (Crow and Kimura 1970; Crow & Denniston 1988).

7.7 Cytoplasmic genes

The effective population size of **cytoplasmic gene** systems (e.g., mitochondria and chloroplasts) is different than the N_e of nuclear genes. We will consider mitochondrial DNA (mtDNA) because so much is known about genetic variation of this molecule. The principles we will consider also apply to genetic variation in chloroplast DNA (cpDNA). However, cpDNA is paternally inherited in some plants (Harris & Ingram 1991).

There are three major differences between mitochondrial and nuclear genes that are relevant for this comparison:

1. Individuals usually possess many mitochondria that share a single predominant mtDNA

Example 7.3 Reduced effective population size in red-winged blackbirds because of the extraordinary reproductive success of one male

Occasionally a truly superior individual graces a population.

(Beletsky & Orians 1989, p. 10)

A long-term study of reproduction of red-winged blackbirds (Figure 7.6) on the Columbia National Wildlife Refuge in central Washington demonstrates the potential for N_e to be greatly reduced in polygamous species with overlapping generations (Beletsky & Orians 1989). Males in this population held breeding territories on average only 2.1 years. Half of all male breeders held territories for just a single year, and annual adult male mortality was ~40%.

Figure 7.6 Male red-winged blackbird. Photo courtesy of John Ashley.

The male known as RYB-AR was banded as a nonterritorial subadult during the 1977 spring breeding season. He first acquired a breeding territory in 1978 and held the same breeding territory through 1988 over 11 consecutive years. The mean annual harem size of RYB-AR was almost double that of other males. Harem size is strongly correlated with reproductive success in this population. Over his lifetime, RYB-AR produced 176 fledged young; this is 17 times greater than the average for males in this population.

RYB-AR fathered 4.2% of the total progeny in this population over the 11 years that he bred. Over these years there were nearly 400 breeding males in this population! As Beletsky and Orians conclude, even if the offspring of RYB-AR are genetically no better than average, he is sure to become a direct ancestor of many individuals in future generations. And, if his exceptional reproductive success is partially inherited by his descendants, his contributions to future generations will be even greater.

sequence. That is, individuals are effectively haploid for a single mtDNA type.
2. Individuals inherit their mtDNA genotype from their mother in most species.
3. There is no recombination between mtDNA molecules.

The effective population size for mtDNA is generally smaller than that for diploid nuclear genes because each individual has only one haplotype (allele) and uniparental inheritance (Birky et al. 1983).

For purposes of comparison, we will use h to compare genetic drift at mtDNA with nuclear genes even though mtDNA is haploid so that individuals are not heterozygous. It might seem inappropriate to use h as a measure of variation for mtDNA since it is haploid and individuals therefore cannot be heterozygous for mtDNA. Nevertheless, h is called gene diversity in this context and is a valuable measure of the variation present within a population (Nei 1987, p. 177). It can be thought of as the probability that two randomly sampled

individuals from a population will have different mtDNA genotypes (Nei 1987, p. 177).

The probability of sampling the same mtDNA haplotype in two consecutive gametes is $1/N_f$, where N_f is the number of females in the population. And since $N_f = 0.5N$,

$$\Delta h = -\frac{1}{N_f} = -\frac{1}{0.5N} \tag{7.10}$$

In the case of a 1:1 sex ratio, there are four times as many copies of each nuclear gene as each mitochondrial gene (N_f):

$$\frac{N_e(\text{nuc})}{N_e(\text{mt})} = \frac{2(N_f + N_m)}{N_f} = 4 \tag{7.11}$$

In general, drift is more important and bottlenecks have greater effects for genes in mtDNA than for nuclear genes because of the generally smaller N_e (Example 7.4). Figure 7.7 shows the relative loss of variation during a bottleneck of a single generation for a nuclear and mitochondrial gene based upon Equation 7.11.

Table 7.3 Expected heterozygosity (H_e), diversity (h) at mtDNA, and average number of alleles ($\bar{A}$) per locus in three populations of the southern Australian spotted mountain trout from Tasmania at 22 allozyme loci and mtDNA (Example 7.4). The Allens Creek and Fortescue Creek populations are coastal populations that are connected by substantial exchange of individuals. The Isabella Lagoon population is an isolated landlocked population. From Ovenden & White (1990).

	Nuclear loci		mtDNA	
Sample	$\bar{A}$	H_e	A	h
Allens Creek	1.9	0.123	28	0.946
Fortescue Creek	1.9	0.111	25	0.922
Isabella Lagoon	1.3	0.104	2	0.038

Things become more complicated with an unequal sex ratio. If there are more females than males in a population, then the N_e for mtDNA can actually be greater than the N_e for nuclear genes. If we use Equation 7.2 for N_e for nuclear genes, then the ratio between the effective number of copies of nuclear genes to the effective number of copies of mitochondrial genes is:

$$\frac{N_e(\text{nuc})}{N_e(\text{mt})} = \frac{2\,(4N_f\,N_m)}{\frac{(N_f + N_m)}{N_f}}$$

which, after a bit of algebra, becomes:

$$\frac{8N_m}{(N_f+N_m)} \tag{7.12}$$

This expression will be less than one if there are more than seven times as many females as males. Therefore, the N_e for mtDNA will be less than the N_e for nuclear genes unless there are at least seven times as many females as males.

We have assumed so far in this section that the variance in reproductive success is equal in males and females. As we saw in Section 7.2, this is often

Example 7.4 Effects of a bottleneck in the Australian spotted mountain trout

Ovenden & White (1990) demonstrated that genetic variation at mtDNA is much more sensitive to bottlenecks than nuclear variation in the southern Australian spotted mountain trout from Tasmania. These fish spawn in fresh water, and the larvae are immediately washed to sea where they grow and develop. The juvenile fish re-enter fresh water the following spring where they remain until they spawn. Landlocked populations of spotted mountain trout also occur in isolated lakes that were formed by the retreat of glaciers some 3,000–7,000 years ago.

Ovenden and White found 58 mtDNA genotypes identified by the presence or absence of restriction sites in 150 fish collected from 14 coastal streams. There is evidence of substantial exchange of individuals among the 14 coastal stream populations. In contrast, they found only two mtDNA genotypes in 66 fish collected from landlocked populations in isolated lakes. However, the lake populations and coastal populations had nearly identical heterozygosities at 22 allozyme loci (Table 7.3). As expected, the allelic diversity of the lake populations was lower than the coastal populations.

The reduced genetic variation at mtDNA in the landlocked populations is apparently due to a bottleneck associated with their founding and continued isolation. Oveden and White suggested that the founding bottleneck may have been exacerbated by natural selection for the landlocked life history in these populations. Regardless of the mechanism, the reduced N_e of the landlocked populations has had a dramatic effect on genetic variation at mtDNA but virtually no effect on nuclear heterozygosity.

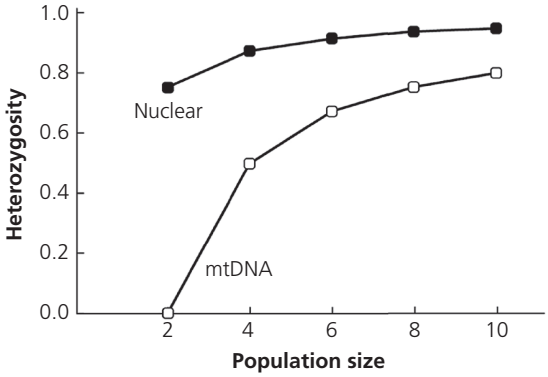

Figure 7.7 Amount of heterozygosity (nuclear) or diversity (mtDNA) remaining after a bottleneck of a single generation for a nuclear and mitochondrial gene with equal numbers of males and females. For example, there is no mitochondrial variation left after a bottleneck of two individuals because only one female is present. In contrast, 75% of the nuclear heterozygosity will remain after a bottleneck of two individuals (see Equation 6.5).

not true. This will decrease the difference in effective population size between nuclear and mitochondrial genes in the many species for which there is much greater variance in reproductive success in males than in females.

7.8 The coalescent

So far we have described genetic changes in populations due to genetic drift by changes in allele frequencies from generation to generation. There is an alternative approach to study the loss of genetic variation in populations that can be seen most easily for the case of mtDNA in which each individual receives the mtDNA haplotype of its mother. We can trace the transmission of mtDNA haplotypes over many generations in the past. That is, we can use a backward-time approach to trace the genealogy of the mtDNA genotype of each individual in a population (Figure 7.8). We can see in the example shown in Figure 7.8 that only one of the original 10 haplotypes remains in a population after just 18 generations due to a process called stochastic **lineage sorting**.

The **gene genealogy** approach also can be applied to nuclear genes, although it is somewhat more complex because of diploidy and recombination. The recent development of the application of genealogical data to the study of population-level genetic processes is perhaps the major advance in population genetics theory in the past 50 years (Hudson 1990; Wakeley 2009). This development has been based upon two primary advances, one technical and one conceptual. The technological advance is the collection of DNA sequence data that allow tracing and reconstructing gene genealogies. The conceptual advance that has contributed to the theory to interpret these results is called "coalescent theory" (Section A10).

Lineage sorting, as in Figure 7.8, will eventually lead to the condition where all alleles in a population are derived from (i.e., coalesce to) a single common ancestral allele. Therefore, the number of generations to coalescence is expected to be shorter for smaller populations. In fact, the mean time to coalescence is approximately equal to N_e generations for

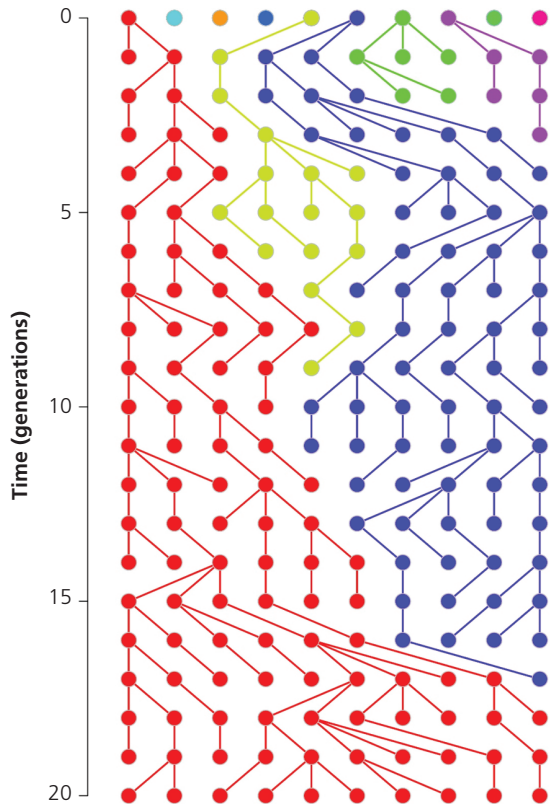

Figure 7.8 Genealogy of mtDNA in a population evolving by genetic drift. Each node represents an individual female and branches lead to daughters. From Revell (2019).

mtDNA, and is four times as long for a nuclear gene (Felsenstein 2019, p. 466). Coalescent theory provides a powerful framework to study the effects of genetic drift, natural selection, mutation, and gene flow in natural populations (Rosenberg & Nordborg 2002; Crandall et al. 2019).

The coalescent approach can be used to study effective population size over relatively long periods of time. Peart et al. (2020) estimated the long-term coalescent N_e for 17 pinniped species (true seals, sea lions, fur seals, and walruses). N_e estimates ranged from ~9,000 to 90,000, and they were strongly correlated with contemporary estimates of N_C ($r^2 = 0.59$, $P < 0.0002$). The N_e/N_C ratios were low (mean, 0.31; median, 0.13) and were strongly associated with demographic history. Residual variation in N_e/N_C, after controlling for past demographic fluctuations, contained information about recent population size changes. Species of conservation concern typically had positive residuals that indicated a smaller contemporary N_C than would be expected from their long-term N_e.

The coalescent is also used to estimate the current or recent effective population size (e.g., Anderson 2005; Luikart et al. 2010). For example, Miller & Waits (2003) estimated N_e for the Yellowstone grizzly bear population to be ~80 from the 1960s to the 1990s using multiple coalescent-based estimators. The coalescent approach enables the extraction of information on genealogical relationships among alleles at a locus, which can improve the estimation of N_e and other parameters (e.g., see Berthier et al. 2002 and Section A10).

7.9 Limitations of effective population size

Effective population size can be used to predict the expected rate of loss of heterozygosity or change in allele frequencies resulting from genetic drift. However, we generally need to know the rate of genetic drift in order to estimate effective population size. Thus, effective population size is perhaps best thought of as a standard, or unit of measure, rather than as a predictor of the loss of heterozygosity. That is, if we know the rate of change in allele frequency or the rate of loss of heterozygosity in a given population, we can use those observed rates to estimate effective population size (Examples 7.1 and 7.4, and Guest Box 7). We will consider the estimation of effective population size in more detail in Chapters 10 and 17.

Perhaps the greatest value of effective population size is heuristic. That is, we can better our understanding of genetic drift by comparing the effects of different violations of the assumptions of ideal populations on N_e (e.g., Figure 7.3). For example, Tanaka et al. (2009) have estimated N_e under different management regimes in order to compare the effects of different measures to control population size in overabundant koala populations. Similarly, in applying the concept of effective population size to managing populations, certain specific effective population sizes are often used as benchmarks. For example, it has been suggested that an N_e of at least 50 is necessary to avoid harmful effects of inbreeding depression in the short term (Franklin 1980; Allendorf & Ryman 2002; Jamieson & Allendorf 2012).

7.9.1 Allelic diversity and N_e

We have considered two measures of the loss of genetic variation in small populations: heterozygosity and allelic diversity. By definition, the inbreeding N_e is an estimate of the rate of loss of heterozygosity, but it is not a good indicator of the loss of allelic diversity within populations. That is, two populations that go through a bottleneck of the same N_e may lose very different amounts of allelic diversity. This difference is greatest when the bottleneck is caused by an extremely skewed sex ratio. Bottlenecks generally have a greater effect on allelic diversity than on heterozygosity. However, a population with an extremely skewed sex ratio may experience a substantial reduction in heterozygosity with little loss of allelic diversity.

The duration of a bottleneck (intense versus diffuse) will also affect heterozygosity and allelic diversity differently (England et al. 2003). Consider two populations that fluctuate in size over several generations with the same N_e, and therefore the same loss of heterozygosity. A brief but very small bottleneck (intense) will cause substantial loss of allelic diversity. However, a diffuse bottleneck spread over several generations can result in the same loss of heterozygosity, but will cause a much smaller reduction in allelic diversity.

In summary, populations that experience the same rate of decline of heterozygosity can experience very different rates of loss of allelic diversity. Therefore, we must consider more than just N_e when considering the rate of loss of genetic variation in populations.

7.9.2 Generation interval

In conservation, we are usually concerned with the loss of genetic variation over some specified number of years in developing policies. For example, according to the International Union for Conservation of Nature (IUCN), species are considered to be "vulnerable" if they have a greater than 10% probability of extinction within 100 years (Table 18.1). The rate of loss of genetic variation through calendar time (e.g., years) depends upon both N_e and mean **generation interval** (G) because $1/(2N_e)$ is the expected rate of loss per generation. Therefore, it is necessary to consider both G and N_e when predicting the expected rate of decline of heterozygosity in natural populations. There are many estimates of N_e in the literature, but very few include estimates of G, which are needed to predict the rate of loss of heterozygosity in calendar time.

There is some confusion in the literature about how to estimate generation interval. The generation interval is the average age of parents (Felsenstein 1971; Hill 1979). Generation interval is not the age of first reproduction, nor is it the average age of reproduction if individuals of different ages produce different numbers of offspring. See Table 7.4 for an example of estimating the generation interval.

It is especially important to estimate the generation interval when comparing the effects of different management schemes on the rate of loss of heterozygosity because conditions that reduce N_e often lengthen the generation interval (Hard et al. 2006). For example, Ryman et al. (1981) found that different harvest regimes for moose in Sweden can have strong effects on both effective population size and generation interval (Figure 7.9). Populations with smaller N_e tended to lose heterozygosity at a slower rate over calendar time because those effects of hunting that reduced N_e (e.g., harvesting young animals) also tended to increase the generation interval. That is, hunted populations with relatively smaller N_e and longer generation interval would lose genetic variation over calendar time (not generations) more slowly than some populations with large N_e and shorter generation interval.

Generation interval was not considered in the koala example that we previously considered (Tanaka et. al. 2009), and it is possible that some

Table 7.4 Hypothetical example of estimation of generation interval (G) in a demographically stable population of sockeye salmon, which die after spawning. The mean age of adult females at sexual maturity is 4.680. However, the mean generation interval of females (4.742) is estimated by using the mean number of eggs produced by females of different ages to estimate the proportion of progeny produced by females of different ages. We assume that males of all ages are equally reproductively successful. The generation interval in this population (4.441) is the mean of the generation interval in females (4.742) and males (4.140).

	Females			Male
Age	**Adults**	**Eggs**	**Progeny**	**Adults**
3	0.010	2,500	0.007	0.230
4	0.310	2,825	0.255	0.510
5	0.670	3,712	0.726	0.210
6	0.010	4,000	0.012	0.060
Mean	4.680	—	4.742	4.140

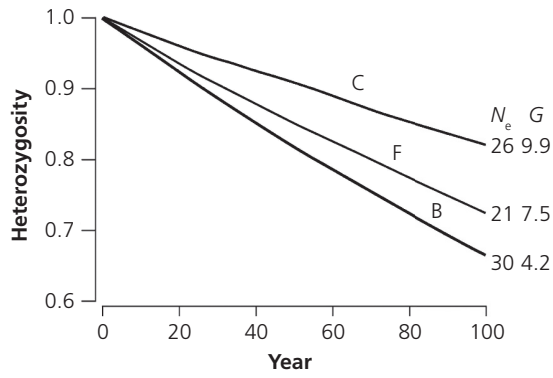

Figure 7.9 Expected decline of heterozygosity under three different sets of hunting regulations in moose from Sweden with a census size of 100 adults following the hunting season. The effective population size and generation interval for each hunting regime is indicated on the right. In hunting regime B, all adults experience identical mortality rates, but calves (less than 1 year old) are protected and are not hunted. In C, only calves are hunted. In F, adult females with calves are protected so that the risk of mortality of an adult female is reduced as a function of the number of calves (0, 1, or 2) with her at the beginning of hunting season. The regime (B) with the largest N_e is expected to lose heterozygosity at nearly twice the rate of the regime (C) with a smaller N_e that has a longer generation interval. Redrawn from Ryman et al. (1981).

strategies producing larger values of N_e might actually lose heterozygosity at a faster rate over calendar time than strategies resulting in smaller values of N_e. In fact, the strategy recommended to increase N_e was to administer contraception to all female koalas beyond a particular age; this strategy is likely to reduce the generation interval, and actually increase the rate of loss of heterozygosity over calendar time for a given N_e!

The inverse relationship between N_e and generation interval also is often true for differences between species. For example, Keall et al. (2001) estimated the census population size of five species of reptiles on North Brother Island in Cook Strait, New Zealand (Table 7.5). The generation interval for these five species was estimated based upon their life history (age of first reproduction, longevity, etc.; C.H. Daugherty, personal communication). As expected, the species with larger body size (e.g., tuatara) have smaller population sizes and longer generation intervals. The loss of heterozygosity over calendar time is strikingly similar in these five species, although they have very different population sizes. In general, species with larger body size (e.g., elephants) will tend to have smaller population sizes but longer generation intervals than species with smaller body size (e.g., mice), and these effects will tend to counteract each other.

Table 7.5 Expected loss in heterozygosity after 1,000 years for five species of reptiles on North Brother Island, New Zealand. N_e values for each species are assumed to be 20% of the estimated census size (N_C, Keall et al. 2001). The estimated generation interval (G) was then used to calculate the number of generations in 1,000 years (t) in order to predict the proportion of heterozygosity (H_e) remaining after 1,000 years using Equation 6.3.

Species	N_C	N_e	G (years)	t	H_e
Tuatara	350	70	50	20	0.866
Duvaucel's gecko	1,440	288	15	67	0.890
Common gecko	3,738	747	5	200	0.875
Spotted skink	3,400	680	5	200	0.863
Common skink	4,930	986	5	200	0.904

7.9.3 Gene flow

Our consideration of effective population size in this chapter has assumed a single panmictic population that is isolated from other populations. However, most natural populations experience some gene flow from other populations. The different measures of N_e are all similar for a stable isolated population, but these values can differ dramatically in populations experiencing migration. Ryman et al. (2019) show that both N_{eI} and N_{eV} are poor indicators of the rate of genetic drift in subpopulations affected by migration, and that they both consistently overestimate the rate of genetic drift in a subdivided population (i.e., they underestimate the local effective population size). This result has important implications in the consideration of how large populations should be in order to avoid serious problems caused by genetic drift (Section 18.8).

7.10 Effective population size in natural populations

The ratio of effective to census population size (N_e/N_C) in natural populations is of general importance for the conservation of populations (Guest Box 7). Census size is often easier to estimate than N_e. Therefore, establishing a general relationship between N_C and N_e would allow us to predict the rate of loss of genetic variation in a wide variety of species (Waples 2002). The actual values of N_e/N_C in a particular population or species will differ greatly depending upon demography and life history. The ratio of N_e to N_C is expected to be in the range of 0.1–0.5 for many populations (Waples 2016).

The effective size can decline without a decline in N_C. For example, a sudden increase in variance of family size where few families produce the entire next generation could reduce N_e with no reduction in N_C. This can happen in species with high reproductive output such as plants, fish, insects, and amphibians. A cryptic genetic bottleneck can also occur when there are few breeders of one sex due to a skewed sex ratio or a polygynous (or polyandrous) breeding system, as mentioned in Section 7.2. Thus, genetic monitoring is important even when demographic monitoring is possible, especially when the N_e/N_C ratio can fluctuate lower than expected (Mimura et al. 2017).

Frankham (1995) provided the first review of estimates of effective population size in natural populations. He concluded that estimates of N_e/N_C averaged ~10% in natural populations for studies

in which the effects of unequal sex ratio, variance in reproductive success, and fluctuations in population size were included. However, Waples (2002) concluded that Frankham (1995) overestimated the contribution of temporal changes by computing the N_e/N_C ratio as a harmonic mean divided by an arithmetic mean. The empirical estimates of N_e that do not include the effect of temporal changes suggest that 20% of the adult population size is perhaps a better general value to use for N_e for many species (Waples 2002).

Palstra & Fraser (2012) provided a critical review of estimates of N_e, N_b, and N_C. Interpreting estimates of N_e and N_b in natural populations is complex. For example, most estimates of contemporary effective population size are based on models that assume N_e is constant over time (Waples 2005a). In real populations, N_e can change dramatically over time. Therefore, it is important to properly match estimates of N_e to the appropriate time periods. In addition, uncertainty in estimates of N_e, N_b, and N_C often have not been considered in estimating N_e/N_C and N_e/N_b ratios.

Palstra & Fraser (2012) presented published N_e/N_b and N_e/N_C estimates including only those studies in which the appropriate time periods were used. Overall, they found a weak and nonsignificant positive regression between both N_e and N_b with N_C. However, they did find strong associations if they used only relatively low values of N_C, less than 3,000 and 600 for N_e and N_b, respectively (Figure 7.10). In general, the effective number of breeders was ~25% of the census size at the time of breeding. There was much greater variability in the estimates of N_e/N_C.

Extremely small values of N_e/N_C have been reported in marine species with high fecundities, high mortalities in early life history stages, and high variance in reproductive success (Hedgecock & Pudovkin 2011). In these species, N_C may be many orders of magnitude greater than N_e (Hauser & Carvalho 2008; Examples 7.5 and 7.6). This suggests that even very large exploited marine fish populations may be in danger of losing crucial genetic variation (Allendorf et al. 2014). However, Waples (2016) has shown that there is a bias in the estimation of N_e when the true N_e is very large so that small estimates of N_e/N_C are expected to occur

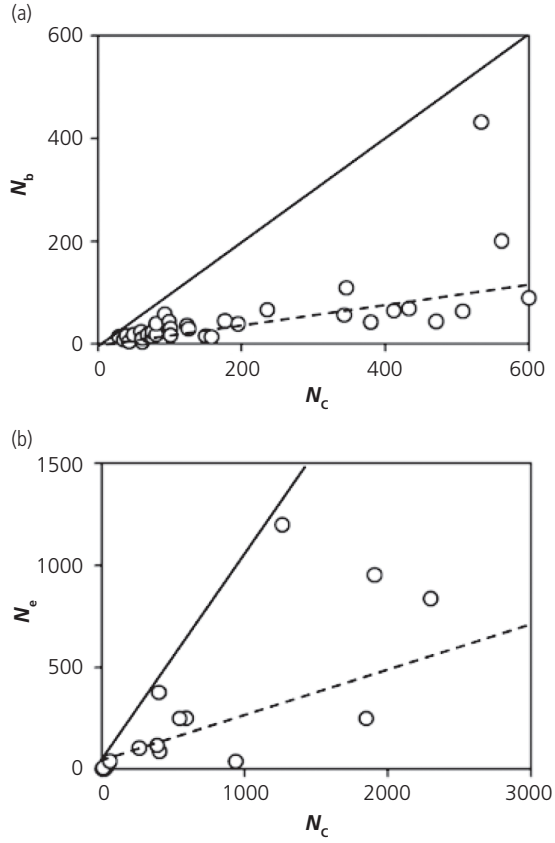

Figure 7.10 Relationships in a variety of species between effective number of breeders (N_b) and census size at the time of breeding (a), and effective population size (N_e) and generational census size (b). The solid line indicates $N_b = N_C$ and $N_e = N_C$; the broken line indicates $N_b/N_C = 0.25$ and $N_e/N_C = 0.25$. Data from Palstra & Fraser (2012).

even when the true N_e/N_C ratio is 0.1 or higher. Therefore, extremely small estimates of N_e/N_C in large populations must be interpreted with caution.

7.11 How can genomics advance understanding of N_e?

Genomics is improving our understanding of the effective population size in natural populations in several ways. First, the use of more loci increases precision and power to detect changes in N_e, and to estimate N_e, which is challenging when N_e is large. A major barrier to understanding N_e in natural

Example 7.5 Effective population size in tiger prawns

A comparison of allele frequencies at eight microsatellite loci in tiger prawns from Moreton Bay, Australia, has shown that the N_e may be nearly three orders of magnitude smaller than N_C in this population (Ovenden et al. 2007). This is an ideal population in which to provide reliable estimates of N_e because it is isolated and does not have overlapping generations. Spawning occurs once a year and only 1% of the individuals live more than 12 months.

Approximately 500 prawns were genotyped in each of three consecutive spawning seasons (2000, 2001, and 2002). Estimates of N_{eV} for the 2001 and 2002 spawning groups were made using the amount of change in allele frequency between consecutive years (i.e., generations) using three different statistical methods. The mean estimated effective populations sizes of the three estimators for the 2001 and 2002 spawning groups was 992 and 1,089. In comparison, the estimated number of adult prawns was 648,898 in 2001 and 464,627 in 2002. Thus, N_e/N_C is ~0.002! These results support the conclusion that the N_e/N_C ratio might be very small in a variety of marine species.

Example 7.6 Effective population size in a seaweed

Fucus serratus (a brown algae) is a key foundation species on rocky intertidal shores of northern Europe. Coyer et al. (2008) estimated the N_e of *F. serratus* in a population from southern Norway sampled in 2000 and 2008 by changes in allele frequencies at 26 microsatellite loci.

Estimates of N_{eV} ranged from 99 to 188, depending on whether the generation interval was assumed to be 1 or 2 years. The estimated census size during this period was 208,000 individuals. Thus, the N_e was approximately nearly three orders of magnitude smaller than N_C in this population. In further support of a small N_e, allelic richness decreased by 14% over this 6-year interval in these samples. Coyer et al. (2008) concluded that this species, and closely related species, are likely to be less resilient to environmental change than generally assumed.

populations has been the low precision of estimators. For example, confidence intervals are often enormous and include infinity. Second, having many loci can provide less biased estimates of N_e by facilitating identification of loci that violate assumptions of N_e estimators (e.g., that loci are independent, no selection, and no genotyping error). For example, Larson et al. (2013) reported imprecise N_e estimates using 39 loci (N_e = 174–infinity) for the population of Chinook salmon from the Tubutulik River. However, N_e estimates became much more precise when using 1,118 loci (N_e = 1,295–3,602).

Genomic approaches also facilitate estimation of N_e at multiple time points in the past to help detect both historical and recent population growth and declines. This is possible thanks to the use of information from linked loci, recombination rates, and runs of homozygosity that can be analyzed using genomic data with mapped loci (e.g., Ceballos et al. 2018; Chapters 10 and 17).

Guest Box 7 Effective population size in brown trout: Lessons for conservation
Linda Laikre and Nils Ryman

The brown trout was one of the first species whose natural population genetic structure was described using the allozyme technique in the 1970s (Allendorf et al. 1976; Ryman 1983). The brown trout is an important model species in conservation genetics. Its status for cultural, sport, and commercial fisheries and the fact that it is often subjected to hatchery breeding and large-scale releases have resulted in many conservation genetics issues being addressed by studying brown trout (Bekkevold et al. 2020).

We initiated a long-term genetic monitoring program of brown trout populations in small mountain lakes and one creek in the Hotagen Nature Reserve in central Sweden in the 1970s. We have genotyped 14 polymorphic allozyme loci continuously for ~100 individuals per population each year from eight sampling locations. We have estimated effective population size in these populations by the amount of allele frequency change between consecutive cohorts (Section 6.2; Jorde 2012). The N_e estimates generally ranged from 20 to 200 (Jorde & Ryman 1996, 2007; Palm et al. 2003).

With such small N_e values, we would expect low genetic variation in these populations. They do not, however, have low genetic variation, and they have maintained genetic diversity over the monitoring period (Charlier et al. 2012; Andersson et al. 2017). Further, the amount of heterozygosity is quite similar in localities with very different local N_e estimates. We explored these patterns further using less frequent monitoring data with SNP genotyping from over 20 additional lakes in the same region. We found the same trend of similar levels of heterozygosity among interconnected lakes in spite of often very low local N_e (Figure 7.11).

These observations suggest that genetic exchange occurs between populations, and that such migration maintains genetic diversity in the separate populations. Ryman et al. (2019) have shown that estimates of local N_e are not good predictors of the rate of loss of genetic variation in populations that are connected to other populations by gene flow. An exception to this pattern of genetic exchange is observed in the one creek locality. This locality appears to be quite isolated. No brown trout occur above a waterfall that constitutes an upstream migration barrier. Similarly, a smaller waterfall below this locality appears to impede migration from downstream populations. This locality exhibits the smallest N_e of only 20, and the amount of heterozygosity is only one-half that of other sites monitored within the same nature reserve.

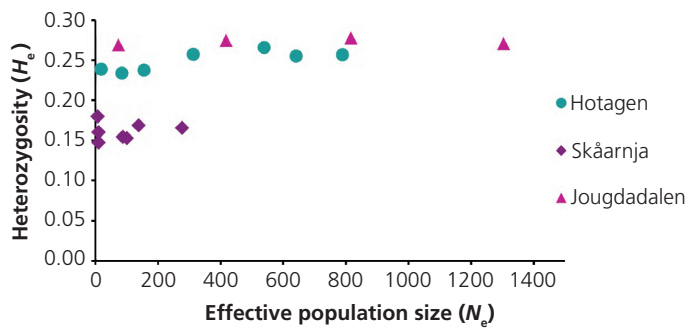

Figure 7.11 Effective population size (N_e) and expected heterozygosity (H_e) estimated from 96 SNPs for populations of naturally occurring brown trout in lakes representing three separate systems of interconnected populations located in different nature reserves in central Sweden (Skåarnja, Hotagen, and Jougadalen). The lack of correlation between N_e and H_e, and the similar amounts of heterozygosity among populations within the different reserves, suggest that gene flow among local populations, rather than N_e, determines the amount of local genetic variation.

Guest box 7 Continued

We assessed changes in N_e over time in detail in one lake and two creek localities and found large temporal differences in the lake, but more stable N_e in the creek localities. This observation suggests that estimating N_e at only one point in time can provide quite different estimates in some cases, underlining the value of monitoring genetic diversity over longer periods.

We estimated census size (N_C) with mark–recapture techniques in Lake Blanktjärnen, and we estimated the ratio N_e/N_C as 0.11, and as 0.04 in a nearby lake (Charlier et al. 2011). These estimates support the common finding that N_e is much smaller than census size. In Lake Blanktjärnen, we observed a correlation between the effective number of breeders per year (N_b; Charlier et al. 2012) and the number of fish caught per annual sampling effort. This observation suggests that genetic techniques are also useful for monitoring or gaining insights into population demography (Schwartz et al. 2007).

Valuable lessons from our long-term genetic monitoring include: (1) the importance of connectivity, which is crucial for maintaining genetic diversity in metapopulations with small local N_e (Ryman et al. 2019); (2) N_e can vary considerably over time, which can make assessments from single samples unrepresentative; and (3) the N_e/N_C ratio is low in this species.