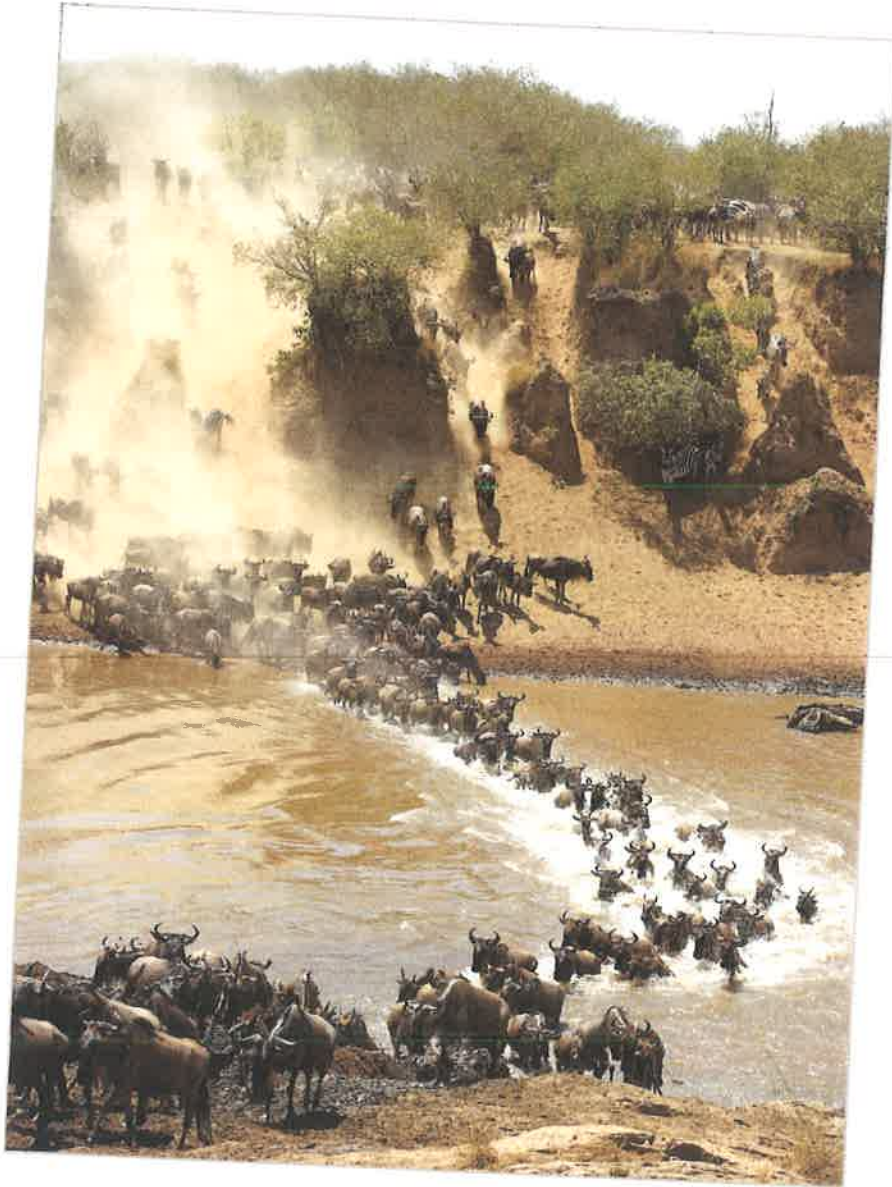


ESSENTIALS OF Conservation Biology

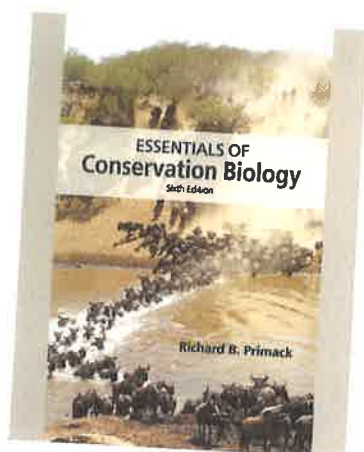
Sixth Edition



Richard B. Primack
Boston University



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About the Cover

The Serengeti National Park in Tanzania and Maasai Mara National Reserve in Kenya protect the annual migrations of roughly 1.2 million wildebeests (*Connochaetes taurinus*), along with zebras and gazelle, from short-grass plains in the southern Serengeti to the grasslands and savannas of the Maasai Mara. Virtually the entire migration occurs within the protected areas—the only mammal migration in Africa that is completely protected.

Essentials of Conservation Biology, Sixth Edition

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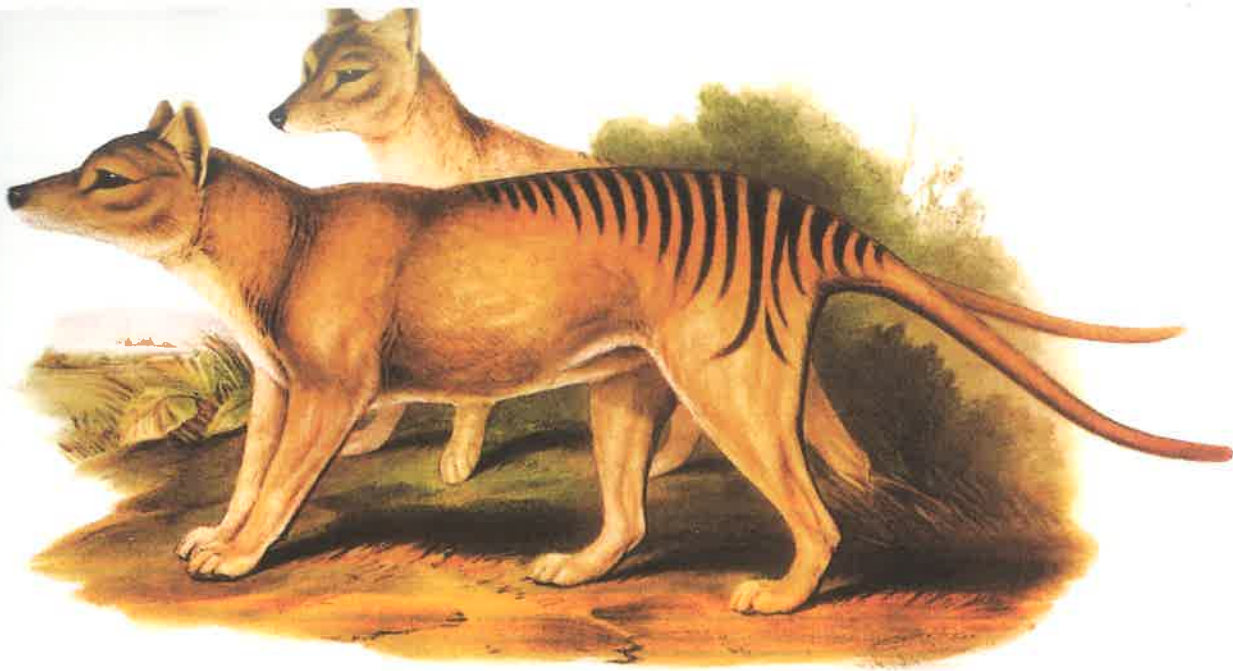
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Chapter 8

Vulnerability to Extinction

Not all species have an equal chance of going extinct. Rare species are considered to be especially vulnerable to extinction, while common species are considered less so. But the term *rare* has a variety of meanings, each of which has a different implication for conservation biology (Feldhamer and Morzillo 2008).

Generally speaking, a species is considered rare if it:

1. Lives in a narrow geographical range
2. Occupies only one or a few specialized habitats
3. Is found only in small populations

The first criterion, based on geographical area, is the most obvious: The Venus flytrap (*Dionaea muscipula*) is rare because it occurs only on the coastal plain of the Carolinas in eastern North America. Many geographically rare species occupy islands, and some may also occupy isolated habitats, such as high mountain peaks in the middle of lowlands or lakes surrounded by a terrestrial landscape. Within their limited geographical range, however, a rare species may be locally abundant.

A species may also be considered rare if it occupies only one or a few specialized habitats. Salt marsh cord grass (*Spartina patens*) is found only in salt marshes and not in other habitats, yet within this habitat, cord grass is quite common. This example contrasts with common species that are found in many different habitats, such as the dandelion (*Taraxacum officinale*), which occupies open meadows, roadsides, river edges, and mown lawns.



Figure 8.1 The Iberian lynx is a critically endangered species. Though they were once found over the entire Iberian Peninsula, they are now believed to number only around 200 in a few scattered areas in Spain. Fragmentation of their habitat and decline of their prey populations have contributed to the lynx's decline.

Species that occupy a narrow range, such as many island species, are particularly vulnerable to extinction.

Finally, a species may be considered rare if it is found only in small populations. The Iberian lynx (*Lynx pardinus*) formerly occurred across Spain and Portugal, but their populations are now always small and isolated (**Figure 8.1**). A common species would have large populations at least in some locations.

The three criteria of rarity discussed above can be applied to the entire geographical range of a species or to the distribution and abundance of species in a particular place. Such an approach can highlight priorities for conservation. A species with a narrow geographical range and specific habitat requirements that is always found in small populations requires immediate habitat protection and, possibly, habitat management to maintain its few, fragile populations. This also applies, to a somewhat lesser degree, to species with larger populations. However, where species have a narrow geographical distribution but a broad habitat specificity, experiments in which individuals are transported to unoccupied but apparently suitable localities to create new populations may be a strategy worth considering (see Chapter 13). These species may have been unable to disperse outside of their narrow geo-

graphical areas because of factors such as geographic barriers or inherent inability to disperse. This suggestion is supported by observations showing that plant species with poor dispersal abilities (no adaptation for long-distance dispersal) tend to have more aggregated populations than do species with good dispersal ability (light, wind-dispersed seeds, or seeds dispersed by mammals and birds), which tend to have more widely dispersed populations (Quinn et al. 1994). Species with broad geographical ranges are less susceptible to extinction and less likely to need rescue efforts, since they tend to have more extant (living) populations and more opportunities to colonize potentially suitable sites.

Endemic Species and Extinction

A species found naturally in a single geographical area and no other place is **endemic** to that location. Endemism is an extremely important factor in a species' risk of extinction. If the populations of an endemic species on Madagascar, or any isolated island, go extinct, the species will be globally extinct. In contrast, mainland species often have many populations distributed over wide areas, so the loss of one population is not catastrophic for a species. Even though 98% of the forests of eastern North America were logged or cleared for farming, for instance, no bird species went extinct because of habitat loss: presumably the remaining forest fragments provided sufficient habitat to allow these widespread species to survive until the forest grew back following the abandonment of farming.

The concept of endemism may seem similar to the properties of those rare species that live in a narrow geographical range. But a species may be endemic to a large area and abundant throughout it. In contrast, a rare species such as the Venus flytrap is typically found only in a limited area (and could be considered a narrowly distributed endemic). Or a rare species may be considered rare in only part of its range. For example, the sweetbay magnolia (*Magnolia virginiana*) is reasonably common throughout the southeastern United States, but in the New England



Chapter 11

Problems of Small Populations

No population lasts forever. Changing climate, succession, disease, and a range of unusual events ultimately lead every population to the same fate: extinction. The real questions to consider are whether a population goes extinct sooner rather than later, what factors cause the extinction, and whether other populations of the same species will continue elsewhere. Will a population of African lions last for more than 1000 years and go extinct only after a change in climate, or will the population go extinct after 10 years because of introduced disease and hunting by humans? Will individual lions from the original population start new populations in currently unoccupied habitat, or has all potential lion habitat disappeared because of new human settlements?

As we discussed in Chapter 7, the extinction of species as a result of human activities is now occurring more than 100 times faster than the natural rate of extinction—far more rapidly than new species can evolve. Because an endangered species may consist of just a few populations, or even a single population, *protecting populations is the key to preserving species*; it is often the few remaining populations of a rare species that are targeted for conservation efforts. In order to successfully maintain species under the restricted conditions imposed by human activities, conservation biologists must determine the sustainability of populations under different circumstances. Will a population of an endangered species persist or even increase in a nature reserve? Is the species in rapid decline, and does it require special attention to prevent it from going extinct?

Many national parks and wildlife sanctuaries have been created to protect “charismatic megafauna” such as lions, tigers, rhinos, bison, and bears, which are important national symbols and attractions for the tourist industry. However, designating the habitats in which these species live as protected areas may not be enough to stop their decline and extinction, even when they are legally protected. Sanctuaries generally are created after most populations of the threatened species have been severely reduced by habitat loss, degradation, and fragmentation or by overharvesting. Under such circumstances, a species tends to dwindle rapidly toward extinction. Also, individuals outside park boundaries remain unprotected and at risk. What, then, is the best strategy for protecting the few remaining populations of an endangered species? Are there special requirements for protecting small populations?

Essential Concepts for Small Populations

An ideal conservation plan for an endangered species would protect as many individuals as possible within the greatest possible area of high-quality, protected habitat (Wilhere 2008). In practical terms, planners, land managers, politicians, and wildlife biologists often must attempt to achieve realistic goals, guided by general principles. For example, they need to know how much longleaf pine habitat a red-cockaded woodpecker (*Picoides borealis*) population requires to persist. Is it necessary to protect habitat containing 50, 500, 5000, 50,000, or more individuals to ensure the survival of the species? Furthermore, planners must reconcile conflicting demands on finite resources—somehow a compromise must be found that allows the economic development required by society while at the same time provides reasonable protection for biodiversity. This problem is vividly demonstrated by the current debate in the United States over the need to protect caribou and other wildlife in the vast Arctic National Wildlife Refuge and the equally compelling need to utilize the considerable oil resources of the area (see Box 17.3).

Minimum viable population (MVP)

In a groundbreaking paper, Shaffer (1981) defined the number of individuals necessary to ensure the long-term survival of a species as the **minimum viable population (MVP)**: “A minimum viable population for any given species in any given habitat is the smallest isolated population having a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental, and genetic stochasticity, and natural catastrophes.” In other words, the MVP is the smallest population size that can be predicted to have a very high chance of persisting for the foreseeable future. Shaffer emphasized the tentative nature of this definition, say-

Plans for protecting a species must determine the number of individuals—the minimum viable population—necessary to maintain the species in both average and harsh years. Protected habitats of adequate size to maintain the MVP can then be established.

ing that the survival probabilities could be set at 95%, 99%, or any other percentage and that the time frame might similarly be adjusted, for example, to 100 or 500 years. The key point is that the MVP size allows a quantitative estimate to be made of how large a population must be to ensure long-term survival.

Shaffer (1981) compares MVP protection efforts to flood control. It is not sufficient to use average annual rainfall as a guideline when planning flood control systems and developing regulations for building on wetlands; instead, we must plan for extreme situations of high rainfall and severe flooding, which may occur only once every 50 or 100 years. In protecting natural systems, we understand that certain catastrophic events, such as hurricanes, earthquakes, forest fires, epidemics, and die-offs of food items, may occur at even greater intervals. To plan for the long-term protection of endangered species, we must provide for their survival, not only in average years, but also in exceptionally harsh years. An accurate estimate of the MVP size for a species often requires a detailed demographic study of the

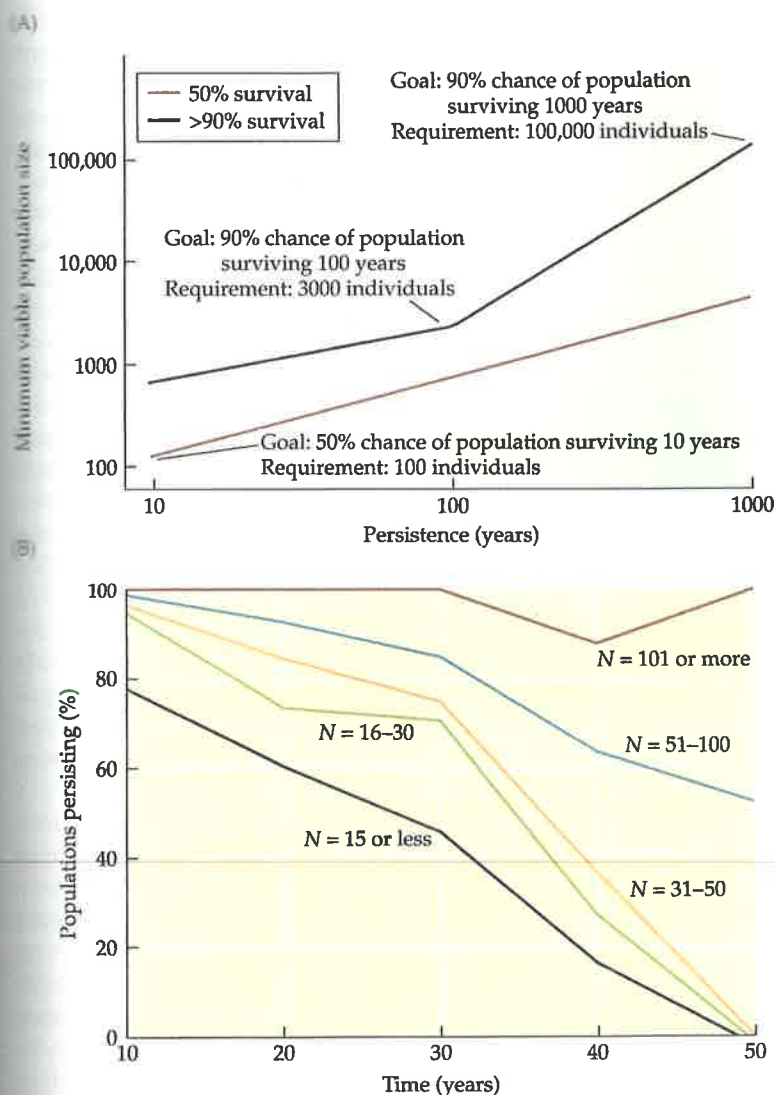


Figure 11.1 (A) If the goal is persistence for a greater number of years, then a larger minimum viable population (MVP) size is needed. A greater MVP is needed to ensure a higher probability of persistence, as illustrated in this case by a 50% probability of survival and a greater than 90% probability of survival. Both axes are on log scales. The values were derived from changes in population size and persistence of 1198 species. (B) The relationship between initial population size (N) of bighorn sheep and the percentage of populations that persist over time. Almost all populations with more than 100 sheep persisted beyond 50 years, while populations with fewer than 50 individuals died out within 50 years. Not included are small populations that were actively managed and augmented by the release of additional animals. (A, after Traill et al. 2010; B, after Berger 1990.)



population and an analysis of its environment. This can be expensive and require months, or even years, of research. Analyses of over 200 species for which adequate data were available, mainly vertebrates, indicated that most MVP values for long time periods fall in the range of 3000–5000 individuals with a median of 4000 (Traill et al. 2010; Flather et al. 2011). In general, protecting a larger population increases the chance of the population persisting for a longer period of time (Figure 11.1A). For species with extremely variable population sizes, such as certain invertebrates and annual plants, protecting a population of about 10,000 individuals might be the ideal strategy.

Unfortunately, many species, particularly endangered species, have population sizes smaller than these recommended minimums. For instance, half of 23 isolated elephant populations remaining in West Africa have fewer than 200 individuals, a number considered to be inadequate for long-term survival of the population (Bouché et al. 2011). The wolf population on Isle Royale, Michigan, has been fluctuating around 20 individuals, but currently has only 8 adults of breeding age and no pups (Mlot 2013).

Field studies confirm that small populations are most likely to decline and go extinct (Grouios and Manne 2009). One of the best-documented studies of MVP size tracked the persistence of 120 bighorn sheep (*Ovis canadensis*) populations (some of

which have been followed for 70 years) in the deserts of the southwestern United States (Berger 1990, 1999). The striking observation is that 100% of the unmanaged populations with fewer than 50 individuals went extinct within 50 years, while virtually all of the populations with more than 100 individuals persisted within the same time period (Figure 11.1B). No single cause was evident for most of the populations that died out; rather, a wide variety of factors appears responsible for the extinctions. For bighorn sheep, the minimum population size is at least 100 individuals. Unmanaged populations below 50 could not maintain their numbers, even in the short term. Additional research on bighorn sheep populations suggests that populations have a greater chance of persisting when they occupy large habitats (which allow populations to increase in size) that are more than 23 km from domestic sheep, a source of disease (Singer et al. 2001). However, despite the factors hindering the survival of small populations of bighorn sheep, habitat management by government agencies and the release of additional animals have allowed some other small populations to persist that might otherwise have gone extinct. Other long-lived species, such as turtles and trees, can often persist for extended periods in small populations (Shoemaker et al. 2013).

Field evidence from long-term studies of birds on the Channel Islands off the California coast supports the fact that large populations are needed to ensure population persistence; only bird populations with more than 100 breeding pairs had a greater than 90% chance of surviving for 80 years (Figure 11.2). In spite of most evidence to the contrary, however, small populations sometimes do prevail: many populations of birds have survived for 80 years with 10 or fewer breeding pairs. Of course, birds are especially mobile and can readily recolonize areas following local extinction. Less mobile species do not have this ability.

Once an MVP size has been established for a species, the **minimum dynamic area (MDA)**—the area of suitable habitat necessary for maintaining the minimum viable population—can be estimated by studying the home range size of individuals and colonies of endangered species (Thiollay 1989; Pe'er et al. 2014). It has been estimated that reserves in Africa of 100–1000 km² are needed to maintain many small mammal populations (see Figure 16.2). To preserve populations of large carnivores, such as lions, reserves of 10,000 km² are needed.

Exceptions notwithstanding, large populations are needed to protect most species, and species with small populations are in real danger of going extinct. Small populations are subject to rapid decline in numbers and local extinction for three main reasons:

1. Loss of genetic variability and related problems of inbreeding depression and genetic drift
2. Demographic fluctuations due to random variations in birth and death rates
3. Environmental fluctuations due to variation in predation, competition, disease, and food supply and due to natural catastrophes that occur at irregular intervals, such as fires, floods, storms, or droughts

We'll now examine in detail each of these causes for decline in small populations.

Small populations are more likely to go extinct than large populations.

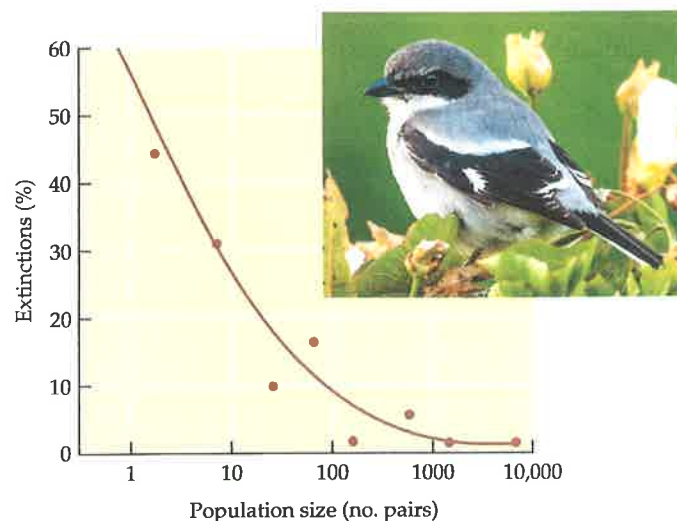


Figure 11.2 Extinction rates of bird species on the Channel Islands, with a loggerhead shrike (*Lanius ludovicianus anthonyi*) as an example of one of the species. Each dot represents the extinction percentage of all the species in that population size class; extinction rate decreases as the size of the population increases. Populations with fewer than 10 breeding pairs had an overall 39% probability of extinction over 80 years, populations of between 10 and 100 pairs averaged about 10% probability of extinction, and populations of over 100 pairs had a very low probability of extinction. (After Jones and Diamond 1976.)

Loss of genetic variability

As was described in Chapter 2, a population's ability to adapt to a changing environment depends on genetic variability, which occurs as a result of individuals' having different **alleles**—different forms of the same gene. Individuals with certain alleles or combinations of alleles may have just the characteristics needed to survive and reproduce under new conditions (Frankham 2005; Allendorf and Luikart 2007). Within a population, the frequency of a given allele can range from common to very rare. New alleles arise in a population either by random mutations or through the migration of individuals from other populations.

In small populations, allele frequencies may change significantly from one generation to the next simply because of chance—based on which individuals survive to sexual maturity, mate, and leave offspring. This random process of allele frequency change is known as **genetic drift**, and it is a separate process from changes in allele frequency caused by natural selection (Hedrick 2005). When an allele occurs at a low frequency in a small population, it has a significant probability of being lost in each generation. For example, if a rare allele occurs in 5% of all the genes present (the "gene pool") in a population of 1000 individuals, then 100 copies of the allele are present ($1000 \text{ individuals} \times 2 \text{ copies per individual} \times 0.05 \text{ allele frequency}$), and the allele will probably remain in the population for many generations. However, in a population of 10 individuals, only 1 copy of the allele is present ($10 \text{ individuals} \times 2 \text{ copies per individual} \times 0.05 \text{ allele frequency}$), and it is possible that the rare allele will be lost by chance from the population in the next generation.

Considering the general case of an isolated population in which there are 2 alleles of each gene in the gene pool, Wright (1931) proposed a formula to express the proportion of original heterozygosity (the proportion of individuals with 2 different allele forms of the gene) remaining after each generation (H). The formula includes the **effective population size** (N_e)—the size of the population as estimated by the number of its breeding individuals:*

$$H = 1 - 1/[2 N_e]$$

According to this equation, a population of 50 breeding individuals would retain 99% of its original heterozygosity after 1 generation:

$$H = 1 - 1/100 = 1.00 - 0.01 = 0.99$$

The proportion of heterozygosity remaining after t generations (H_t) decreases over time:

$$H_t = H^t$$

For our population of 50 animals, then, the remaining heterozygosity would be 98% after 2 generations (0.99×0.99), 97% after 3 generations, and 90% after 10 generations. A population of 10 individuals would retain 95% of its original heterozygosity after 1 generation, 90% after 2 generations, 86% after 3 generations, and 69% after 10 generations (Figure 11.3).

This formula demonstrates that significant losses of genetic variability can occur in isolated small populations. Such small populations often occur on islands and fragmented landscapes (Vranckx et al. 2012). However, the amount of genetic variability within a

Because of genetic drift, small populations lose genetic variation more rapidly than large populations. Some small populations may lack any genetic variation.

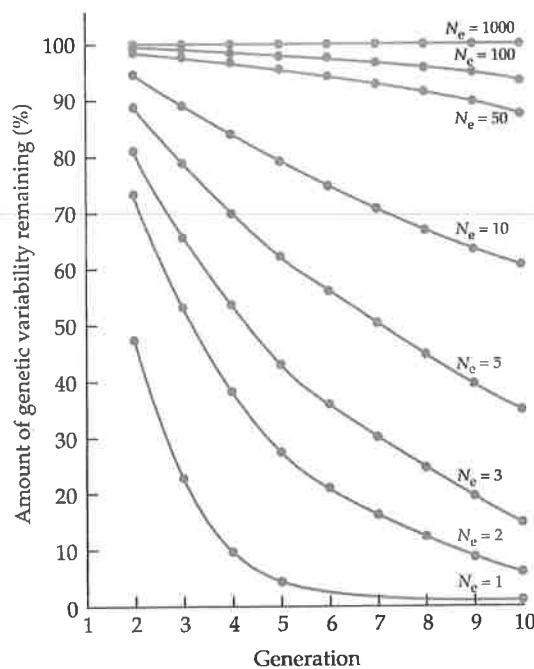


Figure 11.3 Genetic variability is lost randomly over time through genetic drift. This graph shows the average percentage of genetic variability remaining after ten generations in theoretical populations of various effective population sizes (N_e). After 10 generations, there is a loss of genetic variability of approximately 40% with a population size of 10, 65% with a population size of 5, and 95% with a population size of 2. Blue lines indicate minimal loss of genetic variability in large populations; red lines indicate rapid loss of genetic variability in small populations. (After Meffe and Carroll 1997.)

*Factors that affect N_e , the effective population size, are discussed in detail beginning on p. 260.

small population will increase over time through two means: regular mutation of genes and migration of even a few individuals from distant populations. Mutation rates found in nature are between 1 in 10,000 and 1 in 1 million per gene per generation; mutations therefore may make up for the random loss of alleles in large populations and, to a lesser extent, contribute to greater genetic diversity in small populations. However, mutations alone are not sufficient to counter genetic drift in populations of 100 individuals or fewer. Fortunately, even a low frequency of movement of individuals between populations minimizes the loss of genetic variability associated with small population size (Weiser et al. 2013) (Figure 11.4). If even 1 or 2 immigrants arrive each generation in an isolated population of about 100 individuals, the impact of genetic drift will be greatly reduced. With 4–10 migrants arriving

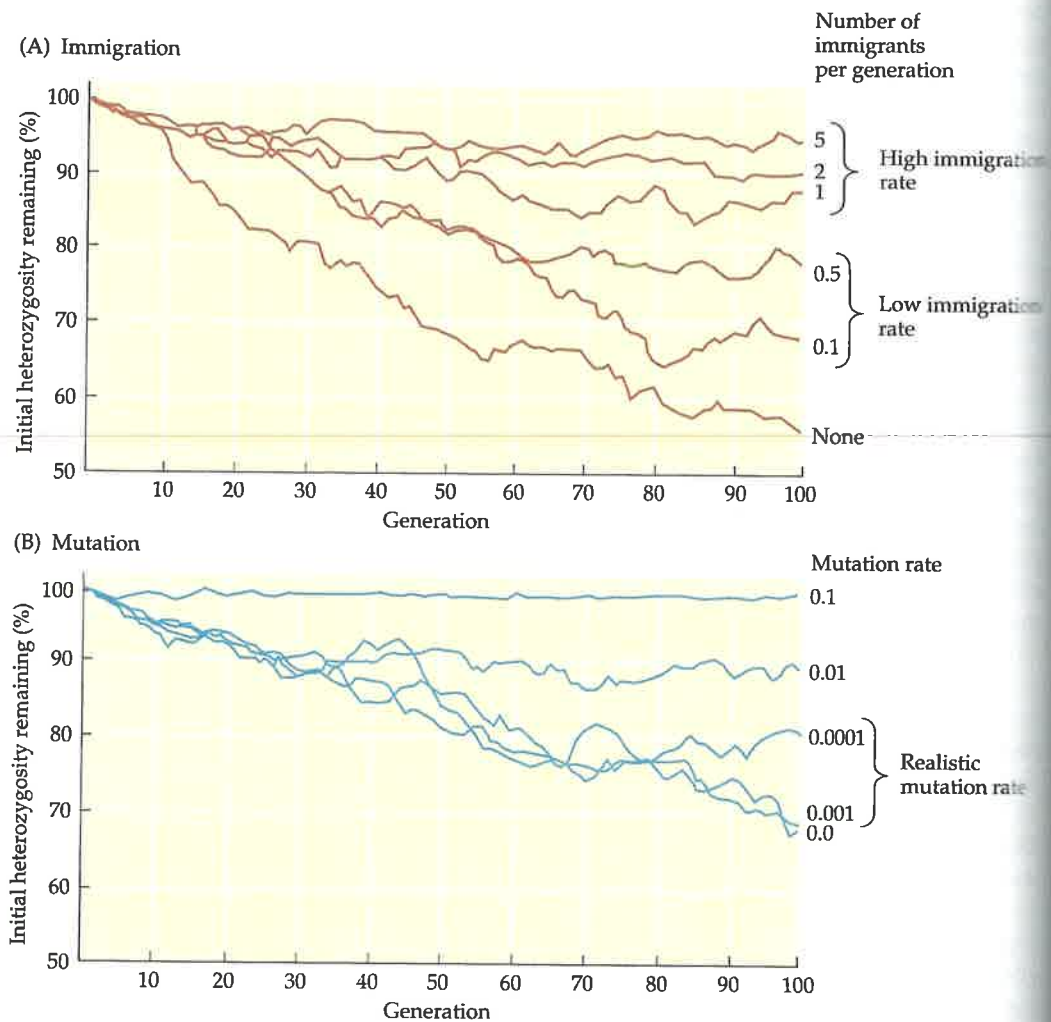


Figure 11.4 The effects of immigration and mutation on genetic variability in 25 simulated populations of size $N_e = 120$ individuals over 100 generations. (A) In an isolated population of 120 individuals, even low rates of immigration from a larger source population prevent the loss of heterozygosity from genetic drift. In the model, an immigration rate as low as 0.1 (1 immigrant per 10 generations) increases the level of heterozygosity, while genetic drift is negligible with an immigration rate of 1 individual per generation. (B) It is more difficult for mutation to counteract genetic drift. In the model, the mutation rate must be 1% (0.01) per gene per generation or greater to affect the level of heterozygosity. Because this mutation rate is far higher than what is observed in natural populations, mutation appears to play a minimal role in maintaining genetic variability in small populations. (After Lacy 1987.)

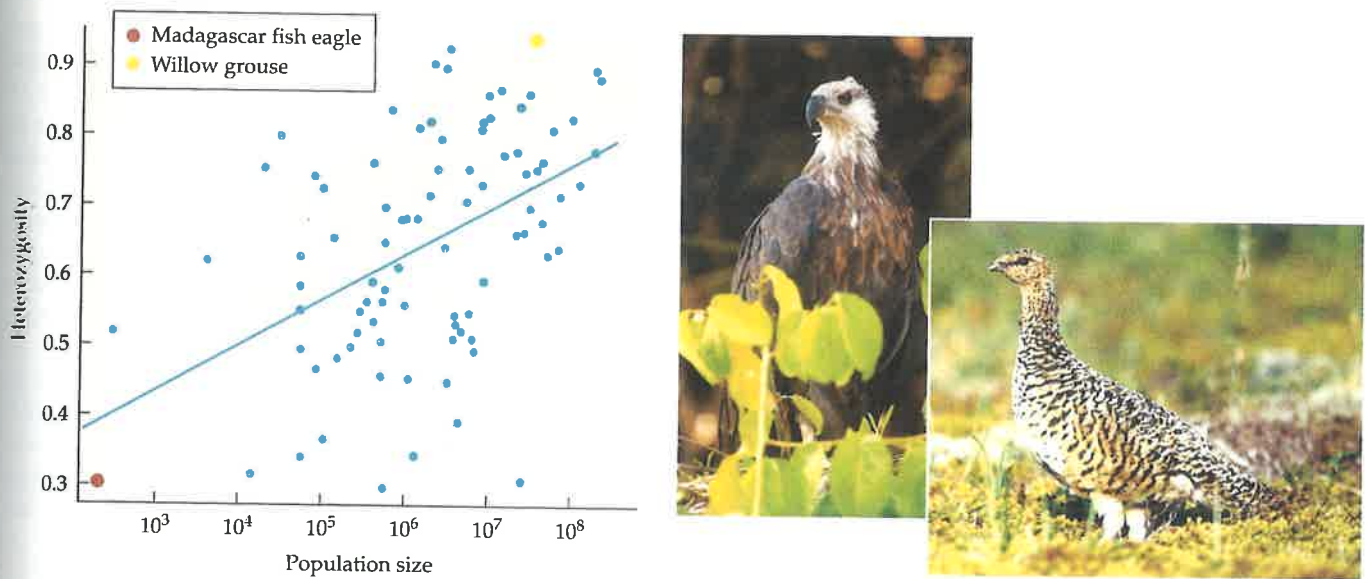


Figure 11.5 For 89 species of birds, the level of heterozygosity is lower with smaller population sizes. The Madagascar fish eagle (*Haliaeetus vociferoides*) represents one extreme with fewer than 40 breeding pairs and very low heterozygosity; at the other extreme, the willow grouse (*Lagopus lagopus*), the state bird of Alaska, has a population size of more than 10 million and high heterozygosity. (After Evans and Sheldon 2008; grouse photograph courtesy of Dave Menke/U.S. Fish and Wildlife Service.)

per generation from nearby populations, the effects of genetic drift are negligible. Gene flow from neighboring populations appears to be the major factor preventing the loss of genetic variability in small populations of Galápagos finches (Grant and Grant 2008). In addition, genetic variation that increases fitness will tend to be retained longer in a population, even when there is genetic drift.

Field data also show that lower effective population size leads to a more rapid loss of alleles from the population (Evans and Sheldon 2008). For example, in a broad survey of 89 bird species, there was a strong tendency for abundant birds to have more heterozygosity than species with small populations (Figure 11.5). Almost all species with populations over 10 million have over 60% heterozygosity, in contrast to less than 60% heterozygosity in most species with fewer than 100,000 individuals.

Unfortunately, rare and endangered species often have small, isolated populations, leading to a rapid loss of genetic variation. In 170 paired comparisons, threatened taxa with narrow ranges had an average of 35% lower genetic diversity than taxonomically related nonthreatened species of wide distribution (Spielman et al. 2004). In some cases, entire species lacked genetic variation. In the evolutionarily isolated Wollemi pine (*Wollemia nobilis*) in Australia, only 40 plants occur in two nearby populations. As might be predicted, an extensive investigation failed to find any genetic variation in this species (Peakall et al. 2003).

It seems safe to assume that to maintain genetic variability, conservation biologists should strive to preserve populations that are as large as possible. But how big should a given population be? How many individuals are needed to maintain genetic variability? Franklin (1980) suggested that 50 reproductive individuals might be the minimum number necessary to avoid short-term inbreeding depression, the lower fitness that results from matings between closely related individuals. This figure is based on the practical experience of animal breeders, and it indicates that animal stocks can be maintained with a loss of 2%–3% of their heterozygosity per generation. Using data on mutation rates in *Drosophila* fruit flies, Franklin further

suggested that in populations of 500 reproductive individuals, the rate of new genetic variability arising through mutation might balance the variability being lost because of genetic drift in small population size. This range of values (at least 50 individuals to prevent inbreeding depression and at least 500 for mutation rates to balance genetic drift) has been referred to as the **50/500 rule**: isolated populations need to have at least 50 individuals, and preferably 500 individuals, to maintain genetic variability. This rule is now considered mainly appropriate for urgent short-term conservation efforts. For conservation efforts targeted for longer time periods and multiple generations, some leading conservation geneticists argue that at least several thousand reproductive individuals must be protected to maintain the genetic variability and long-term survival of a population (Frankham et al. 2009, 2014). This emphasis on protecting large numbers of individuals is due to evidence that inbreeding depression can affect even wild populations with effective sizes of more than 50 individuals and that beneficial mutation rates are lower than previously thought. While this work on genetic variation and MVPs gives us some practical guidelines, the ideal is still to protect as many individuals of rare and endangered species as possible, to maximize their chances of survival.

Consequences of reduced genetic variability

Small populations subjected to genetic drift have greater susceptibility to a number of deleterious genetic effects such as inbreeding depression, outbreeding depression, and loss of evolutionary flexibility. These factors may contribute to a decline in population size, leading to an even greater loss of genetic variability, a loss of fitness, and a greater probability of extinction (Frankham et al. 2009).

Mating among closely related individuals, which occurs in small populations, often results in lower reproductive success and weak offspring.

INBREEDING DEPRESSION A variety of mechanisms prevents **inbreeding**, mating among close relatives, in most natural populations. In large populations of most animal species, individuals do not normally mate with close relatives; this tendency to mate with unrelated individuals of the same species is termed **outbreeding**. Individuals often disperse from their place of birth or are restrained from mating with relatives by behavioral inhibitions, unique individual odors, or other sensory cues. In many plants, numerous morphological and physiological mechanisms encourage cross-pollination and prevent self-pollination. In some cases, particularly when population size is small and no other mates are available, these mechanisms fail to prevent inbreeding. Mating among parents and their offspring, siblings, and cousins, and **self-fertilization** in hermaphroditic species, may result in **inbreeding depression**, a condition that occurs when an individual receives two identical copies of a defective allele from each of its parents. Inbreeding depression is characterized by higher mortality of offspring, fewer offspring, or offspring that are weak or sterile or have low mating success (Frankham et al. 2009) (**Figure 11.6**). These factors result in even fewer individuals in the next generation, leading to more pronounced inbreeding depression.

Evidence for the existence of inbreeding depression comes from studies of human populations (in which there are records of marriages between close relatives for many generations), captive and wild animal populations, and cultivated plants (Frankham et al. 2014). In a wide range of captive mammal populations, matings among close relatives, such as parent–offspring matings and sibling–sibling matings, resulted on average in offspring with a 33% higher mortality rate than in non-inbred animals (**Figure 11.7**). This lower fitness resulting from inbreeding is sometimes referred to as a “cost of inbreeding.” Inbreeding depression can be a severe problem in small captive populations in zoos and in domestic livestock breeding programs. Deleterious effects of inbreeding in the wild have also been demonstrated (Crnokrak and Roff 1999): of over 150 valid data sets, 90% showed

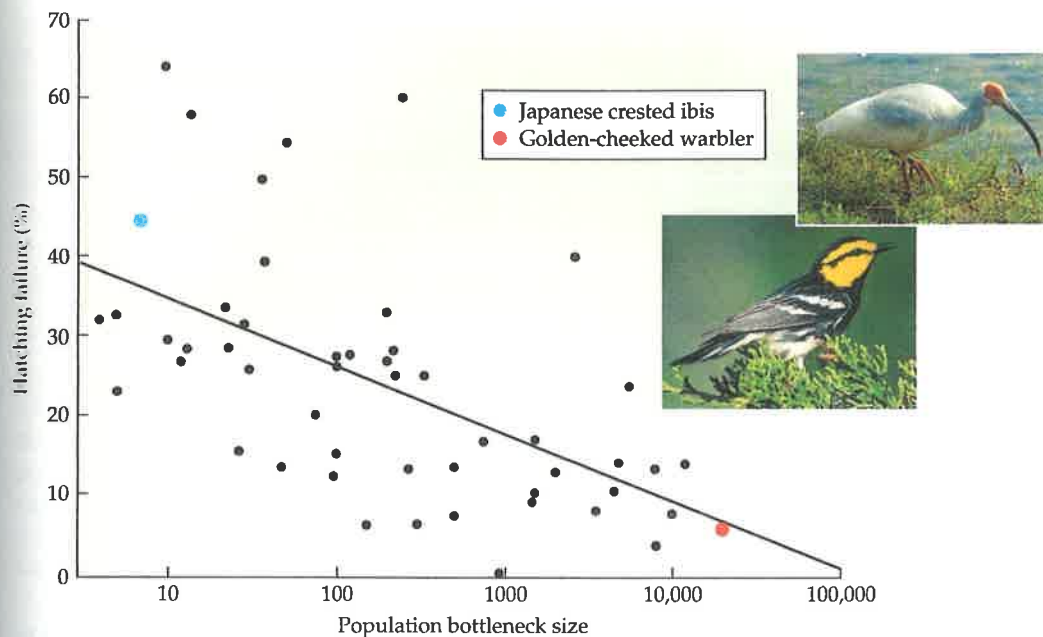


Figure 11.6 For 51 species of birds, the percent hatching failure is highest with the smallest population sizes (as expressed by the bottleneck size—the lowest size recorded for the population). The x-axis is on a log scale. The Japanese crested ibis (*Nipponia nippon*) (top photograph) represents one extreme, with fewer than 10 individuals in one year and hatching failure of about 45%; at the other extreme is the golden-cheeked warbler (*Dendroica chrysoparia*) (bottom photograph), with a population size always over 10,000 individuals and hatching failure of about 5%. (After Heber and Briskie 2010.)

inbreeding to be detrimental. The scarlet gilia (*Ipomopsis aggregata*) provides an example. Plants that come from populations with fewer than 100 individuals produce smaller seeds with a lower rate of seed germination and exhibit greater susceptibility to environmental stress than do plants from larger populations (Heschel and Paige 1995). In a second study, Bouzat et al. (2008) examined isolated small populations of greater prairie chickens (*Tympanuchus cupido pinnatus*) in Illinois. These populations were showing the effects of declining genetic variation and inbreeding depression, including lowered fertility and lowered rates of egg hatching. However, when individuals from large, genetically diverse populations were released among the small populations, egg viability was restored and the populations began to increase in numbers. This result demonstrates the importance of maintaining genetic variation in existing populations and of restoring genetic variation in genetically impoverished populations as a conservation strategy.

OUTBREEDING DEPRESSION Individuals of different species rarely mate in the wild; there are strong ecological, behavioral, physiological, and morphological isolating mechanisms that ensure mating occurs only

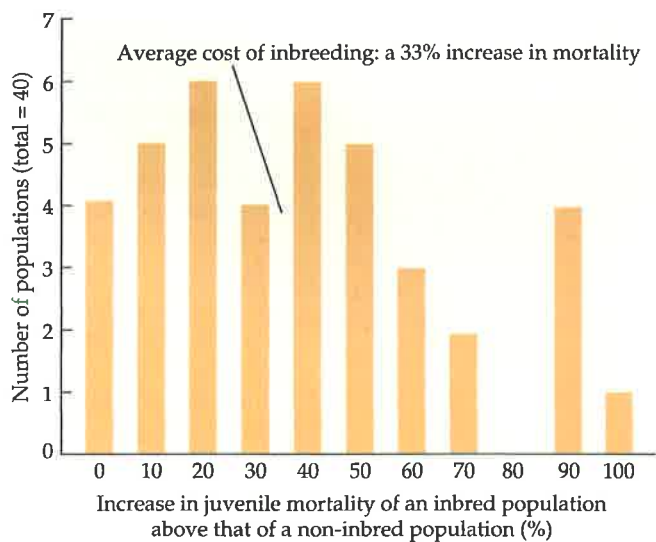
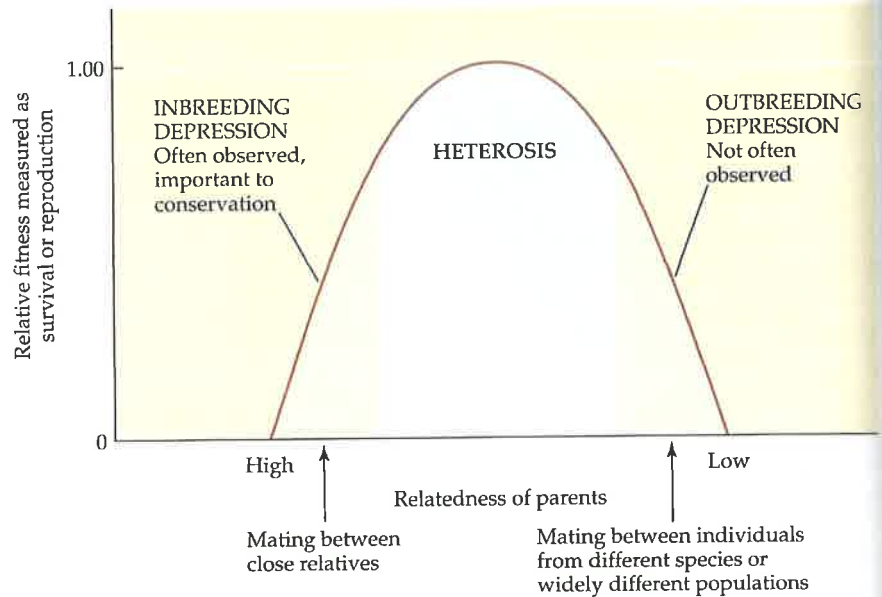


Figure 11.7 A high degree of inbreeding (such as matings between mother and son, father and daughter, brother and sister) results in an average "cost of inbreeding." The data shown in the graph, based on a survey of 40 inbred mammal populations, express the cost as a percentage increase in juvenile mortality above the juvenile mortality rate of outbreeding animals of the same species. (After Ralls et al. 1988.)

Figure 11.8 Mating between unrelated individuals of the same species often results in offspring with a high fitness (or heterosis) as measured by survival or high reproduction (number of offspring produced). Mating among close relatives (sibling–sibling or parent–offspring matings) or self-fertilization in hermaphroditic species leads to low fitness or inbreeding depression. Mating between individuals from widely different populations or even different species sometimes, but not always, results in lowered fitness or outbreeding depression. (After Groom et al. 2006.)



between individuals of the same species. However, when a species is rare or its habitat is damaged, outbreeding—mating between individuals of different populations or species—may occur (Figure 11.8). Individuals unable to find mates within their own species may mate with individuals of related species. The resulting offspring sometimes exhibit **outbreeding depression**, a condition that results in weakness, sterility, or lack of adaptability to the environment (Frankham et al. 2011). Outbreeding depression may be caused by incompatibility of the chromosomes and enzyme systems that are inherited from the different parents. To use an example from artificial selection, domestic horses and donkeys are commonly bred to produce mules. Although mules are not physically weak (on the contrary, they are quite strong, which is why humans find them useful), they are almost always sterile.

Outbreeding depression can also result from matings between different subspecies, or even matings between divergent populations of the same species. Such matings might occur in a captive breeding program or when individuals from different populations are kept together in captivity. In such cases, the offspring of such different genotypes are unlikely to have the precise mixture of genes that allows individuals to survive and reproduce successfully in a particular set of local conditions (Frankham et al. 2009). For example, when the ibex (*Capra ibex*) population of Slovakia went extinct, ibex from Austria, Turkey, and the Sinai were brought in to start a new population. These different subspecies mated and produced hybrids that bore their young in the harsh conditions of winter rather than in the spring, and consequently they had a low survival rate. Outbreeding depression caused by the pairing of individuals from the extremes of the species' geographical range meant failure for the experiment. However, many other studies of animals have failed to demonstrate outbreeding depression or have even shown that some hybrids are *more* vigorous than their parent species (McClelland and Naish 2007), a condition known as **hybrid vigor**. Thus, outbreeding depression may be considered of less concern for animals than inbreeding depression, the negative effects of which are well documented.

Outbreeding depression may be considerably more significant in plants, where the arrival of pollen onto the receptive stigma of the flower is to some degree a matter of the chance movement of pollen by wind, insects, or another pollen vector. A rare plant species growing near a closely related common species may be

overwhelmed by the pollen of the common species and fail to produce seeds (Willi et al. 2007). Even when hybrids are produced by matings between a common and a rare species, the genetic identity of the rare species becomes lost as its small gene pool is mixed into the much larger gene pool of the common species. The seriousness of this threat is illustrated by the fact that more than 90% of California's threatened and endangered plants occur in close proximity to other species in the same genus, with which the rare plants could possibly hybridize. Such a loss of identity can also take place in gardens when individuals from different parts of a species' range are grown next to each other and are cross-pollinated, producing hybrid seed.

LOSS OF EVOLUTIONARY FLEXIBILITY Genetic variation is extremely important to a species' long-term survival. Rare alleles and unusual combinations of alleles that are harmless (or even slightly harmful) but confer no immediate advantage on the few individuals who carry them may turn out to be uniquely suited for a future set of environmental conditions. If such alleles and combinations do become advantageous, their incidence in the population will increase rapidly through natural selection, since the individuals who carry them will be those most likely to survive and reproduce successfully, passing on the formerly rare alleles to their offspring.

Loss of genetic variability in a small population may limit its ability to respond to new conditions and long-term changes in the environment, such as pollution, new diseases, and global climate change (Willi et al. 2007). According to the fundamental theorem of natural selection, the rate of evolutionary change in a population is directly related to the amount of genetic variation in the population. A small population is less likely than a large population to possess the genetic variation necessary for adaptation to long-term environmental changes and so will be more likely to go extinct. For example, in many plant populations, a few individuals have alleles that promote tolerance for high concentrations of toxic metals such as zinc and lead, even when these metals are not present. If toxic metals become abundant in the environment because of pollution, individuals with these alleles will be better able to adapt to them and to grow, survive, and reproduce better than typical individuals; consequently, the frequency of these alleles in the population will increase dramatically. However, if the population has become small and the genotypes for metal tolerance have been lost, the population could go extinct.

Factors that determine effective population size

In this section we will discuss the factors that determine the effective population size, which is the size of the population as estimated by the number of its breeding individuals. The effective population size is lower than the total population size because many individuals do not reproduce, due to factors such as inability to find a mate, being too old or too young to mate, poor health, sterility, malnutrition, small body size, and social structures, such as polygyny (one male mating with more than one female), that restrict which individuals can mate (Hare et al. 2011). Many of these factors are initiated or aggravated by habitat degradation and fragmentation. Furthermore, many plant, fungus, bacteria, and protist species have seeds, spores, or other structures in the soil that remain dormant unless stable conditions for germination appear. These individuals could be counted as members of the population though they are obviously not part of the breeding population. Because of these factors, the effective population size (N_e) of breeding individuals is often substantially smaller than the actual population size (N). Because the rate of loss of genetic variability is based on the effective population size, the loss of genetic variability can be quite severe, even in a large population. For example, consider a population of 1000 alligators with 990 immature animals and only 10 mature breeding animals: 5 males and 5

The effective population size N_e will be much smaller than the total population size N when there is great variation in reproductive output, an unequal sex ratio, or population fluctuations and bottlenecks.

females. In this case, the effective population size is 10, not 1000. For a rare oak species, there might be 20 mature trees, 500 saplings, and 2000 seedlings, resulting in a population size of 2520 but an effective population size of only 20.

In addition, the effective population is often lower than the actual number of breeding individuals because of unequal sex ratio, variation in reproductive output, and large annual changes in population size (Jamieson 2011). This reduced effective population size can lead to further population decline and extinction.

UNEQUAL SEX RATIO A population may consist of unequal numbers of males and females due to chance, selective mortality, or the harvesting of only one sex by people. If, for example, a population of a goose species that is monogamous (with one male and one female forming a long-lasting pair bond) consists of 20 males and 6 females, then only 12 individuals—6 males and 6 females—will be mating. In this case, the effective population size is 12, not 26. In other animal species, social systems may prevent many individuals from mating even though they are physiologically capable of doing so. Among elephant seals, for example, a single dominant male usually mates with a large group of females and prevents other males from mating with them, whereas among African wild dogs, the dominant female in the pack often bears all of the pups.

The effect of unequal numbers of breeding males and females on N_e can be described by this formula:

$$N_e = [4(N_f \times N_m)] / (N_f + N_m)$$

where N_m and N_f are the numbers of adult breeding males and breeding females, respectively, in the population. In general, as the sex ratio of breeding individuals becomes increasingly unequal, the ratio of the effective population size to the number of breeding individuals (N_e/N) also goes down (Figure 11.9). This occurs because only a few individuals of one sex are making a disproportionately large contribution to the genetic makeup of the next generation, rather than the equal contribution found in monogamous mating systems. In the case of Asian elephants (*Elephas maximus*), for example, males are hunted by poachers for their tusks at the Periyar Tiger Reserve in India (Ramakrishnan et al. 1998). In 1997, there were 1166 elephants, of which 709 were adults. Of these adults, 704 were female and 5 were male. If all of these elephants were breeding, this would result in an effective population size of only 20 from a genetic perspective, using the equation shown above.

In many fish and reptiles species, sex is affected by temperature. As global climate change increases water and air temperature in many places, species may have skewed sex ratios, lowering the effective population size. For example, in

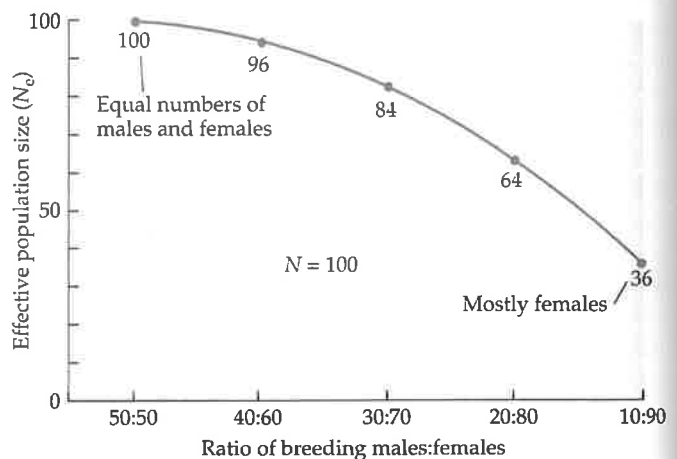


Figure 11.9 The effective population size (N_e) declines when the number of males and females in a breeding population (N) of 100 individuals is increasingly unequal. N_e is 100 when 50 males and 50 females breed, but it is only 36 when 10 males and 90 females breed.

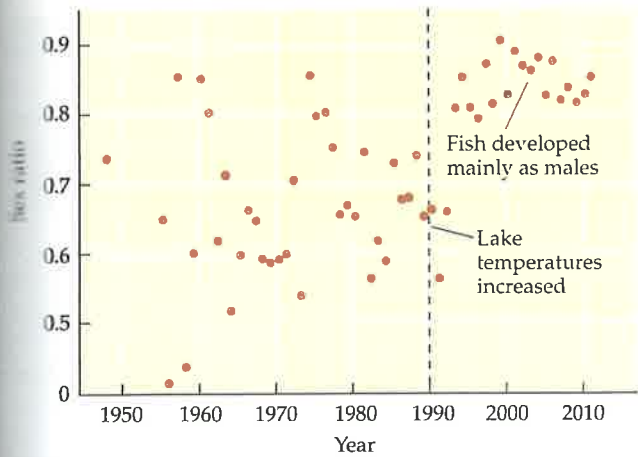


Figure 11.10 (A) The sex ratio of grayling, a fish in the salmon family, in Lake Thun, Switzerland, has shifted from being around 65% male (and highly variable) before 1990, to consistently 80%–90% male after 1990, when lake temperatures increased. The sex ratio is best explained by the temperature fish experience in their first year. (After Wedekind et al. 2013.)

Switzerland, grayling fish (*Thymallus thymallus*) populations that used to have highly variable sex ratios centered around 65% males before 1990, now consistently have 80%–90% males in their population (Figure 11.10). The effective population size will be far less than the number of individuals in the population.

VARIATION IN REPRODUCTIVE OUTPUT In many species the number of offspring varies substantially among individuals. This phenomenon is particularly true of highly fecund species, such as plants and fish (see Hedrick 2005), where many or even most individuals produce a few offspring while others produce huge numbers. Unequal production of offspring leads to a substantial reduction in N_e because a few individuals in the present generation will be disproportionately represented in the gene pool of the next generation. In general, the greater the variation in reproductive output, the more the effective population size is lowered. For a variety of species in the wild, Frankham (1995) estimated that variation in offspring number reduces effective population size by a factor of 54%. In many annual plant populations that consist of large numbers of tiny plants producing one or a few seeds and a few gigantic individuals producing thousands of seeds, N_e could be reduced even more.

POPULATION FLUCTUATIONS AND BOTTLENECKS In some species, population size varies dramatically from generation to generation. Particularly good examples of this are butterflies, annual plants, and amphibians. In extreme fluctuations, the effective population size is somewhere between the lowest and the highest numbers of breeding individuals. This is often the most important factor reducing N_e below the population size. The effective population size can be calculated over a period of t years using the number of individuals (N) breeding in any one year:

$$N_e = t / (1/N_1 + 1/N_2 + \dots + 1/N_t)$$

Consider a butterfly population, monitored for 5 years, that has 10, 20, 100, 20, and 10 breeding individuals in the successive 5 years. In this case,

$$N_e = 5 / (1/10 + 1/20 + 1/100 + 1/20 + 1/10) = 5 / (31/100) = 5(100/31) = 16.1$$

The effective population size over the course of 5 years is above the lowest population size (10) but well below the maximum (100) and the average (32) population size.

The effective population size tends to be determined by the years in which the population has the smallest numbers. A single year of drastically reduced population numbers will substantially lower the value of N_e . This principle applies to a

phenomenon known as a **population bottleneck**, which occurs when a population is greatly reduced in size and loses rare alleles if no individuals possessing those alleles survive and reproduce (Jamieson 2011). With fewer alleles present and a decline in heterozygosity, the overall fitness of the individuals in the population may decline.

A special category of bottleneck, known as the **founder effect**, occurs when a few individuals leave one population to establish another new population. The new population often has less genetic variability than the larger, original population. For example, the Swedish wolf population was established by 5 individuals (Laikre et al. 2013). If a population is fragmented by human activities, each of the resulting small subpopulations may lose genetic variation and go extinct. Such is the fate of many fish populations fragmented by dams (Wofford et al. 2005). Bottlenecks can also occur when captive populations are established using relatively few individuals.

The lions (*Panthera leo*) of Ngorongoro Crater in Tanzania provide a well-studied example of a population bottleneck (Munson et al. 2008). The lion population in the crater consisted of 60–75 individuals until an outbreak of biting flies in 1962 reduced the population to 9 females and 1 male (Figure 11.11). Two years later, 7 additional males immigrated to the crater; there has been no further immigration since that time. The small number of founders, the isolation of the population, and the variation in reproductive success among individuals have apparently created a population bottleneck, leading to inbreeding depression. In comparison with the large Serengeti lion population nearby, the crater lions show reduced genetic variability, high levels of sperm abnormalities (Figure 11.12), reduced reproductive rates, increased cub mortality, and higher rates of infection (Munson et al. 2008). After reaching a peak of 125 animals in the 1980s, the population has since declined again. By 2003, the population had dropped to 34 animals following an outbreak of canine distemper virus that had spread from domestic dogs kept by

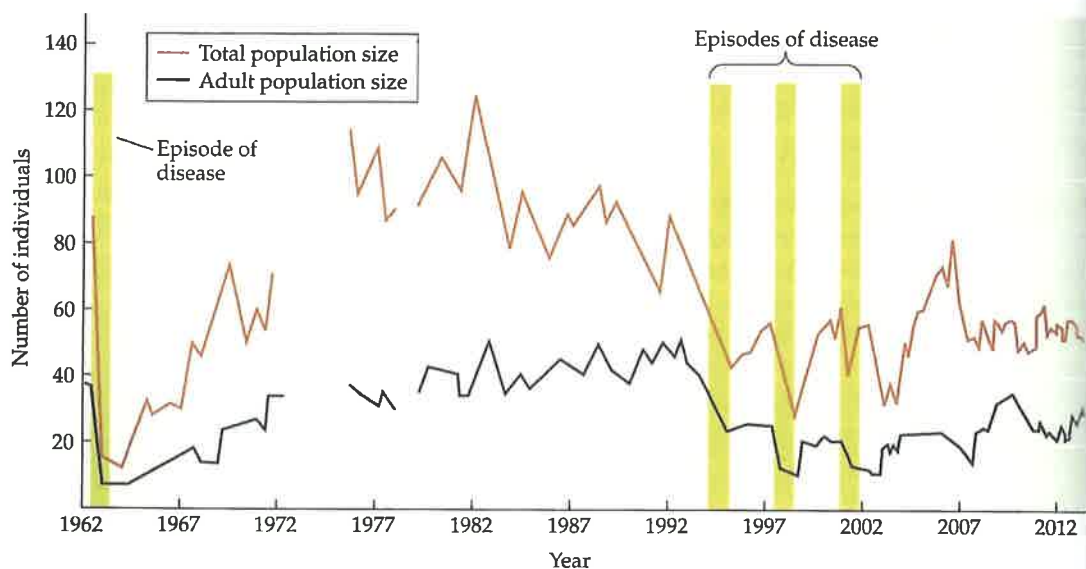


Figure 11.11 The Ngorongoro Crater lion population consisted of about 90 individuals in 1961 before crashing in 1962. Since that time, the population reached a peak of 125 individuals in 1983 before collapsing to 34 individuals (fewer than 20 of which were adults). Small population size, an isolated location, lack of immigration since 1964, and disease have contributed to the loss of genetic variation caused by a population bottleneck. A lack of census data for certain years is the cause of gaps in the lines. The four green bars represent episodes of disease outbreak. (After Munson et al. 2008, with updates from C. Packer.)

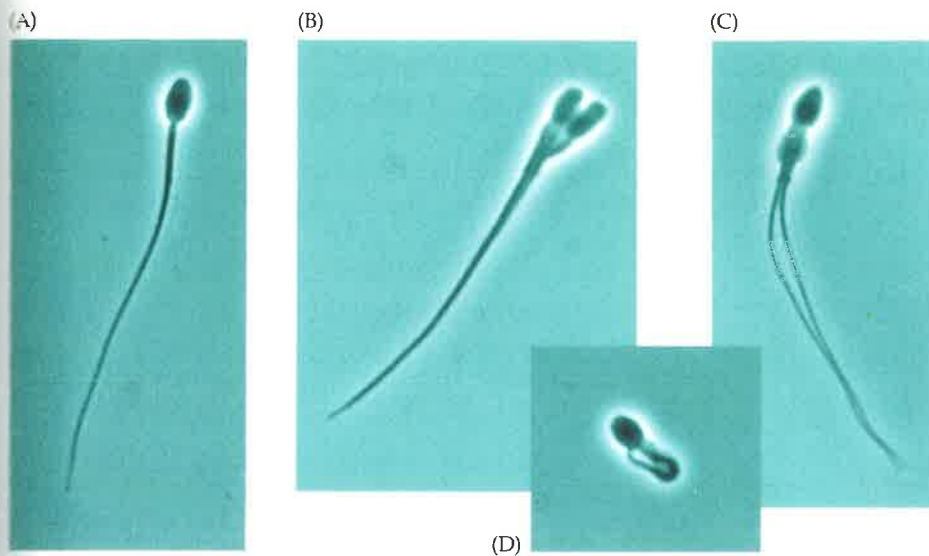


Figure 11.12 Males of the isolated and inbred population of lions at Ngorongoro Crater in Tanzania exhibit a high level of sperm abnormalities. (A) Normal lion sperm. And three non-functional sperm: (B) Bicephalic ("two-headed") sperm, (C) Two-tailed sperm, and (D) Sperm with a coiled flagellum. (Photographs by B. Pukazenthli and D. Wildt, Smithsonian Conservation Biology Institute.)

people living just outside the crater area. For the past 5 years, the population size has been around 50–60 animals.

Population bottlenecks do not always lead to greatly reduced heterozygosity. The effects of population bottlenecks will be most evident when the breeding population is reduced below 10 individuals for several generations. If the population expands rapidly in size after a temporary bottleneck, average heterozygosity in the population may be restored even though the number of alleles present is severely reduced. An example of this phenomenon is the high level of heterozygosity found in the greater one-horned rhinoceros (*Rhinoceros unicornis*) in Nepal, even after the population passed through a bottleneck

Box 11.1). Population size declined from 800 individuals in Chitwan National Park to fewer than 100 individuals; fewer than 30 were breeding. With an effective population size of 30 individuals for one generation, the population would have lost only 17% of its heterozygosity after one generation. As a result of strict protection of the species by park guards, the population recovered to 400 individuals. The Mauritius kestrel (*Falco punctatus*) represents an even more extreme case, with a long population decline that resulted in only one breeding pair remaining in 1974. An intensive conservation program has allowed the population to recover to about 300 adult birds today. A study comparing the present birds with preserved museum specimens and kestrels living elsewhere has found that the Mauritius kestrel lost only about half of its genetic variation after passing through this bottleneck (Ewing et al. 2008).

New populations established from only a few individuals may have reduced genetic variation. Genetic variation may be restored if the population expands rapidly in size.

MANAGING FOR GENETIC VARIATION These examples demonstrate that effective population size is often substantially less than the total number of individuals in a population. Particularly where there is a combination of factors such as fluctuating population size, numerous nonreproductive individuals, and an unequal sex ratio, the effective population size may be far lower than the number of individuals alive in a good year. A review of a wide range of wildlife studies revealed that the effective population size averaged only 11% of the total population size; that is, a population of 300 animals, seemingly large enough to maintain the population, might have an effective population size of only 33, which would indicate that it was in serious danger of extinction (Frankham 2005). If the goal of a conservation program is to protect 5000 reproductive individuals (see p. 251), then the effective population size might be about 550. For highly fecund species, such as fish, seaweed, and many invertebrates, the effective population size may be less than 1% of the total

BOX 11.1 | Rhino Species in Asia and Africa: Genetic Diversity and Habitat Loss

In recent decades, conservationists have focused extraordinary effort on protecting and restoring the numbers of rhinoceroses in parts of their original ranges (Amin et al. 2006). The task is monumental: three of the extant five species of rhinoceros are critically endangered, and all five represent ancient and unusual adaptations for survival. They also include several subspecies that are genetically and, in some cases, morphologically and behaviorally distinct as a result of reproductive isolation and possibly local adaptation. Habitat destruction and poaching are serious threats to the three species of the Asian forests, while the illegal killing of rhinos for their horns (used for medicine and carving) threaten the two African species.

Rhino numbers in Africa and India have increased in recent years, but the numbers of the two critically endangered Southeast Asian species are extremely low, around 50 and 250 animals each. It is estimated that fewer than 30,000 individuals of all five species survive today (IUCN Red List 2013), and they exist in a tiny fraction of their former range. The most numerous of the five is the white rhinoceros (*Ceratotherium simum*) with approximately 20,400 wild animals, although there are only 4 individuals of the distinctive northern subspecies, all in captivity in Kenya. Recent research suggests that this northern subspecies may actually be a sixth, distinct species of rhino, now very near extinction (Groves et al. 2010).

The recovery of each species and subspecies is complicated by the fact that many of the remaining animals live in very small, isolated populations, most notably the Southeast Asian species. Some biologists fear that these small populations may not be viable over the long term, as a result of loss of genetic variability, inbreeding depression, and genetic diseases resulting from mating among closely related individuals.

The question of genetic viability in rhino populations is not as simple as it first appears. Genetic diversity varies greatly among rhino species. Studies of the greater one-horned, or Indian, rhinoceros (*Rhinoceros unicornis*) in Nepal and India indicate that despite its small total abundance—an estimated 3000 animals—the genetic diversity is relatively high, contradicting the common assumption that small populations invariably have low heterozygosity. Long generation times and mobility among populations may have allowed the

Indian rhino to maintain its genetic variability despite passing through a population bottleneck (Pluháček et al. 2007).

Understanding the genetic and demographic characteristics of a species is often needed for effective conservation planning.

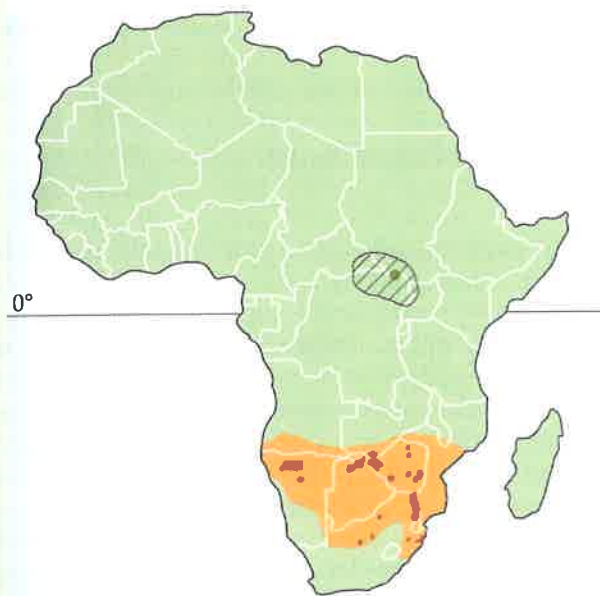
As a contrast with the Indian rhino, the four recognized subspecies of the black rhino are genetically distinct, as shown by microsatellite DNA data (Harley et al. 2005). If black rhinos from a number of different subspecies are placed together in a sanctuary to increase genetic diversity in the species, would the rhinos risk losing adaptive differences that might improve survival of local subspecies? Would distinctive features of each subspecies be lost? Or would increased genetic diversity increase the adaptive capacity of the population?

Maintaining genetic diversity while the abundance of each species of rhinoceros is so low requires limiting outside threats to the breeding population, including logging and illegal poaching, so that populations do not lose any more genetic variability than they already have. Recently, it appears that poaching of rhinos for their horns may be on the rise again. By weight their horns are worth more than gold on the black market. Estimates suggest 2 rhinos a day are being poached in South Africa alone—688 were believed to have been killed there in 2012, and even more in 2013, rates of loss that could reduce population sizes and genetic diversity in some areas.

In addition to managing threats, wildlife managers must maintain conditions to facilitate reproduction and must make decisions on whether to encourage interbreeding among populations or subspecies. Captive breeding can also be targeted to maintain or increase genetic variability and population numbers. This may be especially important for the Southeast Asian species that are on the verge of extinction. However, captive breeding of rhinos is difficult; white rhinos in particular often will not breed in zoo programs.

There is no single, all-encompassing answer to rhino conservation. Management must be tailored to the specific genetic and environmental circumstances of particular species and populations.

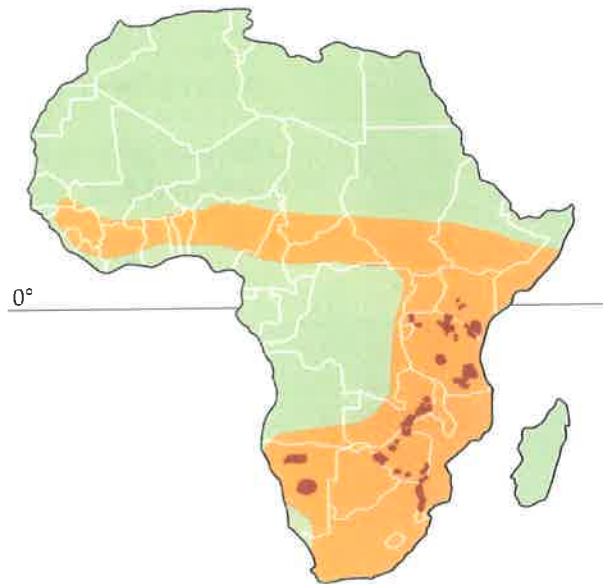
BOX 11.1 | (continued)

**Southern White Rhino**

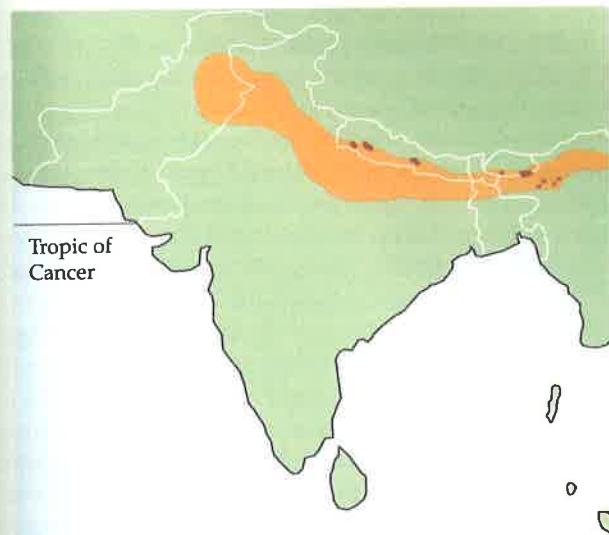
■ Present distribution
■ Former distribution

Northern White Rhino

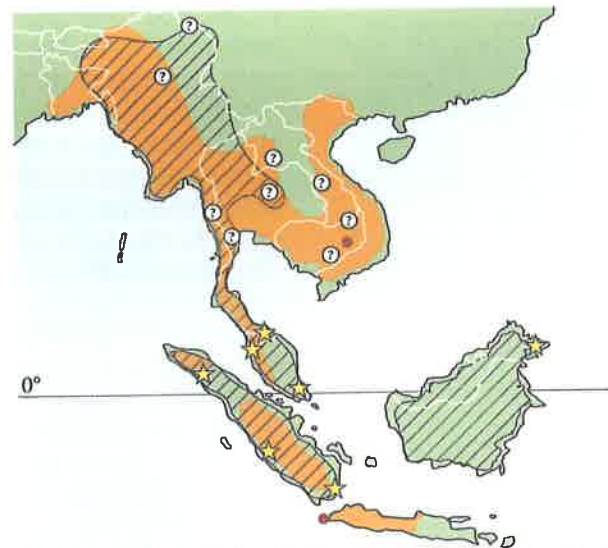
● Present distribution
▨ Former distribution

**Black African Rhino**

■ Present distribution
■ Former distribution

**Indian Rhino**

■ Present distribution
■ Former distribution

**Javan Rhino**

● Present distribution
■ Former distribution

Sumatran Rhino

☆ Present distribution
▨ Former distribution
② Unconfirmed

Each of the five rhinoceros species currently occupies only a tiny fraction of its former range, and their situations and levels of endangerment vary greatly. (After www.rhinos-irf.org)

population size (Frankham et al. 2009). Consequently, management aimed toward simply maintaining large populations may not prevent the loss of genetic variation unless the effective population size is also large. In the case of captive populations of rare and endangered species, genetic variation may be effectively maintained by controlling breeding, perhaps by subdividing the population, periodically removing dominant males to allow subdominant males the opportunity to mate, and periodically transporting a few selected individuals among subpopulations.

Other Factors That Affect the Persistence of Small Populations

In this section we discuss some other factors that affect small populations. Random variation, or **stochasticity**, in the environment can cause variation in the population

Random fluctuations in birth and death rates, disruption of social behavior following decreased population density, and environmental stochasticity all contribute to instability in the population size, often leading to local extinction.

size of a species. For example, the population of an endangered butterfly species might be affected by fluctuations in the abundance of its food plants and the number of its predators. Variation in the physical environment might also strongly influence the butterfly population; in an average year, the weather may be warm enough for caterpillars to feed and grow, whereas a cold year might cause many caterpillars to become inactive and consequently starve. Such **environmental stochasticity** affects

all individuals in the population and is linked to **demographic stochasticity** (or **demographic variation**), which is the variation in birth and death rates among individuals and across years within a given population.

Demographic variation

In an ideal, stable environment, a population would increase until it reached the carrying capacity (K) of the environment, at which point the average birthrate (b) per individual would equal the average death rate (d) and there would be no net change in population size. In any real population, individuals do not usually produce the average number of offspring: they might leave no offspring, somewhat fewer than the average, or more than the average. For example, in an ideal, stable giant panda (*Ailuropoda melanoleuca*) population, each female would produce an average of two surviving offspring in her lifetime, but field studies show that rates of reproduction among individual females vary widely around that number. However, as long as population size is large, the average birthrate provides an accurate description of the population. Similarly, the average death rate in a population can be determined only by examining large numbers of individuals, because some individuals die young and other individuals live a relatively long time. This variation in population size due to random variation in reproduction and mortality rates is known as demographic variation or demographic stochasticity.

Population size may fluctuate over time because of changes in the environment or other factors without ever approaching a stable value. Random fluctuations upward in population size are eventually bounded by the carrying capacity of the environment, and the population may fluctuate downward again. In general, once population size drops below about 50 individuals, individual variation in birth and death rates begins to cause the population size to fluctuate randomly up or down (Schleuning and Matthies 2009). If population size fluctuates downward in any one year because of a higher than average number of deaths or a lower than average number of births, the resulting smaller population will be even more susceptible to demographic fluctuations in subsequent years. Consequently, once a population decreases because of habitat destruction and fragmentation, demographic variation becomes important and the population has a higher probability of declining more and even going extinct due to chance alone (in a year with low reproduction and

high mortality) (Melbourne and Hastings 2008). Species with highly variable birth and death rates, such as annual plants and short-lived insects, may be particularly susceptible to population extinction due to demographic stochasticity. The chance of extinction is also greater in species that have low birthrates, such as elephants, because these species take longer to recover from chance reductions in population size.

As a simple example, imagine a population of three hermaphroditic individuals; each lives for 1 year, needs to find a mate and reproduce, and then dies. Assume that each individual has a 33% probability of producing zero, one, or two offspring, resulting in an average birthrate of 1 per individual; in this instance, there is theoretically a stable population. However, when these individuals reproduce, there is a 1-in-27 chance ($0.33 \times 0.33 \times 0.33$) that no offspring will be produced in the next generation and the population will go extinct. Consider also that there is a 1-in-9 chance that only one offspring will be produced in the next generation ($0.33 \times 0.33 \times 0.33 \times 3$); because this individual will not be able to find a mate, the population will be doomed to extinction in the next generation. There is also a 22% chance that the population will decline to two individuals in the next generation. Thus, random variation in birthrates can lead to demographic stochasticity and extinction in small populations. Similarly, random fluctuations in the death rate can lead to fluctuations in population size that could eliminate the population altogether.

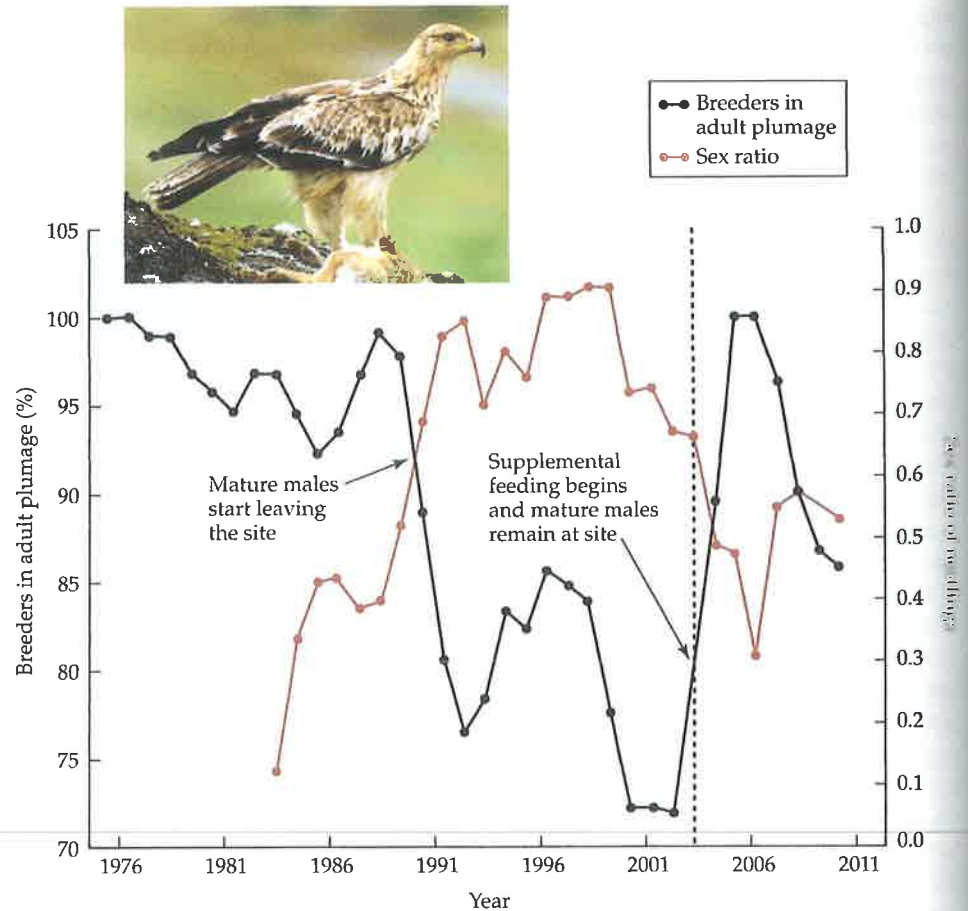
When populations drop below a critical number, deviations from an equal sex ratio may occur, leading to a declining birthrate and a further decrease in population size. For example, imagine a population of four birds that includes two mating pairs of males and females, in which each female produces an average of two surviving offspring in her lifetime. In the next generation, there is a 1-in-8 chance that only male or only female birds will be produced, in which case no eggs will be laid to produce the following generation. There is a 50% (8-in-16) chance that there will be either three males and one female or three females and one male in the next generation, in which case only one pair of birds will mate and the population will decline. This scenario is illustrated by the now extinct dusky seaside sparrow (*Ammodramus maritimus nigrescens*); the last five individuals were males, so there was no opportunity to establish a captive breeding program. Such demographic effects are also seen in the Spanish imperial eagle (*Aquila adalberti*); immature birds are more likely to breed when the population is small than when the population is large, when only mature birds breed. Such immature birds are in turn more likely to produce predominantly male offspring, contributing to further population decline and increasing the probability of local extinction (Figure 11.13) (Ferrer et al. 2009). For these eagles, a management strategy involving supplemental feedings was able to increase population size and restore the sex ratio.

POPULATION DENSITY AND THE ALLEE EFFECT Many small populations are demographically unstable because social interactions (especially those affecting mating) can be disrupted once population density falls below a certain level. This interaction among population size, population density, population growth rate, and behavior is sometimes referred to as the **Allee effect** (Bonsall et al. 2014). Herds of grazing mammals and flocks of birds may be unable to find food and defend themselves against attack from predators when numbers fall below a certain level. Animals that hunt in packs, such as wild dogs and lions, may need a certain number of individuals to hunt effectively.

Perhaps the most significant aspect of the Allee effect for small populations involves reproductive behavior: many species that live in widely dispersed populations, such as bears, spiders, and tigers, have difficulty finding mates once the population density drops below a certain point. Even among plant species, as population size

The social systems and breeding systems of many animals can be disrupted when the population size or density falls below a certain level.

Figure 11.13 In a declining population of Spanish imperial eagles the percentage of mature birds breeding in the population decreased beginning in 1990 as mature male birds left the area to find food elsewhere. As a result, the percentage of immature birds breeding at the site increased; these were mostly immature males mating with mature females (75% breeders in adult plumage means that probably half of the breeding males were immature). Matings involving immature males produce mainly male offspring, contributing to further population decline and increasing the probability of local extinction. Starting in 2004, supplemental food was provided at the site, more of the mature males remained at the site to breed, and the sex ratio of the offspring returned to approximately equal numbers of males and females. (After Ferrer et al. 2009, with updates by M. Ferrer.)



and density decrease, the distance between individual plants increases; pollinating animals may not visit isolated, scattered plants, resulting in insufficient transfer of compatible pollen and a subsequent decline in seed production. In such cases, the birthrate will decline, population density will become lower yet, problems such as unequal sex ratio will worsen, and birthrates will drop even more. Once the birthrate falls to zero, extinction is guaranteed. Detecting and anticipating Allee effects are necessary for the management and recovery of endangered species.

Environmental variation and catastrophes

Random variation in the biological and physical environment, known as **environmental stochasticity**, can also cause variation in the population size of a species. For example, a population of an endangered rabbit species might be affected by fluctuations in the population of a deer species that eats the same types of plants, fluctuations in the population of a fox species that feeds on the rabbits, and fluctuations in the populations of parasites and disease-causing organisms that affect the rabbits. Variation in the physical environment might also strongly influence the rabbit populations—rainfall during an average year might encourage plant growth and allow the population to increase, while dry years might limit plant growth and cause rabbits to starve. Environmental stochasticity affects all individuals in the population, unlike demographic stochasticity, which causes variation among individuals within the population.

Natural catastrophes that occur at unpredictable intervals, such as droughts, storms, earthquakes, and fires, along with cyclical die-offs of the surrounding biological community, can cause dramatic fluctuations in population levels. Natural

catastrophes can kill part of a population or even eliminate an entire population from an area. Numerous examples exist of die-offs in populations of large mammals; in many cases 70%–90% of the population dies (Young 1994). For a wide range of vertebrates, the frequency of catastrophes is about 15% per generation (Reed et al. 2003). Even though the probability of a natural catastrophe in any one year is low, over the course of decades and centuries, natural catastrophes have a high likelihood of occurring.

Even though a population appears to be stable or increasing, an infrequent environmental event or catastrophe can severely reduce population size or even drive it to extinction. Such rare events need to be considered by conservation biologists.

As an example of environmental variation, imagine a rabbit population of 100 individuals in which the average birthrate is 0.2 and an average of 20 rabbits are eaten each year by foxes. On average, the population will maintain its numbers at exactly 100 individuals, with 20 rabbits born each year and 20 rabbits eaten each year. However, if there are 3 successive years in which the foxes eat 40 rabbits per year, the population size will decline to 80 rabbits, 56 rabbits, and 27 rabbits in years 1, 2, and 3, respectively. If there are then 3 years of no fox predation, the rabbit population will increase to 32, 38, and 46 individuals in years 4, 5, and 6. Even though the same average rate of predation (20 rabbits per year) occurred over this 6-year period, variation in year-to-year predation rates caused the rabbit population size to decline by more than 50%. At a population size of 46 individuals, the rabbit population will probably go extinct within the next 5–10 years when subjected to the average rate of 20 rabbits eaten by foxes per year.

Modeling efforts by Menges (1992) and others have shown that random environmental variation is generally more important than random demographic variation in increasing the probability of extinction in populations of small to moderate size. Environmental variation can substantially increase the risk of extinction even in populations showing positive population growth under the assumption of a stable environment (Mangel and Tier 1994). In general, introducing environmental variation into population models, in effect making them more realistic, results in populations with lower growth rates, lower population sizes, and higher probabilities of extinction. For example, a model of a tropical palm using demographic variation predicted that the MVP size, the number of individuals needed to give the population a 95% probability of persisting for 100 years, was about 48 mature individuals (Figure 11.14). When moderate environmental variation was included, however, the MVP size increased to 380 individuals, meaning that a seven times larger population needs to be protected.

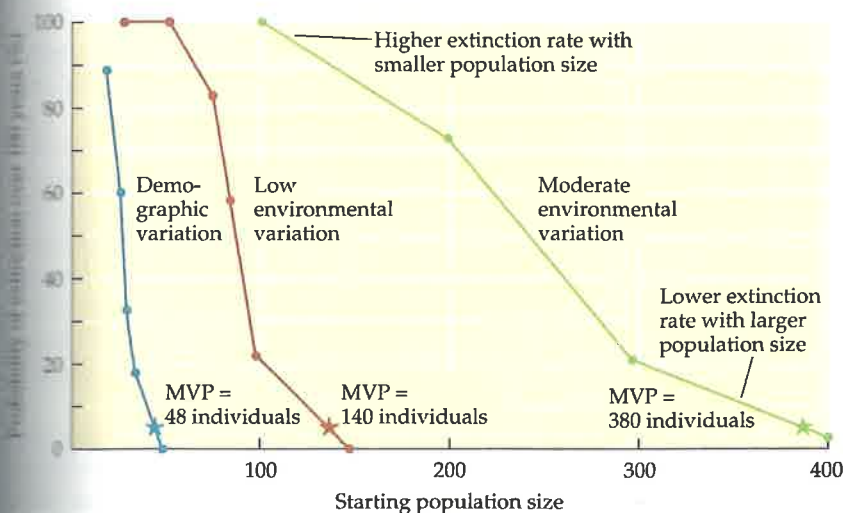


Figure 11.14 The effects of demographic variation, low environmental variation, and moderate environmental variation affect the probability of extinction of a population of a Mexican spiny palm species (*Astrocaryum mexicanum*). In this study, the MVP size, indicated by a star, was defined as the population size at which there is a less than 5% chance of the population's going extinct within 100 years. (After Menges 1992, data from Piñero et al. 1984.)

The interaction between population size and environmental variation was demonstrated using the biennial herb garlic mustard (*Alliaria petiolata*), an invasive plant in the United States, as an experimental subject (Drayton and Primack 1999). Populations of various sizes were assigned at random either to be left alone as controls or to be experimentally eradicated by removal of every flowering plant in each of the 4 years of the study; removal of all plants could be considered an extreme environmental event. Overall, the probability of an experimental population's going extinct over the 4-year period was 43% for small populations (fewer than 10 individuals initially), 9% for medium-sized populations (10–50 individuals), and 7% for large populations (more than 50 individuals). For control populations, the probability of going extinct for small, medium, and large populations was 11%, 0%, and 0%. Large numbers of dormant seeds in the soil apparently allowed most experimental populations to persist even when every flowering plant was removed in 4 successive years. However, small populations were far more susceptible to extinction than large populations.

Extinction Vortices

The smaller a population becomes, the more vulnerable it is to further demographic variation, environmental variation, and genetic factors that tend to lower reproduction, increase mortality rates, and so reduce population size even more, driving the population to extinction. This tendency of small populations to decline toward extinction has been likened to a vortex, a whirling mass of gas or liquid spiraling inward—the closer an object gets to the center, the faster it moves. At the center of an **extinction vortex** is oblivion: the local extinction of the species. Once caught in such a vortex, it is difficult for a species to resist the pull toward extinction (Palomares et al. 2012).

As one example, a decrease in an Iberian lynx (*Lynx pardinus*) population caused by loss of its rabbit prey may cause inbreeding depression and associated higher mortality rates, further decreasing population size (Palomares et al. 2012). Decreased population size may then result in biased sex ratios and the inability to find mates, leading to an even lower population size. The smaller population is then more vulnerable to further population reduction, loss of heterozygosity, and eventual extinction caused by unusual environmental events.

These three forces—environmental variation, demographic variation, and loss of genetic variability—act together such that a decline in population size caused by one factor will increase the vulnerability of the population to the other two factors (Figure 11.15).

It is also important to remember that as a population becomes smaller, it also tends toward becoming ecologically extinct: once a toucan population drops below a certain size or density in a rain forest, for example, fruits might go uneaten and seeds will not be dispersed.

An important implication of the extinction vortex is that addressing the original cause of population decline may not be sufficient to recover a threatened population. Such was the case with the greater prairie chicken population in Illinois described earlier. The original population of over 1 million prairie chickens declined to below 50 following the arrival of European settlers, with a decline in fertility and hatchability. Habitat restoration of the prairie landscape, reversing one of the major original causes of decline, failed to help the population recover. The Illinois prairie chicken population began to grow only after it was outcrossed to populations from other states to reverse inbreeding depression.

As the prairie chicken example illustrates, once a population has declined to a small size, it will probably go extinct unless unusual and highly favorable conditions allow the population size to increase (Shroff et al. 2005). Such populations often

Intensive management is often required to prevent small populations from declining further in size and going extinct.

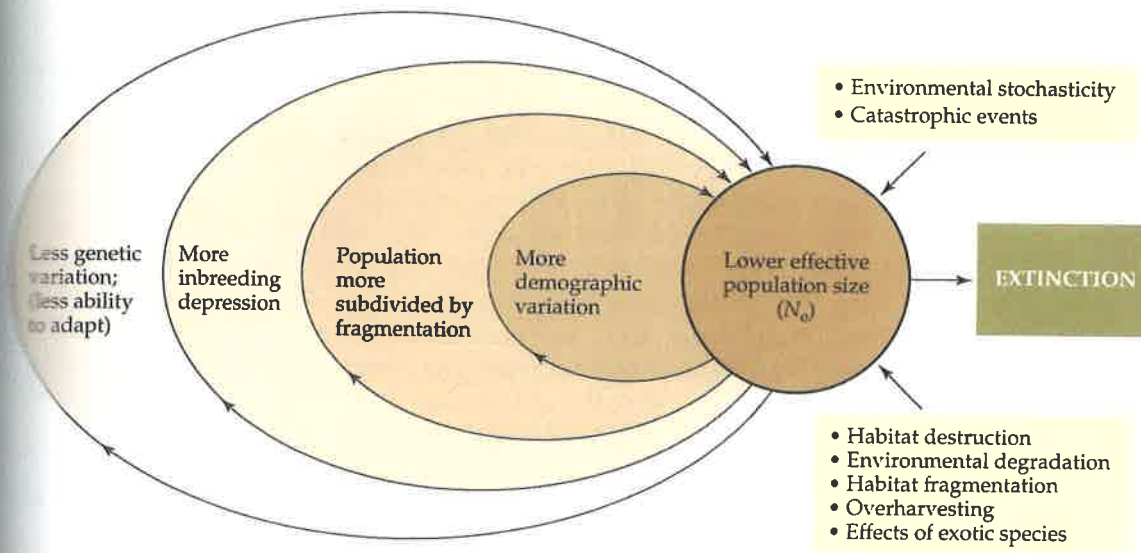


Figure 11.15 Once a population drops below a certain size, it enters an extinction vortex in which the factors that affect small populations tend to drive its size progressively lower. This downward spiral often leads to the local extinction of species. (After Gilpin and Soulé 1986 and Guerrant 1992.)

require a careful program of population and habitat management, as described in later chapters, to increase population growth rate and allow the population to escape from the harmful effects of small population size. In addition, the methods of population viability analysis, described in Chapter 12, allow predictions to be made as to how these actions will affect the probability of population extinction.

SUMMARY

1. In many cases, protecting populations is the key to protecting species from extinction. The minimum viable population (MVP) size is the smallest population size that can be predicted to have a high chance of persisting for the foreseeable future. The MVP for many species is at least several thousand individuals.
2. Biologists have observed that small populations have a greater tendency to go extinct than large populations. Small populations are subject to a more rapid rate of extinction for three main reasons: loss of genetic variability and related problems of inbreeding depression and genetic drift, demographic fluctuations, and environmental variation or natural catastrophes.
3. To protect small populations, we need to determine the effective population size, which is a genetic estimate based on the number of individuals that are actually producing offspring. The calculated effective population size is often much lower than simply the number of living individuals because (1) many individuals are not reproducing, (2) there may be an unequal sex ratio, (3) there may be variation among individuals in number of offspring produced, and (4) populations may show large fluctuations in size over time.
4. Variations in reproductive and mortality rates, known as demographic variation, can cause small populations to fluctuate randomly in size, sometimes leading to extinction. Environmental variation can also cause random fluctuations in population size, with infrequent natural catastrophes sometimes causing major reductions.
5. Once a population's size has been reduced by habitat destruction, fragmentation, and other human activities, it is even more vulnerable to random fluctuations in size and eventual extinction. The combined effects of demographic variation, environmental variation, and loss of genetic variability on small populations create an extinction vortex that tends to accelerate the drive to extinction, and may require population and habitat management to be counteracted.

For Discussion

1. Imagine a species that has four populations, consisting of 4, 10, 40, and 100 individuals. Using Wright's formula, $H = 1 - 1/[2 N_e]$, calculate the loss in heterozygosity over 1, 2, 5, and 10 generations for each population. Calculate the effective population size, N_e , for each population, assuming that there are equal numbers of males and females; then calculate it assuming different proportions of males and females. Allow the population size of each group to fluctuate at random around its average value. Calculate how this affects the loss of heterozygosity and the effective population size.
2. Construct a simple population model of a rabbit that has a stable population size (see p. 269; then add environmental variation (such as severe winter storms or predation) and demographic variation (number of offspring produced per rabbit per year), and determine whether the population would be able to persist over time. Use the methods shown in the text, computer simulations (see Shultz et al. 1999 and Donovan and Welden 2002 for ideas), or random-number generators (flipping coins is the easiest).
3. Find out about a species that is currently endangered in the wild. How is it or how might it be affected by the problems of small populations? Address genetic, physiological, behavioral, and ecological aspects, as appropriate.

Suggested Readings

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- Corlatti, L., K. Hacklander, and F. Frey-Roos. 2009. Ability of wildlife overpasses to provide connectivity and prevent genetic isolation. *Conservation Biology* 23: 548–556. Dispersal is needed to maintain genetic variation in fragmented populations.
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- Ewing, S. R. and 5 others. 2008. Inbreeding and loss of genetic variation in a reintroduced population of Mauritius kestrel. *Conservation Biology* 22: 395–404. The loss of genetic variation is a concern, despite the apparent success of this project.
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- Frankham, R., J. D. Ballou, and D. A. Briscoe. 2009. *Introduction to Conservation Genetics*, 2nd ed. Cambridge University Press, Cambridge, UK. Excellent introduction to the importance of genetics to conservation.
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- Pe'er, G. and 10 others. 2014. Toward better application of minimum area requirements in conservation planning. *Biological Conservation* 170: 92–102. Minimum area requirements have practical application in efforts to protect populations.

- Shoemaker, K. T., A. R. Breisch, J. W. Jaycox, and J. P. Gibbs. 2013. Reexamining the minimum viable population concept for long-lived species. *Conservation Biology* 27: 542–551. Populations of long-lived species can sometimes last for a long time.
- Wedekind, C. and 5 others. 2013. Persistent unequal sex ratio in a population of grayling (Salmonidae) and possible role of temperature increase. *Conservation Biology* 27: 229–234. Case study of the linkage between temperature and sex ratio in fish.