
Principles of Conservation Biology THIRD EDITION

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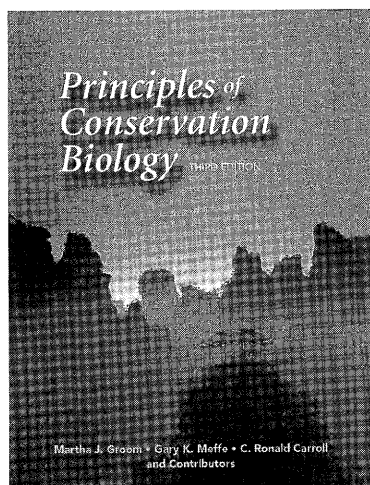
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About the Cover

Mountains from Zhangjiajie National Forest Park, Hunan Province, China. Zhangjiajie was the first national forest park created in China in 1982, and protects 4810 hectares of forests, mountains, and many rare species from the pressures of population growth. Similar areas of high mountains have long been revered in Chinese culture, with protections beginning 4200 B.P. as Imperial or temple gardens. An IUCN Category V protected area, the park is one of over 2000 sites in China's protected area network. (Photograph © John Wong/RubberBall Productions/PictureQuest.)

Principles of Conservation Biology, Third Edition

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tions to more accurately reflect the factors affecting levels of genetic diversity. Such a correction is the genetically effective population size (N_e), which is typically smaller, and often much smaller, than the census size (N). Ratios of effective population size to adult census population size are affected by fluctuations in population size, variance in family size, taxonomic group, and unequal sex ratios (Frankham 1995).

Effective population size is defined as the size of an idealized population that would have the same amount of inbreeding, loss of heterozygosity, or of random gene frequency drift, as the population under consideration (Kimura and Crow 1963). Mathematically, if demographic information is available, N_e can be estimated empirically (Box 11.2). Because N_e is nearly always significantly smaller than the census population size, conservationists have worked to estimate N_e and use this value in planning. Two examples of how N_e is used in conservation planning are discussed in Case Study 11.1 by Fred Allendorf and colleagues.

Mutation

Mutations are the ultimate source of new genetic variation. They occur during errors in replication of a nucleotide sequence or other alteration of the genome. The rate of mutation to new alleles (μ) is generally quite low for a specific locus (typically 10^{-4} to 10^{-6} per locus per generation depending on the segment of DNA), so the net effect of mutation on a single locus is usually weighed over evolutionary time scales rather than on a generation-by-generation basis.

Most mutations are selectively neutral. That is, they have no net effect on the fitness of an individual. However, most mutations that affect fitness are mildly or strongly deleterious. The effects are most often seen when expressed in a homozygous state, depending on the degree of dominance (i.e., the degree to which one or both alleles are expressed in heterozygous genotypes). Even if mutations occur at very low rates, given the large number of genes in most species, it is believed that mildly deleterious mutations arise at a rate perhaps as frequently as one per gamete per generation. In higher organisms, approximately 100 deleterious alleles may be present in each individual.

Mutations are important in a conservation sense because the probability of extinction can be affected by the accumulation of deleterious mutations. Even with very low mutation rates, if the population size is small and remains so for long periods, mutations can accumulate and eventually can become high enough in frequency to be expressed. The probability of **fixation** of a deleterious mutation (where all individuals in a population are homozygous for that mutation) decreases in large populations (i.e., populations with effective sizes greater than a

few hundred individuals). Large populations with high reproductive rates can be expected to be more resistant to accumulations of deleterious mutations than populations of small size.

In many species, only a fraction of offspring survive from birth to reproduce. With low probability of individual survival, a mutant gene newly arisen in one parent will, with high probability, be eliminated. However, in small populations, mutations have a higher probability of being passed on to offspring because inbreeding is more common. Mutations may accumulate to fixation if the strength of selection (S) in eliminating the genotype possessing this allele is lower than the probability of persistence by chance alone (i.e., $S < 1/2N_e$). A mutation that is recessive can become fixed through inbreeding because of the greater probability that individuals will share these mutations, and thus pass them on to their offspring.

As deleterious mutations accumulate, there is a gradual decline in the mean viability of individuals, which can lead to more rapid declines in population size. This precipitates a downward spiral, where mutations continue to accumulate and the population size becomes smaller and smaller, which progressively increases the probability of fixation of future mutations. This phenomenon has been termed **mutational meltdown** (Lynch 1995a).

There are numerous implications of mutational accumulation for conservation and management of natural or captive populations. Current management policies that provide formal protection to species only after they have dwindled to $N = 100$ to 1000 are inadequate if mutational meltdown is possible. The results of Lynch (1995a,b) and others indicate that the accumulation of mutations can pose a substantial threat to the survival of small populations. For "closed" populations that are maintained at levels below 100 individuals, a substantial load of deleterious mutations can be expected to develop within a few dozen generations. Because much of the reduction in fitness will be due to fixation of mutations, it may be essentially irreversible if the population remains closed to immigration from outside sources. Species with low birth rates such as many birds and mammals may be particularly susceptible.

However, a test of this hypothesis using *Drosophila* did not show as severe an effect, although it is unclear why (Gilligan et al. 1997). Some have suggested that several counteracting forces may protect populations from mutational meltdown, such as active preference for mates with fewer mutations, sperm competition, or higher fecundity of individuals with fewer mutations (Jennions et al. 2001; Tregenza and Wedell 2000).

Genetic drift

Genetic drift is the random fluctuation of gene frequencies over time due to chance alone. Because each adult

sophical perspective of the primacy of evolutionary dynamics in life's processes. The fields of evolutionary biology, and population and molecular genetics, which are the foundations of conservation genetics, are well established. Genetic technology does have limitations however, and will not alone be the savior of biodiversity. The application of genetics to conservation problems is a young science that is still developing. Many advances have been made recently that make genetic methodology more accessible to managers and conservation biologists. However, ad hoc or casual genetic analyses are not recommended. Established laboratories with experienced investigators should be consulted.

Plant or animal tissues must be obtained and properly treated. Historically, this meant that fresh or frozen samples had to be obtained from many individuals. For investigators working in remote field sites, difficulties in capture and handling methodology, and the need to return undegraded fresh or frozen samples to the laboratory precluded genetic analysis. However, with the advent of DNA technology, this can be accomplished easily and from minimal sources of material such as hairs or feathers, often noninvasively, and in a manner in which samples can be preserved for long periods at ambient (field) conditions (Palsboll 1999).

Genetics will play a pivotal role in many circumstances, such as studying small isolated populations on real or habitat islands, small numbers of charismatic vertebrates (e.g., large and rare predators or ungulates),

salmon stocks exploited by humans, and captive rearing in zoos, botanical gardens, and aquariums, and by providing critical biological data for species of conservation concern. However, a genetic approach will not save the biological diversity being lost daily in tropical forests, or the coral reefs being killed by coastal development and global climate change. Wholesale habitat destruction is a problem on a different level that cuts across genetic boundaries, and for which solutions are more economic and political than biological. We have much to learn, and we must be realistic about the limitations. Habitat availability and biological interactions and processes should be the primary focus of conservation everywhere. If the habitat is not available, and materials and energy do not flow through an ecosystem, then maintenance of genetic diversity will ultimately degrade to an exercise in ex situ care. Without suitable ecosystems and dynamic ecological processes, high levels of genetic diversity alone would not ensure long-term population viability. Woodruff (1992) stated this concisely when he said, "Genetic factors do not figure among the four major causes of extinction (the Evil Quartet; Diamond 1989): overkill, habitat destruction and fragmentation, impact of introduced species, and secondary or cascade effects." Thus, although genetic factors are major determinants of a population's long-term viability, conservationists can do more for a threatened population in the short-term by managing its habitat. Habitat management is the cheapest and most effective way of conserving genetic diversity.

CASE STUDY 11.1

Genetics And Demography of Grizzly Bear Populations

Fred W. Allendorf, University of Montana, Craig R. Miller and Lisette P. Waits, University of Idaho

Fragmentation and isolation of populations is of increasing concern in conservation. Loss of genetic variation in isolated populations of large mammals is especially serious because of their low population densities and large spatial requirements. Thus, even the largest protected reserves may be too small to maintain viable populations of large mammals.

The most useful concept to estimate the expected rate of loss of genetic variation in isolated populations is effective population size, N_e (Waples 2002). Knowledge of effective population size allows prediction of the expected time when reduced genetic variation is likely to threaten continued existence of an isolated population. In spite of universal agreement about the importance of effective population size for making

management decisions, considerable confusion persists about its estimation in natural populations.

Well-known studies with domestic animals have shown that inbreeding and the concomitant loss of genetic variation has a variety of harmful effects on development, reproduction, survival, and growth rate. Early studies with zoo populations indicated that wild species are susceptible to similar effects (Ralls et al. 1988). In the wild, where conditions tend to be harsher and more variable, the detrimental effects of inbreeding and low diversity on fitness are stronger (Keller and Waller 2002).

Several recent studies have demonstrated that these fitness reductions can increase the probability of extinction. For example, a study on adders (*Vipera berus*) showed how a long-term

decline in demographic rates and a reduction in population size to near zero were rapidly reversed by the influx of genetically diverse individuals (Madsen et al. 1999). A similar effect was observed in a Greater Prairie Chicken (*Tympanuchus cupido pinnatus*) population that had declined to very few individuals on a remnant patch of tallgrass prairie (Westemeier et al. 1998). In a metapopulation of the Glanville fritillary butterfly (*Melitaea cinxia*), subpopulations with lower heterozygosity were more likely to go extinct (Saccheri et al. 1998). It is important to recognize, however, that in all three of these cases, as in most situations, there was not a single cause of decline or extinction. Rather, extinction results from the actions and interactions of genetic, environmental, ecological, and demographic forces.

The rate of loss of genetic variation is generally measured by change in average heterozygosity per individual per locus (H). Heterozygosity is expected to be lost at a rate of $(1/2N)$ per generation in a theoretical "ideal" population of equal numbers of males and females that are all equally likely to contribute offspring to the next generation (Wright 1969). However, as described in the main text, a wild population of N individuals will lose heterozygosity much faster than $1/2N$ due to unequal sex ratios, fluctuations in population size, and non-random reproductive success of individuals, resulting in much greater rate of loss of heterozygosity. Effective population size (N_e) is defined as the size of the ideal population that will result in the same amount of loss in heterozygosity or change in allele frequencies as in the actual population being considered.

The number of alleles will also decline in small populations. Because distinct alleles can respond differently to evolutionary challenges, a population with high allelic diversity may be much more likely to successfully adapt than a population with low allelic diversity (Allendorf 1986). The importance of allelic diversity is perhaps most dramatically illustrated by loci associated with the immune system (MHC loci) where it is not unusual to observe more than 20 alleles at a single locus (Edwards and Hedrick 1998). Unfortunately, the concept of N_e based on the loss of heterozygosity may not be a good predictor of the loss of allelic diversity (Luikart et al. 1999). This is because rare alleles will be lost at population sizes for which there will be little loss in heterozygosity. If rare alleles compose a substantial proportion of the number of alleles in a population, their loss will result in a dramatic drop in allelic diversity. However, because rare alleles have little effect on heterozygosity, their loss will not be reflected in the decline in heterozygosity.

A variety of methods provide estimates of N_e under different violations of the assumptions of the ideal population (Waples 2002). These methods incorporate estimates of demographic parameters such as age at first reproduction, life span, variance in reproductive success, and the number of breeding individuals of each sex. Several problems make it difficult to use these estimations in wild populations. First, these formulas cannot be combined to estimate rate of loss of genetic variation in a wild population because many of the assumptions are not

likely to hold. Second, many of the parameters needed to estimate N_e with these formulas are virtually impossible to estimate in wild populations. Finally, most populations do not consist of a single, randomly mating group. Existing formulas for estimating N_e have not been designed to incorporate effects of gene flow between geographically separated local populations.

The following example from an isolated grizzly bear population (*Ursus arctos*) introduces two other approaches to estimate N_e and illustrates how N_e can be used in a conservation context. In 1975, the grizzly bear was listed as threatened under the U.S. Endangered Species Act. The number of grizzly bears in the contiguous 48 states has declined from an estimated 100,000 in 1800 to less than 1000 at present (Servheen 1999). The inhabited range of the species within this area is now less than 1% of its historic range. The current verified range of the grizzly bear is approximately five million hectares in six separate subpopulations in four states (Servheen 1999). The range reduction isolated subpopulations because continuous habitat was divided and movement corridors disappeared. Population decline accelerated because these isolated subpopulations were small and subject to stochastic demographic influences.

An estimation of the rate of loss of genetic variation in grizzly bear subpopulations is needed to determine population sizes required to maintain viable subpopulations. Moreover, it is also important to determine what management actions can be taken to reduce the rate of loss of genetic variation in the remaining subpopulations. Initial minimum viable population size (MVP) guidelines for the grizzly bear were based on a comprehensive series of computer simulations of demography that did not consider genetics (Shaffer and Sampson 1985). Initial recovery targets for some of the six subpopulations were less than 100 individuals, a size that will lose genetic variation at a rate likely to decrease fitness if the subpopulations are isolated.

We developed a simulation model to estimate effective population size of grizzly bear populations (Harris and Allendorf 1989). The model is a discrete-time, stochastic computer program that follows the history and kinship of each individual (in simulated populations). Values of life history parameters used in the simulations were taken from studies of grizzly bear populations in Montana, Wyoming, and British Columbia. We compared the loss of heterozygosity per generation in model populations to that expected in ideal populations to estimate N_e (Figure A). Our results indicated that the effective population size of grizzly bears is approximately 25% of census size (Allendorf et al. 1991).

An alternative approach is to estimate N_e directly from the amount of genetic drift (as measured by changes in heterozygosity and allele frequencies) observed over time at molecular genetic markers. By definition, heterozygosity will be lost at a rate of $(1/2N_e)$ per generation. N_e can be estimated by measuring the actual loss in heterozygosity at many loci over several generations (Waples 2002). The estimated N_e can be divided by an estimate of N over the same interval to obtain an estimate of