

Interactive Management of Small Wild and Captive Populations (T.J. Foose)

Introduction

Conservation strategies for endangered species must be based on viable populations. While it is necessary, it is no longer sufficient merely to protect endangered species *in situ*. They must also be managed.

The reason management will be necessary is that the populations that can be maintained of many species under the pressures of habitat degradation and unsustainable exploitation will be small, i.e. a few tens to a few hundreds (in some cases, even a few thousands) depending on the species. As such, these populations are endangered by a number of environmental, demographic, and genetic problems that are stochastic in nature and that can cause extinction.

Small populations can be devastated by catastrophe (weather disasters, epidemics, exploitation) as exemplified by the case of the black footed-ferret and the Puerto Rican parrot, or be decimated by less drastic fluctuations in the environment. Demographically, small populations can be disrupted by random fluctuations in survivorship and fertility. Genetically, small populations lose diversity needed for fitness and adaptability.

Minimum Viable Populations

For all of these problems, it is the case that the smaller the population is and the longer the period of time it remains so, the greater these risks will be and the more likely extinction is to occur. As a consequence, conservation strategies for species which are reduced in number, and which most probably will remain that way for a long time, must be based on maintaining certain minimum viable populations (MVP's), i.e. populations large enough to permit long-term persistence despite the genetic, demographic and environmental problems.

There is no single magic number that constitutes an MVP for all species, or for any one species all the time. Rather, an MVP depends on both the genetic and demographic objectives for the program and the biological characteristics of the taxon or population of concern. A further complication is that currently genetic and demographic factors must be considered separately in determining MVP's, although there certainly are interactions between the genetic and demographic factors. Moreover, the scientific models for assessing risks in relation to population size are still in rapid development. Nevertheless, by considering both the genetic and demographic objectives of the program and the biological characteristics pertaining to the population, scientific analyses can suggest ranges of population sizes that will provide calculated protection against the stochastic problems.

Genetic and demographic objectives of importance for MVP

Probability of survival (e.g., 50% or 95%) desired for the population:

Percentage of the genetic diversity to be preserved (90%, 95%, etc.);

Period of time over which the demographic security and genetic diversity are to be sustained (e.g., 50 years, 200 years).

In terms of demographic and environmental problems, for example, the desire may be for 95% probability of survival for 200 years. Models are emerging to predict persistence times for populations of various sizes under these threats. Or in terms of genetic problems, the desire may be to preserve 95% of average heterozygosity for 200 years. Again models are available. However, it is essential to realize that such terms as viability, recovery, self-sustainment, and persistence can be defined only when quantitative genetic and demographic objectives have been established, including the period of time for which the program (and population) is expected to continue.

Biological characteristics of importance for MVP

Generation time: Genetic diversity is lost generation by generation, not year by year. Hence, species with longer generation times will have fewer opportunities to lose genetic diversity within the given period of time selected for the program. As a consequence, to achieve the same genetic objectives, MVP's can be smaller for species with longer generation times. Generation time is qualitatively the average age at which animals produce their offspring; quantitatively, it is a function of the age-specific survivorships and fertilities of the population which will vary naturally and which can be modified by management, e.g. to extend generation time.

The number of founders. A founder is defined as an animal from a source population (the wild for example) that establishes a derivative population (in captivity, for translocation to a new site, or at the inception of a program of intensive management). To be effective, a founder must reproduce and be represented by descendants in the existing population. Technically, to constitute a full founder, an animal should also be unrelated to any other representative of the source population and non-inbred.

Basically, the more founders, the better, i.e. the more representative the sample of the source gene pool and the smaller the MVP required for genetic objectives. There is also a demographic founder effect: the larger the number of founders, the less likely is extinction due to demographic stochasticity. However, for larger vertebrates, there is a point of diminishing returns (Figure 1), at least in genetic terms. Hence a common objective is to obtain 20-30 effective founders to establish a population. If this objective cannot be achieved, then the program must do the best with what is available. If a pregnant female woolly mammoth were

discovered wandering the tundra of Alaska, it would certainly be worth trying to develop a recovery plan for the species even though the probability of success would be low. By aspiring to the optima, a program is really improving the probability of success.

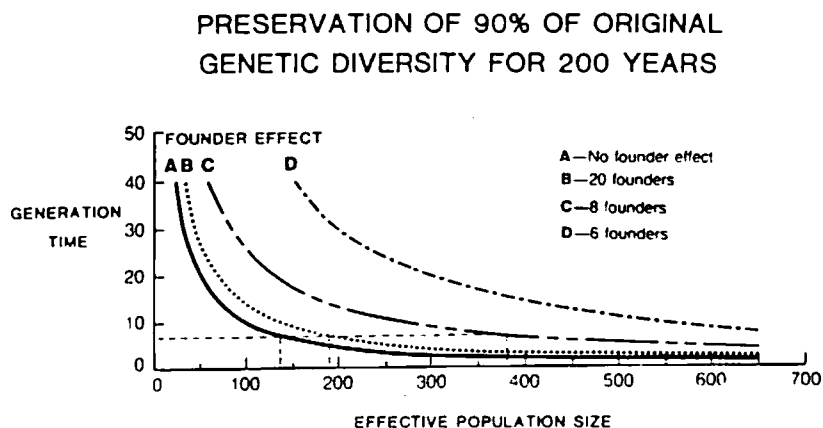


Figure 1. Interaction of number of founders, generation time of the species, and effective population size required for preserving 90% of the starting genetic diversity for 200 years.

Effective Population Size. Another very important consideration is the effective size of the population, designated N_e . N_e is not the same as the census size, N . Rather, N_e is a measure of the way the members of the population are reproducing with one another to transmit genes to the next generation. N_e is usually much less than N . For example in the grizzly bear, N_e/N ratios of about .25 have been estimated (Harris and Allendorf 1989). As a consequence, if the genetic models prescribe an N_e of 500 to achieve some set of genetic objectives, the MVP might have to be 2000.

Growth Rate. The higher the growth rate, the faster a population can recover from small size, thereby outgrowing much of the demographic risk and limiting the amount of genetic diversity lost during the so-called "bottleneck". It is important to distinguish MVP's from bottleneck sizes.

Population viability analysis

The process of deriving MVP's by considering various factors, i.e. sets of objectives and characteristics, is known as Population Viability (sometimes Vulnerability) Analysis (PVA). Deriving applicable results in PVA requires an interactive process between population biologists, managers, and researchers. PVA has been applied to a number of species (e.g., Parker and Smith 1988, Seal et al. 1989, Ballou et al. 1989, Lacy et al. 1989, Lacy and Clark, in press).

As mentioned earlier, PVA modelling often is performed separately with respect to genetic and demographic events. Genetic models indicate it will be necessary to maintain populations of hundreds or thousands to preserve a high percentage of the gene pool for several centuries. Recent models allow simultaneous consideration of demography, environmental uncertainty, and genetic uncertainty.

MVP's to contend with demographic and environmental stochasticity may be even higher than to preserve genetic diversity especially if a high probability of survival for an appreciable period of time is desired. For example, a 95% probability of survival may entail actually maintaining a much larger population whose persistence time is 20 times greater than required for 50% (i.e., average) probability of survival; 90%, 10 times greater. From another perspective, it can be expected that more than 50% of actual populations will become extinct before the calculated mean persistence time elapses.

Species of larger vertebrates will almost certainly need population sizes of several hundreds or perhaps thousands to be viable. In terms of the stochastic problems, more is always better.

Metapopulations and Minimum Areas

MVP's imply minimum critical areas of natural habitat, that will be vast for large carnivores like the Key deer. Consequently, it will be difficult or impossible to maintain single, contiguous populations of the hundreds or thousands required for viability.

However, it is possible for smaller populations and sanctuaries to be viable if they are managed as a single larger population (a metapopulation) whose collective size is equivalent to the MVP (Figure 2). Actually, distributing animals over multiple "subpopulations" will increase the effective size of the total number maintained in terms of the capacity to tolerate the stochastic problems. Any one subpopulation may become extinct or nearly so due to these causes; but through recolonization or reinforcement from other subpopulations, the metapopulation will survive. Metapopulations are evidently frequent in nature with much local extinction and recolonization of constituent subpopulations occurring.

Unfortunately, as wild populations become fragmented, natural migration for recolonization may become impossible. Hence, metapopulation management will entail moving animals around to correct genetic and demographic problems (Figure 3). For migration to be effective, the migrants must reproduce in the new area. Hence, in case of managed migration it will be important to monitor the genetic and demographic performance of migrants

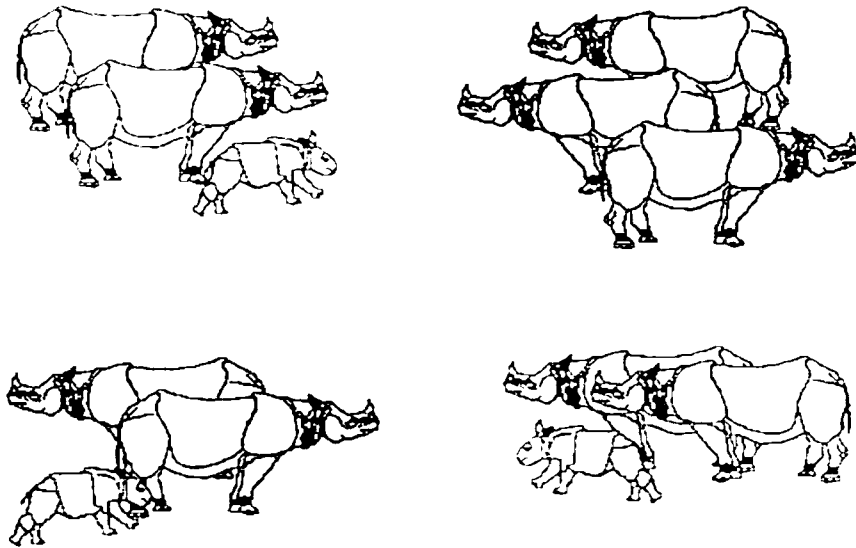


Figure 2. Multiple subpopulations as a basis for management of a metapopulation for survival of a species in the wild.

Managed migration is merely one example of the kinds of intensive management and protection that will be desirable and necessary for viability of populations in the wild. MVP's strictly imply benign neglect. It is possible to reduce the MVP required for some set of objectives, or considered from an alternative perspective, extend the persistence time for a given size population, through management intervention to correct genetic and demographic problems as they are detected. In essence, many of these measures will increase the N_c of the actual number of animals maintained.

The Key deer is already subject to intervention: animals are fed by residents, movements are obstructed and the population is being fragmented by development, and deer are killed by collisions with automobiles. Such interventions are manifestations of the fact that as natural sanctuaries and their resident populations become smaller, they are in effect transforming into megazoos that will require much the same kind of intensive genetic and demographic management as species in captivity.

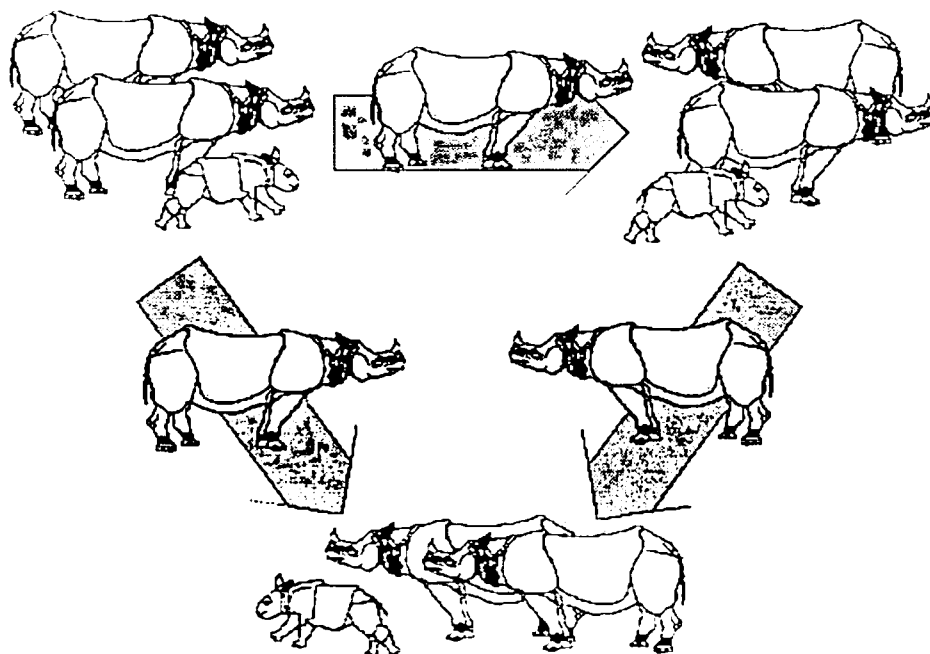


Figure 3. Managed migration among subpopulations to sustain gene flow in a metapopulation.

Captive Propagation

Another way to enhance viability is to reinforce wild populations with captive propagation. More specifically, there are a number of advantages to captive propagation: protection from unsustainable exploitation, e.g. poaching; moderation of environmental vicissitudes for at least part of the population; more genetic management and hence enhance preservation of the gene pool; accelerated expansion of the population to move toward the desired MVP and to provide animals more rapidly for introduction into new areas; and increase in the total number of animals maintained.

It must be emphasized that the purpose of captive propagation is to reinforce, not replace, wild populations. Captive colonies and zoos must serve as reservoirs of genetic and demographic material that can periodically be transfused into natural habitats to re-establish species that have been extirpated or to revitalize populations that have been debilitated by genetic and demographic problems.

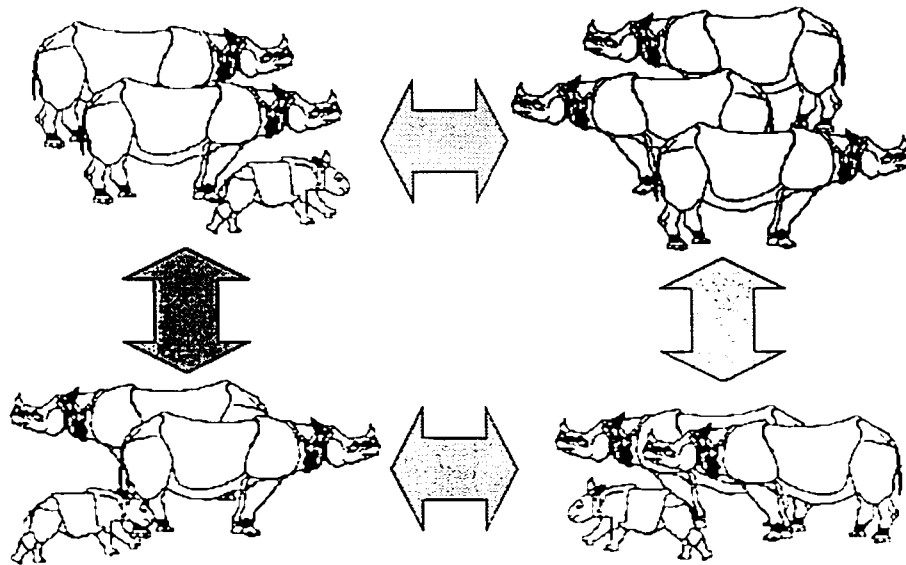


Figure 4. The use of captive populations as part of a metapopulation to expand and protect the gene pool of a species.

The survival of a great and growing number of endangered species will depend on assistance from captive propagation. Indeed, what appears optimal and inevitable are conservation strategies for the species incorporating both captive and wild populations interactively managed for mutual support and survival (Figure 4). The captive population can serve as a vital reservoir of genetic and demographic material; the wild population, if large enough, can continue to subject the species to natural selection. This general strategy has been adopted by the IUCN (the world umbrella conservation organization) which now recommends that captive propagation be invoked anytime a taxon's wild population declines below 1000 (IUCN 1988).

Species Survival Plans

Zoos in many regions of the world are organizing scientifically managed and highly coordinated programs for captive propagation to reinforce natural populations. In North America, these efforts are being developed under the auspices of the AAZPA, in coordination with the IUCN SSC Captive Breeding Specialist Group (CBSG), and are known as the Species Survival Plan (SSP).

Captive propagation can help, but only if the captive populations themselves are based on concepts of viable populations. This will require obtaining as many founders as possible, rapidly expanding the population normally to several hundreds of animals, and managing the population closely genetically and demographically. This is the purpose of SSP Masterplans. Captive programs can also conduct research to facilitate management in the wild as well as in captivity, and for interactions between the two.

A prime examples of such a captive/wild strategy is the combined USFWS Recovery Plan/SSP Masterplan for the red wolf. Much of the captive propagation of red wolves has occurred at a special facility in Washington state, but there is also a growing number of zoos providing captive habitat, especially institutions within the historical range of the red wolf.

Another eminent example of a conservation and recovery strategy incorporating both captive and wild populations is the black-footed ferret. This species now evidently survives only in captivity. Because the decision to establish a captive population was delayed, the situation became so critical that moving all the animals into captivity seemed the only option, circumstances that also applied to the California condor. Another option may have been available if action to establish a captive population had occurred earlier as was done with the Puerto Rican parrot and plain pigeon. Consideration of the survivorship pattern, which exhibited high juvenile mortality for ferrets, as it does for many mammals and birds, suggested that young animals destined to die in the wild might be removed with little or no impact on the population. The AAZPA and CBSG/SSC/IUCN are involved in these kinds of strategies and programs worldwide.

Population Viability Analysis (R. C. Lacy)

Many wildlife populations that were once large, continuous, and diverse have been reduced to small, fragmented isolates in remaining natural areas, nature preserves, or even zoos. For example, black rhinos once numbered in the 100s of thousands, occupying much of Africa south of the Sahara; now a few thousand survive in a handful of parks and reserves, each supporting a few to at most a few hundred animals. Similarly, the Puerto Rican parrot, the only psittacine native to Puerto Rico, was formerly widespread on the island and numbered perhaps a million birds. By 1972 the species was reduced to just 20 birds (4 in captivity). Intensive efforts since have accomplished a steady recovery to 46 captive and 34 wild birds at the end of 1988. In 1989, the Luquillo forest which is home to both the captive and wild flocks of Puerto Rican parrots was severely damaged by a hurricane. Apparently about half of the wild parrots were killed, most of the traditional nest trees were destroyed, the food supply was decimated, and it is unlikely that a viable population remains in the wild.

When populations become small and isolated from any and all other conspecifics, they face a number of demographic and genetic risks to survival: in particular, chance events such as the occurrence and timing of disease outbreaks, random fluctuations in the sex ratio of offspring,

and even the randomness of Mendelian gene transmission can become more important than whether the population has sufficient habitat to persist, is well adapted to that habitat, and has an average birth rate that exceeds the mean death rate. Unfortunately, the genetic and demographic processes that come into play when a population becomes small and isolated feed back on each other to create what has been aptly but depressingly described as an "extinction vortex". The genetic problems of inbreeding depression and lack of adaptability can cause a small population to become even smaller --which in turn worsens the uncertainty of finding a mate and reproducing -- leading to further decline in numbers and thus more inbreeding and loss of genetic diversity. The population spirals down toward extinction at an ever accelerated pace. The size below which a population is likely to get sucked into the extinction vortex has been called the Minimum Viable Population size (or MVP).

The final extinction of a population usually is probabilistic, resulting from one or a few years of bad luck, even if the causes of the original decline were quite deterministic processes such as over-hunting and habitat destruction. Recently, techniques have been developed to permit the systematic examination of many of the demographic and genetic processes that put small, isolated populations at risk. By a combination of analytic and simulation techniques, the probability of a population persisting a specified time into the future can be estimated: a process called Population Viability Analysis (PVA) (Soule 1987). Because we still do not incorporate all factors into the analytic and simulation models (and we do not know how important the factors we ignore may be), the results of PVAs almost certainly underestimate the true probabilities of population extinction.

The value of a PVA comes not from the crude estimates of extinction probability, but rather from identification of the relative importance of the factors that put a population at risk and assessment of the value (in terms of increased probability of population persistence) of various possible management actions. That few species recognized as Endangered have recovered adequately to be delisted and some have gone extinct in spite of protection and recovery efforts attests to the acute risks faced by small populations and to the need for a more intensive, systematic approach to recovery planning utilizing whatever human, analytical, biological, and economic resources are available.

Genetic Processes in Small and Fragmented Populations

Random events dominate genetic and evolutionary change when the size of an interbreeding population is on the order of 10s or 100s (rather than 1000s or more). In the absence of selection, each generation is a random genetic sample of the previous generation. When this sample is small, the frequencies of genetic variants (alleles) can shift markedly from one generation to the next by chance, and variants can be lost entirely from the population -- a process referred to as "genetic drift". Genetic drift is cumulative. There is no tendency for allele frequencies to return to earlier states (though they may do so by chance), and a lost variant cannot be recovered, except by the reintroduction of the variant to the population through

mutation or immigration from another population. Mutation is such a rare event (on the order of one in a million for any given gene) that it plays virtually no role in small populations over time scales of human concern (Lacy 1987a). The restoration of variation by immigration is only possible if other populations exist to serve as sources of genetic material.

Genetic drift, being a random process, is also non-adaptive. In populations of less than 100 breeders, drift overwhelms the effects of all but the strongest selection: Adaptive alleles can be lost by drift, with the fixation of deleterious variants (genetic defects) in the population. For example, the prevalence of cryptorchidism (failure of one or both testicles to descend) in the Key deer (*Felis concolor coryi*) is probably the result of a strongly deleterious allele that has become common, by chance, in the population; and a kinked tail is probably a mildly deleterious (or at best neutral) trait that has become almost fixed within the Key deer.

A concomitant of genetic drift in small populations is inbreeding -- mating between genetic relatives. When numbers of breeding animals become very low, inbreeding becomes inevitable and common. Inbred animals often have a higher rate of birth defects, slower growth, higher mortality, and lower fecundity ("inbreeding depression"). Inbreeding depression has been well documented in laboratory and domesticated stocks (Falconer 1981), zoo populations (Ralls et al. 1979, Ralls and Ballou 1983, Ralls et al. 1988), and a few wild populations. The male-biased sex ratio of Key deer fawns may be a consequence of inbreeding, as might the low rate of twinning.

Inbreeding depression probably results primarily from the expression of rare, deleterious alleles. Most populations contain a number of recessive deleterious alleles (the "genetic load" of the population) whose effects are usually masked because few individuals in a randomly breeding population would receive two copies of (are "homozygous" for) a harmful allele. Because their parents are related and share genes in common, inbred animals have much higher probabilities of being homozygous for rare alleles. If selection were efficient at removing deleterious traits from small populations, progressively inbred populations would become purged of their genetic load and further inbreeding would be of little consequence. Because random drift is so much stronger than selection in very small populations, even decidedly harmful traits can become common (e.g., cryptorchidism in the Florida panther, biased sex ratio in the Key deer) and inbreeding depression can drive a population to extinction.

The loss of genetic diversity that occurs as variants are lost through genetic drift has other, long-term consequences. As a population becomes increasingly homogeneous, it becomes increasingly susceptible to disease, new predators, changing climate, or any environmental change. Selection cannot favor the more adaptive types when all are identical and none are sufficiently adaptive. Every extinction is, in a sense, the failure of a population to adapt quickly enough to a changing environment.

To avoid the immediate effects of inbreeding and the long-term losses of genetic variability a population must remain large, or at least pass through phases of small numbers ("bottlenecks") in just one or a few generations. Because of the long generation times of the

Puerto Rican parrot, the present bottleneck has existed for just one or two generations, and could be exited (successfully, we hope) before another generation passes and further genetic decay occurs. The Florida Key deer has evidently been in a bottleneck for thousands of years, perhaps 2-3 thousand generations. Although we cannot predict which genetic variants will be lost from any given population (that is the nature of random drift), we can specify the expected average rate of loss. Figure 5 shows the mean fate of genetic variation in randomly breeding populations of various sizes. The average rate of loss of genetic variance (when measured by heterozygosity, additive variance in quantitative traits, or the binomial variance in allelic frequencies) declines by drift according to:

$$V_g(t) = V_g(0) \times (1 - 1/(2N_e))^t,$$

in which V_g is the genetic variance at generation t , and N_e is the effective population size (see below) or approximately the number of breeders in a randomly breeding population. As shown in Figure 6, the variance in the rate of loss among genes and among different populations is quite large: some populations may (by chance) do considerably better or worse than the averages shown the Figure 5.

The rate of loss of genetic variation considered acceptable for a population of concern depends on the relationship between fitness and genetic variation in the population, the decrease in fitness considered to be acceptable, and the value placed by humans on the conservation of natural variation within wildlife populations. Over the short-term, a 1% decrease in genetic variance (or heterozygosity), which corresponds to a 1% increment in the inbreeding coefficient, has been observed to cause about a 1-2% decrease in aspects of fitness (fecundity, survival) measured in a variety of animal populations (Falconer 1981). Appropriately, domesticated animal breeders usually accept inbreeding of less than 1% per generation as unlikely to cause serious detriment. The relationship between fitness and inbreeding is highly variable among species and even among populations of a species, however. A few highly inbred populations survive and reproduce well (e.g., northern elephant seals, Pere David's deer, European bison), while attempts to inbreed many other populations have resulted in the extinction of most or all inbred lines (Falconer 1981).

Concern over the loss of genetic adaptability has led to a recommendation that management programs for endangered taxa aim for the retention of at least 90% of the genetic variance present in ancestral populations (Foose et al. 1986). The adaptive response of a population to selection is proportional to the genetic variance in the traits selected, so the 90% goal would conserve a population capable of adapting at 90% the rate of the ancestral population. Over a timescale of 100 years or more, for a medium-sized vertebrate with a generation time of 5 years such a goal would imply an average loss of 0.5% of the genetic variation per generation, or a randomly breeding population of about 100 breeding age individuals.

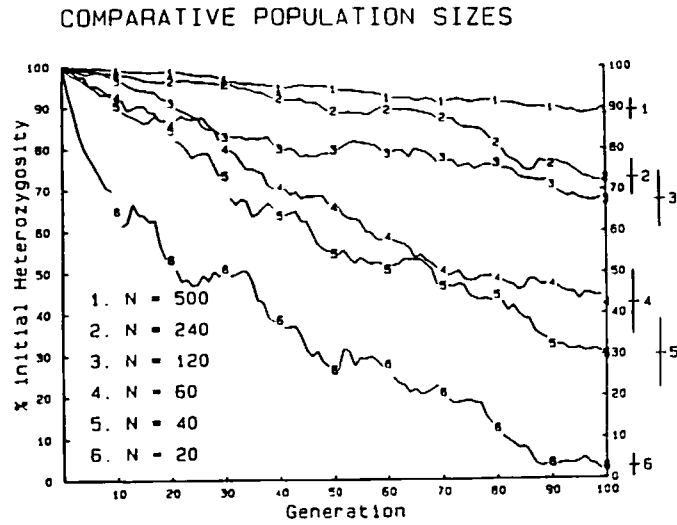


Figure 5. The average losses of genetic variation (measured by heterozygosity or additive genetic variation) due to genetic drift in 25 computer-simulated populations of 20, 50, 100, 250, and 500 randomly breeding individuals. Figure from Lacy 1987a.

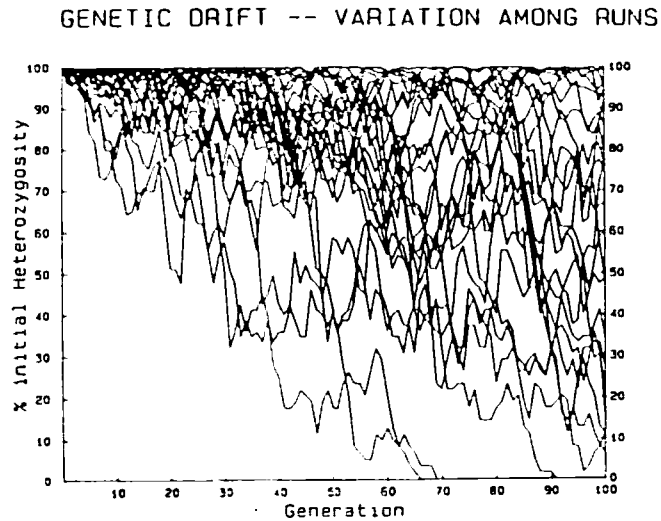


Figure 6. The losses of heterozygosity at a genetic locus in 25 populations of 120 randomly breeding individuals, simulated by computer. Figure from Lacy 1987a.

Most populations, whether natural, reintroduced, or captive, are founded by a small number of individuals, usually many fewer than the ultimate carrying capacity. Genetic drift can be especially rapid during this initial bottleneck (the "founder effect"), as it is whenever a population is at very low size. To minimize the genetic losses from the founder effect, managed populations should be started with 20 to 30 founders, and the population should be expanded to carrying capacity as rapidly as possible (Foose et al. 1986, Lacy 1988, 1989). With twenty reproductive founders, the initial population

would contain approximately 97.5% of the genetic variance present in the source population from which the founders came. The rate of further loss would decline from 2.5% per generation as the population increased in numbers. Because of the rapid losses of variability during the founding bottleneck, the ultimate carrying capacity of a managed population may have to be set substantially higher than the 100 breeding individuals given above in order to keep the total genetic losses below 90% (or whatever goal is chosen).

The above equations, graphs, and calculations all assume that the population is breeding randomly. Yet breeding is random in few if any natural populations. The "effective population size" is defined as that size of a randomly breeding population (one in which gamete union is at random) which would lose genetic variation by drift at the same rate as does the population of concern. An unequal sex ratio of breeding animals, greater than random variance in lifetime reproduction, and fluctuating population sizes all cause more rapid loss of variation than would occur in a randomly breeding population, and thus depress the effective population size. If the appropriate variables can be measured, then the impact of each factor on N_e can be calculated from standard population genetic formulae (Crow and Kimura 1970, Lande and Barrowclough 1987). For many vertebrates, breeding is approximately at random among those animals that reach reproductive age and enter the breeding population. To a first approximation, therefore, the effective population size can be estimated as the number of breeders each generation. In managed captive populations (with relatively low mortality rates, and stable numbers), effective population sizes are often 1/4 to 1/2 the census population. In wild populations (in which many animals die before they reach reproductive age), N_e/N probably rarely exceeds this range and often is an order of magnitude less.

The population size required to minimize genetic losses in a medium sized animal, therefore, might be estimated to be on the order of $N_e = 100$, as described above, with $N = 200$ to 400. More precise estimates can and should be determined for any population of management concern from the life history characteristics of the population, the expected losses during the founding bottleneck, the genetic goals of the management plan, and the timescale of management.

Although the fate of any one small population is likely to be extinction within a moderate number of generations, populations are not necessarily completely isolated from conspecifics. Most species distributions can be described as "metapopulations", consisting of a number of partially isolated populations, within each of which mating is nearly random. Dispersal between populations can slow genetic losses due to drift, can augment numbers following population decline, and ultimately can recolonize habitat vacant after local extinction.

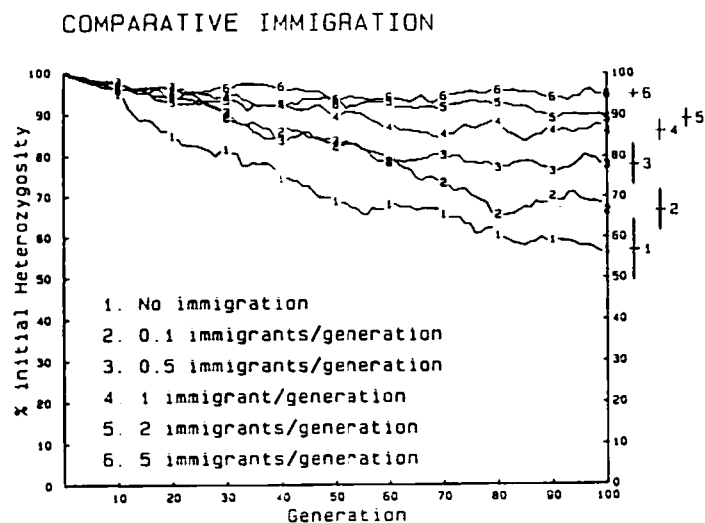


Figure 7. The effect of immigration from a large source population into a population of 120 breeding individuals. Each line represents the mean heterozygosity of 25 computer-simulated populations (or, equivalently, the mean heterozygosity across 25 non-linked genetic loci in a single population). Standard error bars for the final levels of heterozygosity are given at the right. Figure from Lacy 1987a.

If a very large population exists that can serve as a continued source of genetic material for a small isolate, even very occasional immigration (on the order of 1 per generation) can prevent the isolated subpopulation from losing substantial genetic variation (Figure 7). Often no source population exists of sufficient size to escape the effects of drift, but rather the metapopulation is divided into a number of small isolates with each subjected to considerable stochastic forces. Genetic variability is lost from within each subpopulation, but as different variants are lost by chance from different subpopulations the metapopulation can retain much of the initial genetic variability (Figure 8). Even a little genetic interchange between the subpopulations (on the order of 1 migrant per generation) will maintain variability within each subpopulation, by reintroducing genetic variants that are lost by drift (Figure 9). Because of the effectiveness of even low levels of migration at countering the effects of drift, the absolute isolation of a small population would have a very major impact on its genetic viability (and also, likely, its demographic stability). Population genetic theory makes it clear that no small, totally isolated population is likely to persist for long.

A. ABSOLUTE SUBDIVISION

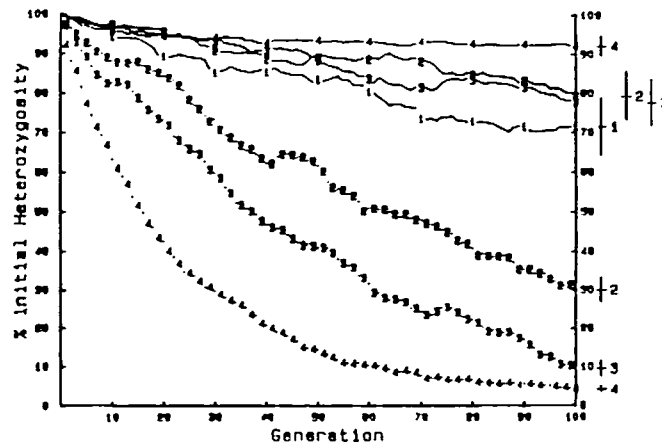


Figure 8. The effect of division of a population of 120 breeders into 1, 3, 5, or 10 isolated subpopulations. Dotted lines (numbers) indicate the mean within-subpopulation heterozygosities from 25 computer simulations. Lines represent the total gene diversity within the simulated metapopulation. Figure from Lacy 1987a.

MIGRATION AMONG 5 SUBPOPULATIONS

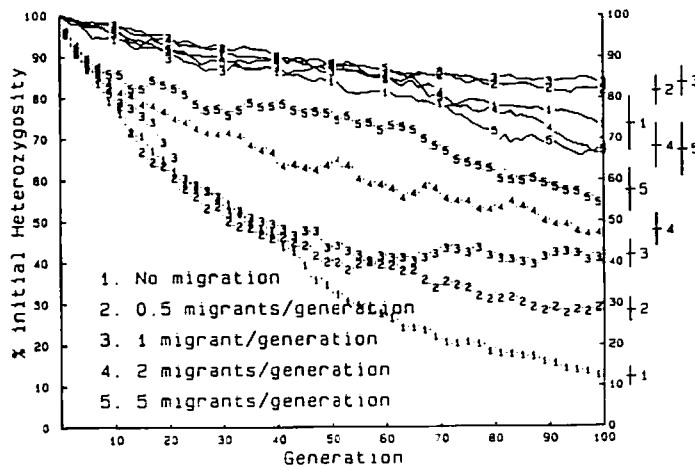


Figure 9. The effect of migration among 5 subpopulations of a population of 120 breeders. Dotted lines (numbers) indicate the mean within-subpopulation heterozygosities from 25 simulations. Lines represent the total gene diversity within the metapopulation. Figure from Lacy 1987a.

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