# Introduction to Conservation Genetics

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Cambridge & New York

CAMBRIDGE
UNIVERSITY PRESS

2002

pp. xxi, 617

In their classic study, Bonnell & Selander (1974) showed that this bottlenecked population had no genetic diversity at 20 allozyme loci, while the related southern elephant seal had normal levels of genetic diversity. Subsequently, Hoelzel et al. (1993) found that the northern elephant seal had only two mtDNA variants compared to 23 in southern elephant seals.

Following protection from hunting, the northern elephant seal has recovered to numbers of over 100000 and it has been removed from the endangered species list. This demonstrates that a population size bottleneck does not necessarily doom a species to immediate extinction. However, the loss of genetic diversity is likely to make it more prone to extinction from new diseases or other environmental changes. Further, the population will be partially inbred (Chapter 11), and is likely to have reduced reproductive fitness as a consequence (Chapter 12). An important feature of such bottleneck events is the large chance element in the outcome. Some situations will be relatively harmless if few deleterious mutations are, by chance, present in the remaining population. In other cases, populations are not so lucky: deleterious mutations are fixed and they decline to extinction.

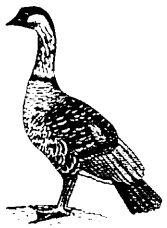


**Table 8.1** Bottlenecks in endangered species (numbers of founders breeding in captivity)

| Species | Bottleneck size | Reference |
|---|---|---|
| *Mammals* | | |
| Arabian oryx | 10 | 1 |
| Black-footed ferret | 10 | 2 |
| European bison | 13 | 3 |
| Indian rhinoceros | 17 | 3 |
| Pere David's deer | 5 | 4 |
| Przewalski's horse | 12 (11 domestic mare) | 5 |
| Red ruffed lemur | 7 | 5 |
| Siberian tiger | 25 | 3 |
| *Birds* | | |
| California condor | 14 (3 clans) | 6 |
| Chatham Island black robin | 5 | 7 |
| Guam rail | 12 | 8 |
| Mauritius kestrel | 2 | 9 |
| Mauritius pink pigeon | 6 | 10 |
| Nene (Hawaiian goose) | 17 | 11 |
| Puerto Rican parrot | 13 | 12 |
| Whooping crane | 14 | 13 |

*References*: 1, Marshall et al. (1999); 2, Russell et al. (1994); 3, Hedrick (1992); 4, Balbar (1985); 5, Hedrick & Miller (1992); 6, Geyer et al. (1993); 7, Ardern & Lambert (1997); 8, Haig et al. (1994); 9, Groombridge et al. (2000); 10, Wayne et al. (1994); 11, Rave et al. (1994); 12, Brock & White (1992); 13, Glenn et al. (1999)



The impact of single pair bottlenecks on allele frequencies in experimental populations of fruit flies is shown in Fig. 8.5. Note the loss of alleles, particularly of rare alleles. Allele frequencies have changed from those in the parent population. Replicate bottlenecked populations varied in the allele they lost and in the frequencies of the alleles that remained. On average, heterozygosity dropped from 0.61 in the base population to 0.44 in the bottlenecked populations, and the number of alleles from 6.7 to 2.4. Note that the cumulative effects of $N_e = 100$ over 57 generations has resulted in a similar loss of genetic diversity. In what follows we present the theory relating to the effects of single generation population bottlenecks, while the effects of sustained small population size are deferred until Chapter 10.

Population bottlenecks result in loss of alleles (especially rare ones), reduced genetic diversity and random changes in allele frequencies.

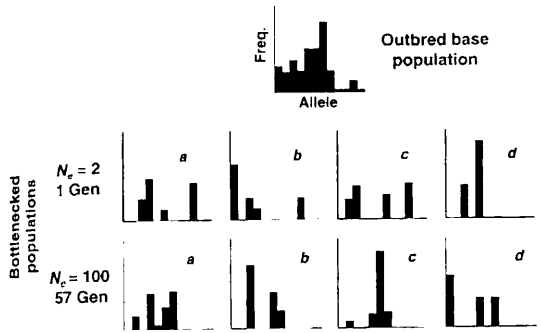



**Fig. 8.5** Effect of single pair population bottlenecks on experimental populations of fruit flies (England 1997). The distribution of allele frequencies at a microsatellite locus is shown in the large outbred base population, in four replicate populations subjected to a bottleneck of one pair of flies, and in four populations maintained at $N_e = 100$ for 57 generations. *Alleles are lost, especially rare ones, and allele frequencies distorted in the bottlenecked populations.*

The impact of a bottleneck on heterozygosity is simplest to derive for a single pair bottleneck (Table 8.2). From that we can generalize to larger sized bottlenecks. Following a single pair bottleneck heterozygosity is reduced from $2pq$ to $1.5pq$, a decline of 25%. In general, the proportion of initial heterozygosity retained after a single generation bottleneck is

$$H_1 / H_0 = 1 \quad (1/2N) \tag{8.2}$$

where $H_1$ is the heterozygosity immediately after the bottleneck, and $H_0$ that before. Upon rearrangement we obtain an expression for the change in heterozygosity between the two generations ($\Delta H$):

$$\Delta H = H_1 - H_0 = -(1/2N) H_0 \tag{8.3}$$

A proportion $1/(2N)$ of the original heterozygosity is lost. Thus, single generation bottlenecks have to be severe before they have a substantial impact on heterozygosity. A bottleneck of $N = 25$ only reduces heterozygosity by 2%, while a bottleneck of 100 reduces it by only 0.5%. Loss of genetic diversity arises predominantly from sustained reductions in population size, rather than single generation bottlenecks (Chapter 10).

The impact of a bottleneck on allelic diversity is often greater, although correlated. Overall, the number of alleles ($A$) retained following a single generation bottleneck is

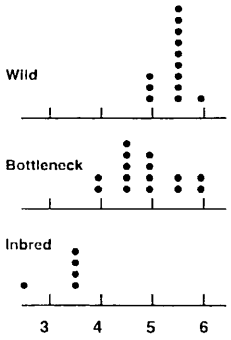



**Fig. 8.6** Effects of population bottlenecks on evolutionary potential in fruit flies (Frankham *et al.* 1999). Populations were subjected to a single pair bottleneck for one generation. These populations, their base population and highly inbred (homozygous) populations from the same stock were all increased to the same population size, placed in cages and subjected to a regime of increasing concentrations of NaCl until extinction. Extinction concentrations for the three treatments are plotted. *Evolutionary potential was significantly reduced in the bottlenecked populations and they were more variable than the base population.*

**Table 8.2** Effect on heterozygosity of a single pair, single generation bottleneck. The heterozygosities given are the Hardy–Weinberg equilibrium $H_e$ following the single pair bottleneck. The base population has two alleles $A_1$ and $A_2$ at frequencies $p$ and $q$, respectively (and a heterozygosity of $2pq$)

| Possible alleles in samples of two individuals | Frequency ($f$) | Heterozygosity ($H_e$) | $f \times H_e$ |
|---|---|---|---|
| 4 $A_1$ | $p^4$ | 0 | 0 |
| 3 $A_1$ : 1 $A_2$ | $4p^3q$ | 0.375 | $1.5p^3q$ |
| 2 $A_1$ : 2 $A_2$ | $6p^2q^2$ | 0.5 | $3p^2q^2$ |
| 1 $A_1$ : 3 $A_2$ | $4pq^3$ | 0.375 | $1.5pq^3$ |
| 4 $A_2$ | $q^4$ | 0 | 0 |
| Total | 1 | | $1.5pq\,(p^2 + 2pq + q^2)$ $= 1.5pq$ |

Mean heterozygosity in bottlenecked populations: $H_1 = 1.5pq$

Consequently, $H_1 / H_0 = 1.5pq / 2pq = 0.75 = [1 - (1/2N)]$

Thus a single pair bottleneck, on average, reduces heterozygosity by 25% of the initial value.

$$A = n - \sum_{i=1}^{\text{No. of alleles}} (1 - p_i)^{2N} \qquad (8.4)$$

where $n$ is the number of alleles before the bottleneck and $p_i$ is the frequency of the $i$th allele. The sigma term is the number of alleles lost.

Loss of heterozygosity and allelic diversity in the bottlenecked fruit fly populations (Fig. 8.5) are close to those expected from the theory above. For example, the heterozygosity was predicted to fall from 0.61 to $0.61 \times (1 - \frac{1}{4}) = 0.45$ in the bottlenecked populations. The observed change was to 0.44. In the Mauritius kestrel, heterozygosity declined 57% from 0.23 to 0.10 as a result of single pair bottleneck (Box 8.1). This was greater than expected from a single pair bottleneck. However, the population suffered several generations of bottlenecks. Additional genetic diversity would have been lost during the six generations it spent at sizes of less than 50.

Many threatened wildlife populations show evidence of loss of genetic diversity due to population size bottlenecks (Chapter 3). For example, polymorphism is significantly reduced in artiodactyls (swine, hippopotamus, ruminants, deer and bison) that have suffered known bottlenecks (Hartl & Pucek 1994). In contrast, the Indian rhinoceros in Chitwan, Nepal has gone through a recent bottleneck of 60–80 individuals but retains a high level of genetic diversity (9.9% heterozygosity for allozymes; Dinerstein & McCracken 1990). Such a bottleneck is too large to generate any detectable reduction in heterozygosity within a few generations (see Problem 8.5).



## Effect of population bottlenecks on quantitative genetic diversity

Population size bottlenecks reduce evolutionary potential

For quantitative characters showing only additive genetic variation, the expected loss of quantitative genetic variation due to a bottleneck is also a $1/(2N)$ proportional reduction in variation. This expectation has been verified in several selection experiments in fruit flies (Frankham 1980). The situation is more complex for characters exhibiting non-additive genetic variation, as bottlenecks can actually increase additive genetic variation due to increased homozygosity for rare recessive alleles (Robertson 1952). Increases in additive genetic variation in bottlenecked population for characters exhibiting non-additive variation have been reported by Bryant *et al.* (1986) and by Lopez-Fanjul & Villaverde (1989), but their relevance to evolutionary potential is questionable as the mean values for the characters dropped due to the inbreeding involved. A direct test of the impact of population bottlenecks on evolutionary potential in fruit flies found clear reductions due to the bottleneck (Fig. 8.6). The bottlenecked populations also showed a greater variance in evolutionary potential among populations than did the outbred controls (see also Whitlock & Fowler 1999).

## Inbreeding

Inbreeding is unavoidable in small populations and leads to reductions in reproduction and survival

In small populations, matings among relatives (inbreeding) is inevitable. With time, every individual becomes related so that no matings between unrelated individuals are possible. This is illustrated in the Mexican wolf pedigree (Fig. 8.7). Every individual beyond the third generation has parents that are related, i.e. they are all inbred. This is not a result of deliberate mating of relatives, it is simply a consequence of the small number of founders and the small population size. Inbreeding also becomes inevitable in larger populations, but it takes longer. For example, a population of size 100 over 57 generations becomes, on average, as inbred as the progeny of a brother–sister mating (Chapter 10).

Inbreeding is of profound importance in conservation biology as it leads to reductions in heterozygosity, to reduced reproduction and survival (inbreeding depression) and to increased risk of extinction (Chapter 2, 11 and 12).

## Measuring population size

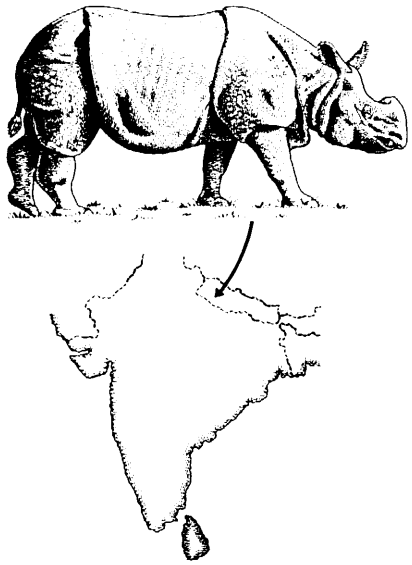
Natural populations have many different structures and breeding systems that have different genetic consequences. For example, some populations of small mammals fluctuate wildly in size. Further, species vary in mating system (e.g. monogamy, harems), and from approximately random mating to selfing and asexual reproduction. The same

Chapter 14

# Genetically viable populations

**Terms:**
Minimum viable population size (MVP).
mutational meltdown

As resources for threatened species are limited, it is important to define the minimum size needed to retain genetic 'health.' To avoid inbreeding depression and retain fitness in the short-term $N_e > 50$ is required. For threatened species to permanently retain their evolutionary potential $N_e$ of 500–5,000 is required. Current sizes of threatened species are typically too small to avoid genetic deterioration



Endangered Indian one-horned rhinoceros.



## Shortage of space for threatened species

There is a severe shortage of space for threatened species, both in wild reserves and in captivity

Habitat loss is equivalent to loss of living space for threatened species. Substantial proportions of mammals (56%), birds (53%), reptiles (62%), amphibians (64%), fish (56%), gymnosperms (32%) and angiosperms (9%) are threatened, largely through this reduction (Chapter 1). The financial and physical resources required to conserve them are enormous. Providing reserves, such as national parks, is costly, and often conflicts with human demands for increased land use. Captive breeding programs have been suggested as a partial solution. However, there is also a shortage of resources for this strategy. About 2000 endangered vertebrate species require captive breeding, but space exists for only about 800 species (Tudge 1995). Pragmatic decisions must be made in allocating scarce breeding spaces. Retention of too few individuals will lead to the deleterious genetic effects we have discussed, and ultimately jeopardize the outcome of programs. Conversely, allocating too many resources to one species will be at the expense of others, for which no space will be available.

Consequently, there is an urgent need to define the minimum population size required for species to be viable in the long term. This chapter addresses the question: 'How large must populations be, to be genetically viable?' This issue has been discussed under the title of minimum viable population size (MVP), yet the population sizes are not necessarily minimum, nor viable. Rather, we are considering the minimum size required to maintain a population that suffers no reduction in reproductive fitness or evolutionary potential over thousands of years. This does not signify that populations of lesser size have no future, only that their reproductive fitness and evolutionary potential are likely to be compromised, and they have an increased risk of extinction. As Soulé (1987) noted 'there are no hopeless cases, only people without hope and expensive cases.'

For a particular population or species, the question above reduces to:

- Is the population size large enough to avoid loss of reproductive fitness?
- Does the species have enough genetic diversity to evolve in response to environmental change?

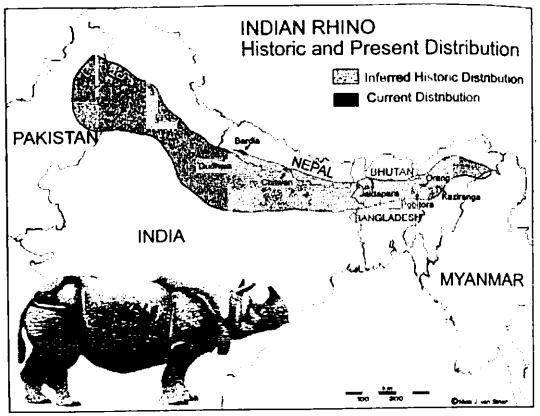
These questions are illustrated for the endangered Indian rhinoceros and the northern elephant seal in Box 14.1.

### Box 14.1 Is the species genetically viable in the medium to long term?

IS THE RHINOCEROS POPULATION SIZE LARGE ENOUGH?

The Indian one-horned rhinoceros, like many wildlife populations, numbered many hundreds of thousands. With habitat reduction and fragmentation and poaching for

[illegible] numbers have been reduced to about 2,000 individuals [illegible] graphically illustrate [illegible] the figure and its [illegible] Rhino Fund personal communication). The species has [illegible] genetic diversity (Dinerstein & McCracken 1990). The largest population [illegible] and the smallest [illegible] for the entire species, are there sufficient individuals to avoid extinction due to inbreeding and compromised ability to undergo adaptive evolutionary change? Regrettably, the arguments presented in this chapter lead us to anticipate that the one-horned rhinoceros will undergo slow genetic deterioration in the long term.




| Area | Population size (1999) |
|---|---|
| *Areas with large populations* | |
| Kaziranga (India, Assam) | ~ 1800 |
| Chitwan (Nepal) | ~ 600 |
| *Areas with smaller populations* | |
| Pobitora (India, Assam) | 76 |
| Dudhwa/Bardia (Nepal/India) | 72 |
| Jaldapara (India, W. Bengal) | 53 |
| Orang (India, Assam) | 46 |
| Gorumia (India, W. Bengal) | 19 |
| Mamas (India, Assam) | ~ 5 |
| *Total* | 2175–2225 |

DOES THE NORTHERN ELEPHANT SEAL HAVE ENOUGH GENETIC DIVERSITY?
The northern elephant seal underwent a population size bottleneck of about 20–30 individuals, but has since recovered to well over 100 000 individuals and is no longer [illegible] endangered. However it displays no allozyme genetic diversity (Bonnell & Selander 1974, Hoelzel *et al.* 1993) and only two mtDNA haplotypes (compared to 23 in related southern elephant seals). Many other threatened species lack genetic diversity (Chapter 3). Are these species doomed to extinction? Below we will see that such species are likely to have compromised ability to evolve in response to environmental change and thus increased extinction risk. However, they are not predicted to become extinct in the near future, unless they experience an unexpected catastrophe (e.g. a new disease).

## How large?

How large do populations need to be to ensure their genetic 'health'? This involves three critical genetic goals:

- Retaining reproductive fitness by avoiding inbreeding depression
- Retaining the ability to evolve in response to changes in the environment (evolutionary potential)
- Avoiding the accumulation of new deleterious mutations.

Various predictions of population sizes required to achieve these goals are given in Table 14.1. We consider each of these issues below.

Table 14.1 | How large must populations be to retain genetic 'health'? Various estimates of the required effective population size ($N_e$) are given. The times to recover normal levels of genetic diversity following complete loss of diversity are also given in generations

| Goal | $N_e$ | Recovery time (generations) | Reference |
|---|---|---|---|
| Retain reproductive fitness | 50 | | 1, 2 |
| Retain evolutionary potential | 500 | $10^3$–$10^4$ | 1, 3 |
| | 5000 | | 4 |
| | 570–1250 | | 5 |
| Retain single locus genetic diversity | $10^2$–$10^3$ | $10^2$–$10^3$ | 3 |
| Avoid accumulating deleterious mutations | 1000 | | 4 |
| | 100 | | 6 |
| | 12 | | 7 |

References: 1, Franklin (1980); 2, Soulé (1980); 3, Lande & Barrowclough (1987); 4, Lande (1995a); 5, Franklin & Frankham (1998); 6, Lynch *et al.* (1995); 7, Charlesworth *et al.* (1993).

## Retaining reproductive fitness

Small populations of naturally outbreeding species become inbred and suffer reductions in reproductive fitness (Chapter 12). What amount of inbreeding can be tolerated without significant inbreeding depression?

No finite population is immune from eventual inbreeding depression

Franklin (1980) and Soulé (1980) both suggested that an effective population size of 50 was sufficient to avoid inbreeding depression in the short term, based on the experience of animal breeders.

Is there a population size that is immune from inbreeding depression? Since inbreeding increases at a rate of $1/2N_e$ per generation, all finite closed populations eventually become inbred. Further, as inbreeding depression is linearly related to the inbreeding coefficient (Chapter 12), there is no threshold below which inbreeding is not deleterious. Even low levels of inbreeding are expected to result in some low level of inbreeding depression. Based upon the median number of lethal equivalents of 3.14, as found in captive mammals (Ralls *et al.* 1988), we would expect about 2% inbreeding depression when $F = 0.005$, 4% when $F = 0.01$, and 15% when $F = 0.05$ for juvenile survival alone.

An effective size of 50, suggested by Franklin and Soulé, corresponds to an increase in inbreeding coefficient of 1% per generation. The context of their predictions was that over a period of perhaps 5–10 generations, there would be little detectable inbreeding depression when the $N_e$ was 50. However, little relevant data were available at the time of their predictions.

Populations with effective sizes of 50 in fruit flies and 90 in houseflies show inbreeding depression

Subsequently, inbreeding depression was described in fruit fly populations maintained at effective sizes of about 50 for 210 generations. One-quarter of the populations became extinct (Latter *et al.* 1995). Inbreeding depression was also evident in fruit fly populations maintained with effective sizes of 50, or less, for 50 generations (Fig. 14.1). In housefly populations inbreeding depression was evident in populations with $N_e = 50$ after 12 generations, and even in those of $N_e = 90$ after only five generations (Bryant *et al.* 1999; Reed & Bryant 2000).

We do not know precisely how large populations must be to avoid meaningful inbreeding depression in the long term, but the required size is clearly much greater than an effective size of 50. Disturbingly, about one-half of all captive populations of threatened mammals have $N$ of less than 50 (Magin *et al.* 1994), and are likely to suffer inbreeding depression relatively soon.

At what point will inbreeding become sufficient to cause extinctions? Estimated times to extinction for different sized housefly populations approximated the effective size in generations, i.e. 480 generations for $N_e = 500$, 80 for $N_e = 87$, 54 for $N_e = 50$ and 32 for $N_e = 15$ (Reed & Bryant 2000). Extinction risks in rapidly inbred populations of mice and fruit flies increase markedly at $F = 0.5$ and beyond (Fig. 12.2). $F$ values for the housefly populations at extinction were 0.38 to 0.66, consistent with the fruit fly data.

In practice, wild populations that were listed as endangered in 1985–91 numbered 100–1000 individuals (Wilcove *et al.* 1993). Similarly, the IUCN scheme for categorization of extinction risk lists 50, 250 and 1000 adults as cut-offs for the critically endangered, endangered and vulnerable categories (IUCN 1996). Since $N_e/N$ ratios are about 0.1, many of these populations will have effective sizes of 50 or less and are at risk of extinction from inbreeding depression (without considering other factors) unless their sizes are substantially increased.



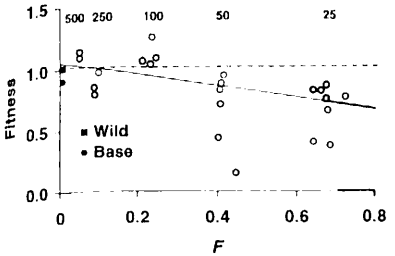



**Fig. 14.1** How large must populations be to avoid inbreeding depression? Reproductive fitness of populations of fruit flies maintained for 50 generations with different effective sizes (numbers at the top of the figure), compared to the wild population from which they were founded (after Woodworth 1996). There is a significant regression of fitness on inbreeding coefficient, $F$, as indicated by the fitted line. *All populations with sizes of 50 or less had lower fitness than the wild population (dotted line).*

## Retaining evolutionary potential

Effective population sizes of 500–5000 have been suggested as necessary to maintain evolutionary potential

Since our objective is conservation of species as dynamic entities capable of evolving to cope with environmental change, evolutionary potential must be retained. While there is a range of estimates of the size of populations required, there is general agreement that it is an $N_e$ of at least 500 (Table 14.1). Since the debate about this issue has major implications for the genetic management of wild and captive populations, we consider the estimations in some detail.

In his classic paper, Franklin (1980) predicted that an effective size of 500 was required. He argued that additive genetic variation, rather than allelic diversity, determined evolutionary potential, and this is directly related to heterozygosity (Equation 5.3). Finally Franklin assumed that the level of additive genetic variation for peripheral characters at equilibrium was dependent on the balance between loss of quantitative genetic variation and its replenishment by mutation.

The $N_e$ required to balance additive genetic variation lost by drift and with that gained by mutation (under a neutral model), is obtained as follows:

$$\Delta V_A = V_m - V_A / 2N_e \qquad (14.1)$$

where $\Delta V_A$ is the change in additive genetic variation in one generation, $V_m$ the gain in genetic variation per generation due to mutation, and $V_A$ the additive genetic variation. The $V_A/2N_e$ term is the loss of additive genetic variation per generation due to drift. At equilibrium, $\Delta V_A = 0$, so

$$N_e = V_A / 2V_m \qquad (14.2)$$

Thus, the required population size depends upon the initial additive genetic variation and the rate at which it is regenerated by mutation.

Franklin (1980) noted that $V_m = 10^{-3} V_E$ for bristle characters in fruit flies (one of the few estimates of $V_m$ then available), where $V_E$ is the environmental variation for the quantitative character. Upon substituting this value into Equation 14.2, he estimated the required $N_e$ as

$$N_e = V_A / [2 \times 10^{-3} \times V_E] = 500 V_A / V_E \quad (14.3)$$

and since the heritability $h^2 = V_A / V_P = V_A / (V_A + V_E)$

$$N_e = 500 h^2 / (1 - h^2) \quad (14.4)$$

To obtain his estimate of $N_e$, Franklin (1980) assumed a heritability of 50%. This is a reasonable estimate of the heritability for peripheral characters (Table 5.3). Consequently, Franklin predicted that an effective size of 500 was required to retain additive genetic variation and long-term evolutionary potential.

Lande and Barrowclough (1987) reached a similar conclusion, based on a model involving an equilibrium between stabilizing selection, drift and mutation. However, Lande (1995a) later revised his estimate and suggested that a value of 5000 was required. He argued that only about 10% of newly generated mutations are useful for future genetic change because most newly arisen mutations are deleterious (based on data from Lopez & Lopez-Fanjul 1993). Since $V_m$ has been found to be approximately $10^{-3} V_E$ for a wide range of quantitative characters (Table 7.1), Lande adjusted for the deleterious mutations by using $V_m = 10^{-4} V_E$. Upon substituting this value into equation 14.2, he estimated $N_e$ as:

$$N_e = V_A / [2 \times 10^{-4} \times V_E] = 5000 h^2 / (1 - h^2) \quad (14.5)$$

Like Franklin (1980), Lande (1995a) also assumed a heritability of 50%. This yielded an estimate of 5000 to retain evolutionary potential.

Reservations have been expressed about this estimate (Frankham & Franklin 1998). First, estimates of $V_m = 10^{-3} V_E$ already include, in part, a correction for deleterious alleles. Some estimates are derived from long-term experiments, which provide the opportunity for unconditionally deleterious mutations to be eliminated, i.e. many of the 90% of deleterious mutations have already been excluded in obtaining the estimate.

Second, by introducing the issue of deleterious mutations, Lande was beginning to consider fitness, rather than peripheral characters. For these, heritabilities are often much less than 0.5 (see Tables 5.2 and 5.3). Heritabilities for fitness characters are typically 10%–20%, or less. If we use a heritability of 10%, and $V_m = 10^{-4} V_E$, then $N_e = 560$, and for a heritability of 20% is $N_e = 1250$ (Franklin & Frankham 1998).

Third, the effects of mutations depend on environmental conditions. Mutations that are deleterious in the current environment may be favourable under altered conditions in the future. For example, genetic adaptation to captivity in fruit flies seems to be due to rare alleles that are deleterious in the wild (Woodworth 1996). Since evolutionary potential is concerned with the capacity to adapt to environmental change, the genetic diversity that must be preserved may be deleterious, or neutral, in the current environment. We do not know what proportion of mutations are unconditionally deleterious versus those that are deleterious in some conditions and beneficial in others.

The calculations above are based on models that ignore natural selection, or do not consider it adequately. Reproductive fitness is the central character for evolutionary potential, as it is fitness that is involved in evolutionary change. The above expressions are of dubious validity when applied to reproductive fitness subject to directional natural selection. There is currently no theory allowing us to predict the equilibrium additive genetic variation under a model of mutation, drift and natural selection operating on reproductive fitness. The issue must be resolved empirically. Preliminary experimental estimates from fruit flies indicate that the effective population sizes required to retain evolutionary potential are from several hundred to several thousand (Gilligan 2001).

We should emphasise that estimates of the required $N_e$ are very approximate. There are uncertainties about mutational variances for reproductive fitness, and especially about the proportion of mutations that are deleterious (Keightley 1996). Further, the above estimates assume that heterozygosity determines evolutionary potential. Some authors argue that allelic diversity may be critical (Allendorf 1986; Fuerst & Maruyama 1986). For example, particular alleles may confer disease, pest or parasite resistance. If allelic diversity is important in determining evolutionary potential, the sizes required to preserve it (particularly for rare alleles) are much larger than those required to preserve heterozygosity (see below).

What population size is required to maintain evolutionary potential for wild populations in nature? Only very rarely is $N_e$ known for wild populations. Since comprehensive estimates of $N_e/N$ are about 0.1 (Chapter 10), census sizes in wild populations must be about one order of magnitude higher than the $N_e$ values we have calculated, i.e. 5000–50 000. This sets a lower limit for the minimum size to maintain long-term viability (Soulé 1987), and is within the range of values reached from consideration of other threats (Chapter 20).

Wild populations in nature require adult census sizes about 10 times larger than the $N_e$ values estimated above, i.e. several thousand to tens of thousands

## How large are threatened populations?

We have concluded that effective sizes of at least 500 and actual numbers of adult census sizes of at least 5000 are required to retain genetic diversity and to minimize inbreeding depression in perpetuity. However, we operate in a climate of severely restricted resources. The following section examines the population sizes being recommended in practical endangered species programs.

The population size criteria used by IUCN to define endangerment are well below the 5000 minimum required to retain long-term genetic health

The population size criteria used in the IUCN (1996) system for categorizing endangerment of species reflect the current scientific consensus on the relationship between population size and degree of endangerment (Chapter 1). Under this system, populations (species) are considered critically endangered, endangered, or vulnerable if populations sizes are less than 50, 250 or 1000 mature individuals, respectively. These

correspond to $N_e$ of about 5, 25 and 100 respectively, all within the range where inbreeding and loss of genetic diversity will undoubtedly occur over a relatively short period of time. These will certainly impact on the viability of populations within the time frames specified for the endangered IUCN categories (Table 1.3). For example, the critically endangered category refers to three generations. A critically endangered species with $N_e = 5$ would have an inbreeding coefficient in excess of that for full-sib mating after three generations and would suffer substantial inbreeding depression. An endangered species with $N_e = 25$ would have $F = 0.18$ after the 10-generation time frame specified by the IUCN.

Population sizes of endangered species are usually smaller than those required to meet genetic objectives

Actual census population sizes for a variety of endangered species are given in Table 14.2. Most of these have population sizes of less than 500 and, presumably, effective population sizes much less than this.

## What happens to species with $N_e < 500$?

Species with effective sizes of less than 500 are not doomed to extinction, but will become increasingly vulnerable with time, and have increased extinction risk

Species with effective sizes insufficient for long-term maintenance of genetic diversity are not doomed to immediate extinction. On average they will suffer depletion of genetic diversity and suffer reduced ability to evolve in response to novel environmental threats. They will slowly become inbred, with consequent reduction in reproduction and survival rates, and require increasing human intervention to ensure their survival. This may take the form of providing them with more benign environments (isolating them from competitors, avoiding introduction of diseases and improving their environment), or managing them to increase reproduction and survival.

## Reduced long-term evolutionary potential in endangered species

Endangered species have substantially compromised ability to evolve in response to environmental change, as long-term evolutionary potential depends on $N_e$ and reproduction rates, in addition to initial additive genetic variation

The long-term ability of populations to evolve is proportional to the effective population size, both for evolutionary change due to current genetic variation in the population and for changes due to new mutations. This dependence arises through the impact of drift on current genetic diversity and because more new mutations occur in larger populations. The combination of these effects puts a limit on the extent of adaptation to novel environmental conditions that can be wrought by natural selection. We now extend several of the concepts relating to quantitative genetic variation and selection response in small populations, first presented in Chapter 5 and 8.

For genetic variation from the initial population, the total response to selection in the long term ($R_{\text{limit}}$, the limit to selection) is predicted to be approximately (Robertson 1960)

$$R_{\text{limit}} = 2N_e S h^2 \qquad (14.6)$$

where $S$ = selection differential and $h^2$ = heritability (Chapter 5).



**Table 14.2** | Population sizes in the wild ($N$) and category of endangerment for a variety of threatened taxa. The categories are based primarily on the IUCN system and account for more than population size (Chapter 1)

| Species | Location | Category | $N$ | Reference |
|---|---|---|---|---|
| *Mammals* | | | | |
| Australian | Israel | I | 284 | 1 |
| Baiji dolphin | China | Cr E | 150 | 2 |
| Eastern barred bandicoot | Australia (mainland) | Cr E | 200 | 3 |
| Ethiopian wolf | Ethiopia | Cr E | 500 | 4 |
| Darwin's fox | Chile | E | 500 | 4 |
| Florida panther | USA | Cr E | 30–50 | 5 |
| Giant panda | China | E | 1000 | 6 |
| Golden lion tamarin | Brazil | Cr E | 400 (+200) | 7 |
| Humpback whale | Oceans | V | 6000 | 8 |
| Javan rhinoceros | Indonesia | Cr E | 60 | 9 |
| Javan rhinoceros (different sub-species) | Vietnam | Cr E | 5 | 9 |
| Northern hairy-nosed wombat | Australia | Cr E | 70 | 10 |
| Northern right whale | N. Oceans | E | 350 | 6 |
| Tana River crested mangabey | Kenya | E | 2000–15000 | 11 |
| *Birds* | | | | |
| Attwater's prairie chicken | USA | E (USA) | 42 | 12 |
| Bali starling | Indonesia | Cr E | 50 | 5 |
| Black stilt | New Zealand | Cr E | 70 | 13 |
| Kirtland's warbler | USA | V | 1350 | 14 |
| Lord Howe Island woodhen | Australia | E | 20–30 | 15 |
| | | E (NSW) | 210 | 15 |
| Mauritius pink pigeon | Mauritius | Cr E | 220 | 16 |
| Puerto Rican parrot | Puerto Rico | Cr E | 40 | 5 |
| Seychelles magpie robin | Seychelles | Cr E | 22 | 17 |
| Seychelles warbler | Seychelles | Cr E | 26 | 18 |
| | | V | 1500 | 18 |
| Red-cockaded woodpecker | USA | V (USA E) | 9270 | 19 |
| Whooping crane | N. America | E | 140 (+73) | 20 |
| *Reptiles* | | | | |
| Aruba Island rattlesnake | Caribbean | Cr E | 350 | 21 |
| Komodo dragon | Indonesia | V | 3000 | 22 |
| *Invertebrates* | | | | |
| Palos Verdes blue butterfly | California | E (USA) | 200 | 23 |
| *Plants* | | | | |
| Apalachicola rosemary | Florida | E | 5555 | 24 |
| *Bidens micrantha kalealana* | Hawaii | E | 2000 | 25 |
| Catalina mahogany | California | E | 6 | 27 |
| Conigan greenhood | Australia | E | 27 | 28 |
| Mauna Kea silversword | Hawaii | L | 240 | 24 |
| *Schiedea nal-akaiensis* | Hawaii | E | 100–200 | 25 |
| Small whorled pogonia | N. America | V | 2600 | 24 |

**Table 14.3** | Population size targets specified for de-listing a range of endangered species

| Species | Target population size for de-listing | Reference |
|---|---|---|
| *Mammals* | | |
| Asian rhinoceros | 2500 ($N_e$ = 500) in 10 + populations | 1 |
| Black-footed ferret | 1500 adults in 10 + populations | 2 |
| Sea otter | 2650 | 3 |
| *Birds* | | |
| Attwater's prairie chicken | 5000 in 3 different areas | 4 |
| Bald eagle | 3900 pairs | 5 |
| California condor | 2 × 150 wild + 150 captive | 6 |
| Lord Howe Island woodhen | 200 (endangered to threatened) | 7 |
| Peregrine falcon | 456 breeding pairs | 8 |
| Red-cockaded woodpecker | 5 populations of 500 = 2500 | 9 |
| *Plants* | | |
| Lakeside daisy | 1000 plants | 10 |

*References*: 1. Foose *et al.* (1995); 2. Clark (1994); 3. Ralls *et al.* (1996); 4. Bowdoin & Williams (1996); 5. Millar (1999); 6. Ralls *et al.* (2000); 7. Brook *et al.* (1997a); 8. Mesta (1999); 9. Kulhavy *et al.* (1995); 10. Dennison (1994)

endangered list (Table 14.3). Target sizes are based on many considerations, but frequently ignore genetic concerns. While most target sizes are in the thousands, they are generally less than genetic arguments require, based on a $N_e/N$ ratio of about 0.1. The numbers for peregrine falcons and California condors are particularly alarming at about 900 and 450. The peregrine falcon has now been de-listed as it exceeded its target population size.

## Genetic goals in management of captive populations – a compromise

Captive populations of endangered species are usually managed to retain 90% of their genetic diversity for 100 years

There are many fewer captive breeding resources available than would be required to maintain all the species deserving captive breeding, especially if the numbers recommended above are used (e.g. $N_e$ = 500 per species). Zoos house about 540000 mammals, birds, reptiles and amphibians. At most, only half of the spaces are suitable for propagating endangered animals (Conway 1986). It is estimated that about 2000 vertebrate species require captive breeding to save them from extinction (Tudge 1995). To maintain each of these species at an effective size of 500



(assuming $N_e/N$ = 0.3 in captivity) would require 3.3 million animal spaces, about 12 times the space available for captive breeding. At an average population census size of 500, only 540 species can be accommodated. Currently only 15% of mammal spaces in zoos house threatened species (Magin *et al.* 1994), and the situation is even worse than indicated above. There is a trade-off. If some loss of genetic diversity is accepted, smaller populations of more species can be accommodated.

The current compromise is to manage endangered species in captivity to conserve 90% of the wild population's genetic diversity for 100 years. The background to the 100 years time frame is that wild habitat may become available following the predicted human population decline in 100–200 years (Soulé *et al.* 1986). This requires different sized populations for species with different generation lengths. An approximate expression for the required size can be obtained using Equation 10.1, as follows:

$$H_t/H_0 = (1 - 1/2N_e)^t = e^{-t/2N_e}$$

Upon taking natural logarithms, substituting 0.9 for $H_t/H_0$, 100/$L$ for $t$ (where $L$ is generation length in years), and rearranging, we obtain

$$N_e = 475/L \qquad (14.9)$$

Consequently, the required size is inversely proportional to the generation length for the species in question. A range of examples is given in Table 14.4. For example, the effective size required to maintain 90% of the original heterozygosity is 475 for a species with one generation per year, 18 for Caribbean flamingos with a generation time of 26 years and 1759 for the white-footed mouse with a generation length of 14 weeks. This is one of the few circumstances where long-lived species are at an advantage.

Maintaining 90% of genetic diversity for 100 years is a reasonable practical compromise. However, even with this compromised goal, it is unlikely that all the species requiring captive breeding can be accommodated. Species are being maintained with lesser goals (and smaller sizes) due to shortage of resources.

The cost of this compromise is increased inbreeding and reduced reproductive fitness. From Chapter 11:

$$F = 1 - (H_t/H_0)$$

The accepted 10% loss of heterozygosity corresponds to an increase of $F$ of 10%, with consequent inbreeding depression. After 100 years, individuals will be related to each other to a degree somewhere between that of first cousins ($F$ = 0.0625) and half-siblings ($F$ = 0.125). This will reduce juvenile survival on average by about 15% and total fitness by about 25%, in captivity (Chapter 12). The fitness costs are likely to be much greater if species are subsequently reintroduced into harsher wild environments (Crnokrak & Roff 1999). Thus, captive breeding programs are balancing the cost of permitting a moderate degree of inbreeding over 100 years against the benefits of maintaining additional endangered species within the limited resources available.