Animal Conservation (1998) **1**, 69–73

How large must populations be to retain evolutionary potential?

I. R. Franklin[1] and R. Frankham[2]

[1] CSIRO Division of Animal Production, Locked Bag 1, Blacktown, NSW 2148, Australia
[2] Key Centre for Biodiversity and Bioresources, School of Biological Sciences, Macquarie University, NSW 2109, Australia
(Received 20 June 1997; accepted 3 December 1997)

Abstract

Maintaining genetic variation for future evolutionary change is an important issue for conservation biology. However, there is controversy over the effective population size (N_e) required for endangered species to retain their evolutionary potential, with proposed sizes ranging from 500 to 5000. The highest estimate is based on the assumption that 90% of mutations are deleterious. We review the arguments for an effective size of 5000 and conclude that it assumes effective mutation rates that are too low, and heritabilities that are, in general, very high. We conclude that an N_e of 500–1000 is appropriate at this time.

The effective population size (N_e) required for a population to retain its evolutionary potential sets a lower limit to viable population size for wildlife (Soulé, 1987). Franklin (1980), in reviewing the genetical considerations for conservation policy, suggested that there were two primary considerations – an immediate danger in small populations due to inbreeding and, in the longer term, a loss of quantitative genetic variation that would limit future evolutionary change. In addressing the latter issue, he argued that, in small populations, the rate of change in additive genetic variability is, essentially, determined by the rate of loss by drift and the rate of gain by mutation. That is,

$$\Delta V_A = V_m - V_A/2N_e,$$

where V_A is the additive genetic variance and Vm the increment in additive variance per generation due to mutation. At equilibrium, $\Delta V_A = 0$, so

$$N_e = V_A/2V_m.$$

Franklin (1980) noted that $V_m \sim 10^{-3} V_E$ for abdominal bristle number in *Drosophila*, where V_E is the environmental variance. Consequently,

$$N_e = V_A/[2 \times 10^{-3} V_E] = 500 V_A/V_E = 500 h^2/(1 - h^2).$$

The heritability (h^2) of bristle number is approximately 0.5, hence $N_e = 500$. Lande & Barrowclough (1987) reached a similar conclusion. While the principle that the conservation of quantitative genetic variation is an important factor in managing endangered species has found general acceptance, there is disagreement about the appropriate value for N_e (Culotta, 1995).

Lande (1995) argued that only a fraction of newly generated variation is useful for future genetic change as newly arisen mutations with large effects are often deleterious. Interpreting the results of López & López-Fanjul (1993), Lande concluded that 90% of the new variation is associated with deleterious alleles, leaving 10% that is 'quasineutral'. A V_m around 10^{-3} V_E is appropriate for a wide range of quantitative characters (Houle, Morikawa & Lynch, 1996). Hence, Lande argues, N_e of 5000 is necessary to maintain evolutionary potential.

Genetic considerations are only one of many factors influencing conservation policy (Franklin, 1980; Lande, 1988; Caughley & Gunn, 1996); ecological or other considerations may dictate much higher population sizes. However, recommendations that raise the limit on effective population size from 500 to 5000 cannot be taken lightly.

Several observations suggest that Lande's argument should be treated with caution. First, estimates of V_m are often derived from long-term experiments (with or without selection); these provide an opportunity for unconditionally deleterious mutations to be eliminated (Keightley, Mackay & Caballero, 1993). Estimates of mutational variances derived from response to selection in initially homozygous lines are approximately 10^{-3} V_E (Mackay *et al.*, 1994). Hence, the value 10^{-3} V_E already includes, in part, a correction for deleterious alleles.

Second, alleles deleterious under one set of environmental conditions may be advantageous under other conditions; the concept of evolutionary potential in the conservation context is concerned with coping with environmental change. There is extensive evidence for such alleles as demonstrated by the occurrence of genotype × environment interactions (Falconer & Mackay 1996). Clearly, such alleles should not be discounted.

Third, heritabilities are often less than 0.5. Of traits in *Drosophila* and other non-domestic animals classified as life history, behaviour, physiology and morphology, only morphological traits in animals excluding *Drosophila* average about 0.5; all other categories are less (Roff, 1997). This is particularly important for traits closely related to reproductive fitness where heritabilities are typically 10–20% (Roff, 1997). Using Lande's (1995) discount factor of 90%, so that $V_m = 10^{-4} V_E$, then if we assume $h^2 = 0.1$, $N_e = 556$, while for $h^2 = 0.2$, $N_e = 1250$.

Wild populations need to be about an order of magnitude higher than these N_e values (i.e. about 5000–12 500) to maintain their evolutionary potential, as N_e/N ratios that contain all relevant variables average 0.10–0.11 (Frankham, 1995). This range sets a lower limit for the minimum size that populations should be maintained at for long-term viability (Soulé, 1987), and is within the range of values reached from consideration of environmental stochasticity and catastrophes (Nunney & Campbell, 1993) and from empirical observation (Thomas, 1990).

Acknowledgements

We thank B. Brook, D. Gilligan, R. Lande and M. Soulé for comments. R. F.'s research is supported by ARC and Macquarie University Research grants. Publication 236 of the Key Centre for Biodiversity and Bioresources.

REFERENCES

Caughley, G. & Gunn, A. (1996). *Conservation biology in theory and practice*. Cambridge, MA: Blackwell.

Culotta, E. (1995). Endangered species: minimum population size grows larger. *Science* **270**: 31–32.

Falconer, D. S. & Mackay, T. F. C. (1996). *Introduction to quantitative genetics*. (4th edn). Harlow: Longman.

Frankham, R. (1995). Effective population size / adult population size ratios in wildlife: a review. *Genet. Res.* **66**: 95–107.

Franklin, I. R. (1980). Evolutionary change in small populations. In *Conservation biology: an evolutionary–ecological perspective*: 135–150. Soulé, M. E. & Wilcox, B. A. (Eds). Sunderland: Sinauer.

Houle, D., Morikawa, B. & Lynch, M. (1996). Comparing mutational variabilities. *Genetics* **143**: 1467–1483.

Keightley, P. D., Mackay, T. F. C. & Caballero, A. (1993). Accounting for bias in estimates of the rate of polygenic mutation. *Proc. R. Soc. (B)* **253**: 291–296.

Lande, R. (1988). Genetics and demography in biological conservation. *Science* **241**: 1455–1460.

Lande, R. (1995). Mutation and conservation. *Conserv. Biol.* **9**: 782–791.

Lande, R. & Barrowclough, G. F. (1987). Effective population size, genetic variation, and their use in population management. In *Viable populations for conservation*: 87–123. Soulé, M. E. (Ed.). Cambridge: Cambridge University Press.

López, M. A. & López-Fanjul, C. (1993). Spontaneous mutation of a quantitative trait in *Drosophila melanogaster*. II. Distribution of mutant effects on the trait and fitness. *Genet. Res.* **51**: 117–126.

Mackay, T. F. C., Fry, J. D., Lyman, R. F. & Nuzhdin, S. V. (1994). Polygenic mutation in *Drosophila melanogaster*. Estimates from response to selection of inbred strains. *Genetics* **136**: 937–951.

Nunney, L. & Campbell, K. A. (1993). Assessing minimum viable population size: demography meets population genetics. *Trends Ecol. Evol.* **8**: 234–239.

Roff, D. A. (1997). *Evolutionary quantitative genetics*. New York: Chapman & Hall.

Soulé, M. E. (1987). Introduction. In *Viable populations for conservation*: 1–10. Soulé, M. E. (Ed.). Cambridge: Cambridge University Press.

Thomas, C. D. (1990). What do real populations tell us about minimum viable population sizes? *Conserv. Biol.* **4**: 324–327.

The critical effective size for a genetically secure population

Michael Lynch and Russell Lande

Department of Biology, University of Oregon, Eugene, Oregon 97403, USA
(Received 18 November 1997; accepted 3 December 1997)

For practical reasons, managers and policy-makers have to make rapid decisions with limited information on the status of endangered species. Because of its relative ease of acquisition, the most common surrogate used to derive inferences about the risk of extinction is population size. This is not to say that population size is the best indicator of risk; other considerations, such as the recent rate of population decline, are of clear importance (Mace & Lande, 1991). A popular rule of thumb for the critical population size necessary for the maintenance of adequate genetic variance for adaptive evolution in quantitative traits, originally espoused by Franklin (1980) and Soulé (1980), has been an effective population size (N_e) of 500 individuals. More recent assessments, based on both empirical and theoretical developments, suggest that this number should be revised upwards to $N_e \simeq 1000$–5000 (Lande, 1995*a*; Lynch, 1995; National Research Council, 1995; Bürger & Lynch, 1997). Here we address the arguments of Franklin & Frankham