



## Letter to the Editor

**The 50/500 rule is still valid – Reply to Frankham et al.**

Frankham et al. (2014) provide revised recommendations for application of the 50/500 rule and other genetic considerations in population viability analyses. While their paper includes much that is valuable, we disagree with their primary recommendation that the 50/500 rule be revised upwards to at least 100/1000.

The authors give primacy to inbreeding depression, even at effective sizes of 500. While one cannot, in general, discount the importance of inbreeding depression as a threat to endangered species, the formula they use to predict its magnitude is based on one derived in the 1950s to distinguish between various kinds of genetic load. First, in a random mating population, there will be variation both in the inbreeding coefficient itself, and in the proportion of the genome homozygous by descent. Therefore, the formula takes no account of the role of natural selection, which will tend to eliminate individuals that are most affected by inbreeding. Secondly, the formula assumes that loci homozygous for deleterious alleles act independently and multiplicatively. The paradoxes of genetic load theory foundered on these assumptions, as it became obvious that more realistic models of selection, in which deleterious genotypes are eliminated in bunches, can be a much stronger force in removing these from populations. The statement “Theory predicts that  $N_e = 142$  is required for a population to retain 90% of current fitness after inbreeding of  $F = 5\%$ ,” makes numerous assumptions about the action of natural selection and the relationship between the fitness of populations and the fitness of individuals within it. It is hard to argue that an effective population of size 100 is not preferable to one of size 50, but the degree to which the fitness of such populations is reduced by inbreeding depression is better answered empirically rather than on shaky theoretical arguments.

Their approach to conserving genetic variation for future adaptive change is even more contentious. Primarily, Frankham et al. draw a curious distinction between fitness and “peripheral traits”, discount the latter, and then attempt to determine how much genetic variation for loci directly affecting fitness can be maintained in finite populations. This is a crucial question, dating back to old genetic load arguments but, again, they ignore the fact that natural selection operates on phenotypes, and may be more effective in eliminating deleterious genotypes than they suppose. Their approach runs counter to Franklin's (1980) view, that polygenic traits, such as body size, behavioral avoidance of threats, metabolic adjustment to stress, etc. are the essence of adaptive change. These “peripheral” traits are invariably subjected to stabilizing selection, and under these circumstances very little of this variation is eroded by selection. This standing variation represents a pool of genetic variance that the population can use to respond to environmental deterioration.

We agree with Frankham et al. (2014) that it is important to be explicit about what is meant by “short term”. They define short term as five generations based on conversations they had with the authors of the seminal papers (Soulé, 1980; Franklin, 1980). We believe that it is better to select the most appropriate number of generations based on the particular conservation problem or species (short-lived animals require more immediate remedial action than long-lived ones) rather than the unstated values used by these authors when they first proposed the rule. We also have concerns whether a ratio of  $N_e/N$  between 0.1 and 0.2 should be used as a default when it is based on just 100 existing (and rather variable) measurements, and may not be a robust estimate for the half million or so poorly known threatened species.

We have other concerns about the proposed 100/1000 rule and that the genetically derived IUCN Red List population-size thresholds should be doubled on the basis of their review. Revising  $N_e$  from 500 to 1000 would have little effect on the increase of inbreeding and the loss of genetic variation, and the costs may well outweigh the benefits. Further, we worry about the advocacy of a triage approach where species with long-term MVPs less than 10,000 are effectively written off. However, these concerns are based more on political and logistic criteria rather than scientific arguments, and therefore will be discussed elsewhere.

There are many problems associated with the use of simple rules in a complicated world – indeed there are no real thresholds such as 50 or 500. In general, of course, larger  $N_e$  values are better. Nevertheless, the 50/500 rule has served as a useful guide in applying genetics to conservation. In our opinion, Frankham et al. (2014) have not presented new empirical results or convincing theory that justifies changing this guideline to larger values, where such a change would have far reaching consequences.

**References**

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