



## Perspective

## Genetics in conservation management: Revised recommendations for the 50/500 rules, Red List criteria and population viability analyses

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## ABSTRACT

Conservation managers typically need to make prompt decisions based on limited information and resources. Consequently, generalisations have essential roles in guiding interventions. Here, we (i) critique information on some widely accepted generalisations and variables affecting them, (ii) assess how adequately genetic factors are currently incorporated into population viability analysis (PVA) models used to estimate minimum viable population sizes, and (iii) relate the above to population size thresholds of the IUCN Red List criteria for threatened species that were derived from genetic considerations. Evidence accumulated since 1980 shows that genetically effective population size ( $N_e$ ) = 50 is inadequate for preventing inbreeding depression over five generations in the wild, with  $N_e \geq 100$  being required to limit loss in total fitness to  $\leq 10\%$ . Further, even  $N_e = 500$  is too low for retaining evolutionary potential for fitness in perpetuity; a better approximation is  $N_e \geq 1000$ . Extrapolation from census population size ( $N$ ) to  $N_e$  depends on knowing the ratio of  $N_e/N$ , yet this information is unavailable for most wild populations. Ratio averages ( $\sim 0.1$ – $0.2$ ) from meta-analyses are sufficient, provided adjustments are made for dissimilar life histories. Most PVA-based risk assessments ignore or inadequately model genetic factors. PVA should routinely include realistic inbreeding depression, and genetic impacts on evolutionary potential should be incorporated where appropriate. Genetic generalisations used in conservation, the treatment of genetics in PVAs, and sections of the IUCN Red List criteria derived from genetic considerations, all require revision to be more effective conservation tools.

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Abbreviations:  $d$ , dominance; MVP, minimum viable population size;  $N_e$ , effective population size;  $N$ , census population size; PVA, population viability analysis;  $q_e$ , equilibrium frequency;  $s$ , selection coefficient;  $V_A$ , additive genetic variation;  $V_m$ , mutational variation for a quantitative character;  $u$ , mutation rate.

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## 1. Introduction

Conservation biology is a crisis discipline requiring urgent management for threatened species often with inadequate information (Soulé, 1985). As most species have inadequate information on which to base effective intervention decisions, conservation action is frequently opportunistic, seeking compromise under competing demands, and/or politically expediency (Pressey and Bottrill, 2008). For example, parcels of land offered for sale require that decisions to purchase for conservation must be made promptly (McDonald-Madden et al., 2008). Given limited resources and sparse information for most threatened species, scientific generalisations are often required. Some authors have criticised these (Flather et al., 2011), but the alternative is usually unscientific conservation decisions made at the political and bureaucratic levels, especially in poorer countries and for non-charismatic species (Brook et al., 2011).

The International Union for Conservation of Nature and Natural Resources (IUCN) recognises the need to conserve biodiversity at three level: genetic diversity, species and ecosystems (McNeely et al., 1990), with genetic issues being involved in all three (Frankham et al., 2010). We concentrate on the first two. Species are usually driven to extinction by a combination of systematic human-associated threats (habitat loss, over-exploitation, introduced species, pollution and climate change) and stochastic events associated with small population size (demographic, ecological and genetic stochasticity, and catastrophes) (Shaffer, 1981), typically interacting in a synergistic feedback (Brook et al., 2008) termed the 'extinction vortex' (Gilpin and Soulé, 1986). In this *Perspective* we focus on controversial aspects of genetic stochasticity (see Glossary in Appendix A1), primarily encompassing inbreeding depression, and reduced evolutionary potential (Frankham et al., 2010; Jamieson and Allendorf, 2012).

Inbreeding and loss of genetic diversity are unavoidable in small, closed, sexually reproducing populations, and accumulate in a ratchet-like manner over generations for diploid random-mating populations, as follows (Wright, 1969):

$$H_t/H_0 = \left(1 - \frac{1}{2N_e}\right)^t = 1 - F \quad (1)$$

where  $H_t$  is heterozygosity at generation  $t$  (for neutral variation),  $H_0$  initial heterozygosity,  $N_e$  genetically effective population size and  $F$  the inbreeding coefficient (with generation zero defined as having  $F=0$ ). In naturally outbreeding species, this typically results in inbreeding depression (unless they have already experienced it) and reduced ability to evolve (Frankham et al., 2010).

To work, generalizations depend on different taxa responding similarly, or at least groups of them doing so. While ecologists typically emphasise species distinctiveness (e.g. Flather et al., 2011), evolutionary and conservation geneticists usually focus on the similarity of evolutionary processes across species with similar breeding systems. For example, across most major taxa: (i) inbreeding has consistently deleterious effects on fitness in wild outbreeding diploid and polyploid species (Crnokrak and Roff,

1999), (ii) population mean genetic diversity, mean fitness and population size are positively correlated (Frankham, 2012), (iii) heritabilities (genetic variation as a proportion of phenotypic variation) are lower for fitness than for quantitative traits peripherally related to fitness (Mousseau and Roff, 1987; Falconer and Mackay, 1996), (iv) non-additive genetic variation is greater for fitness than peripheral traits (Frankham et al., 2010), and (v) mutation rates for quantitative characters are relatively similar (Houle et al., 1996). Consequently, generalisations are often justifiable for genetic issues in conservation biology (see also Appendix A2).

Our focus is on three genetic issues relating to generalisations. First, an effective population size of at least 50 (Franklin, 1980; Soulé, 1980) has been long recommended as a 'rule' for avoiding inbreeding depression in the short term. Second,  $N_e = 500$  has been considered sufficient to retain evolutionary potential in perpetuity (Franklin, 1980; Lande and Barrowclough, 1987). These two issues had important roles in the development and implementation of the IUCN Red List categorisation system for threatened species (Mace et al., 2008), especially criterion C that relates to population size (Appendix A3). Third, minimum viable population sizes (MVP; Shaffer, 1981) provide estimates of the sizes required for species to persist with high probability in the long-term. Given that over 30 years have elapsed since the classic  $N_e = 50$  and  $N_e = 500$  recommendations were proposed, and their tenacity in conservation management circles, we now ask whether current evidence supports them, and how they might be modified. Jamieson and Allendorf (2012) reviewed these issues, but we reach different conclusions to them on several important issues.

We critique and make recommendations (Table 1) on (i) the  $N_e = 50$  and 500 rules, (ii) how best to translate  $N_e$  into census population size ( $N$ ), (iii) the genetic consequences of fragmented populations, and (iv) the treatment of genetic issues in PVA and their effect on estimation of MVPs. Finally, we (v) evaluate the implications of these for the IUCN Red List categorisation system.

## 2. Population size required to avoid inbreeding depression in the short term: $N_e = 50$ ?

Soulé (1980) and Franklin (1980) proposed  $N_e = 50$  as sufficient to prevent inbreeding depression in naturally outbreeding diploid species in the short term, and most authors, including Jamieson and Allendorf (2012) still endorse this value. However, specifying the duration as 'short term' is too vague, because it can mean different things in different disciplines. Since Soulé and Franklin had ~5 generations in mind (from discussions with RF), we recommend that 5 generations be used (because genetic effects scale to generations).

Franklin (1980) and Soulé (1980) based their  $N_e = 50$  on the opinion of animal breeders, plus limited data from domestic and laboratory animals. However, inbreeding depression is generally greater in stressful, wild environments than in benign, captive ones (Fox and Reed, 2010), and domestic animals might have different susceptibility to inbreeding depression compared to wild populations because they have been subjected to artificial selection,

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