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Review

Pragmatic population viability targets in a rapidly changing world

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ABSTRACT

To ensure both long-term persistence and evolutionary potential, the required number of individuals in a population often greatly exceeds the targets proposed by conservation management. We critically review minimum population size requirements for species based on empirical and theoretical estimates made over the past few decades. This literature collectively shows that thousands (not hundreds) of individuals are required for a population to have an acceptable probability of riding-out environmental fluctuation and catastrophic events, and ensuring the continuation of evolutionary processes. The evidence is clear, yet conservation policy does not appear to reflect these findings, with pragmatic concerns on feasibility over-riding biological risk assessment. As such, we argue that conservation biology faces a dilemma akin to those working on the physical basis of climate change, where scientific recommendations on carbon emission reductions are compromised by policy makers. There is no obvious resolution other than a more explicit acceptance of the trade-offs implied when population viability requirements are ignored. We recommend that conservation planners include demographic and genetic thresholds in their assessments, and recognise implicit triage where these are not met.

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1. Introduction

Extinction is the natural endpoint in the evolutionary process, with most species typically persisting 1–10 million years (Frankham et al., 2002). Evolutionary theory and numerical simulation of population persistence (or demise) has allowed the estimation of thresholds, or key 'turning points', after which extinction is more likely. The turning point in the trajectory of a population is complex, such that simplifications of the process are often used to make conservation decisions in an imperfectly measured world. This is why the concept (and applied use) of population viability and minimum viable population size (MVP) gained momentum in the early years of conservation biology (Beissinger and McCullough, 2002), and why population thresholds remain in use today (Traill et al., 2007), albeit concomitant with extinction correlates such as habitat loss (Mace et al., 2008). Importantly, these thresholds imply the moment at which a *declining* population becomes a *small* population, with increased vulnerability to extinction (Caughley, 1994). Small populations are uniquely vulnerable to demographic stochasticity at this crucial stage (Melbourne and Hastings, 2008). Moreover, the number of individuals

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required to maintain the *small* population is generally underestimated.

But are people really listening to the key, inconvenient truths that emerge here? The present-day increase in the rate of extinction is rapid and can be principally attributed to an explosion of modern human activity (IUCN, 2008). In response to the perceived biotic crisis that looms as a result (Ehrlich and Pringle, 2008), multi-lateral conservation organisations such as the World Conservation Union (IUCN) and the scientific community have worked hard to understand and quantify extinction risk, and communicate this knowledge to policy-makers, governments and the general public (Beissinger and McCullough, 2002). Here we review the evolutionary and demographic requirements of populations and argue that evidence-based scientific estimates of what is required to achieve viability are (often considerably) larger than targets outlined by conservation organisations. While we cannot provide an exhaustive review of the practical challenges of conservation biology, we suggest that most vulnerable species are not really being managed for viability (continued existence under trying environmental circumstances); rather, conservation targets in most cases merely aim to maximise short-term persistence and fit with complex political and financial realities (see Duffy, 2008). The problem is similar to the dilemma faced by climate scientists, where national and international policy seems incapable of meeting the emissions reduction implied by the available geophysical and biological evidence to avert severe anthropogenic interference with the climate system, let alone to reverse the damage already done (Chakravarty et al., 2009; Hare, 2009). Numerous socio-political impediments (IPCC, 2007; Working Group III) do not invalidate the science behind climate change and its impacts (Working Group I and II); rather, they capitulate to the reality of what is considered politically possible. Here we argue that preventing species extinctions by applying knowledge derived from the discipline of conservation biology has an analogous problem, admittedly with no immediate resolution.

2. The scientific basis for minimum viable population sizes

Despite a good deal of empirical development of the concept of minimum viable population size (Frankham, 1995; Franklin and Frankham, 1998; Reed et al., 2003; Brook et al., 2006; Traill et al., 2007), there is a disconnect between associated theory and conservation practice. It is irrefutable that population size matters for extinction risk, with small and isolated populations being particularly vulnerable to: (1) demographic fluctuation due to random variation in birth and death rates and sex ratio, (2) environmental fluctuation in resource or habitat availability, predation, competitive interactions and catastrophes, (3) reduction in co-operative interactions and subsequent decline in fertility and survival (Allee effects), (4) inbreeding depression reducing reproductive fitness, and (5) loss of genetic diversity reducing the ability to evolve and cope with environmental change (see Caughley, 1994; Frankham, 1995).

The idea of a MVP has its foundation in efforts to capture, in population viability analyses (PVA), the many and interacting determinants of extinction risk. In this original context, MVP is defined as the smallest number of individuals required for a population to persist in its natural environment (Shaffer, 1981). The likelihood of success is measured on a probability scale (0–1), and projections into the future can be scaled to years or generations (Reed et al., 2003).

Alternatively, evolutionarily determined MVPs are based solely on the maintenance of evolutionary potential, that is, the population size required at equilibrium to balance the loss of quantitative genetic variation with the gain from mutation (Franklin, 1980; Franklin and Frankham, 1998). Although the arguments are theoretically different, both recommend similar turning points toward extinction, as we demonstrate below.

2.1. Empirical MVP

Estimates of MVP size can be derived by empirical simulation, experiments, or long-term monitoring. An example of long-term census study is that by Berger (1990) who evaluated the persistence of isolated populations of bighorn sheep (*Ovis canadensis*) over 50 years. Populations <50 individuals went locally extinct, while those containing $\geqslant$100 individuals generally persisted.

Most empirical MVPs are probabilistic estimates of population persistence over a stipulated period: by arbitrary convention at least 90% certainty of persistence for at least 100 years (Shaffer, 1981). Typically, PVAs are stochastic systems models which project changes in population abundance over time and account for demographic and environmental variation, catastrophic events, density dependence and inbreeding depression (Gilpin and Soulé, 1986). PVAs are used to predict population persistence in the short (a few years) to medium term (10s–100s of years) and allow quantitative comparison and qualitative ranking of alternate management strategies. Persistence over generations (from as low as 3 to 40 or more generation spans) is used as an alternate to time steps in years, and is seen as biologically more appropriate when working across taxonomic groups (O'Grady et al., 2008). Simulation models can be individual- or matrix/cohort-based and implemented using generic computer software packages (see Lindenmayer et al., 1995) or tailored models. Most estimates of empirical MVP have been obtained using PVAs; indeed, a recent review of MVP-related literature found that 95% of 141 published articles used PVA as their basis for estimating extinction risk (Traill et al., 2007).

Median estimates of the empirical MVP derived from PVAs range from ~1300 (Brook et al., 2006) to ~5800 individuals (Reed et al., 2003), depending on the method and underlying assumptions. The lower estimate derives from scalar population growth models that do not include demographic stochasticity, fluctuation in age structure or genetic deterioration. The upper estimates of MVP (Reed et al., 2003) accounted for all major deterministic and stochastic threats and some positive feedbacks, including inbreeding depression. Of note, Melbourne and Hastings (2008) find that most population analyses have under-estimated viability by not accounting for all major factors contributing toward stochasticity.

A recent review and meta-analysis reported that 60% of published PVAs included genetic effects (Traill et al., 2007). Yet, even PVAs that take genetic factors into account usually underestimate their impacts on extinction risk. First, these only encompass the deleterious genetic impacts of inbreeding on reproduction and survival (inbreeding depression), but do not consider the loss of genetic diversity which effectively reduces a population's ability to evolve and cope with environmental change (Visser, 2008). Second, all studies that include inbreeding depression underestimate its effect on population viability. Many use small impacts of inbreeding depression based on juvenile mortality in captive populations, rather than those for all components of reproduction and survival in wild populations (O'Grady et al., 2006). Further, all assume Poisson-type variation in family size, but variation is typically much greater leading to lower effective population sizes (Box 1), more rapid inbreeding and greater reduction in reproductive fitness (Frankham et al., 2002).