Review

Pragmatic population viability targets in a rapidly changing world

Lochran W. Traill [a,*], Barry W. Brook [a], Richard R. Frankham [b], Corey J.A. Bradshaw [a,c]

[a] Environment Institute and School of Earth and Environmental Sciences, University of Adelaide, South Australia 5005, Australia
[b] Department of Biological Sciences, Macquarie University, NSW 2109, Australia
[c] South Australian Research and Development Institute, P.O. Box 120, Henley Beach, South Australia 5022, Australia

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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.

Contents

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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* Corresponding author. Tel.: +61 8 83036070.
   E-mail address: lochran.traill@gmail.com (L.W. Traill).

required to maintain the *small* population is generally under-estimated.

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 ≥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).

Box 1 Genetically effective population sizes.

The genetically effective population size (N_e) is a measure of a population's genetic behaviour relative to that of an 'ideal' population (Frankham et al., 2002). Technically, it is the size of an idealised population that would result in the same inbreeding or loss of genetic diversity as that in the population under study. An idealised population is a conceptual closed, random-mating population of hermaphrodites that have Poisson variation in family size, constant numbers of breeding individuals in successive, non-overlapping generations, and no mutation or selection (Wright, 1931). Real populations deviate from the idealised population due to fluctuations in population size, unequal sex ratios, family size variation greater than Poisson and overlapping generations. The first three factors reduce N_e to below the census size, while the effects of overlapping generations are not consistent in direction (Frankham, 1995). Genetic impacts depend on N_e, rather than N, with genetic diversity being lost at a rate of $1/(2N_e)$ per generation within closed populations, and inbreeding increasing at this same rate in random-mating populations. The N_e is the 'currency' used to describe the evolutionary MVP.

Critics argue that PVAs are only practically useful for predicting extinction risk where data are extensive and reliable and projection time frames are short (Fieberg and Ellner, 2000). Further, the IUCN Red List does not base the categorisation of any threatened species on PVAs alone (IUCN, 2008). However, Boyce (1992) and Burgman (2006) suggest that PVAs are indispensable when done properly because they cause assumptions regarding the processes leading to decline to be made explicit, and bring together scientists and policy-makers to assess the costs and benefits of alternative approaches to population management.

2.2. Evolutionary MVP

Few conservation programs (for wild-living populations) explicitly incorporate genetic goals or attempt to maintain wild populations large enough to retain a substantial fraction of genetic diversity (Frankham et al., 2002). Genetically viable populations are those large enough to avoid inbreeding depression, prevent the accumulation of deleterious mutations, and maintain evolutionary potential. Small populations can persist in the wild for some time, but the reproductive fitness of these, and especially the ability to adapt to change (evolutionary potential) is compromised and extirpation is likely (Spielman et al., 2004; Kristensen et al., 2008). So what population sizes are required to ensure genetic viability, and how do these compare to empirical MVPs?

The MVP to retain evolutionary potential in perpetuity is the equilibrium population size where loss of quantitative genetic variation due to small population size (genetic drift) is matched by gains through mutation. Franklin (1980) estimated this to be a genetically effective population size (N_e) of ~500 individuals (50 to avoid inbreeding). Critically though, the mean ratio of the N_e to the census population size (N) is ~0.1 (Frankham, 1995) and therefore a census population of ~5000 adults. The concept of N_e is described in Box 1, but we note here that the estimation of the census N allowed biologists to move on from the 50/500 rule (after Franklin, 1980). Other estimates of the evolutionary MVP have attained a N_e of ~5000, corresponding to an adult population size of 50,000 (Lande, 1988; Franklin and Frankham, 1998).

Unfortunately, the population sizes of many threatened species are likely to fall below this range (perhaps >2000 species, given the total number of *Critically Endangered* populations in the Red List; IUCN, 2008). The loss of genetic variation within these populations can be regenerated through mutation, but this will typically take hundreds to thousands of generations (Frankham et al., 2002). Small populations have therefore reached a point-of-departure: away from the ability to adapt to changing environmental circumstances and toward inflexible vulnerability to these same changes (Frankham and Ralls, 1998).

3. Generalities

The bottom line is that both the evolutionary and demographic constraints on populations require sizes to be at least 5000 adult individuals. These seem to be large requirements, but a number of studies across taxonomic groups have made similar findings: the median MVP derived from PVA of 102 vertebrate species was 5816 individuals (Reed et al., 2003), and 4169 individuals from a meta-analysis of 212 species (Traill et al., 2007). The census-based MVP of 5500 reported by Thomas (1990) is also remarkably congruent; all similar to the recommended census N of 5000 individuals (Frankham, 1995). We note though that similarities are not strictly equivalent, and are a result of evaluation of some non-overlapping factors, meaning minimum viable population size in many circumstances will be larger still.

4. Conservation in the long term

The science of more than 30 years of empirical and genetic research on the viability of wild-living populations thus implies that the number of individuals (required to avoid a turning point toward extinction) is greater than generally appreciated or implemented within conservation management. Although our contention that conservationists often manage below a biologically reasonable extinction threshold is not new (see Tear et al., 1993; Reed et al., 2003), debate persists. Disagreement hinges on two main issues: (i) the accuracy of predictions and (ii) their real-world applicability to conservation action (Beissinger and Westphal, 1998; Coulson et al., 2001).

Regarding accuracy, criticism centres on the general low quality of available population data and the high sensitivity of predictions to assumptions made. A response to this is that the rapidity with which the extinction crisis is unfolding means that biologists and managers cannot afford to wait for the collection of the necessary high-quality data before making decisions (Lee and Jetz, 2008) – and that given their relative simplicity, most biases are likely to underestimate rather than over-estimate risk (though see Brook, 2000 for a counter-example). Many conservationists also question the real-world relevance of MVP estimates given their high associated uncertainty bounds and the wide cross-species range. For example, some published PVAs have specified MVP sizes as low as 20 individuals (Sæther et al., 1998) and others as high as 100,000 (Reed, 2005). However, variation arises in part from the complexity, biological reality and type of PVA used, and median confidence intervals from meta-analysis of standardised MVPs still provide reasonable guidance on the most likely targets that will be required (e.g., 3577–5129, 95% CI; Traill et al., 2007). Further, conservationists working within developing nations will rarely have the resources available to collect the demographic and other data necessary to model viability for specific species or taxa; there is thus a compelling argument to develop rules of thumb for population size extinction-risk thresholds. Moreover, related species tend to have similar characteristics and response.

Differences between published MVP estimates, even for the same species, can also be explained by the different survival probabilities and timescales used. For example, median MVP values estimated from time series models fitted to 1198 species (Brook et al., 2006) differed substantially (by up to 10,000 individuals) depending on whether the risk criteria specified a >50% or >90% probability of survival (Fig. 1). The first is a 'coin toss' level of risk acceptance, the latter is equivalent to being listed as *Threatened* by the IUCN (Criterion E). Further, median MVP values increase by many thousands of individuals as the projection interval increases from 10 to 1000 years (Fig. 2). The implication here (of selecting a particular frame of reference) is that conservation decision-makers must explicitly choose a period over which they are managing for persistence, and with a specified certainty of success. Beyond that chosen frame of reference, nothing useful can be said about the long-term persistence of a given species.

The science of integrated population biology is now clear enough that we can state that if conservation practitioners purportedly manage for population viability with a few hundred individuals or less, then they effectively manage at a 50:50 odds of success on a century time scale (see Fig. 1). Clearly, any conservation project that is serious about the long-term survival (and continued ability to evolve) of a species must aim for a meta-population of thousands of individuals (Figs. 1 and 2), or else re-evaluate their stated position. Practitioners can validly take issue with high population targets, because of the impracticality of preserving adequate contiguous habitat, especially for large-bodied species (e.g., Armbruster and Lande, 1993). In reality, most populations presently exist as fragmented sub-populations within a larger meta-population (Akçakaya et al., 2004), with their successful conservation depending on genetic exchange among units to maintain high genetic diversity (Hoegh-Guldberg et al., 2008).
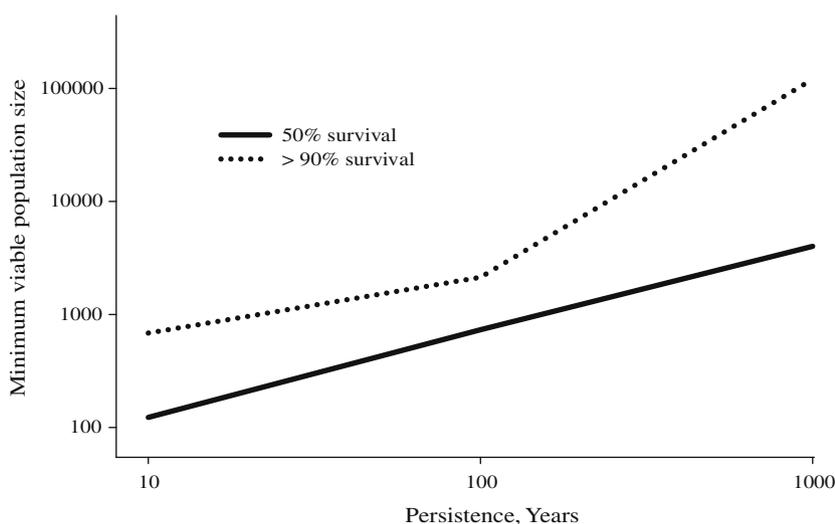
Fig. 1. Line plot of median minimum viable population estimates (scaled to log$_{10}$) for 1198 species derived from time series analyses (see Brook et al., 2006) along a logged timescale (10–1000 years). The full line represents median MVP size at 50% probability of persistence. The dotted line is the median MVP at greater than 90% probability of persistence.
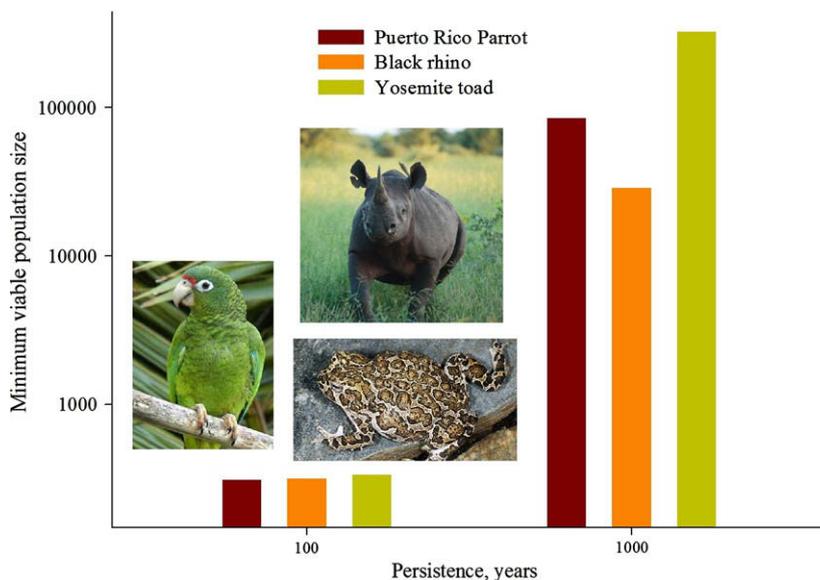
Fig. 2. Bar chart of (log$_{10}$) MVP estimates for three threatened vertebrate species from time series population viability analyses (Brook et al., 2006). Selected species are the Yosemite toad (*Bufo canorus*), black rhinoceros (*Diceros bicornis*) and the Puerto Rico parrot (*Amazona vittata*). Data are model-averaged MVP values for 100 years (90% probability of survival, as used by the IUCN, 2008) and 1000 years (99% probability of survival). Images, PR parrot (http://kevinschafer.com), black rhino (http://wildcast.net) and Yosemite toad (http://calacademy.org).

5. Conclusions

We maintain that given demographic, genetic and phenomenological consensus, the concept of the minimum viable population is a useful benchmark, and highly relevant in today's biodiversity crisis. The poor implementation of empirically derived MVP targets is not the fault of the available data or theory arising; rather, we argue it is more constrained by political and logistic challenges. In other words, MVP estimates bring scientific frankness to the socio-political arena. Geophysical scientists use climate models to advise decision makers on the risks posed by global warming associated with different scenarios of carbon emission reductions (IPCC, 2007). Similarly, conservation biologists have a critical role to play in providing a scientific reality check on whether, and to what degree, decisions made in the interests of threatened species management or under the motivation of avoiding extinctions, will be effective. This can be done openly, thereby avoiding the tag of stealth policy (see Lackey, 2007; Wilhere, 2008). By explicit presentation of threshold data at alternate probabilities of success (Fig. 1), biologists leave the ultimate decision to the political process.

Current evidence from integrated work on population dynamics shows that setting conservation thresholds at a few hundred individuals only is a subjective and non-scientific decision, not an evidence-based biological one which properly accounts for the synergistic impacts of deterministic threats (Brook et al., 2008; Visser, 2008). Many existing conservation programs might therefore be managing inadvertently or implicitly for extinction – a clearly illogical and counter-intuitive aspiration. If practitioners cannot justify using conservation triage to alleviate problems associated with unrealistic targets (see Box 1), where small, inbred populations are neglected in preference to more viable options, then they must manage for biologically relevant MVPs at least 5000 adult individuals (or 500 simply to prevent inbreeding) whilst addressing the concomitant mechanisms of decline (Balmford et al., 2009).

Box 2 Ecological triage.

Ecological (or conservation) triage is a concept enveloped in an evolving, but unfortunately acrimonious, debate at the centre of conservation biology. Polarity centres on two fundamentally different approaches toward conservation, *viz.* 'no species extinction, at any cost' and 'extinction is inevitable for some species, let's manage the process rationally' (e.g., Jachowski and Kesler, 2009).

The debate has a long history. Walker (1992) advocated the prioritisation of species (conservation status) according to the necessary functions that species or populations provided to ecosystem function; and the abandonment of functionally redundant, or highly diminished species. While few conservationists explicitly advocate extinction of no-hopers, triage is implicit through recognition that current threats to biodiversity outweigh the resources available to mitigate these (Bottrill et al., 2008). Thus, a number of approaches can be taken to optimise conservation effort, albeit acknowledging that preventing extinction altogether is at the very least daunting. For example, Hobbs and Kristjanson (2003) advocate adaptive management strategies ranging from *no immediate management action* (say, for non-threatened species) to *urgent protection or restoration,* without stating that populations should be abandoned. Carefully thought-out resource allocation thus allows more efficient conservation effort, and hopefully, better outcomes.

Recent advances in the science include 'prioritisation protocols' that optimise (conservation) resource allocation through cost-benefit analyses (Murdoch et al., 2007) and the likelihood of management success (Joseph et al., 2009). The authors build on the *Noah's Ark* framework (Weitzman, 1998) through consideration of conservation costs and benefits, species utility and value; but take these a step further by accounting for the probability of management success. Wilson et al. (2007) developed a conservation prioritisation framework that addressed geographic priorities, fund allocation and area-specific threats. By applying this framework across Mediterranean ecoregions, they found that more species could be conserved through targeted conservation actions than through sole reliance on acquisition of appropriate habitat.

Conservation planning uses many criteria to guide decisions on conservation action, principally based on (biodiversity) representation and persistence (see Sarkar et al., 2006). Among the principles relevant to biodiversity persistence are population viability and evolutionary potential. Nonetheless, the point we make is that even (conservation) planners practice an implicit form of triage through recognition that entire conservation networks are not feasible. Conservation is one form of land use among many, and planners optimise conservation outcomes given the constraints.

Criticism of triage basically comes down to 'defeatism'. Pimm (2000) argues that triage is inappropriately seductive because "it combines the semblance of tough decision-making style with the substance of doing nothing." The argument to let species X go will be repeated years later for species Y. Further, triage inhibits science; saving the very rarest pushes the technical frontiers of conservation biology. To quote Pimm (2000) again, "nothing concentrates the mind like impending extinction, nor so openly tests whether our knowledge of ecology, genetics and is up to task."

More recent critics point out that a shift in philosophical stance by conservation biologists will have ramifications far beyond the current debate. If conservation biologists, the very people dedicated to prevent extinction via scientific investigation and restorative problem solving, sanction this, then what is there to stop others with no sympathy for conservation from justifying extinction (Jachowski and Kesler, 2009)? Others highlight conservation success stories such as the whooping crane (*Grus americana*), or indicate new funding possibilities for conservation through carbon financing (Pimm, 2000; Parr et al., 2009).

The debate is not likely to go away. In the interim, and on a positive note, the explicit nature of triage-based analyses will likely prompt funding from Government and donor sources that may not otherwise have been freed.

One partial remedy is for prioritisation of conservation funds to be based on indices of the distance of species population sizes from MVP. So for example, a small population of 50 individuals will score 0.01 (percent of 5000), and the inverse of this can be used as a modifier for fund allocation. A simple scoring system such as this can be the basis of a decision-framework for threatened species within a particular management region, and conservationists can factor in other considerations such as likelihood of success and economic value (see Joseph et al., 2009). Indeed, both

demographic and evolutionary MVPs have been, and continue to be influential to real-world conservation planning (Sarkar et al., 2006). As with the use of biodiversity surrogates in conservation planning (Pressey, 2004), rules of thumb on species' demographic and genetic requirements are often the only option when dealing with the current crisis under conditions of great uncertainly and severe resource constraints.

Further, minimum viable population sizes are legitimate and concrete targets that policy-makers can digest and implement. While scientists debate MVP variance, the extinction crisis deepens. Thresholds at 500/5000 are communicated more effectively to policy-makers who do not have the time to read the extensive literature surrounding viability. Indeed, the lack of communication between science and conservation policy can be improved through dissemination of generalities (such as thresholds) that can be formulated as policy (see Gibbins et al., 2008).

If, on the other hand, scientists regard MVP thresholds to be too high to implement practically, then what are the alternatives? Is managing for hundreds of individuals over short time-frames sensible? If biologists believe that meta-populations numbering less than a few thousand individuals are capable of survival in a globally changing world, then this needs to be argued with relevant empirical and genetic data as support. Other than that, a more explicit and honest acceptance of the biological trade-offs implied in ignoring MVPs on logistical grounds is needed, for credibility's sake.

Acknowledgements

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