Review

Minimum viable populations: is there a 'magic number' for conservation practitioners?

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Establishing species conservation priorities and recovery goals is often enhanced by extinction risk estimates. The need to set goals, even in data-deficient situations, has prompted researchers to ask whether general guidelines could replace individual estimates of extinction risk. To inform conservation policy, recent studies have revived the concept of the minimum viable population (MVP), the population size required to provide some specified probability of persistence for a given period of time. These studies conclude that long-term persistence requires $\geq$5000 adult individuals, an MVP threshold that is unaffected by taxonomy, life history or environmental conditions. Here, we re-evaluate this suggestion. We find that neither data nor theory supports its general applicability, raising questions about the utility of MVPs for conservation planning.

Conservation planning and the viability of populations

Establishing species conservation priorities and quantitative management objectives is enhanced by the ability to estimate the extinction risk faced by populations. In particular, two topical, linked concepts in conservation (triage and return on investment) often require an estimate of the risk faced by a population and the financial costs of strategies to mitigate that risk [1]. Early work on estimating extinction risk focused on population viability analysis (PVA) and related methods for estimating a threshold population size below which extinction risks were deemed unacceptably high (the so-called 'minimum viable population', MVP) [2–4] (Box 1). Formal application of these methods requires extensive, high-quality data, usually drawn from intensive, long-term studies [5–10]. Even with quality data, extinction probabilities will often be estimated with considerable uncertainty, unless populations are rapidly growing or declining [11], and forecasts of population fates should be restricted to short time horizons [10]. Unfortunately, for many species, especially those of conservation concern, quality long-term data on which to base estimates of persistence remain limited [12–14].

The need to make rapid decisions about conservation targets, often in the absence of necessary data, has prompted interest in identifying robust, general guidelines for MVPs [15,16]. Taking advantage of growing access to population and life-history data for large numbers of species, several recent papers [17–20] explore the credibility of a lower limit to robust MVPs. Despite apparent caution about overinterpreting the strength of evidence, the most recent review [20] asserts that '[t]he bottom line is that both the evolutionary and demographic constraints on populations require sizes to be at least 5000 adult individuals.' A popular science summary of the article goes further, christening 5000 adults 'a magic number' that applies to 'mammals, amphibians, insects, plants and the rest' [21]. The conservation implications of this claim are profound, because it asserts that a population threshold of 5000 must be reached or exceeded, regardless of taxon (plant, invertebrate or vertebrate) or environmental context (either short-term stressors or more fundamental properties of the local environment).

Given the importance of managing for viable populations, it is essential that conservation biologists engage in robust debate regarding MVP. Our intention here is to focus on the analyses and conclusions from recent studies that advocate a universal threshold for MVP [17–20]. We begin by considering whether ecological principles support the notion of a universally applicable MVP threshold and by outlining crucial conservation policy outcomes of recent MVP papers [17–20]. Using data from three of the key papers [17–19], we identify aspects of analysis and interpretation that do not support the existence of a universally applicable estimate of MVP. Finally, we offer suggestions for how conservationists might proceed in the absence of such an estimate.

A universal threshold for MVP?

Traill *et al.* [20] argue that conservationists working in developing countries lack the resources to estimate MVPs accurately for conservation targets and, thus, that there is 'a compelling argument to develop rules of thumb for population size extinction-risk thresholds.' By contrast,

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Box 1. History and estimation of a MVP

The MVP concept emerged in 1981 from Shaffer's [2] pioneering paper that defined a minimum viable population as 'the smallest isolated population having a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental, and genetic stochasticity, and natural catastrophes.' The criteria for evaluating viability (the time frame and associated extinction risk) were 'tentatively and arbitrarily' chosen by Shaffer, recognizing that risk criteria were within the purview of society as well as science. Operationally, time horizons of 50–100 years and extinction risk of 5% became the most frequently used criteria.

Shaffer [2] outlined five possible approaches for determining MVPs: experiments, biogeographic patterns, theoretical models, simulation models and genetic considerations. Experimentally manipulating the size of replicated populations and then following their trajectories is rarely possible in nature. Examining biogeographic patterns of distribution can lead to estimates of minimum area requirements, densities, or population sizes versus occupancy (i.e. incidence). However, because of the indirect tie to extinction, this approach is rarely used. Theoretical models can be used to predict the time required for a population of a given size to go extinct (see [26]), but the idiosyncratic or contextual situation that characterizes most wild populations precludes the application of such models to real-world conservation. Genetic considerations consisted of comparing an estimate of the effective size (N_e) of a population to the 50/500 'rule' of conservation genetics (i.e. an N_e exceeding 50 for short-term and 500 for long-term survivability). However, the 50/500 values of N_e are simply viability goals for maintaining genetically diverse populations; they provide little direct connection with extinction risk.

The remaining method, simulation modelling (also known as PVA), is the most general and popular approach to estimating MVPs. A stochastic population projection model is constructed from estimates of the mean and variance of demographic rates (from studies of individuals) or from population growth rates (i.e. r or λ, estimated from time series of counts or indices). Simulation models project populations into the future using Monte Carlo methods, incorporating chance events (e.g. demographic and environmental stochasticity, genetic effects of inbreeding and catastrophes) as well as other processes that affect the population, to produce extinction probabilities at specified time periods in the future. The minimum viable population size is found by iteratively changing the initial population size to find the smallest size that has a 95% chance of remaining extant at the end of the time period evaluated in the simulation.

The initial promise of MVP estimates as conservation yardsticks faded as conservation biologists realized that estimates of extinction risk from PVA models were often imprecise, inaccurate, contingent upon threats currently acting, and affected by model structure, study duration and other uncontrolled factors [5,71–73]. Many conservation biologists recognized that PVA models were best used for ranking relative extinction risk [5,50]. The focus on MVP was reversed to emphasize the importance of PVAs for understanding the relative probability of persistence for populations in a variety of scenarios. This approach, which focused on understanding population drivers and processes, was of broader utility to land managers and conservation practitioners. When used to evaluate multiple scenarios, PVA can bring together Caughley's [25] small and declining population paradigms in a tool that helps practitioners search for solutions to conservation problems, rather than focusing only on a static, small population paradigm answer (MVP) [74].

we argue that there are compelling reasons to suspect that no single MVP is likely to apply adequately to all populations because extinction risks are often context dependent (Box 1), and manifest from a complex interaction between life history, environmental context and threat [22–24] that can be difficult to detect with noisy data [5,10]. Theory strongly suggests that the size of a population is only marginally relevant to the extinction risk when the rate of decline is rapid and continuous [25,26]. Characteristics of both a 'fast life style' associated with small body size and short generation times [27], and the 'slow life style' represented by large organisms with long generation times [24,28] can make some species and lineages more or less likely to go extinct, affecting any estimation of MVP. Moreover, extinction risks differ between lineages threatened by habitat loss, lineages threatened by human persecution and introduced novel predators [22,24] and lineages threatened by loss of food resources [29]. Thus, theory indicates that populations of equal size will vary greatly in their extinction risk depending on their life histories, long-term population growth rates, habitat quality and current threats.

The findings of recent MVP papers [17–19] are at odds with theoretical expectations. A brief overview of the approaches and findings used in these three recent papers is given in Table 1. These papers have been characterized by largely measured tones (see also [30]), with the authors using generally careful analyses to expose sources of uncertainty in estimates of MVP. Against that backdrop, the authors' emergent conclusions [20] are surprising. In particular, the assertion that practitioners 'must manage for biologically relevant MVPs [of] at least 5000 adult individuals' [20] is made without reference to the specifics of the situation of any population. The suggestion that funding could be allocated on the basis of the numerical distance of a population from 5000 adults [20], if strictly implemented, does not adequately acknowledge that some populations might persist safely at lower population sizes, whereas others might need to be considerably larger to ensure persistence. The concern that '[w]hile scientists debate MVP variance, the extinction crisis deepens' [20], discourages further discussion of the issue. However, if a generally applicable MVP is to guide policy and funding allocation, then a robust debate culminating in a workable consensus is essential. Such a debate has yet to occur, but will need to focus on the value judgements inherent in estimating MVPs, as well as on the methods underlying MVP estimates. In the next section, we direct our attention to the latter.

What do data on MVP tell us?

Using 5000 individuals as a rule-of-thumb for the MVP of a population (the robust conservation threshold advocated by Traill *et al.* [20,21]) would disregard substantial uncertainty in existing estimates of MVPs that suggests that 5000 is likely to be a very poor estimate for any specific population. Analyses underlying the derivation of the 5000 benchmark are complex and, inevitably, analytical decisions were required to make disparate data comparable for a wide range of species and from a large number of sources. Here, we focus on three important issues. Technical details are provided to support our arguments. We demonstrate that uncertainty and contingency in the data have not been accounted for adequately, and that a failure to find taxonomic or ecological differences in measures of central tendency among highly variable data does not, in and of

Table 1. Data sets and analyses used to estimate MVPs, and results and conclusions from papers advocating the use of generally applicable MVP thresholds

Data analysed	MVP analyses	Results and conclusions	Refs
Demographic data on 102 vertebrate species; estimates of the frequency and magnitude of catastrophes, and default assumptions about the consequences of inbreeding depression	Standard PVA software package (VORTEX [81]) used to estimate MVPs conferring a 99% probability of persistence for 40 generations; estimates standardized to their expected values if 40 generations of demographic data were available (see Box 2)	No statistically significant difference detected among MVPs across taxa; overall mean standardized MVP = 7316. '[C]onservation programs, for wild populations, need to be designed to conserve habitat capable of supporting approximately 7000 adult vertebrates to ensure long-term persistence'	[17]
Time series data (acquired from the Global Population Dynamics Database [82]) on 1198 populations of plants, vertebrates and invertebrates	Information theoretic approaches used to assess support among five population growth models ranging in complexity from a random walk to a θ-logistic [80,83]. Numerical simulations based on each model determined initial population size (i.e. the MVP) conferring 99% probability of persistence for 40 generations or 90% probability of persistence for 100 years. Average MVP determined for each criterion by model averaging [84]	Median MVP = 1181 and 1377 for 40-generation and 100-year criteria, respectively; 'a striking lack of predictability in MVP'; 'although MVPs provide a useful rule of thumb for species conservation, they should not be used as precise conservation targets'	[18]
287 published MVP estimates, covering 212 species	Meta-analysis; all published estimates of MVP standardized to those expected if the generating model had sought a 99% probability of persistence for 40 generations, and had included both inbreeding depression and the potential for catastrophes	Model including desired probability and time-frame for persistence, the inclusion of inbreeding effects, and the inclusion of catastrophes explained 6.3% of the deviance among published MVP estimates. Median standardized MVP = 4169; 'a species' or population's MVP is context-specific, and there are no simple short-cuts to its derivation'	[19]

Box 2. Data standardization and uncertainty

Environmental stochasticity is a major driver of the dynamics of many populations. To model the effects of environmental stochasticity, it is necessary to have good estimates of variance in vital rates, which, in turn, require data collected over many years to sample the extent of environmental variation [5,75]. Short studies will often underestimate the range of vital rate variation, providing optimistic estimates of population stability and viability [76]. As a result, Reed and colleagues found that raw estimates of MVP (termed MVPA) produced by VORTEX were strongly affected by the study length (in generations; SLG) from which data were drawn [17]; they 'corrected' MVP estimates to the value expected from 40 generations of population data (MVPC) using the process depicted in Figure I. Essentially, the correction amounts to extrapolating an estimated MVP at point *a* along a line parallel to the regression (Equation (1)):

$$\ln(MVPA) = \beta_o + \beta_1(\ln[SLG]) + \varepsilon_i \tag{1}$$

until it intersects a study length of 40 generations at point *c*.

Two aspects of this process are problematic. First, the correction approach assumes that a regression of estimated ln(MVP) against ln(SLG) for any individual population would have an independent intercept, but a common slope defined by the overall regression of 102 different populations. Thus, the correction method is predicated on the belief that collecting an equal amount of additional data on individual populations (i.e. increasing the study lengths by a given number of generations) would increase each estimated MVP by the same absolute amount. No theory exists to support this assumption.

The second concern is that the regression equation used to standardize MVPs to a span of 40 generations included only two investigations with >15 generations of data. Assessing the consequences of this is problematic. Although theory exists to guide the assessment of prediction intervals around a standard regression (Figure I), such theory cannot be applied in a straightforward manner to data points assumed to lie on independent regression lines, with a shared slope but independent intercepts. Owing to this complexity, we consider only that component of uncertainty in MVPC estimates [17] that is associated with error in the estimated regression slope.

We examined the uncertainty in MVPC based on the statistics associated with re-fitting Reed *et al.*'s regression model to the data presented in their appendix [17]. If we assume that MVPA and SLG are known, such that the variance associated with these quantities is zero, then the variance associated with each corrected estimate *i* of MVP (MVPC) is given by Equation (2):

$$Var[\ln(MVPC_i)] = Var(\beta_1)(\ln[40/SLG_i])^2 \tag{2}$$

The 95% confidence interval for each corrected value, which we call an extrapolation interval, can then be estimated using Equation (3):

$$\ln(M\hat{V}PC_i) \pm 1.96\sqrt{\mathrm{var}(\ln[MVPC_i])} \tag{3}$$

We observed that the extrapolation intervals for the 102 species analysed by Reed *et al.* [17] failed to include the universal MVP of 5000 adult individuals in 60% of the cases (Figure II).

Although this analysis illustrates the high degree of uncertainty surrounding efforts to estimate persistence over the long term with limited empirical data, uncertainty is still greatly underestimated here. For example, assigning an SLG to each study in [17] assumes that generation length is a fixed life-history property within species. However, it is well known that estimating mean generation time is a challenge among species with overlapping generations [77,78], and examples illustrate that intraspecific generation length estimates can vary substantially (e.g. Ethiopian wolf generation time estimates range from 3 to 8 years [79]). Thus, the uncertainty bounds associated with the extrapolation process reported here are, at best, minimum estimates.

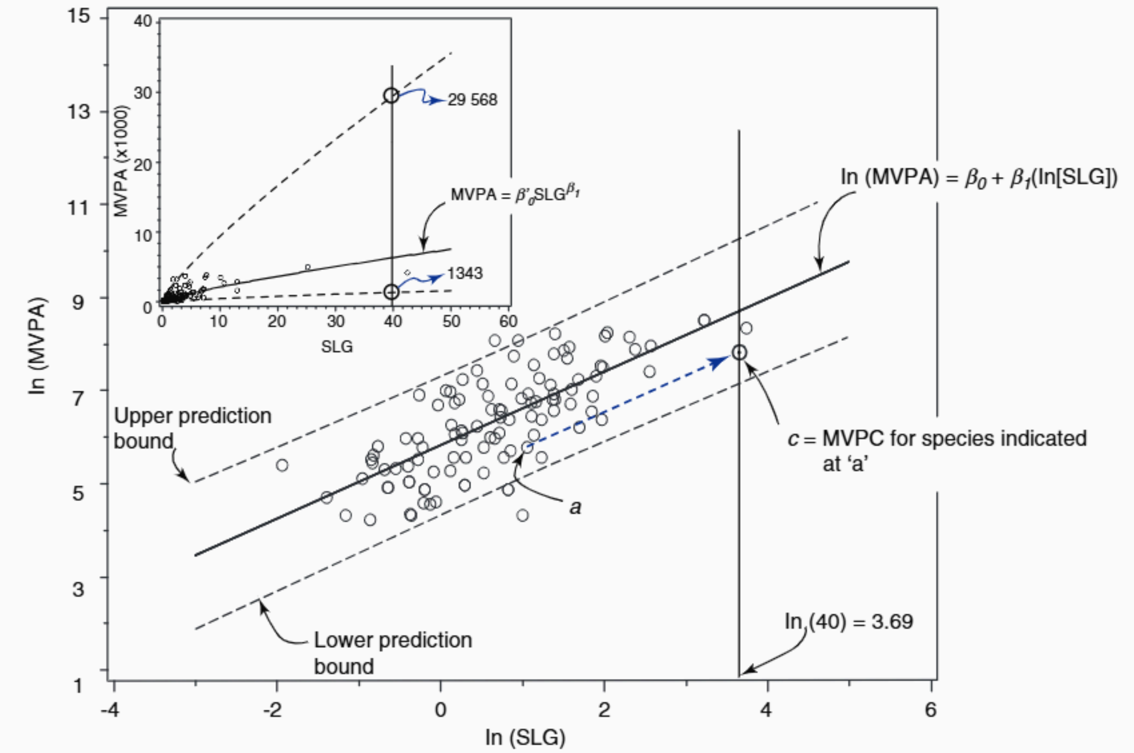

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Figure I. Correcting reported MVPA to that expected if the study used to estimate VORTEX parameters had been conducted for 40 generations (MVPC). The process is illustrated in the transformed log scale and back-transformed arithmetic scale (inset). SLG represents the study length (in generations) of the investigation used to parameterize the model of any individual population in VORTEX. The standardized MVP for species *a* is found at point *c*. Conventional lower and upper prediction intervals are displayed in log and arithmetic scales.

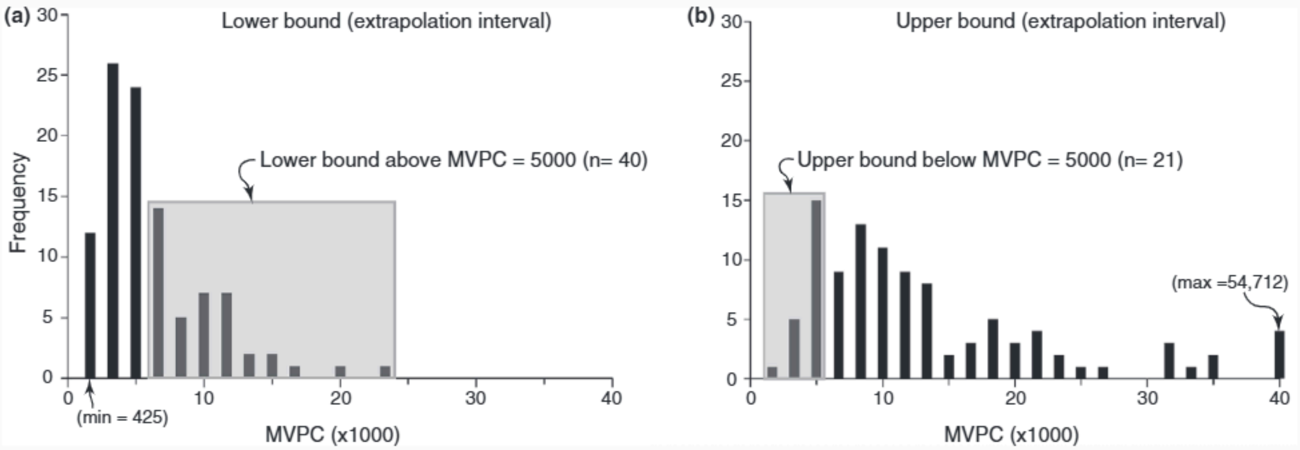

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Figure II. Frequency distributions of the lower **(a)** and upper **(b)** bounds of the extrapolation interval (based on Equation (3)) for the MVPC for the 102 species used by Reed *et al.* [17]. The union of the sets where the lower bound exceeds 5000 and the upper bound is less than 5000 defines the number of species ($n = 61$) whose extrapolation interval does not include MVPC = 5000.

itself, provide evidence for a generally applicable MVP threshold.

Standardization and extrapolation

Reed *et al.* observed a strong effect of study duration on MVP estimates [17]. Furthermore, variation in vital rates among species with different life histories (e.g. large- versus small-bodied animals) was reduced when scaled to a common generation length [31]. To account for these observations, MVP estimates were 'corrected' to MVPC, the value expected if 40 generations of population data had been available [17–19]. The standardization process by which this was achieved, together with the statistical shortcomings of that approach, are summarized in Box 2. Reconsidering uncertainty in the data, we estimated that the lower and upper bound of the corrected (standardized) MVP for each individual population studied ranged from a minimum of 425 individuals to a maximum of 54 712 individuals (Box 2,

Figure II). This outcome suggests to us, as it has to others, that the size of populations required for long-term persistence '…are generally believed to be highly circumstance and species specific, depending on the environment and life history characteristics of the species' [31].

A similar process was used by Traill *et al.* to standardize the MVPs estimated through many disparate modelling exercises [19]. A statistical model was used to standardize MVP estimates to control for varying methodology in the literature (Table 1). As with the standardization process applied by Reed *et al.* (Box 2), this amounts to assuming that the effect of a given factor (e.g. the inclusion of inbreeding effects) across populations would apply with the same absolute magnitude within each population. Although it would be testable, no theory exists to support this notion. Even accepting the standardization process, it is telling that the fitted model explained only 6.3% of the deviance among MVP estimates; remaining variability is presumably attributable to inherent differences among the focal populations and their environmental context (see following section). The explanatory power of the fitted model does little to justify the claim [20] that, '[d]ifferences between published MVP estimates, even for the same species, can also be explained by the different survival probabilities and timescales used.'

Determinism, outliers and environmental context

Reed *et al.* [17] investigated whether MVPs were higher than is usually acknowledged. To eliminate data from populations subject to strong deterministic declines (probably arising from anthropogenic effects), they excluded populations with 'strong negative growth rates' [17]. By contrast, Brook *et al.* [18] were actively interested in the relationship between population growth rate and MVP. Consequently, the 1198 populations in their analysis included 561 populations with negative growth rates [including species in very steep decline, such as the Steller sea lion (*Eumetopias jubatus*), for which $r = -0.72$]. Unsurprisingly, the population growth rate was found to have an important influence on estimated MVP [18], with the highest MVPs associated with situations characterized by low growth rates combined with high population variance. That MVPs are useful only in cases where strong deterministic effects have been removed [25] does not appear to have influenced the selection of species assessed by Brook *et al.* [18] or Traill *et al.* [19]. Indeed, if only the relatively stable populations (i.e. those with $-0.02 \leq r \leq 0.02$) are considered, the median MVP estimate reported by Brook *et al.* shifts from 1181 ($n = 1198$) to 355 ($n = 408$) based on the 40-generation criterion. Therefore, the inclusion of populations known to be in decline owing to strong deterministic threats suggests that median estimated MVPs are overly pessimistic (see Box 3), as shown by Lande in his analytical treatment of this question [26].

Some indication of the potential importance of environmental context can be gained by considering the data presented by Traill *et al.* [19]. These data enable one to focus on the effects of extrinsic factors (rather than intrinsic ecology) by looking at species for which multiple estimates of MVP have been produced. From Traill *et al.*'s supplementary data [19], we found 52 species that each had two to nine independent MVP estimates. Even after standardization, MVPs varied substantially within species (see Table S1 in supplementary material online). The grizzly bear (*Ursus arctos*) had the greatest number of independent estimates ($n = 9$) with standardized MVPC ranging from 395 (MVPC_{min}) to 44 259 (MVPC_{max}). Other notable species with at least four independent estimates included the wolf (*Canis lupus;* $\text{MVPC}_{\text{min}} = 248$; $\text{MVPC}_{\text{max}} = 6332$), Asian elephant (*Elephas maximas*; $\text{MVPC}_{\text{min}} = 266$; $\text{MVPC}_{\text{max}} = 4737$), mountain gorilla (*Gorilla gorilla*; $\text{MVPC}_{\text{min}} = 630$; $\text{MVPC}_{\text{max}} = 11\,919$), and red-cockaded woodpecker (*Picoides borealis*; $\text{MVPC}_{\text{min}} = 422$; $\text{MVPC}_{\text{max}} = 20\,868$). Overall, maximum MVP estimates were many times greater than minimum estimates for the same species, often exceeding two orders of magnitude ($\text{MVPC}_{\text{max}} / \text{MVPC}_{\text{min}}$: median = 15.4). The reported range of MVPC estimates also failed to include 5000 individuals in 42% of the cases ($n = 22$), with 19 cases failing because $\text{MVPC}_{\text{max}} < 5000$, and three cases failing because $\text{MVPC}_{\text{min}} > 5000$; these results illustrate well the strong dependence of MVP estimates on the environmental context of a population (see also Figure 1).

Density dependence and stability

Density dependence is profoundly important to the regulation of many natural populations, and fundamental to the recovery of populations from perturbation. The form of density dependence can exert a strong influence on extinction probabilities associated with different population sizes [32,33]. Papers analysing MVPs [17–19] have differed in their treatment of density dependence, leading to some contradictory interpretations of the importance of the phenomenon (Box 4). Clearly, a failure to include density dependence appropriately is likely to inflate estimates of MVP substantially. The difficulty of inferring the form of density dependence, even from relatively long population time series, highlights that meaningful estimates of MVP are likely to be derived only from very long, and therefore rare, data sets [8].

Re-evaluating support for a generally applicable MVP threshold

Reconsideration of the underlying data indicates that uncertainty in MVP estimates is substantial, regardless of the analytical approach used in recent treatments [17–19]. The vast uncertainty associated with MVP estimates for single populations or groups of populations probably underlies the tendency to find no evidence for statistical differences of MVPs among taxa [17] or strong life-history predictors of MVP size [18,19]. An alternative, more robust interpretation of that finding is that there is no significant difference in MVPs *between* taxa simply because there is such enormous variation in MVPs *within* taxa. Indeed, variation among populations is perhaps the most striking finding of recent analyses; for example, within-species estimates of standardized MVP varied more than 100-fold for the whooping crane (*Grus americana*), Eurasian beaver (*Castor fiber*), muskox (*Ovibos moschatus*), and others ([19] see Table S1 in supplementary material online]. *Thus, regardless of the taxon to which a population belongs, any 'rule of thumb' MVP is likely to be a poor estimate of*

Box 3. Outlier MVPs

In our re-examination of the Brook *et al.* supplemental data [18], it was apparent that their original Figure 1 truncated observations at ln[MVP] = 20 (~0.5 billion individuals). A replotting of their figure based on all observations in their supplemental data ($n = 1198$) revealed that the number of species with MVPs that exceeded 0.5 billion individuals varied by the population growth model fitted to the time-series data (Figure I), with higher frequencies of exceptionally large MVPs associated with models lacking density dependence (Figure Ia,b). These large MVP estimates could be an artefact of the method used to estimate MVP, for it seems difficult to argue that species such as the rough-legged hawk (*Buteo lagopus*), northern harrier (*Circus cyaneus*), or rook (*Corvus frugilegus*) require >1 billion individuals (model-averaged estimate) to remain viable, unless the studies supplying the empirical data were on populations subject to strong deterministic threats or severe catastrophic events. To remove the potential bias caused by what could be termed 'methodological outliers', we deleted any observations with an estimated ln[MVP] >20. This filtering shifted the median MVP estimate from 1181 ($n = 1198$) to 462 ($n = 756$) using the 40-generation criterion. If we further restricted our consideration to those species with relatively stable populations ($-0.02 \leq r \leq 0.02$), then the median MVP was further reduced to 280 individuals ($n = 339$).

Our point here is not to argue that MVP targets should be lower than those advocated by others [17–20], but to highlight two observations: (i) median MVP estimates are sensitive to the set of species used in their estimation; and (ii) there appear to be legitimate circumstances where reported MVPs can be overly pessimistic. Both of these observations indicate that summary statistics applied to empirically derived estimates of MVP are characterized by a degree of sensitivity that is inconsistent with the notion of a robust universal MVP.

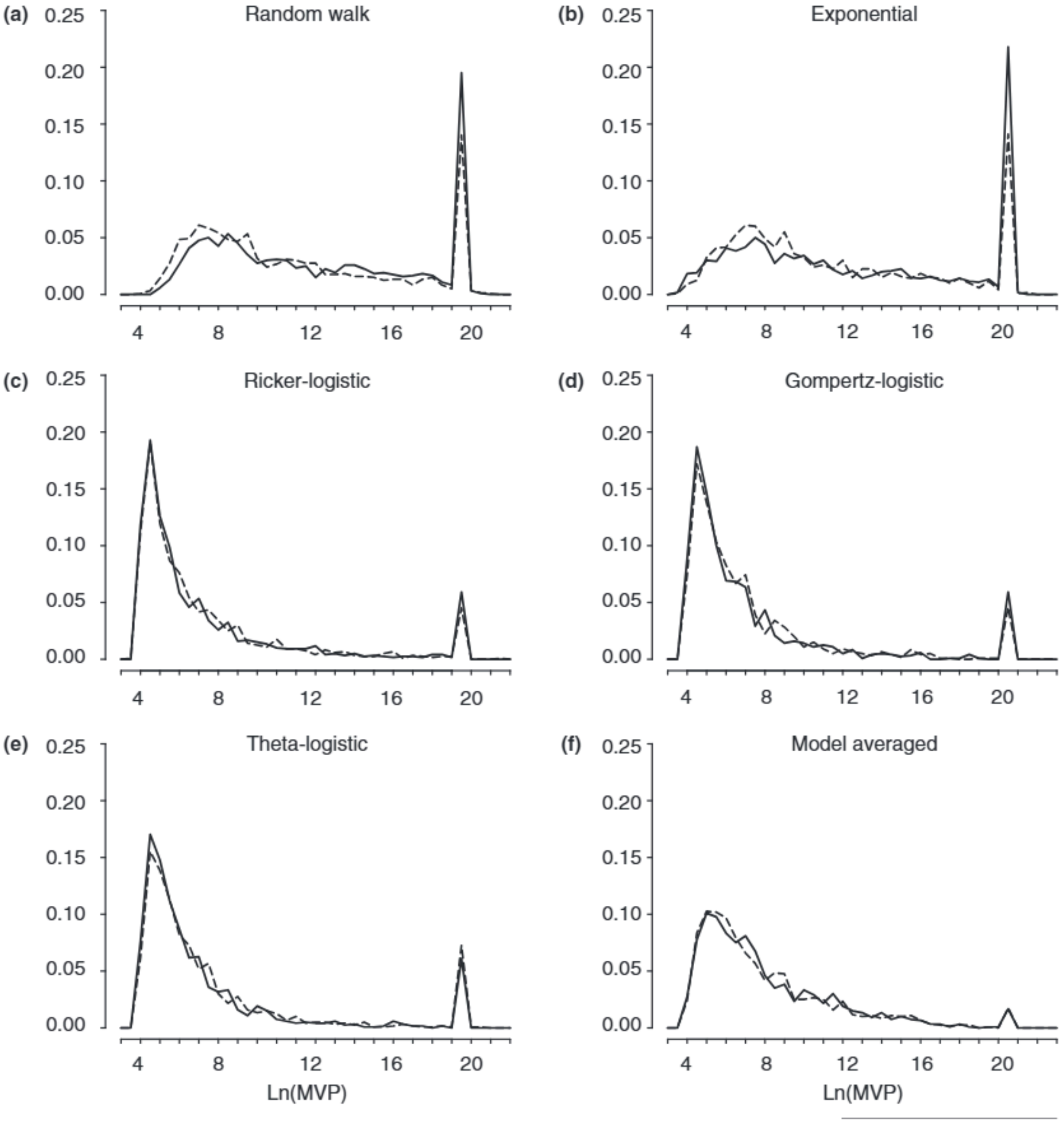

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Figure I. Full frequency distributions of ln[MVP] from Brook et al. supplemental data [18] among five population growth models **(a–e)** and model-averaged **(f)** estimates using Brook et al.'s 40-generation (dashed line) and 100-year (solid line) viability criteria. Potential methodological outliers are associated with a frequency spike at ln(MVP) ≈ 20.

the MVP of that population, highlighting the improbability that a universal threshold for MVP would be useful to conservation practitioners.

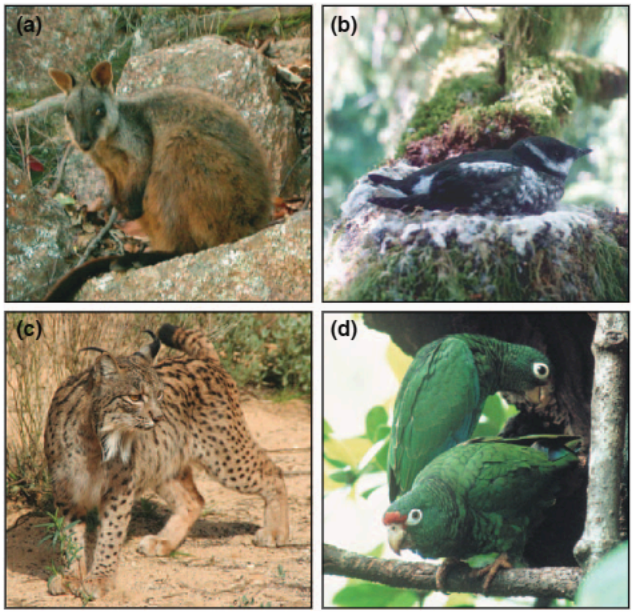

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Figure 1. The viability of a population of given size is strongly related to its environmental context as well as its life history. This can confound efforts to set a guideline figure at which a population ceases to have long-term viability. For example: **(a)** the brush-tailed rock wallaby (*Petrogale penicillata*) is thought to number in the region of 10^4–10^5 individuals but is declining steadily, owing to the effects of introduced predators and competitors; **(b)** the marbled murrelet (*Brachyramphus marmoratus*) of the pacific northwest USA is thought to number in the order of 10^4 individuals but is endangered, nevertheless, by a range of threats (habitat loss and fragmentation, increasing populations of nest predators and depletion of food resources at sea); **(c)** the Iberian lynx (*Lynx pardinus*), numbering approximately 10^2 individuals, is unlikely to be viable in the long term (owing to prey depletion, habitat loss and fragmentation and high rates of unnatural mortality); and **(d)** globally, mature Puerto Rican parrots (*Amazona vittata*) number only 10–10^2 but, nevertheless, the species has shown an increasing trend over recent decades. Reproduced, with permission, from Glen Fergus **(a)**; Thomas Hamer, Hamer Environmental L.P. **(b)**; Programa de Conservación Ex-situ del Lince Ibérico (http://www.lynxexsitu.es) **(c)**; and James W. Wiley and Noel F. R. Snyder **(d)**.

Alternatives to a ‘magic number’ for viability

Our reconsideration of recent MVP papers suggests that there are good reasons for managers and conservation practitioners to regard advocacy of a universal MVP threshold with considerable scepticism. That, in turn, prompts two questions. First, if published estimates of MVP are insufficient to identify the characteristics of a population or organism that will determine its approximate MVP, can one identify those attributes? Second, if one is unable to identify (and, therefore, plan for) a generally applicable minimum number of individuals to conserve, what are the consequences for conservation?

The concept of viable minima is of interest not only to conservation biologists. Minimum population densities are closely tied to several aspects of ecology, such as understanding consumer–resource relationships, the use of energy within ecosystems and the relative roles of factors that limit population persistence, whether genetic, behavioural or energetic. Although relationships between population density and body size have long been a focus of macroecology [34], theory has not yet been used to predict the lower limits to this relationship [35]. Viable minima are also closely tied to Allee effects [36] and, in particular, to the concept of ‘Allee thresholds’ (the point at which mean per-capita population growth rates become negative) [37]. This suggests that alternative, active fields of ecology could yield insights into the factors that predispose a population to be tolerant of low densities and (given an understanding of space use) small population sizes. It would be useful for researchers in those areas to consider how their work might relate to traits affecting MVP.

Box 4. MVPs and density dependence

Reed *et al.* recognized the importance of density dependence and included it where its impact on vital rates had been measured, or where there were strong indications of its operation [17]. Although they gave no details of the number of their studied populations for which adequate data on density dependence were available, we can gain a sense of their empirical challenge by examining the frequency distribution of study lengths for the populations considered. Study duration estimates for each population that we derived from Reed *et al.*'s appendix [17] show that over a quarter of the 102 populations used had been studied for one generation or less, half had been studied for less than two generations, and only one population had a study length that exceeded 25 generations (Box 2, Figure I). With these limitations on the temporal extent of available data, establishing plausible patterns of density dependence would be difficult for most, if not all, of the populations for which MVP was estimated.

A more rigorous approach was taken by Brook *et al.*, who analysed evidence for different forms of density dependence in population time series [18]. They found strong evidence that the inclusion of negative density dependence had an important bearing on MVP estimates. MVPs determined from shorter time series (which lacked strong evidence of density dependence) were more pessimistic (i.e. larger) than those based on longer time series (from which, evidence of density dependence was typically strong); overall, the estimated MVP was approximately an order of magnitude larger for short than for long time series [18].

Brook *et al.*'s [18] findings suggest an intriguing contrast with the earlier findings of Reed *et al.* [17]. Specifically, although Reed *et al.* found that longer studies led to more pessimistic MVP estimates, it appears that when density dependence is incorporated, the insights gained from longer studies provide reasons for greater optimism (smaller MVP estimates). Although some authors have subsequently expressed doubts about the model used to determine the form of density dependence [80], the emergent message remains that a failure to include density dependence is likely to inflate estimates of MVP substantially.

Given the clear importance of density dependence, it is perhaps surprising that Traill *et al.* found no evidence that the way in which density dependence was incorporated into models had a bearing on the estimated MVP [19]. Nevertheless, it is likely that the role of density dependence is more complex than could be detected by Traill *et al.*'s statistical approach. In particular, there are good reasons to expect that the form of density dependence would interact with other aspects of modelling and environmental context to influence MVP estimates.

If, at present, it is not possible to identify a universally applicable MVP, what might be the consequences for conservation? Traill *et al.* have linked uncertainty over MVPs to the current extinction crisis [20]. Thus, it is reasonable to ask to what extent the failure to agree on a universally applicable MVP contributes to the current extinction crisis? It seems more probable that: (i) extinctions occur because of a failure to identify and treat the causes of population declines [25,38], not because populations are assumed to be safe when, in fact, they are not; and (ii) failures to treat the major causes of decline are often related to political or economic issues [39–42], rather than to a lack of adequate scientific information on population viability.

What, then, is the utility of estimates for MVPs? In spite of the enthusiasm with which the MVP concept was initially embraced by conservation biologists, we can distil from literature only two advantages of having an estimate of MVP. First, an MVP can serve as a useful tool to persuade policy-makers that extinction is a possibility and action is required [43,44]. In this way, PVA and other quantitative criteria are used to classify taxonomically diverse species into threat categories under the International Union for Conservation of Nature (IUCN) Red List of Threatened Species [45], identifying populations that merit further scrutiny. In these cases, policy-makers should interpret estimates of extinction risk and its accompanied uncertainty for various scenarios, rather than comparing recent estimates of population size to an estimate of a ‘secure’ MVP population size. Second, MVPs can be used to determine conservation targets, either proactively or reactively (*sensu* [46]). Proactive targets set minimum size thresholds that, if reached, would place populations in unacceptable danger. Reactive targets suggest objectives for population recovery programs (e.g. delisting decisions). Value judgements are likely to differ in the two cases. Reactive MVPs could be used in prioritization, for example, as a tool for determining probable return on investment and, thus, as an aid to ecological triage [20]. Specifically, Traill *et al.* suggest prioritizing spending based on the distance a population is below a generalized target size of 5000 adults, in conjunction with the cost and likelihood of elevating the population to that target [20], ‘...to abandon hopeless-case species in favour of greater returns elsewhere’ [21]. Given the poor support for a universal MVP, this approach lacks credibility.

In keeping with numerous other authors (e.g. [9,45,47–54]), we recognize the value of PVA in bringing together relevant information on a population, formalizing understanding of the important processes, exposing gaps in knowledge, and serving as a focus for both scientists and policy-makers. However, in agreement with those same authors, we recommend against using the outcomes of such modelling exercises to set conservation targets unless there are strong reasons to believe that modelling outcomes are robust and defensible for the focal population. Embracing a single, estimated MVP threshold would release biologists from the obligation to assess the situation of the focal population, thereby forfeiting the diagnostic benefits that emerge from doing so [25]. Much of modern conservation is directed towards landscape- or ecosystem-level processes [55–57]. However, in situations in which populations remain the focus of conservation action, particularly when trying to salvage populations that are already in trouble, we suggest that there is no substitute for diagnosing and treating the mechanisms behind the decline of a population [25,38], actions that are unlikely to be informed by using a ‘magic number’ to set a target for conservation.

Conclusions

We applaud recent efforts [17–20] to encourage more quantitative approaches to evaluating population viability than a reliance on the oft-cited 50/500 MVP rule of conservation genetics [58,59]. The findings that MVP estimates are sensitive to the duration over which data were gathered and that meta-analytic comparisons among MVP estimates require rigorous standardization emphasize the need to obtain good estimates of demographic variability. We also suspect (as have others long before [60]) that multiple populations totalling thousands (not hundreds) of individuals will be needed to ensure long-term persistence. Nevertheless, MVP estimates both among and within species show striking variation for many reasons. The fundamentally contingent nature of MVPs means that we cannot support a universally applicable MVP threshold.

Ecology has been characterized as a science built on ‘contingent generalizations’ [61,62]. Such contingency has long been acknowledged in the PVA literature [2] and continues to foil attempts to generalize about crucial levels of habitat or abundance [16,63], even among populations of a single species [64]. Uncertainty, even when dealing with populations of the same species, suggests that generalizing among species is a dangerous undertaking. Failing to account for uncertainty is a common problem in conservation [65], and can lead to biased expectations and to the misdirection of scarce conservation resources [66].

The MVP concept is a key example of one of the hardest questions faced in conservation biology: how much is enough? Key national legislations governing endangered species decisions (e.g. the US Endangered Species Act, Canada’s Species at Risk Act, and Australia’s Environmental Protection and Biodiversity Act), as well as efforts by national and international organizations committed to species conservation [67], use MVP concepts that can revolve around listing decisions (has the species declined to a number that is threatened with extinction?), delisting decisions (has it recovered enough that it is no longer so threatened?), extinction risk categorizations, and determining the number and size of protected areas that a threatened species needs. MVP analyses and PVA modelling can be used to assist in these decisions, but their value is constrained by large uncertainty in model outcomes [68]. Realistic MVPs might well be in the thousands for many life histories, but uncertainty around any guideline figure would be of a similar order of magnitude. The extinction of the passenger pigeon (*Ectopistes migratorius*), perhaps the most abundant land bird in North America during the 1800 s (numbering 3–5 billion individuals [69]), stands as a sobering reminder that population size alone is no guarantee against extinction. As others have remarked, ‘population viability analysis is an inexact science,’ [17] and there is ‘no single ‘magic’ population size that guarantees’ population persistence [70].

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tree.2011.03.001.

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