

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Minimum viable population size: A meta-analysis of 30 years of published estimates

Lochran W. Traill^a, Corey J.A. Bradshaw^b, Barry W. Brook^{a,*}

^aResearch Institute for Climate Change and Sustainability, School of Earth and Environmental Sciences, University of Adelaide, South Australia 5005, Australia

^bSchool for Environmental Research, Institute of Advanced Studies, Charles Darwin University, Darwin, Northern Territory 0909, Australia

ARTICLE INFO

Article history:

Received 5 April 2007

Received in revised form

5 June 2007

Accepted 15 June 2007

Available online 6 August 2007

Keywords:

MVP

Extinction correlates

Population viability

Generalized linear mixed-effects models

Meta-analysis

ABSTRACT

We present the first meta-analysis of a key measure in conservation biology: minimum viable population (MVP) size. Our analysis is based on studies published since the early 1970s, and covers 141 sources and 212 species (after filtering 529 sources and 2202 species). By implementing a unique standardization procedure to make reported MVPs comparable, we were able to derive a cross-species frequency distribution of MVP with a median of 4169 individuals (95% CI = 3577–5129). This standardized database provides a reference set of MVPs from which conservation practitioners can generalize the range expected for particular species (or surrogate taxa) of concern when demographic information is lacking. We provide a synthesis of MVP-related research over the past 30 years, and test for ‘rules of thumb’ relating MVP to extinction vulnerability using well-known threat correlates such as body mass and range decline. We find little support for any plausible ecological and life history predictors of MVP, even though correlates explain >50% of the variation in IUCN threat status. We conclude that a species’ or population’s MVP is context-specific, and there are no simple short-cuts to its derivation. However, our findings are consistent with biological theory and MVPs derived from abundance time series in that the MVP for most species will exceed a few thousand individuals.

© 2007 Elsevier Ltd. All rights reserved.

1. Introduction

Conservation practitioners are challenged to make informed choices about the allocation of finite resources to mitigate the current extinction crisis (Ceballos and Ehrlich, 2002; Thomas et al., 2004), while being cognizant of the complex ecological (Shaffer, 1985) and socio-political (Woodroffe et al., 2005) systems in which such decisions are embedded. Accelerating habitat and species losses have mandated consideration of this problem in terms of the number of individuals required for persistence within a specified timeframe (Shaffer, 1981;

Shaffer, 1987) because small and range-restricted populations are highly vulnerable to extinction (Terborgh and Winter, 1980; Gilpin and Soulé, 1986; Schoener and Spiller, 1987). The concept of a ‘minimum viable population’ (MVP; Shaffer, 1981; Lacava and Hughes, 1984) has been used extensively in species recovery and conservation management programs (Clark et al., 2002), and is relevant to the IUCN’s Red List (www.iucnredlist.org) criteria concerning small and range-restricted populations. However, the biological and utilitarian value of MVP to species conservation has remained controversial (Shaffer, 1987; Caughley, 1994; Reed et al., 1998).

* Corresponding author. Tel.: +61 8 8303 3745; fax: +61 8 8303 4364.

E-mail addresses: lochran.traill@adelaide.edu.au (L.W. Traill), corey.bradshaw@cdu.edu.au (C.J.A. Bradshaw), barry.brook@adelaide.edu.au (B.W. Brook).

0006-3207/\$ - see front matter © 2007 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2007.06.011

Past reviews of the concept (Samson, 1983; Gilpin and Soulé, 1986; Ewens, 1990) and its application (Sjogren-Gulve and Ebenhard, 2000; Bulte, 2001; Stinchcombe et al., 2002) have been theoretical, qualitative or cursory, with the primary literature tending to focus on inherent problems of estimation (Reed et al., 1998; Brook et al., 2000) rather than utility *per se*. Despite both debate on the real-world applicability of the concept (Caughley, 1994; Reed et al., 1998) and its sustained popularity (Bulte, 2001; Reed et al., 2003; Tear et al., 2005; Brook et al., 2006), there has been no broad-scale quantitative assessment of the MVP literature. This is perhaps due in part to the difficulty of standardization (e.g., definition of risk and timeframe, alternative model structures) across studies.

Individual case studies of MVP for any given species cannot reveal: (a) the form and variance of the cross-species distribution of MVP, and whether these agree with theoretical predictions, or match with genetic, demographic or environmental rules of thumb for MVP; (b) the existence (or absence) of taxonomic or life history patterns in MVP; and (c) generalizations useful for conservation management. Here we provide the first quantitative meta-analysis of published MVP estimates, to determine the ensemble properties of MVP and whether useful generalizations emerge.

2. Methods

2.1. Dataset

We conducted an exhaustive meta-analysis of the MVP-relevant literature. All MVP data were obtained from published articles, book chapters and scientific reports. Primary literature was identified through ISI's Web of Science (www.isinet.com) and Elsevier's Science Direct (www.sciencedirect.com) databases. The online search engines Google (www.scholar.google.com) and Yahoo (www.yahoo.com) were used to identify, and where possible source, scientific reports and other grey literature. Search terms such as "minimum & viable" and "extinction" were used, among others. Monographs and book chapters were sourced through university library databases. A cross-check of the reference list of each article permitted further collation, especially for sources published prior to 1992. Each article was reviewed for MVP estimates, and where population viability analysis (PVA) methods were used, populations were considered 'viable' only where $\geq 80\%$ of the initial population survived for ≥ 20 years (Shaffer, 1981). If the initial population was considered unviable but a target MVP estimate provided, the latter was used. Where MVP was not specified explicitly, we required at least the risk of extinction for a defined timeframe and initial population size to be reported. Data from baseline PVA models were selected and hypothetical scenarios ignored. MVP estimates derived through genetic analyses or population censuses were also included. A database was collated and structured according to taxonomic group. Attributes such as species IUCN Red listing (IUCN, 2006) were later assigned, and the completed database is available online as [Supplementary Material](#) (Table S1).

2.2. Controlling for differences in the modelling technique used to derive MVP

Data were collated for 287 MVP estimates, initially by collecting all parameters that some or all of the models used to derive MVP. These were (1) probability of persistence, (2) duration of persistence in years, (3) duration of persistence in generations, (4) model type or method used to derive MVP estimate, (5) sex ratio at birth, (6) adult sex ratio, (7) form of density dependence, (8) carrying capacity, (9) Allee effect (present/absent), (10) inbreeding depression considered, (11) probability of catastrophe, (12) birth to adult survival, (13) adult survival, (14) per cent of female population breeding, (15) fecundity, (16) age at parturition, (17) longevity, (18) density and (19) dispersal ability. In many cases, data for the above parameters were omitted or not given by the authors.

Using logic and previous hypotheses based on extinction theory (Akcakaya, 1998; Brook et al., 2006), we reduced the initial 19 model attributes to six predictors which we hypothesized would be relatively independent and explain much of the methodological variation in MVP among studies: (1) Model used [MOD]: a categorical index of method or model used to derive MVP. This was restricted to: (a) individual-based simulation, (b) matrix/cohort-based simulation (including time series methods), (c) empirical census or (d) genetic analysis; (2) Persistence probability [PER]: a continuous variable of the probability of population persistence over a given time period. If not used, and where the population was stated as viable, the probability was assumed to be 100%; (3) Duration [DUR]: a continuous variable being the period of time over which a population was deemed viable, expressed as a continuous variable in generations (3–1200). When generation length of the species was not provided, we assumed it to be equal to the age at primiparity. Where a MVP was estimated from a census or genetic analysis, or where the time frame of viability was not stated explicitly ($n = 13$), viability was assumed to be 100 years and the number of generations estimated on this basis; (4) Density dependence [DEN]: a categorical factor classified as: (a) density-independent, (b) ceiling-type density dependence or (c) functional-type density dependence. The differentiation between categories (b) and (c) was necessary to account for their opposite effect on MVP – ceiling density dependence increases extinction risk, whereas non-Allee functional density dependence (negative feedback) decreases extinction risk, relative to density-independent models (Ginzburg et al., 1990); (5) Inbreeding depression [INB]: a categorical factor indicating whether the loss of genetic variation in the population was modelled or not. This was most commonly, although not universally, applied as 3.14 diploid lethal equivalents on juvenile survival; and (6) Catastrophes [CAT]: a categorical factor indicating whether random catastrophe outside the normal distribution of environmental stochasticity was included or not.

2.3. Ecological extinction predictors

Following previous work (Brook et al., 2006), we reduced a set of postulated ecological, life history and anthropological extinction correlates to a set of eight composite predictors. Where these correlates were not given in the sourced litera-

Table 1 – Summary of generalized linear and generalized linear mixed-effect model (GLM and GLMM, respectively) comparisons using Akaike's Information Criterion corrected for small sample sizes (AIC_c) and Bayesian Information Criterion (BIC): (a) GLMMs of the MVP-generating model correlates used for standardization (PER = persistence probability, MOD = model type, DUR = duration in generations, DEN = form of density dependence, INB = inbreeding included, CAT = catastrophes included) against the original MVP estimates; (b) GLMMs of the standardized MVP (MVP_{st}) against ecological and life history correlates (BWT = body weight, GNL = generation length, FEC = fecundity SOC = social grouping, HMP = human impact, DSP = dispersal, RAN = range, TRE = population trend); (c) GLM of the ecological and life history correlates against MVP_{st}; and (d) binomial GLMM relating species IUCN Red-Listing (listed or not listed) to ecological and life history correlates

Candidate models	LL	k	ΔAIC _c	wAIC _c	ΔBIC	wBIC	%DE
(a) MVP-generating model correlates							
MVP ~ PER + DUR + INB + CAT	−425.935	7	0.056	0.439	0.000	0.800	6.3
MVP ~ DEN + PER + DUR	−427.324	7	2.834	0.109	2.778	0.199	6.0
MVP ~ PER + DUR	−438.280	5	20.489	<0.001	13.978	<0.001	3.6
MVP ~ MOD + PER + DUR + DEN + INB + CAT	−420.397	12	0.000	0.451	15.708	<0.001	7.5
MVP ~ MOD + PER + DUR	−435.307	8	20.961	<0.001	24.102	<0.001	4.2
MVP ~ null	−454.568	3	48.889	<0.001	35.841	<0.001	0.0
(b) GLMM of ecological and life history correlates							
MVP _{st} ~ null	−1.151	3	0.000	0.364	0.000	0.757	0.0
MVP _{st} ~ BWT	−1.116	4	2.025	0.132	5.096	0.059	3.0
MVP _{st} ~ TRE	−1.127	4	2.046	0.131	5.114	0.059	2.1
MVP _{st} ~ HMP	−1.146	4	2.084	0.128	5.151	0.058	0.5
MVP _{st} ~ GNL	−1.147	4	2.087	0.128	5.155	0.058	0.4
MVP _{st} ~ BWT + GNL	−1.112	5	4.136	0.046	10.247	0.005	3.4
MVP _{st} ~ HMP + TRE	−1.127	5	4.167	0.045	10.272	0.004	2.1
MVP _{st} ~ BWT + GNL + FEC	−0.973	6	6.003	0.018	15.142	0.000	15.5
MVP _{st} ~ BWT + GNL + DSP + RAN	−1.052	7	8.333	0.006	20.451	0.000	8.6
MVP _{st} ~ BWT + GNL + SOC	−1.016	8	10.456	0.002	25.555	0.000	11.8
MVP _{st} ~ BWT + GNL + FEC + SOC + DSP + RAN + HMP + TRE	−0.914	13	21.646	0.000	51.184	0.000	20.6
(c) GLM of ecological and life history correlates							
MVP _{st} ~ BWT + GNL + FEC	196.466	5	0.000	0.746	0.000	1.000	15.5
MVP _{st} ~ BWT	181.859	3	25.039	0.000	18.502	0.000	3.0
MVP _{st} ~ null	178.585	2	29.528	0.000	19.692	0.000	0.0
MVP _{st} ~ BWT + GNL + SOC	191.868	7	13.454	0.001	19.909	0.000	11.8
MVP _{st} ~ TRE	180.875	3	27.006	0.000	20.469	0.000	2.1
MVP _{st} ~ BWT + GNL + DSP + RAN	188.197	6	18.658	0.000	21.896	0.000	8.7
MVP _{st} ~ BWT + GNL	182.293	4	26.248	0.000	22.989	0.000	3.4
MVP _{st} ~ HMP	179.103	3	30.551	0.000	24.014	0.000	0.5
MVP _{st} ~ GNL	178.968	3	30.821	0.000	24.283	0.000	0.4
MVP _{st} ~ BWT + GNL + FEC + SOC + DSP + RAN + HMP + TRE	203.025	12	2.159	0.253	24.379	0.000	20.6
MVP _{st} ~ HMP + TRE	180.878	4	29.079	0.000	25.820	0.000	2.1
(d) GLMM of ecological and life history correlates							
IUCN ~ BWT + GNL + FEC + SOC + DSP + RAN + HMP + TRE	−60.328	13	74.329	0.000	0.000	0.867	54.0
IUCN ~ HMP + TRE	−74.019	5	0.000	0.556	4.571	0.088	43.6
IUCN ~ HMP	−76.136	4	0.452	0.444	5.912	0.045	42.0
IUCN ~ BWT + GNL + DSP + RAN + TRE	−84.747	8	32.400	0.000	36.731	0.000	35.4
IUCN ~ BWT + GNL + DSP + RAN	−89.857	7	37.429	0.000	44.222	0.000	31.5
IUCN ~ BWT + GNL + FEC + TRE	−100.322	7	56.577	0.000	66.842	0.000	23.6
IUCN ~ GNL + TRE	−107.006	5	63.603	0.000	73.362	0.000	18.5
IUCN ~ BWT + GNL + TRE	−105.896	6	64.494	0.000	74.464	0.000	19.3
IUCN ~ TRE	−112.062	4	70.888	0.000	80.100	0.000	14.6
IUCN ~ BWT + GNL + SOC + TRE	−104.677	9	73.018	0.000	82.254	0.000	20.2
IUCN ~ BWT + TRE	−111.778	5	73.039	0.000	83.116	0.000	14.8
IUCN ~ BWT + GNL + FEC	−116.044	6	84.142	0.000	95.822	0.000	11.6
IUCN ~ BWT + GNL	−119.315	5	87.930	0.000	98.583	0.000	9.1
IUCN ~ GNL	−121.283	4	89.159	0.000	99.019	0.000	7.6
IUCN ~ BWT + GNL + SOC	−115.406	8	89.623	0.000	101.176	0.000	12.1
IUCN ~ null	−131.254	3	106.551	0.000	115.564	0.000	0.0
IUCN ~ BWT	−130.474	4	107.425	0.000	117.768	0.000	0.6

All GLMMs include the taxonomic Class (e.g., Mammalia, Aves, etc.) as a random effect. Shown are model log-likelihood (LL), number of parameters (k) change in AIC_c (ΔAIC_c), AIC_c weight (wAIC_c), change in BIC (ΔBIC), BIC weight (wBIC) and the per cent deviance explained (%DE). %DE is a measure of the structural goodness-of-fit of the model. Models sequences are ordered by wBIC for all model sets, because we were primarily interested in main rather than tapering effects.

ture, data were derived from online databases or published papers on that species (see [Appendix S1, Supplementary Material](#)). Predictors used were: (1) Body weight [BWT]: an allometric scaling covariate (mass in g). Body mass data for the mostly herbaceous plants were estimated using a benchmark wet-weight for a similar-sized species, and forestry timber data used to estimate mass for large Monocotyledons; (2) Generation length [GNL]: taken as age at sexual maturity and estimated in months; (3) Fecundity [FEC]: a continuous variable representing the mean number of young produced per female per year. This included the average number of eggs laid/young born, but did not account for the probability of survival to adulthood (such as in birds and herptiles). Multiple broods within a year were taken into consideration to calculate a total yearly output of offspring; (4) Social grouping [SOC]: a categorical index of mating systems. These were (a) colonial (i.e., large breeding colonies and spawning sites), (b) polygamous or gregarious, (c) monogamous and (d) solitary (i.e., a brief period of copulation only or asexual/hermaphroditic breeding, and plants); (5) Dispersal [DSP]: the migratory or dispersive capability of a species, where dispersal and migration are used interchangeably, and categorized broadly as (a) migratory or (b) constrained. A species was considered constrained if it remained within a 20-km radius of its place of birth/hatching; (6) Range [RAN]: the geographic distribution scored as either (a) geographic range spanning more than one major biome ([Smith and Smith, 2003](#)), or (b) the species was primarily restricted to a single biome; (7) Human impact [HMP]: a categorical index of the (a) beneficial or (b) generally adverse influence of people. Species considered to benefit from humans were domesticated animals, harvested crops and commensals, for example; and (8) Population trend [TRE]: a categorical index of (a) stable or increasing population or (b) a population in general decline. TRE was assumed to account for deterministic population decline.

2.4. Statistical analyses

For all analyses we reduced the population dataset from 287 populations to 212 unique species to avoid potential problems of pseudo-replication caused by multiple representations (different populations) of the same species. Two a priori model sets ([Burnham and Anderson, 2002](#)) were constructed to examine the amount of variation explained in MVP ([Table 1](#)): (a) six models encompassing a selection of the model characteristics used to derive MVP, and (b) eleven models encompassing a selection of ecological, life history and anthropogenic threat terms.

To gauge the relative importance of each derived variable for predicted MVP, we fitted a series of generalized linear mixed-effects models (GLMM) to \log_e MVP in the R Language ([R Development Core Team, 2004](#)), using the `lmer` function (in the `lme4` library). MVP was assumed on a priori grounds to be log-normally distributed ([Brook et al., 2006](#)). The random effects error structure of GLMM was used to correct for non-independence of species due to potential shared evolutionary life history traits ([Felsenstein, 1985](#)) by decomposing the variance across species by hierarchical Linnaean taxonomy (Class) (following [Blackburn and Duncan, 2001](#)). Class was selected as the taxonomic random term in preference to Order

because of sample size limitations: many Orders were represented by a single species only. The importance of considering taxonomy in the GLMM was assessed also by repeating the analyses using a series of generalized linear models (GLM) with the same ecological and life history correlates. Asymptotic indices of information loss were used to assign relative strengths of evidence to the different competing models ([Burnham and Anderson, 2002](#)), with both Akaike's Information Criterion corrected for small sample sizes (AIC_c) and Bayesian Information Criterion (BIC) weights used as an objective means of model comparison ([Burnham and Anderson, 2002](#)). AIC_c identifies tapering effects where n , per term, exceed approximately 20 data, whereas BIC only identifies main effects ([Link and Barker, 2006](#)). Full model results are shown in [Table 1](#).

Because MVP estimates taken from the literature vary due to the particular methods employed in each case, it was necessary to standardize estimates (MVP_{st}) to a consistent model structure. To do this we used the best-ranked GLMM based on BIC ([Table 1](#)) for the model characteristics set (the model including persistence probability, duration of persistence, inbreeding depression and catastrophes, and a phylogenetic correction), setting persistence probability (PER) to 99%, the number of generations (GNL) over which MVP was estimated to 40, and set the β coefficients for the factors to have inbreeding depression (INB) and catastrophes (CAT) included. The standardizing equation was therefore:

$$\log_e MVP_{st} = \log_e MVP_{orig} + \beta_{PER} \cdot \log_e \left(\frac{0.99}{PER} \right) + \beta_{GNL} \cdot \log_e \left(\frac{40}{GNL} \right) + \beta_{INB} + \beta_{CAT}$$

where $\beta_{PER} = 22.5618$, $\beta_{GNL} = 0.4365$, $\beta_{INB} = 1.2306$, $\beta_{CAT} = 0.4258$. The distributions of the original versus standardized MVP estimates are shown in [Fig. 1](#). For each species, the

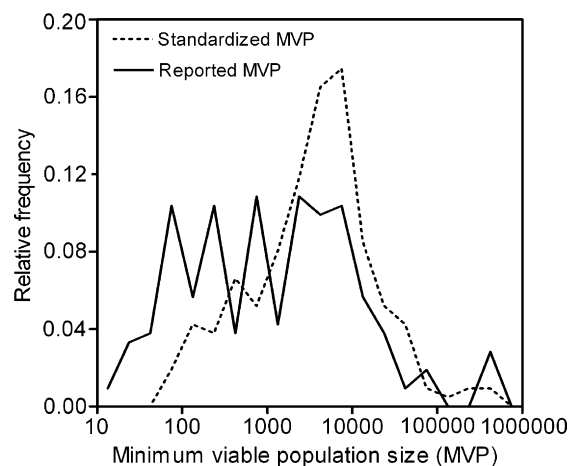


Fig. 1 – Comparison of original versus standardized minimum viable population sizes. Relative frequencies of the 212 MVP species estimates (\log_{10} scale) for the original, uncorrected values, taken directly from the literature (solid line, [Supplementary Notes](#)) and the same values after standardization for differing structure of the MVP-generating method/model (dotted line).

respective coefficients were set to zero when its original MVP-generating model matched the defined standardization criterion. Although the per cent deviance explained in MVP by the highest BIC-ranked model was only ~6%, standardization was still required to avoid potentially spurious relationships in the analysis of MVP and ecological correlates.

We tested the ecological predictors by fitting GLMM to $\log_e \text{MVP}_{\text{st}}$ with Class set as a random effect for phylogenetic control, and then fitted GLM without random effects to examine the importance of including phylogenetic control in the models. To provide an independent check of the biological authenticity of the derived ecological predictors with respect to a measure of extinction proneness, we constructed analogous models using the IUCN Red Listing (IUCN, 2006) of species (17 models). Of the 212 species represented in the meta-analysis, 92 were Red-Listed (anything other than 'Least Concern').

3. Results

We sourced 529 relevant articles published between January 1974 and December 2005, describing up to 2202 species and a minimum of 1444. The exact count of distinct species could not be determined because one large study (Fagan et al., 2001) did not report which species were examined. Excluding a recent study on MVP which fitted a set of simple phenomenological models to 1198 abundance time series (Brook et al., 2006), 141 articles met the selection criteria and listed 287 MVP estimates for 212 species. A gradual increase in MVP-related publications over the past 30 years was matched by a concomitant rise in the number of species studied (Fig. 2). The establishment of public-access online databases (e.g., IUCN Red list and Global Population Dynamics Database

[GPDD], www.cpbnts1.bio.ic.ac.uk/gpdd/) and subsequent multi-species analyses (Fagan et al., 2001; Reed et al., 2003; Brook et al., 2006) in recent years were responsible for large increases in the number of species evaluated (Fig. 2).

A bias toward large-bodied species in extinction-related research was evident. Ultimately, we found that the frequency distribution of species studied was skewed towards heavier species, with 53.8% of all species and 85.3% of mammals exceeding 1000 g (Fig. 3). By contrast, only 31% of 4049 extant mammals listed in a large database of body masses (Smith et al., 2003) are >1000 g. Moreover, vertebrates accounted for 47% of all species studied, despite this taxon representing only a few percent of named species (IUCN, 2006), and of the 92 species in the meta-analysis that were IUCN Red-Listed, 62.0% were mammals. Surprisingly, the Red Listing of species included in all MVP-related studies showed an over-representation of non-threatened species (Fig. S1, Supplementary Material), likely due to larger studies (Brook et al., 2006) being based on abundance time series collected for purposes not directly related to conservation, such as monitoring and harvesting.

The reported MVP values were not comparable in a quantitative meta-analysis because of differences in the specified risk definitions and structure of the generating models. We therefore collated relevant model type and structure data for each species and fitted a set of GLMM and used AIC_c and BIC to select the most parsimonious model(s) for standardizing MVP (see Section 2). The most parsimonious model relating MVP to 'generating-model structure' was, according to AIC_c, the one that included all model characteristics; however only 7.5% of the deviance was explained by the saturated model after controlling for phylogeny (Table 1). An analysis on a reduced dataset, using Class/Order as a nested random effect, yielded an equivalent result. It has been shown that with sufficient sample sizes, the Kullback–Leibler prior used to justify AIC_c weighting favours more complex models (Link and

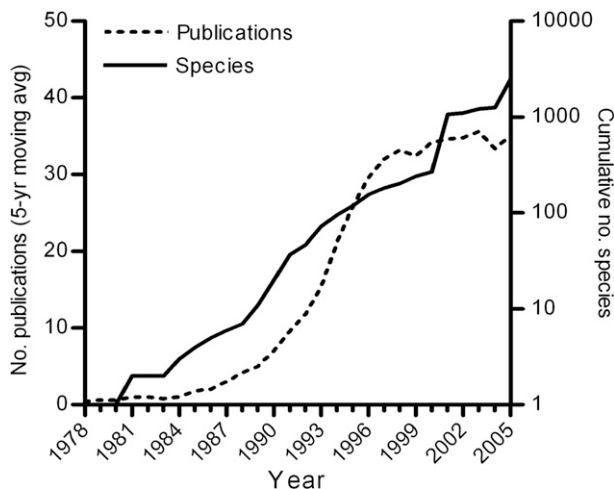


Fig. 2 – Publication trends for minimum viable population size (MVP), 1974–2005. The cumulative number of species in studies related to population viability and extinction (\log_{10} scale, solid line), and a 5-year moving-average of the number MVP-related peer-reviewed and unpublished literature sources (dotted line). A large increase in species studied since 2001 marked the advent of freely-accessible online population databases.

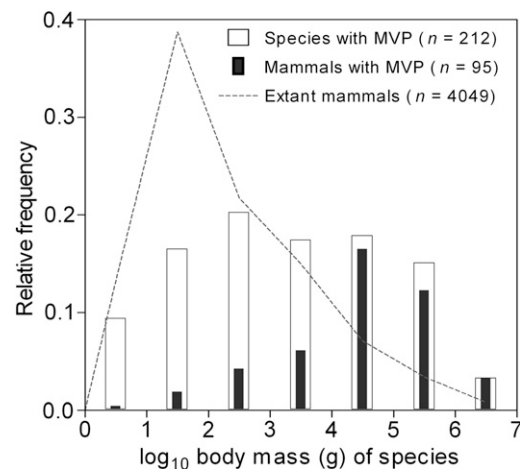


Fig. 3 – Relative frequency distribution of body weight (\log_{10} scale in g). All species (open bars) and mammals (solid bars) with estimates of minimum viable population size are shown, with the relative distribution of body weights for all extant mammals for which data are available (Smith et al., 2003) (dotted line) for comparison.

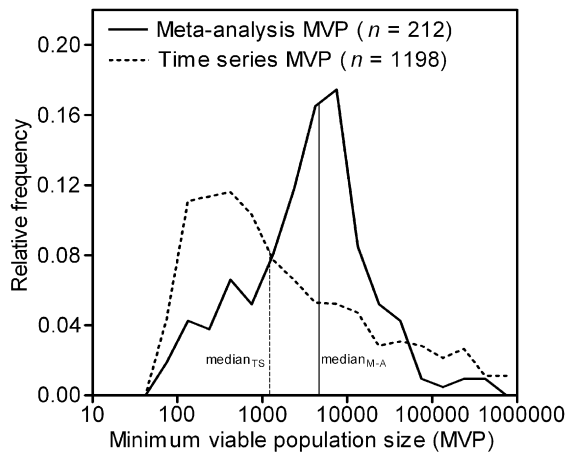


Fig. 4 – Relative frequency distribution of minimum viable population (MVP) estimates (\log_{10} scale). Standardized MVPs from the meta-analysis of 212 species examined since 1976 (solid line) are compared to MVP estimates derived independently from models fitted to 1198 species' time series of abundance data (dotted line) (Brook et al., 2006). Median values are represented by vertical lines for each distribution.

Barker, 2006), so we also considered model ranking according to the dimension-consistent BIC weights to identify the main drivers of structural variation in MVP (i.e., ignoring tapering effects). The latter metric signalled that only four of the six correlates considered (probability of persistence, duration,

inbreeding and catastrophe – see Section 2) explained an important component (6.3%) of the deviance in MVP (Table 1). Thus, using the best BIC-supported model's coefficients, we standardized MVPs (MVP_{st}) to a 99% persistence probability, and time frame of 40 generations (a previously used time frame – Brook et al., 2006).

Median MVP_{st} was 4169 individuals (3577–5129, 95% CI), compared to the median reported uncorrected MVP of 3299 individuals. This is similar to the recommended effective population size of 4500 individuals based on genetic data (Frankham, 1995), and the median MVP of 5816 reported for vertebrates (Reed et al., 2003). The frequency distribution of the standardized published MVP estimates (Fig. 4) was more symmetrical and peaked at a higher MVP than the model-averaged distribution of MVPs derived from an independent time series analysis (Brook et al., 2006). This result contradicts the view that estimates of population viability derived from scalar models may be overly precautionary (Dunham et al., 2006), probably because Brook et al. (2006) considered functional density dependence, whereas Dunham et al. (2006) only used a population ceiling function.

4. Discussion

Deciding how much habitat is needed to achieve conservation goals requires robust rules of thumb because in many situations there are insufficient data to develop a species-specific population viability analysis (Shaffer et al., 2002). So, can we provide any generalities from this meta-analysis of MVP? Models relating ecological attributes predicted *a priori* to

Table 2 – Summary of median (and bootstrapped 95% confidence bounds) minimum viable population sizes from all available literature (n = number of species; standardized = MVP_{st} ; original = MVP_{orig})

	n	MVP_{st}	MVP_{st} 95% CI	MVP_{orig}
<i>Vertebrates</i>				
Birds	48	3742	2544–5244	3310
Fish	8	1,239,727	211,171–2,085,032	500,000
Mammals	95	3876	2261–5095	2901
Herptiles ^a	31	5409	3611–6779	3999
Sum/median	182	4102	3325–5096	3697
<i>Other taxa</i>				
Plants ^b	22	4824	2512–15,992	2097
Insects	5	10,841	1650–103,625	2000
Marine invertebrates ^c	3	3611	1984–1,047,547	2500
Sum/median	30	6111	3165–10,768	2100
<i>Body mass</i>				
<1 kg	98	5137	3577–6947	2509
≥1 kg	114	3956	2575–4961	3697
<i>IUCN</i>				
Listed	92	3611	2261–5033	2484
Not listed	120	4824	3867–5878	3435
All species	212	4169	3577–5129	3299

^a Reptiles and amphibians.

^b Mosses, ferns, dicotyledons, monocotyledons and gymnosperms.

^c Molluscs and crustaceans.

correlate with extinction risk failed to explain much of the variation in MVP_{st}; the saturated correlates model accounted for 20.6% of the explained deviance after taking phylogeny into account as a random effect (Table 1). The most parsimonious GLMM, according to BIC, failed to find evidence for any main effects. Yet these predictors explained 54% of the deviance in whether or not a species was IUCN Red-Listed. This contrast between the predictability of MVP versus IUCN status has been described in previous work (Brook et al., 2006), using MVP estimated from an independent source (time series data), and effectively highlights two different paradigms (Caughley, 1994). Ecological predictors of threatened status indicate a species' sensitivity to the largely systematic drivers of extinction (Cardillo, 2003), confirmed here by the support for IUCN listing. MVP represents, on the other hand, the small population paradigm (Caughley, 1994); that is, a population already reduced in size and subject to a host of population-specific threats (many stochastic) which cannot be accounted for in broad species comparisons such as ours.

MVP is thus an appropriate measure of the viability of populations that have declined deterministically (or catastrophically) to a small size, but subsequently 'stabilized' (though they continue to fluctuate stochastically). As such, context-specific factors such as variability of the local environment are more relevant for determining MVP than the broad-scale extinction drivers that cause endangerment. MVP size and regional or global extinction risk are thus unrelated (Brook et al., 2006). Note that the majority of vertebrates considered threatened by IUCN are listed under Criterion A, which relates threat to rate and magnitude of population size or range decline (IUCN, 2006). The assessment of vulnerability of IUCN is complementary, but essentially unrelated, to that derived from MVP.

Despite the lack of predictability of MVP based on plausible (and measurable) correlates of extinction risk, we can draw some broad generalizations from the meta-analysis. MVP-related studies have gradually increased over the past three decades, with no apparent decline in the concept's use, and with a trend toward multi-species analyses (Fig. 2). Depending on the strength of density dependence, MVP follows either a weakly right-skewed or symmetrical distribution (Fig. 4), with the highest probability density in the range of a few thousand, rather than hundreds, or tens of thousands of individuals, comparable to the findings of Brook et al. (2006) and Reed et al. (2003). While there was some broad taxonomic variation, the true magnitude of any differences is uncertain because some taxa have been poorly sampled to date (fish and invertebrates – Table 2).

A major product of this collation and standardization of published MVPs, especially when coupled with a previous phenomenological analysis (Brook et al., 2006), is a database of MVPs and species attributes that span a broad range of biomes, body sizes, life histories and threat status. This resource (Table S1, provided as a searchable spreadsheet table in the Supplementary Material) can be used by conservation practitioners as a preliminary guide to the MVP range expected for particular species or surrogate taxa of concern, or indeed to derive a target MVP for data-deficient species (we recommend the upper 95% confidence limit of MVP for the taxon in question, excluding poorly sampled taxa such as insects, fish and

marine invertebrates). Moreover, these results provide important baseline data for testing future research hypotheses regarding population size and extinction risk, particularly with the now-evident shift toward the Bayesian paradigm within ecology and the concomitant need for robust informative prior information (Clark and Gelfand, 2006). We also support a disciplinary shift away from charismatic species (as highlighted by the lack of data available for fishes, insects and marine invertebrates) and focus of expertise and resources on IUCN-listed species and hotspots of latent extinction risk (Cardillo et al., 2006).

Acknowledgements

We thank Julian O'Grady for his assistance with some of the correlates data, and Marcel Cardillo and an anonymous referee for helpful review comments. Funding came from the Australian Research Council (DP02851634). B.W.B. conceived the work, L.W.T. compiled the data, and all authors contributed to the data analysis and writing of the paper.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2007.06.011](https://doi.org/10.1016/j.biocon.2007.06.011).

REFERENCES

- Akcakaya, H.R., 1998. RAMAS Metapop: viability analysis for stage-structured metapopulations (version 3.0). Applied Biomathematics, Setauket, NY.
- Blackburn, T.M., Duncan, R.P., 2001. Establishment patterns of exotic birds are constrained by non-random patterns in introduction. *Journal of Biogeography* 28, 927–939.
- Brook, B.W., O'Grady, J.J., Chapman, A.P., Burgman, M.A., Akçakaya, H.R., Frankham, R., 2000. Predictive accuracy of population viability analysis in conservation biology. *Nature* 404, 385–387.
- Brook, B.W., Traill, L.W., Bradshaw, C.J.A., 2006. Minimum viable population size and global extinction risk are unrelated. *Ecology Letters* 9, 375–382.
- Bulte, E.H., 2001. Minimum viable populations and sluggish management. *Environmental Conservation* 28, 191–193.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information Theoretic Approach*, second ed. Springer-Verlag, New York.
- Cardillo, M., 2003. Biological determinants of extinction risk: why are smaller species less vulnerable? *Animal Conservation* 6, 63–69.
- Cardillo, M., Mace, G.M., Gittleman, J.L., Purvis, A., 2006. Latent extinction risk and the future battlegrounds of mammal conservation. *Proceedings of the National Academy of Sciences of the United States of America* 103, 4157–4161.
- Caughley, G., 1994. Directions in Conservation Biology. *Journal of Animal Ecology* 63, 215–244.
- Ceballos, G., Ehrlich, P.R., 2002. Mammal population losses and the extinction crisis. *Science* 296, 904–907.
- Clark, J.S., Gelfand, A.E., 2006. A future for models and data in environmental science. *Trends in Ecology & Evolution* 21, 375–380.
- Clark, J.A., Hoekstra, J.M., Boersma, P.D., Kareiva, P., 2002. Improving U.S. Endangered Species Act recovery plans: key findings and recommendations of the SCB recovery plan project. *Conservation Biology* 16, 1510–1519.

- Dunham, A.E., Akçakaya, H.R., Bridges, T.S., 2006. Using scalar models for precautionary assessments of threatened species. *Conservation Biology* 20, 1499–1506.
- Ewens, W.J., 1990. The minimum viable population size as a genetic and a demographic concept. In: Adams, J., Lam, D.A., Hermalin, A.I., Smouse, P.E. (Eds.), *Convergent Issues in Genetics and Demography*. Oxford University Press, New York, pp. 307–316.
- Fagan, W.F., Meir, E., Prendergast, J., Ayoola, F., Kareiva, P., 2001. Characterizing population vulnerability for 758 species. *Ecology Letters* 4, 132–138.
- Felsenstein, J., 1985. Phylogenies and the comparative method. *American Naturalist* 70, 115.
- Frankham, R., 1995. Effective population-size adult-population size ratios in wildlife – a review. *Genetical Research* 66, 95–107.
- Gilpin, M.E., Soulé, M.E., 1986. Minimum viable populations: processes of species extinction. In: Soule, M.E. (Ed.), *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer, Sunderland, MA, pp. 19–34.
- Ginzburg, L.R., Ferson, S., Akçakaya, H.R., 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. *Conservation Biology* 4, 63–70.
- IUCN, 2006. IUCN Red List of Threatened Species. World Conservation Union. www.redlist.org.
- Lacava, J., Hughes, J., 1984. Determining minimum viable population levels. *Wildlife Society Bulletin* 12, 370–376.
- Link, W.A., Barker, R.J., 2006. Model weights and the foundations of multimodel inference. *Ecology* 87, 2626–2635.
- R Development Core Team, 2004. R: A language and environment for statistical computing. URL <http://www.R-project.org>.
- Reed, J.M., Murphy, D.D., Brussard, P.F., 1998. Efficacy of population viability analysis. *Wildlife Society Bulletin* 26, 244–251.
- Reed, D.H., O'Grady, J.J., Brook, B.W., Ballou, J.D., Frankham, R., 2003. Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. *Biological Conservation* 113, 23–34.
- Samson, F.B., 1983. Minimum viable populations – a review. *Nature Areas Journal* 3, 15–23.
- Schoener, T.W., Spiller, D.A., 1987. High population persistence in a system with high turnover. *Nature* 330, 474–477.
- Shaffer, M.L., 1981. Minimum population sizes for species conservation. *BioScience* 31, 131–134.
- Shaffer, W.M., 1985. Order and chaos in ecological systems. *Ecology* 66, 93–106.
- Shaffer, M., 1987. Minimum viable populations: coping with uncertainty. In: Soule, M.E. (Ed.), *Viable Populations for Conservation*. Cambridge University Press, Cambridge, pp. 69–86.
- Shaffer, M., Watchman, L.H., Snape III, W.J., Latchis, I.K., 2002. Population viability analysis and conservation policy. In: Beissinger, S.R., McCullough, D.R. (Eds.), *Population Viability Analysis*. University of Chicago Press, Chicago, pp. 123–142.
- Sjogren-Gulve, P., Ebenhard, T., 2000. The Use of PVA in Conservation Planning.
- Smith, R., Smith, T., 2003. *Elements of Ecology*. Benjamin Cummings, San Francisco, CA.
- Smith, F.A., Lyons, S.K., Ernest, S.K.M., Jones, K.E., Kaufman, D.M., Dayan, T., Marquet, P.A., Brown, J.H., Haskell, J.P., 2003. Body mass of late quaternary mammals. *Ecology* 84, 3403.
- Stinchcombe, J., Moyle, L.C., Hudgens, B.R., Bloch, P.L., Chinnadurai, S., Morris, W.F., 2002. The influence of the academic conservation biology literature on endangered species recovery planning. *Conservation Ecology* 6, 15–26.
- Tear, T.H., Kareiva, P., Angermeier, P.L., Comer, P., Czech, B., Kautz, R., Landon, L., Mehlman, D., Murphy, K., Ruckelshaus, M., Scott, J.M., Wilhere, G., 2005. How much is enough? The recurrent problem of setting measurable objectives in conservation. *Bioscience* 55, 835–849.
- Terborgh, J., Winter, B., 1980. Some causes of extinction. In: Soulé, M.E., Wilcox, B.A. (Eds.), *Conservation Biology: An Ecological-Evolutionary Perspective*. Sinauer, Sunderland, MA, pp. 119–134.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. *Nature* 427, 145–148.
- Woodroffe, R., Thirgood, S., Rabinowitz, A., 2005. *People and Wildlife. Conflict or Co-existence?* Cambridge University Press, Cambridge, UK.