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

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## 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.

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## 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](http://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).

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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](http://www.isinet.com)) and Elsevier's Science Direct ([www.sciencedirect.com](http://www.sciencedirect.com)) databases. The online search engines Google ([www.scholar.google.com](http://www.scholar.google.com)) and Yahoo ([www.yahoo.com](http://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  $\geq 20$  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 (Akçakaya, 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<sub>c</sub>) 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<sub>st</sub>) 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<sub>st</sub>; and (d) binomial GLMM relating species IUCN Red-Listing (listed or not listed) to ecological and life history correlates**

| Candidate models  | LL       | k  | ΔAIC <sub>c</sub> | wAIC <sub>c</sub> | ΔBIC    | wBIC   | %DE  |
|---|----------|----|-------------------|-------------------|---------|--------|------|
| <i>(a) MVP-generating model correlates</i>                        |          |    |                   |                   |         |        |      |
| 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  |
| <i>(b) GLMM of ecological and life history correlates</i>         |          |    |                   |                   |         |        |      |
| MVP <sub>st</sub> ~ null  | -1.151   | 3  | 0.000             | 0.364             | 0.000   | 0.757  | 0.0  |
| MVP <sub>st</sub> ~ BWT   | -1.116   | 4  | 2.025             | 0.132             | 5.096   | 0.059  | 3.0  |
| MVP <sub>st</sub> ~ TRE   | -1.127   | 4  | 2.046             | 0.131             | 5.114   | 0.059  | 2.1  |
| MVP <sub>st</sub> ~ HMP   | -1.146   | 4  | 2.084             | 0.128             | 5.151   | 0.058  | 0.5  |
| MVP <sub>st</sub> ~ GNL   | -1.147   | 4  | 2.087             | 0.128             | 5.155   | 0.058  | 0.4  |
| MVP <sub>st</sub> ~ BWT + GNL                                     | -1.112   | 5  | 4.136             | 0.046             | 10.247  | 0.005  | 3.4  |
| MVP <sub>st</sub> ~ HMP + TRE                                     | -1.127   | 5  | 4.167             | 0.045             | 10.272  | 0.004  | 2.1  |
| MVP <sub>st</sub> ~ BWT + GNL + FEC                               | -0.973   | 6  | 6.003             | 0.018             | 15.142  | 0.000  | 15.5 |
| MVP <sub>st</sub> ~ BWT + GNL + DSP + RAN                         | -1.052   | 7  | 8.333             | 0.006             | 20.451  | 0.000  | 8.6  |
| MVP <sub>st</sub> ~ BWT + GNL + SOC                               | -1.016   | 8  | 10.456            | 0.002             | 25.555  | 0.000  | 11.8 |
| MVP <sub>st</sub> ~ BWT + GNL + FEC + SOC + DSP + RAN + HMP + TRE | -0.914   | 13 | 21.646            | 0.000             | 51.184  | 0.000  | 20.6 |
| <i>(c) GLM of ecological and life history correlates</i>          |          |    |                   |                   |         |        |      |
| MVP <sub>st</sub> ~ BWT + GNL + FEC                               | 196.466  | 5  | 0.000             | 0.746             | 0.000   | 1.000  | 15.5 |
| MVP <sub>st</sub> ~ BWT   | 181.859  | 3  | 25.039            | 0.000             | 18.502  | 0.000  | 3.0  |
| MVP <sub>st</sub> ~ null  | 178.585  | 2  | 29.528            | 0.000             | 19.692  | 0.000  | 0.0  |
| MVP <sub>st</sub> ~ BWT + GNL + SOC                               | 191.868  | 7  | 13.454            | 0.001             | 19.909  | 0.000  | 11.8 |
| MVP <sub>st</sub> ~ TRE   | 180.875  | 3  | 27.006            | 0.000             | 20.469  | 0.000  | 2.1  |
| MVP <sub>st</sub> ~ BWT + GNL + DSP + RAN                         | 188.197  | 6  | 18.658            | 0.000             | 21.896  | 0.000  | 8.7  |
| MVP <sub>st</sub> ~ BWT + GNL                                     | 182.293  | 4  | 26.248            | 0.000             | 22.989  | 0.000  | 3.4  |
| MVP <sub>st</sub> ~ HMP   | 179.103  | 3  | 30.551            | 0.000             | 24.014  | 0.000  | 0.5  |
| MVP <sub>st</sub> ~ GNL   | 178.968  | 3  | 30.821            | 0.000             | 24.283  | 0.000  | 0.4  |
| MVP <sub>st</sub> ~ BWT + GNL + FEC + SOC + DSP + RAN + HMP + TRE | 203.025  | 12 | 2.159             | 0.253             | 24.379  | 0.000  | 20.6 |
| MVP <sub>st</sub> ~ HMP + TRE                                     | 180.878  | 4  | 29.079            | 0.000             | 25.820  | 0.000  | 2.1  |
| <i>(d) GLMM of ecological and life history correlates</i>         |          |    |                   |                   |         |        |      |
| 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<sub>c</sub> (ΔAIC<sub>c</sub>), AIC<sub>c</sub> weight (wAIC<sub>c</sub>), 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.

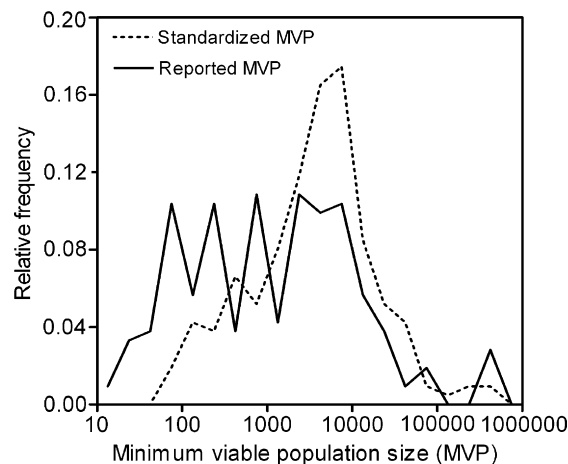
To gauge the relative importance of each derived variable for predicted MVP, we fitted a series of generalized linear mixed-effects models (GLMM) to  $\log_e MVP$  in the R Language (R Development Core Team, 2004), using the `lmer` function (in the `lme4` library). MVP was assumed on a priori grounds 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  $\beta$  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



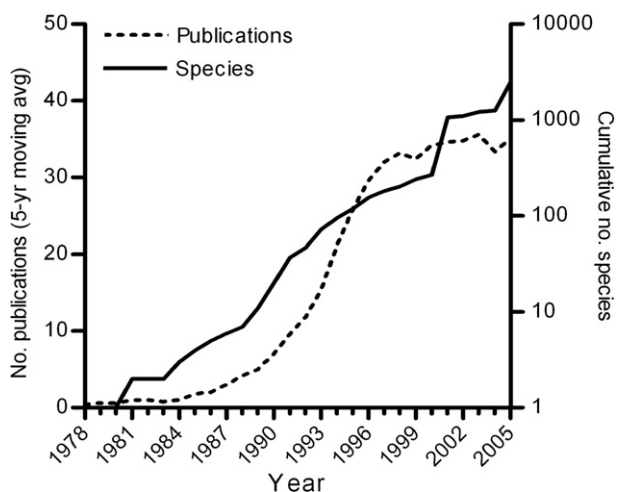
**Fig. 1 – Comparison of original versus standardized minimum viable population sizes. Relative frequencies of the 212 MVP species estimates ( $\log_{10}$  scale) for the original, uncorrected values, taken directly from the literature (solid line, [Supplementary Notes](#)) and the same values after 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  $\log_e MVP_{st}$  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

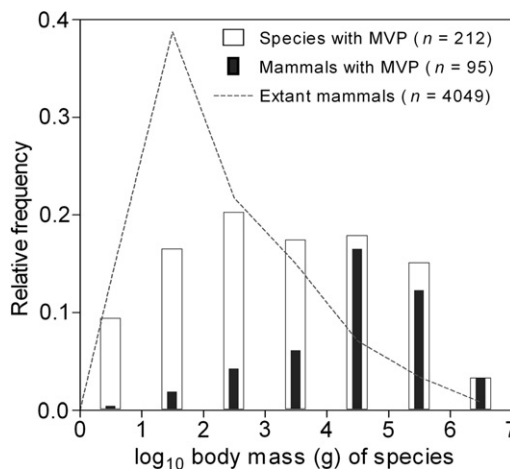


**Fig. 2 – Publication trends for minimum viable population size (MVP), 1974–2005. The cumulative number of species in studies related to population viability and extinction ( $\log_{10}$  scale, solid line), and a 5-year moving-average of the number MVP-related peer-reviewed and unpublished literature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

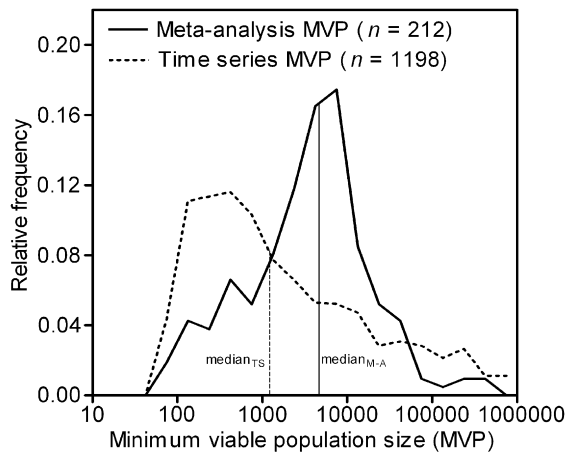
[GPDD], [www.cpbnts1.bio.ic.ac.uk/gpdd/](http://www.cpbnts1.bio.ic.ac.uk/gpdd/)) and subsequent multi-species analyses (Fagan et al., 2001; Reed et al., 2003; Brook et al., 2006) in recent years were responsible for large increases in the number of species evaluated (Fig. 2).

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. 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*

**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 <sup>a</sup>            | 31  | 5409       | 3611–6779         | 3999         |
| Sum/median                        | 182 | 4102       | 3325–5096         | 3697         |
| <i>Other taxa</i>                 |     |            |                   |              |
| Plants <sup>b</sup>               | 22  | 4824       | 2512–15,992       | 2097         |
| Insects                           | 5   | 10,841     | 1650–103,625      | 2000         |
| Marine invertebrates <sup>c</sup> | 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).

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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.biocon.2007.06.011.

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