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Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates

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Abstract

Population size is a major determinant of extinction risk. However, controversy remains as to how large populations need to be to ensure persistence. It is generally believed that minimum viable population sizes (MVPs) would be highly specific, depending on the environmental and life history characteristics of the species. We used population viability analysis to estimate MVPs for 102 species. We define a minimum viable population size as one with a 99% probability of persistence for 40 generations. The models are comprehensive and include age-structure, catastrophes, demographic stochasticity, environmental stochasticity, and inbreeding depression. The mean and median estimates of MVP were 7316 and 5816 adults, respectively. This is slightly larger than, but in general agreement with, previous estimates of MVP. MVPs did not differ significantly among major taxa, or with latitude or trophic level, but were negatively correlated with population growth rate and positively correlated with the length of the study used to parameterize the model. A doubling of study duration increased the estimated MVP by approximately 67%. The increase in extinction risk is associated with greater temporal variation in population size for models built from longer data sets. Short-term studies consistently underestimate the true variances for demographic parameters in populations. Thus, the lack of long-term studies for endangered species leads to widespread underestimation of extinction risk. The results of our simulations suggest that conservation programs, for wild populations, need to be designed to conserve habitat capable of supporting approximately 7000 adult vertebrates in order to ensure long-term persistence.

Keywords: Demographic stochasticity; Endangered species; Extinction; Minimum viable population size; Population variability; Population viability analysis

1. Introduction

The Earth is currently suffering a catastrophic loss of biodiversity (Lawton and May, 1995). A primary goal of conservation biology is to arrest this loss. Population size has been shown to be the major determinant of persistence in populations of a variety of animal species (Brown, 1971; Jones and Diamond, 1976; Toft and Schoener, 1983; Diamond et al., 1987; Newmark, 1987; Pimm et al., 1988, 1993; Richman et al., 1988; Soulé et al. 1988; Berger, 1990; Kindvall and Ahlén, 1992; Schoener and Spiller, 1992; Rosenzweig, 1995; Foufopoulos and Ives, 1999). As the catastrophic loss of biodiversity continues unabated, guidelines for how extinction risk is related to population size should be a high priority in conservation biology (Shaffer et al., 2000).

Population viability analysis (PVA) provides a quantitative means for predicting the probability of extinction and for prioritizing conservation needs (Shaffer, 1981; Gilpin and Soulé 1986; Beissinger and Westphal, 1998). PVA can take into account the combined impacts of stochastic factors (demographic, environmental and genetic stochasticity) and deterministic factors (e.g.

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habitat loss, over exploitation) (Miller and Lacy, 1999; Beissinger and McCullough, 2002). Individual-based stochastic models of population dynamics typically use population-specific life history information to forecast future population sizes using computer simulation (Miller and Lacy, 1999; Sjögren-Gulve and Ebenhard, 2000; Beissinger and McCullough, 2002).

A number of scientists have pointed out the limitations of PVA (Beissinger and Westphal, 1998; Coulson et al., 2001). However, despite criticism, the use of PVA models in conservation continues to grow and no attractive alternatives have arisen (Mann and Plummer, 1999; Beissinger and McCullough 2002; Brook et al., 2002). Consequently, it is extremely important that variables affecting the predictive power of PVA be identified, so that there can be improvement in this important conservation tool.

A minimum viable population size (MVP) can be defined as the smallest size required for a population or species to have a predetermined probability of persistence for a given length of time (Shaffer, 1981). During the last decade, the concept of a generally applicable minimum viable population size has fallen into disfavor. This lack of interest in the concept of a minimum viable population size seems to be due to two major causes. (1) The perception that there is a great deal of taxonomic and environmental specificity involved in population dynamics, and (2) a greater emphasis on ecosystem and landscape conservation (e.g. Christensen 1997).

Reed et al. (2002) suggest that PVA should never be used to estimate minimum viable population sizes. Yet, they provide no reasoning for this statement. Any estimate of extinction risk is a de facto estimate of minimum viable population size. Because the resources available to conservation programs are finite and because political and administrative decisions are frequently made without the time for case-specific evaluations, general yet scientifically defensible estimates of minimum population sizes and habitat areas are essential (Shaffer et al., 2000). With this information, time, money and habitat areas can be rationally and efficiently allocated (Lacy, 1992). We suggest that using PVA to estimate MVPs can have great heuristic value and lead to scientifically defensible generalizations concerning viable populations.

We developed, or found in the literature, population viability models for 102 vertebrate species based on actual life history data. This approach allows us to estimate MVPs for a wide range of vertebrate species with a high level of replication. It also allows us to include most of the variables believed to be important to population persistence, using the best demographic and life history data available for wild populations. Further, PVA has been shown to provide reasonable predictions of extinction risk for well-studied species (Brook et al., 2000; McCarthy and Broome 2000; McCarthy et al., 2000; but see Lindenmayer et al., 2001; McCarthy et al., 2001).

It is not feasible to estimate MVPs from field studies for a wide variety of species within a reasonable time. The only realistic way to obtain MVPs for a large number of species and develop general guidelines is to use PVA, as originally envisaged by Shaffer (1981). The aims of our study were to: (1) Use PVA to estimate MVPs for 102 vertebrate populations, allowing us to make recommendations based on the characteristics of this distribution. (2) Search for explanatory variables causing the variation in MVPs using a large number of case studies. This allows for the specification of MVPs for different groups of species or circumstances. (3) Use the data from this study, and a review of pre-existing data, to address the arguments, presented above, against a widely applicable MVP. We use these 102 PVA models to test for the underlying phenomena causing variation in minimum viable population sizes across demographic, ecological, study, and taxonomic parameters and groupings.

2. Methods

2.1. Definition of minimum viable population size

All MVP estimates in this data set are for a 99% probability of persistence for 40 generations. We estimated minimum viable population sizes using three different criteria. (1) The primary variable manipulated in this study is the mean carrying capacity required for a 99% probability of persistence for 40 generations (MVP_K). This was determined by setting the *initial* population size (N_i) equal to the carrying capacity (K) and varying these until the threshold risk of extinction is reached, as detailed later. (2) Output from the population viability analysis software used (VORTEX; Miller and Lacy, 1999) allows the calculation of the number of adults expected in a population of size N_i (with N_i set equal to K), assuming a stable age distribution. Since the practical imperative is usually to define a minimum habitat area suitable for establishment of breeding territories, hunting grounds, etc., we will focus on this minimum viable adult population size (MVP_A). This is a particularly relevant measure, as most conservation organizations couch population size in terms of the number of sexually mature individuals. (3) Output on heterozygosity can be used to calculate the effective population size (N_e) for any given K. This is the minimum viable effective population size MVP_{Ne}. This measure is relevant as a comparison with predictions of minimum viable population size based on genetic theory.

The three measures of MVP all correlate very strongly with each other ($r > 0.93$ in all comparisons) and the choice of measure does not qualitatively change the conclusions reached in any of the analyses.

2.2. PVA models

VORTEX version 8.01 (Miller and Lacy, 1999) was used to model the 102 populations examined in this study. VORTEX is an individual-based, age-structured population simulation model that can include carrying capacity, demographic stochasticity (in mortality and breeding structure), environmental stochasticity, catastrophes, density-(in)dependent reproductive rates, inbreeding depression, and allows a range of user defined functions to replace fixed parameter terms (Miller and Lacy, 1999). VORTEX has been extensively applied to endangered species conservation by the Conservation Breeding Specialist Group of the World Conservation Union and others (Seal et al., 1998).

2.3. Vortex inputs and outputs

Most model inputs were gathered directly from the species–specific studies. Age-specific birth and death rates and their variance, mean age at first breeding, mean litter size and its variance, and proportion breeding and its variance, were all calculated from the available demographic information. If no data on maximum age were available, it was estimated from the shape of the mortality curve.

The frequency and magnitude of catastrophes was estimated from the species-specific study, from data available on the Global Population Dynamics Database (NERC Centre for Population Biology, 1999), or estimated from Reed et al. (in press).

Inbreeding depression is the one variable where a default value was used. A conservative figure of five lethal equivalents, per diploid genome, for juvenile survival was used. The actual number of lethal equivalents for juvenile mortality may be higher (Jiménez et al., 1994; Crnokrak and Roff, 1999; Keller et al., 2002) and certainly inbreeding depression in natural populations affects adult survival and fecundity as well as juvenile survival (Keller, 1998; Cheptou et al., 2000; Meagher et al., 2000; Keller et al., 2002). The model allowed for the purging of the genetic load via selection against deleterious recessive alleles. The evidence for genetic effects on fitness and persistence in wild populations now seems irrefutable (Vrijenhoek, 1994; Saccheri et al., 1998; Westermeier et al., 1998; Crnokrak and Roff 1999; Madsen et al., 1999; Hedrick and Kalinowski, 2000; Richards, 2000; Nieminen et al., 2001; Reed and Frankham, in press).

Density-dependence as a form of regulation for population size is very common (Woiwood and Hanski, 1992; Godfray and Hassell, 1992; Holyoak, 1993; Turchin, 1995; Lande et al., 2002). It is thought by many to greatly influence the probability of population persistence (e.g. Den Boer, 1968; Hanski et al., 1996; Dennis et al., 1998). However, whether density-dependence in reproductive and mortality rates increases or decreases the probability of extinction depends on the shape of the density-dependent function. All populations modeled had at least one form of density dependence, in that population size could not exceed a ceiling size (K). Where density-dependent rates of mortality or fecundity for a specific species had been measured, the species-specific density-dependent function was used. For species where evidence of strong density-dependence was available, but no details of the form provided, a logistic model of density-dependence was used. There is no consensus about the prevalent form of density dependence in real populations, however, ceiling and logistic models of density-dependence differ little in their extinction rates when all else is equal (Foley, 1997).

Many of the parameters analyzed are outputs of the model (population growth rate, generation length) or are calculated from model outputs (CV_N). Thus, no information from the literature was required for these parameters. Rather, they are the result of the demographic and life history data entered into the model.

2.4. Estimating minimum viable population size

To estimate MVP_K, a series of runs of each PVA model was performed using different values of K, until the estimates encompassed the threshold extinction probabilities of population survival for the required definition of MVP. Extinction risk at various K values were plotted and MVP interpolated from the regression line. Subsequently, runs around this predicted value are done to refine the MVP estimate ($\pm 0.5\%$). One thousand replicate simulations are used to provide adequate precision (Harris et al., 1987; Burgman et al., 1993).

2.5. Choice of species

The 102 vertebrates modeled for this study include two amphibians, 28 birds, one fish, 53 mammals, and 18 reptiles. Populations with strong negative growth rates were not included in this data set. Even populations in excess of 100,000 will not be viable if strong deterministic (anthropogenic) factors and habitat destruction are the forces driving the population to extinction. For these cases, the cause of decline must be identified and ameliorated before a useful estimate of MVP can be made (Caughley, 1994). No other filter was applied. The populations represent a wide range of habitats, ecologies, and geographic locations. The species modeled, their estimated MVP, and other pertinent information are listed in the Appendix.

2.6. Methodological assumptions

There are two fundamental assumptions associated with our approach. (1) No habitat loss (since we are

concerned with the minimum habitat area to be maintained over a given time frame). (2) Individual populations are discrete and isolated (not distributed in a source-sink or metapopulation configuration).

2.7. Factors influencing MVP

Backwards stepwise regression and factor analysis were performed to identify the key variables responsible for variation among species in MVP. We used two measures of population fitness and growth, two measures of population variability and two measures of study duration (Table 1). The relationships between coefficient of variation in population size (CV_N) and both MVP and duration of study (in generations) were assessed using linear regressions with natural log transformed data.

In the test for a causal link between study duration and extinction risk, a paired t-test was used to determine whether a random sequential one-third sample of the data reduced MVP compared to that for the full data set within each of 10 species.

Analysis of variance was used to test whether MVP differs among major taxonomic groups (birds, mammals, and poikilotherms) and trophic levels (carnivores, omnivores, and herbivores). Linear regression was used to test whether there was an effect of latitude on MVP.

2.8. Adjusting for bias

There is a strong and highly significant relationship between the length of the study (in generations) used to parameterize the population viability model and the estimated minimum viable population size ($r^2 = 0.467$, $P < 0.0001$) (Fig. 1). This relationship is the result of an increase in the temporal variation in population size in models created from longer data sets. Because of this increasing variance with increasing study length, uncorrected estimates of minimum viable population size would obviously be underestimates (i.e. the longer data sets provide the better parameter estimates). Therefore, all 102 minimum viable population size estimates were corrected, using the following formula:

$$\ln\ MVP_C = \ln\ MVP_A + 0.75423\ [\ln(40/SLG)]$$

where MVP_C is the minimum viable adult population size corrected to 40 generations worth of data for each species, MVP_A is the minimum viable adult population size as estimated from the available data regardless of study length, and SLG is the study length in years divided by the species' generation length in years. This is similar to using residuals from the linear regression, and provides estimates of MVP for all species under the assumption that 40 generations of data were available for each. This correction makes the variance in MVP_C due to variance in study length equal to zero.

MVP values were transformed using natural logarithms to normalize data prior to statistical analyses. F tests were carried out to determine whether major taxa, global latitiude, or trophic level affected MVP.

Table 1
Test of predictors of minimum viable population size using stepwise multiple regression[a]

Variable	F	P-value
Study duration (generations)	20.58	<0.0001
Population growth rate (ln R_0)	9.68	0.0025
Standard deviation of r	1.09	0.2992
Study duration (years)	0.92	0.3410
Coefficient of variation of r	0.87	0.3536
Intrinsic rate of increase (r)	0.22	0.6378
Adjusted $R^2 = 0.630$		
Study duration (generations)	96.11	<0.0001
Population growth rate (ln R_0)	53.00	<0.0001
Adjusted $R^2 = 0.639$		

[a] The top panel shows significance levels for individual variables, and the total variance explained when all six of the original variables are included in the model. The bottom panel shows the results of the multiple regression model when only the two significant variables are included.

3. Results

3.1. Effect of study duration

We performed backwards stepwise multiple regression and factor analysis to examine underlying causes of variation among minimum viable population sizes. Both analyses produced very similar results. Thus, only the results of the multiple regression are shown (Table 1).

To our surprise, study duration had a major impact on minimum viable population size (Table 1, Fig. 1). Critically, shorter studies caused a systematic underestimation of extinction risk, rather than simply a less precise estimation, as often assumed. Further, the relationship was significant only when study duration was measured relative to the generation length of the organism.

A doubling of study duration increased minimum viable population size by approximately 67%, based on the regression equation. Study duration explained 47% of the variation in MVP among species. Further, study duration was the most important variable predicting differences in MVP when multiple regression was used to test two measures of population fitness and growth, two measures of population variability and two measures of study duration (Table 1). The only other variable explaining a significant proportion of the variance in MVP was the rate of population growth per generation (ln R_0).

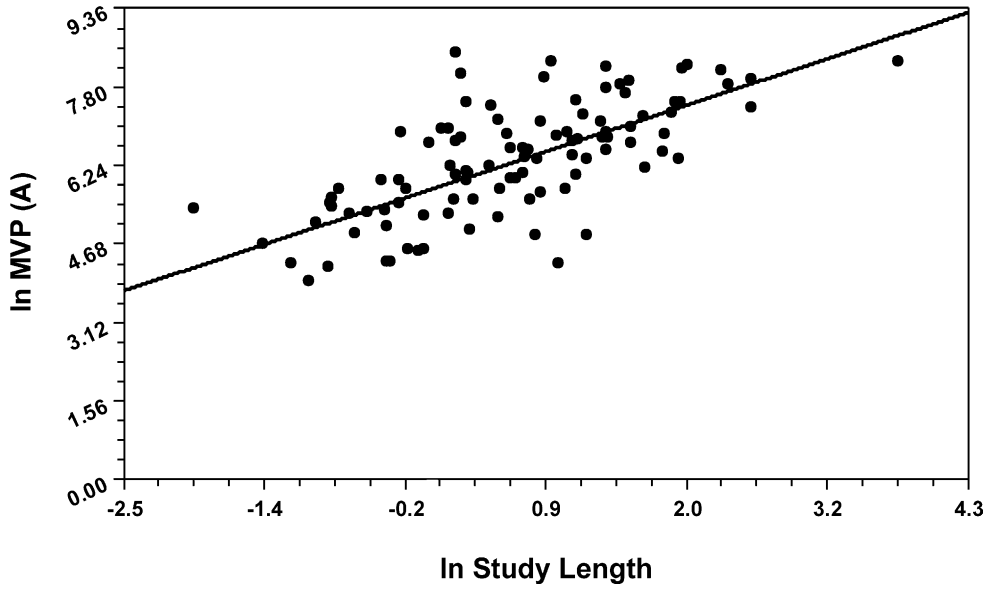

Fig. 1. The relationship between the study duration (in generations) used in the population viability model and the minimum population size (MVP) required for 99% persistence for 40 generations ($F=87.7$, $r^2=0.467$, $P<0.0001$). Both variables were natural log transformed.

As greater temporal variability in population size is positively correlated with extinction risk (Vucetich et al., 2000), we hypothesized that the relationship between study duration and predicted extinction risk was a result of an increase in CV_N with length of time the population was studied. Thus, MVP (extinction risk) and length of the study used to parameterize the model should both be strongly related to variability in population size. These predictions were confirmed. CV_N was strongly correlated with MVP, explaining 65% of the variation in MVP among species ($r^2=0.649$, $P<0.0001$). The relationship between study duration and CV_N was also positive and highly significant ($r^2=0.340$, $P<0.0001$).

If study duration causes the differences in predicted extinction risk, then the effect should also be found within species. This was evaluated by comparing predicted extinction risk for ten species, based either on the use of the full data set, or a random sequential one-third subset. Minimum viable population size estimates were significantly greater for the total data set than for the data sub-set ($t=3.58$, d.f. $=9$, $P<0.005$).

3.2. Minimum viable population sizes

The distribution of MVP_c is presented in Fig. 2. Means and medians for the three measures of MVP are presented in Table 2. The mean for MVP_C is 7316 and the median is 5816. All MVP distributions are positively skewed. MVP_c is the most relevant measure in conservation terms and the median and mean provide our estimate that a minimum habitat area capable of supporting approximately 7000 sexually mature adults is required to maintain long-term minimum viable populations of vertebrates in the wild.

Estimates of minimum viable population size are very scale dependent. Based on a subset ($n=38$) of the 102 species used in this study, approximately 5800 adult animals are needed for a 95% chance of persistence over 40 generations, 4700 for 90% persistence, and 550 for a 50% chance of persistence.

3.3. Variables affecting MVP

There were no significant differences in minimum viable population size, among the 102 species modeled, due to global latitude ($r^2=0.006$, $P=0.455$), taxonomic grouping ($F=0.053$, $P=0.949$), or trophic level ($F_{2,97}=0.479$, $P=0.621$). The statistical power of these tests was sufficient to detect a 7% or greater difference among groups with at least a 87% probability (Zar, 1999).

Table 2
Mean (with standard error) and median minimum viable population sizes for the 102 vertebrate species modeled[a]

	Mean	Median
MVP_A	7316 (±562)	5816
MVP_K	11,410 (±849)	8514
MVP_{Ne}	1752 (±156)	1341

[a] MVP_A is the carrying capacity (model ceiling), providing a 99% probability of persistence for 40 generations, stated as a number of adults. MVP_K represents the carrying capacity in number of total individuals. MVP_{Ne} the minimum viable effective population size. The estimates are corrected for the length of study as explained in the methods section.

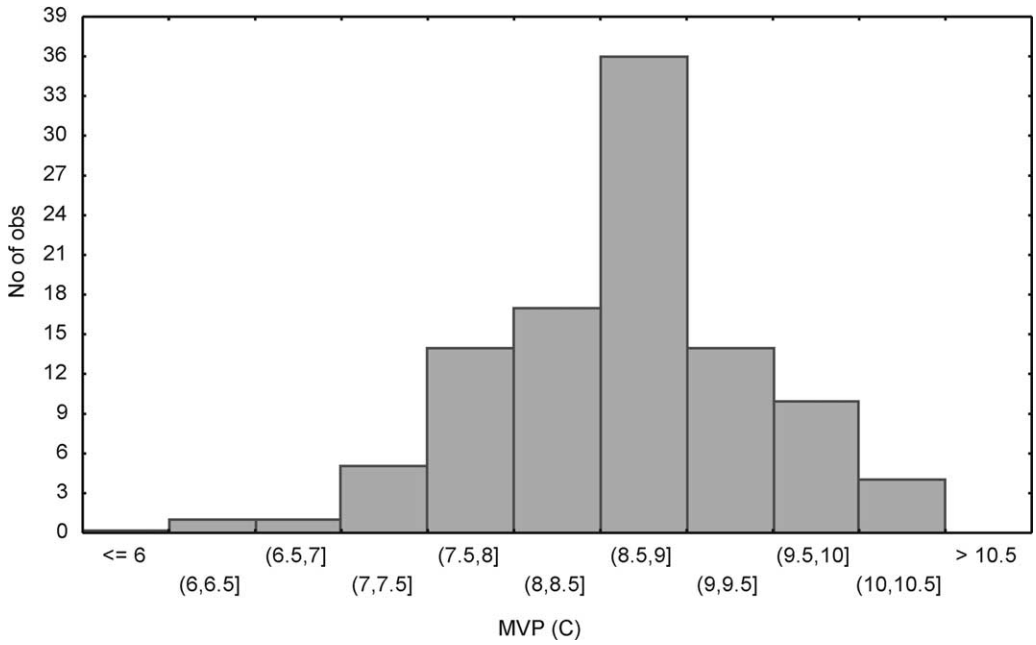

Fig. 2. The distribution of minimum viable population sizes (ln MVP_C) for the 102 vertebrate species, as determined by population viability analysis. The smallest MVP is an estimate from a herd of domestic goats released on an island without predators.

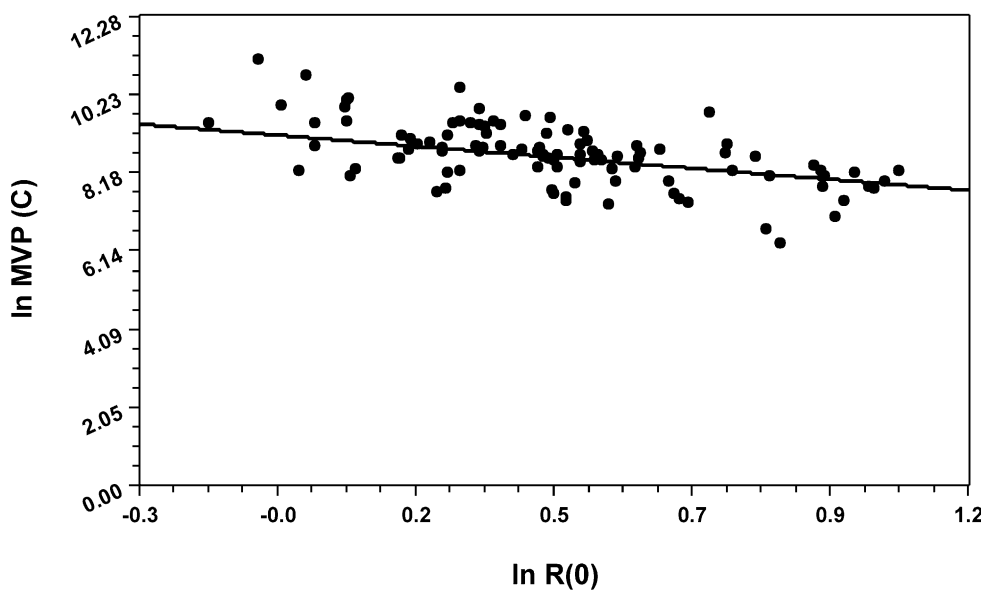

Fig. 3. The minimum number of adults (ln MVP_C) required, for a 99% chance of persistence for 40 generations, at a given population growth rate (ln R_0). The linear regression is highly significant ($r^2 = 0.351$, $P < 0.0001$). The regression formula predicts an MVP_C of 13,455 when the growth rate is 0 ($R_0 = 1.0$), 2221 when the growth rate is 1 ($R_0 = 2.72$), and 6006 when the growth rate is the mean value ($R_0 = 1.565$) for the 102 vertebrate species modeled in this study.

All else being equal, minimum viable population sizes should be larger for more variable populations. Indeed, in these 102 models, minimum viable population size is closely correlated with temporal variability in population size. There were also no significant differences in population variability among mammalian orders on a per generation scale ($F_{4.72} = 0.967$, $P = 0.431$) or between carnivores and herbivores ($F_{1.75} = 0.257$, $P = 0.614$) in our analysis of the data collected by Sinclair (1996).

Linear regression shows MVP to be significantly and negatively related to the population growth rate per generation (ln R_0) ($r^2 = 0.351$, $P < 0.0001$) (Fig. 3). The regression formula predicts an MVP_A of 13,455 when

the growth rate is 0 ($R_0 = 1.0$), 2221 when the growth rate is 1 ($R_0 = 2.72$), and 6006 when the growth rate is the mean value ($R_0 = 1.565$) for the 102 vertebrate species modeled in this study.

4. Discussion

The major findings of this investigation are: (1) Estimated MVPs were strongly influenced by the duration of the study, relative to the generation length of the organism, used to parameterize the model. Larger MVPs are predicted from longer studies because those models produce greater temporal variation in population size. (2) MVPs did not differ among major taxa, or with latitude or trophic level. (3) MVPs were significantly and substantially affected by the population growth rate, being larger with smaller growth rates. (4) The mean and median estimated MVP was 7316 and 5816, respectively. Each of these findings and their conservation implications are elaborated on later.

4.1. Factors influencing MVP estimates

The predicted MVP increased with increasing length of the study used to parameterize the model. This relationship was only statistically significant when study duration was measured relative to the generation length of the organism. Thus, shorter studies caused a systematic underestimation of extinction risk, rather than simply a less precise estimation, as often assumed (Boyce, 1992; Ludwig, 1999; Coulson et al., 2001). Besides underestimating the risk of extinction, the study-duration effect compromises the use of PVA in determining relative risk among different species and prioritizing management decisions unless explicitly accounted for.

Both study duration and MVP were significantly correlated with the temporal variability of population size, measured as the coefficient of variation in population size (CV_N). Increases in the length of the study used to parameterize the model, relative to the generation length of the organism, increases the amount of temporal variability in population size produced by the model, therefore increasing the MVP necessary to maintain a given level of extinction risk.

The explanation for why shorter studies consistently underestimate extinction risk is that fluctuations in population size through time are positively autocorrelated and the range of fluctuations increases over time (Halley, 1996; Morales, 1999). Thus, random samples from any continuous time period will underestimate the true variance. While it has been shown previously that variation in population size increases over time for census data (Pimm and Redfearn, 1988; Inchausti and Halley, 2001) and that under some conditions this can lead to underestimates of extinction risk (Ripa and Lundberg, 1996; Johst and Wissel, 1997; Morales, 1999), this is the first time that it has been demonstrated that extinction risk estimated from individually estimated demographic parameters increases with study duration. Further, we provide the first estimate of the magnitude of the effect. PVA models built from short-term studies will systematically underestimate extinction risk. Interestingly, Thomas et al. (2002) have found that a short-term (four generation) study of the metapopulation dynamics of a butterfly greatly underestimated the 30-generation colonization and extinction rates within the metapopulation. Thus, the underestimation of population variability with short-term data sets seems to exist at the demographic, population, and metapopulation levels.

How long do populations have to be studied to allow the possibility of accurate predictions of extinction risk? The relationship between CV_N and the study duration was determined using a wide variety of non-linear functions. Yet, the best fitting relationship between study duration and CV_N was linear. Thus, the variance in population size is still increasing across the range of study durations examined (up to 43 generations) in this study. Similarly, temporal variability in population size had not reached an asymptote for the majority of the 544 data sets studied by Inchausti and Halley (2001). Greater than 12 generations of data are required to produce minimum viable population sizes that are in broad agreement with theoretical and empirically based approximations (Soulé, 1987; Thomas, 1990; Reed and Bryant, 2000).

The median generation length of the 102 vertebrates modeled in this study was greater than 5 years. Thus, many decades or even centuries of research would be required to encompass most of the variation in demographic parameters. Since most ecological studies are of very short duration, typically two or three years (Tilman, 1989; Baskin, 1997), the underestimation of extinction risk will be ubiquitous.

It has been suggested that PVA models routinely overestimate extinction risk due to the inclusion of error variance (Beissinger and Westphal, 1998). Every attempt should be made to remove error variance from the estimates of demographic parameters, however, three circumstantial lines of evidence suggest that the study length is the stronger effect. (1) As mentioned earlier, the study length required to produce minimum viable population sizes in accordance with theoretical and empirical evidence is quite large. Yet, small studies with greater error variance do not produce MVPs in accordance with theory. (2) Population variability and population growth rate explain $>75\%$ of the variation in MVP. (3) Brook et al. (2000) found that PVA predicted without bias quasi-extinction events in 20 well-studied species. This would not be expected if error

Table 3
Estimates of minimum viable population size from the literature. The estimates are generally smaller than the 7,000 predicted from PVA in this study[a]

Reference	MVP_A	Time Frame	Factors Considered
Franklin (1980)	4500[a]	Into perpetuity	Mutation/drift
Newmark (1987)	>3250	40 generations	All (observation)
Reed and Bryant (2000)	>2000[a]	50 generations	Adaptation/fitness
Schultz and Lynch (1997)	~2000[a]	Into perpetuity	Mutation/fitness
Thomas (1990)	5500	100 years	Population variability
Whitlock (2000)	~2000[a]	Into perpetuity	Mutation/fitness

PVA likely includes a larger number of factors than any other single study. More details of the studies can be found in the discussion.
[a] Minimum viable population sizes were originally presented as effective population sizes. The effective population size (N_e) presented in the original paper was multiplied by nine to produce the MVP_A listed here (see Frankham, 1995).

variance wildly exaggerated extinction risk. Two other recent studies have also shown broad agreement between the predictions of PVA models, created from long-term data sets, and the actual population dynamics of the population modeled (McCarthy and Broome, 2000; McCarthy and Lindenmayer, 2000).

How can the systematic underestimation of extinction risk be avoided? It is not feasible to delay decisions while adequate data are collected for each species. The alternative to PVA is to rely on human intuition, but this is notoriously inaccurate (Zeckhauser and Viscusi, 1990). One remedy is to use default values for stochastic parameters derived from data on well-studied species. Default values are used already, especially in VORTEX (Miller and Lacy, 1999), but their origin is unclear and they are not sourced to published analyses of long-term data sets.

In addition to study length, differences in MVPs based on population growth rate exist. As would be expected, populations with larger growth rates ($\ln R_0$) required smaller numbers of adults to avoid extinction than did populations with lower growth rates. Because the differences in MVP are not due to broad-scale environmental differences or taxonomy, it is likely that the differential growth rates reflect habitat quality and the extent of anthropogenic interference. The actual population size required for long-term persistence may range from 2000 in pristine habitat to >13,000 in substantially degraded habitats. This implies that the amount of habitat required to maintain minimum viable population sizes, can be reduced through habitat restoration and by increasing population fitness through immigration into inbred populations (Westermeier et al., 1998).

4.2. Minimum viable population size

We estimate that in order to ensure long-term persistence of vertebrate populations, sufficient habitat must be conserved to allow for approximately 7000 breeding age adults. How do our estimates, using detailed PVAs on 102 species, compare with the small amount of empirical data available? Pimm et al. (1988) provide population sizes and median extinction times for multiple populations of 62 species of birds. We divided median extinction time by generation length and regressed this against population size. The regression suggests that approximately 125 breeding pairs would be required for a 50% probability of persistence over 40 generations. Similarly, Berger (1990) gathered data on extinction times for more than 102 populations of bighorn sheep. Linear regression of population size against time until extinction suggests that 775 animals are needed for a 50% probability of persistence for 40 generations. These two numbers are in rough agreement with our estimate of 550 adults for a 50% probability of persistence for 40 generations.

Extinction records from national parks in the western USA (Newmark, 1987; Soulé, 1987) shed some light on what is likely to constitute a minimum viable population size. Of 69 populations of lagomorphs (rabbits and hares), the 9 populations (13%) that went extinct had median population sizes of 3276. The parks were established about 75 years prior to the study and, therefore, would represent 40–50 generations for a lagomorph. Thus, 3000 animals do not appear to be sufficient to ward off extinction during these time frames.

Table 3 illustrates how our estimates, using PVA, compare with estimates of minimum viable population size derived using other methods, such as genetic theory or simple models of population variability. Probably the first attempt to arrive at a generalized minimum viable population size was by Franklin (1980). His estimate of an effective population size of 500 was based on an expected equilibrium between the loss of quantitative genetic variation due to drift and its replenishment by mutation. An effective population size of 500 is approximately 4500 adults (Frankham, 1995). Reed and Bryant (2000) monitored fitness and adaptability in laboratory populations of the housefly and estimated that >2000 individuals would likely be necessary for

long-term persistence in wild populations. Schultz and Lynch (1997) and Whitlock (2000) have used mathematical models, incorporating the decline in fitness due to the fixation of deleterious alleles and the restoration of fitness through beneficial mutations, to estimate minimum viable population sizes. Both studies suggest that an effective population size of greater than 200 ($N \sim 2000$) is needed to maintain equilibrium fitness. Although this approach holds promise, the genetic parameters used in the model are known with very little precision. Thomas (1990), using data on the fluctuations in population size of small vertebrates and some invertebrates, concluded that a minimum viable population size of 5500 is needed to avoid an unacceptable risk of extinction.

4.3. Homogeneity of population dynamics

In the introduction, we presented two reasons that are often cited as failings of the general minimum viable population size concept. These were: (1) The perception that there is a great deal of taxonomic and environmental specificity involved in population dynamics. (2) A retreat from 'single species' conservation to ecosystem and landscape conservation. We will address both of these later.

The second objection can be dealt with briefly. The goal of basing conservation efforts at ecosystem and landscape scales is a laudable one. However, regardless of whether we manage conservation efforts on the basis of conserving ecosystems, landscapes, or 'hotspots' of biodiversity, those conservation units must contain viable populations of any species we seek to have remain extant. Conservation efforts directed at carefully selected, charismatic, land-intensive species probably provide the best and most pragmatic means to protect, not only that particular population but, the ecosystem and other species falling under its 'umbrella' (Foose et al., 1995).

The first objection is more contentious. It has long been believed that there is no single value for population size that may be applied to all populations to ensure persistence (Gilpin and Soulé, 1986; IUCN 1994). However, recent evidence calls this into question. In this study, no differences in MVP were found due to taxon, trophic level, or global latitude. Likewise, studies examining temporal variability of population sizes, which is expected to correlate strongly with extinction risk, have found little evidence for large-scale patterns. The variability in population size for 123 vertebrate species was remarkably similar regardless of taxonomy or trophic level (Inchausti and Halley, 2001). Temporal variation in the population size of herbivores is similar regardless of body mass, taxonomic group, or ecological habitat (Gaillard et al., 2000). An analysis of data, originally presented in Sinclair (1996), also fails to show differences in population variability, among mammals, due to taxonomic grouping or trophic level. The applicability of default values is strengthened by this growing body of evidence demonstrating homogeneity in population variability among environments and taxonomic groups.

Much of the perceived variation in previous estimates of minimum viable population size is due to differences in the temporal scale being measured (e.g. 50 years, 200 years, 10 generations), the extinction risk assumed (e.g. 1, 10, 50%), or what is actually being considered a population (e.g. number of adults, effective population size). When generation length is controlled for and the units of measure made the same, much of the variation in estimates of minimum viable population size disappear.

With the possible exception of Amazonia, the Russian Far East, and Canada, continuous blocks of land capable of supporting populations of 7000 large vertebrates, especially carnivores, is not available. Thus, the need to coordinate networks of smaller populations to ensure viable populations through the use of corridors, or managed immigration, should be a high priority.

Our estimate for MVP is designed to provide broad guidelines for species conservation planning. Population viability analysis is an inexact science, the variance among species estimates was large, and some of the variance around our estimated MVPs is unexplained. A number of upward and downward biases in estimating extinction risk exist (Brook, 2000). Many of our models unavoidably incorporated sampling error, so our MVP estimates may be too large. However, since we use a population ceiling, conservative estimates of inbreeding depression, and do not model Allee effects, we may underestimate MVP (Lacy, 1993, 2000; Lindenmayer et al., 1995). In short, we can provide no 'magic number' that will ensure persistence.

However, population viability analysis provides a holistic method for estimating MVPs and is the method that most capably brings all the factors considered important to population persistence under one umbrella. Thus, our goal in writing this paper is to stimulate a quantitative assessment of MVP approaches to conservation planning and to add to the body of literature that suggests that we should be thinking in terms of several thousands—not hundreds—of individuals in our goal to maintain viable populations of vertebrates.

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Appendix

Species	MVPA	MVP_C	ln R_0	Taxon
Accipiter nisus	915	5244	0.456	bird
Acinonyx jubatus	831	4036	0.123	mammal
Aepyceros melampus	69	2123	0.671	mammal
Agkistrodon contortrix	1932	13,091	0.320	RAF
Ailuropoda melanoleuca	440	6224	0.272	mammal
Alligator mississipiensis	265	3783	1.060	RAF
Amazona vittata	1073	15,802	0.417	bird
Ambystoma tigrinium	1103	16,939	0.733	RAF
Anolis limifrons	4189	3,999	0.566	RAF
Anser caerulescens	635	4,412	0.911	bird
Aphelocoma coerulescens	3223	25,379	0.302	bird
Aquila chrysaetos	744	7480	0.763	bird
Brachyteles arachnoides	78	1664	0.695	mammal
Bubo virginianus	721	4090	0.471	bird
Canis lupus	1403	6332	0.438	mammal
Capra	75	566	0.854	mammal
Caretta caretta	331	9472	0.202	RAF
Cercopithecus aethiops	996	19,547	0.105	mammal
Cervus eldi hainanus	155	3326	0.932	mammal
Cervus eldi thamin	1688	19,298	0.336	mammal
Cervus elephus	626	5768	0.541	mammal
Chelydra serpentina	728	6779	0.440	RAF
Chrysemys picta	249	7594	0.231	RAF
Crocidura russula	1,660	3865	0.925	mammal
Crocodylus acutus	138	3611	0.982	RAF
Crocodylus rhombifer	132	2468	1.008	RAF
Crotalus horridus	1282	13,958	0.302	RAF
Cygnus columbianus	97	1720	0.965	bird
Delichon urbica	3584	12,689	0.373	bird
Dendroca kirtlandii	1256	7323	0.329	bird
Diceros bicornis	325	6199	0.531	mammal
Dipodomys stephansi	2590	13355	0.053	mammal
Elephas maximus	218	4737	0.509	mammal
Emydoidea blandingii	99	1856	0.487	RAF
Enhydra lutris	523	7623	0.510	mammal
Eumetopias jubatus	450	4204	0.437	mammal
Falco peregrinus anatum	266	2385	0.279	bird
Felis concolor	923	5162	0.196	mammal
Ficedula hypoleuca	2878	6688	0.647	bird
Fratercula arctica	261	3323	0.113	bird
Fulmarus glacialis	197	2885	1.035	bird
Gorilla gorilla beringei	842	11,919	0.346	mammal
Grus americana	1131	5449	0.447	bird
Gulo gulo	1265	10,612	0.517	mammal
Gypaetus barbatus	102	1713	0.485	bird
Haliaeetus leucocephalus	193	3297	0.836	bird
Halichoerus grypus	2344	19,165	0.111	mammal
Hippotragus equinus	110	5037	0.546	mammal
Kinosternon subrubrum	1413	18,636	0.108	RAF
Leontopithecus rosalia	722	6587	0.410	mammal
Liasis fuscus	200	5409	0.812	RAF
Lichenostomus melanops	233	7009	0.271	bird
Loxodonta africana	166	5474	0.574	mammal
Lycaon pictus	500	2229	0.461	mammal
Lynx lynx	1816	6563	0.214	mammal
Lynx rufus	2208	11,079	0.490	mammal
Marmota flaviventris	3857	13,277	−0.131	mammal
Martes americana	1867	6884	0.344	mammal
Meles meles	427	2901	0.572	mammal
Melospiza melodia	3520	9870	0.452	bird
Mirounga angustirostris	596	5095	0.611	mammal
Mirounga leonina	3249	31,791	0.038	mammal
Monachus schauinslandi	76	1597	0.558	mammal
Nannopterum harrisi	207	5029	0.464	bird
Nestor meridionalis	279	8349	0.522	bird
Nipponia nippon	301	2544	0.929	bird
Odocoileus virginianus	2809	13,733	0.360	mammal
Ovibos moschatus	399	3876	0.772	mammal
Ovis aries	1026	7334	0.607	mammal
Ovis dalli dalli	982	10,164	0.349	mammal
Panthera leo	1023	5792	0.446	mammal
Panthera leo persica	1449	9405	0.281	mammal
Panthera tigris altaica	876	5840	0.395	mammal
Panthera tigris tigris	329	2377	1.017	mammal
Papio cynocephalus	934	7097	0.374	mammal
Parus atricapillus	694	2776	0.501	bird
Phacochoerus aethiopicus	406	4114	0.604	mammal
Phascolarctos cinereus	2429	13,774	0.109	mammal
Picoides borealis	3720	20,868	−0.004	bird
Python reticulatus	813	13,418	0.290	RAF
Rana catesbeiana	451	5909	0.613	RAF
Rhinoceros sondaicus	395	8771	0.218	mammal
Rhinoceros unicornis	75	2895	0.664	mammal
Rissa tridactyla	264	1678	0.830	bird
Salvelinus fontinalis	984	3869	0.026	RAF
Sauromalus obesus	515	5912	0.761	RAF
Sceloporus graciosus	1514	5768	0.470	RAF
Strix uralensis	329	3543	0.283	bird
Sus scrofa	144	1849	0.680	mammal
Tetrao tetrix	841	5846	0.509	bird
Trichechus manatus latirostris	4982	7044	−0.044	mammal
Tricholimnas sylvestris	592	2151	0.262	bird
Trichosurus caninus	386	5116	0.200	mammal
Ursus americanus	189	2045	0.463	mammal
Ursus arctos horribilis	600	3811	0.302	mammal
Ursus arctos	469	6221	0.335	mammal
Ursus marittimus	250	4961	0.535	mammal
Urus thibetanus japonicus	395	7823	0.252	mammal
Uta stansburiana	133	1149	0.948	RAF
Varanus komodoensis	221	15,283	0.459	RAF
Vipera berus	913	12,381	0.335	RAF
Zosterops lateralis	2660	7141	0.054	bird

A complete set of references for the building of the models, or for any single species, can be obtained by e-mailing the corresponding author.

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