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Expected minimum population size as a measure of threat

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Abstract

Risks of population decline are studied extensively in conservation biology, but are difficult to estimate because they change abruptly over a relatively narrow range of parameters. We propose that risks of decline may be usefully summarized by the expected minimum population size. This is the smallest population size that is expected to occur within a particular time period. Analytical solutions for the expected minimum population size are obtained for a stochastic population model of exponential growth. In more complex models that are analyzed by Monte Carlo simulation, the expected minimum population size may be determined by recording the smallest population size obtained in each interval and taking the average of these values. Whereas risks of decline change abruptly with changes in parameter values, the expected minimum population size changes more gradually. The results demonstrate that the expected minimum population size provides a better indication of the propensity for decline than the risk of extinction (or risk of decline to some other small population size), especially when the risk of extinction is small.

INTRODUCTION

The risk of extinction within a particular time frame is the most commonly-used index for assessing the vulnerability of a population or species. It has obvious appeal, because the goal of conservation biology is to minimize the number of extinctions, which may be achieved by minimizing the extinction risk. However, the risk of extinction is difficult to predict reliably for most species, partly because relatively small errors in parameter estimates can lead to large errors in the predicted risk of extinction. This occurs in part because over a range of parameter estimates, most risks of extinction are close to zero or one, with intermediate risks occurring for a relatively narrow range of parameter values (Dennis, Munholland & Scott, 1991; Fieberg & Ellner, 2000).

The mean time to extinction (T_e) is a commonly-used alternative to the risk of extinction. Because distributions of time to extinction are skewed to the right, the majority of extinctions occur prior to the mean (Burgman, Ferson & Akçakaya, 1993). Therefore, the mean time to extinction may give a misleading impression of the risk of extinction faced by a species. A second alternative to the probability of extinction is the risk of decline to small population sizes, termed quasi-extinction risk by Ginzburg *et al.* (1982). The advantage of this alternative is that conservation is concerned with decline to small population sizes, not just extinction, and predicted risks may be more unreliable at smaller population sizes (e.g., Possingham & Davies, 1995). However, risks of quasi-extinction behave similarly to risks of extinction, being relatively insensitive across a wide range of parameter estimates, and changing abruptly over a narrow range.

Burgman *et al.* (1993) extended the use of quasi-extinction risks to construct quasi-extinction risk curves that show the risk of decline to any population size. These curves provide additional information about characterizing the risk of population decline, but cannot do so with a single number, instead relying on a graphical representation of the results. McCarthy (1996) introduced the expected minimum population size as a way of summarizing a risk curve. The expected minimum population size is obtained by recording the smallest population size observed in each iteration of a stochastic model and taking the average of these minimums. It is equivalent to the area to the left of a quasi-extinction risk curve (McCarthy, 1996, see also Methods and Results below).

In this paper, we argue that the expected minimum population size is extremely useful for identifying the threat faced by a species. Importantly, the propensity for decline and effects of management strategies are often better summarized by the expected minimum population size than the risk of population decline. Because of this, the expected minimum population size gives a better indication of the threat faced by a population and the propensity for decline, especially when the predicted risk of extinction is low.

METHODS

Risks of population decline were examined for a stochastic model of exponential growth $N_{t+1} = \lambda_t N_t$, where N_t is the population size in year t and λ_t is the rate of population increase. Stochasticity was incorporated by drawing the growth rate randomly from a log-normal distribution. Thus, $\ln(\lambda_t)$ has a normal distribution with mean r and variance σ^2 . Ginzburg *et al.* (1982) provide a solution of the risk of population decline for this model. Expressing the future population size as a proportion of the initial population size, the probability of falling to or below a particular threshold within a given time period (T) is (Ginzburg *et al.*, 1982; Dennis *et al.*, 1991; Fieberg & Ellner, 2000)

$$Q(n) = \varphi(-u-v) + \exp(-2uv)\varphi(u-v), \quad (1)$$

where $\varphi()$ is the standard normal cumulative distribution function, $u=r\sqrt{T}/\sigma$, $v=-\ln(n)/(\sigma\sqrt{T})$, and n is the threshold population size as a proportion of the initial population size, so that $0 \leq n \leq 1$.

The function $Q(n)$ (eqn (1)) is a quasi-extinction risk curve. It is also, by definition, the cumulative distribution function for the minimum population size observed within T years. It is possible to use this function to determine the expected minimum population size, which is the mean of the distribution $Q(n)$. It can be shown that for the stochastic model of exponential growth the expected minimum population size is equal to (see Appendix)

$$\begin{aligned} E(n) &= \int_0^1 nq(n)dn = 1 - \int_0^1 Q(n)dn \\ &= 2u\varphi(u)/y + 2(u+w)\exp(wy/2)(1-\varphi(u+w))/y, \end{aligned} \quad (2)$$

where $w=\sigma\sqrt{T}$, $y=2u+w$, $q(n)=dQ(n)/dn$, and in the first step we have integrated by parts (showing incidentally that $E(n)$ is equal to the area to the left of the quasi-extinction risk curve $Q(n)$). Some useful approximations of eqn (2) are provided in the Appendix.

The expected minimum population size (eqn (2)) was calculated across a range of values for r (-0.1 to 0.1) and σ (0.05 to 0.2) at $T=100$, as was the risk of decline to 1% and 10% of the initial population size (eqn (1)). If the size of the population is expressed as a percentage of the initial population size, the expected minimum population size will have a possible range between 0 and 100%. A value of 0% corresponds to certain extinction and a value of 100% indicates no risk of decline from the initial population size.

Although this study is largely limited to a population model without density dependence and only considering environmental stochasticity, analyses with other models have produced results that are similar to those reported here (McCarthy, unpublished). As one example, results of a simulation model of *Burramys parvus* are also presented below. This model includes density dependence, environmental stochasticity and high levels of demographic stochasticity due to the small population sizes being considered (McCarthy & Broome, 2000). Risks of population decline within 100 years were calculated from 10,000 iterations with an equilibrium population size of 20 females. To examine the response of the different predictions to changes in parameter values, risks were also calculated for cases in which the population growth rate was reduced by 40% through to cases where it was increased by 40%. Analytical solutions are not available in this case, so the expected minimum population size was determined by recording the smallest population size observed in each of the 10,000 iterations and taking the average of these.

RESULTS

As reported elsewhere (Dennis *et al.*, 1991; Fieberg & Ellner, 2000), risks of population decline change abruptly with changes in the mean population growth rate, with the sharpest change occurring when the variation in the population growth rate is low (Fig. 1). In contrast, the expected minimum population size tends to change more gradually across the range of parameter values. Thus, when there is only a low risk of decline to a small population size, the expected minimum population size might still indicate that the population has a considerable propensity to decline, especially when the standard deviation in the growth rate is low. For example, when $r=0.0$, risks of decline to 1% of

the initial population size are only between 0-2% ($\sigma=0.05-0.2$), whereas the expected minimum population sizes are between 34-70% of the initial population size, indicating a considerable propensity for decline (Fig. 1).

Quasi-extinction risk curves illustrate how the expected minimum population size summarizes the propensity for decline. Fig. 2 shows risks of decline for three different mean growth rates ($r=-0.05, 0.0, 0.05$; $\sigma=0.2$). Comparison with Fig. 1 ($\sigma=0.2$) demonstrates how the change in the expected minimum population size is equal to the area between the quasi-extinction curves. For example, moving from $r=-0.5$ to 0.0 changes the expected minimum population size by approximately 30% of the initial population size (Fig. 1, $\sigma=0.2$), which is equal to the average horizontal distance between the risk curves (Fig. 2). Differences in the expected minimum population size summarize how changes in a parameter (in this case, mean population growth rate) move the population closer to or further from extinction.

Similar results were obtained in the case of the simulation of *Burramys parvus* population dynamics (Fig. 3). The risk of declining to extinction and the risk of declining to 5 individuals or fewer within the next 100 years changed relatively abruptly over a narrow range of values for the population growth rate. Over the same range of parameter values, the expected minimum population size changed relatively uniformly (Fig. 3).

DISCUSSION

Risks of population decline typically follow a sigmoidal shape in response to parameter values (e.g., Burgman *et al.*, 1993; McCarthy *et al.*, 1995; Fieberg & Ellner, 2000; McCarthy & Broom, 2000). The consequence of this is that risks of decline vary very little over the range of most parameters, but change from very small to close to unity over a relatively narrow range (Fig. 1). This was illustrated in the current study. For example, in cases where there was a 95% chance of the populations remaining above 10% of the initial population size, the populations were still likely to decline substantially (Fig. 1). In the case of the *Burramys parvus* simulations, the expected minimum population size remained less than 50% of the initial population size, even when the chance of remaining above 5 individuals (25% of the initial population) was greater than 90%. In these cases, if risks of declining to particularly small population sizes were examined, the propensity for decline would be overlooked.

For the risk of decline to usefully characterize the relationship between the propensity for decline and parameter values, the risk of decline must be approximately 50% at intermediate parameter values. This could be achieved by selecting the appropriate threshold population size, but the consequence is inconsistency with the threshold varying between populations, species and management strategies. An alternative is to measure the threshold population size such that the risk of decline is 50%. Variation in this population size will also indicate variation in the propensity to decline. In fact, the threshold population size corresponding to a 50% risk of decline is equivalent to the median of the minimum population size, and it will equal the expected minimum population size when the distribution of this variable is symmetric. Thus, the two values will often be similar; for example, compare threshold population sizes corresponding to a 50% risk of decline in Fig. 2 with the expected minimum population sizes in Fig. 1 ($\sigma=0.2$). One notable difference between the median and expected minimum population sizes is that when risks of extinction are greater than 50%, the expected minimum population size will vary with changes in the model, whereas the median will not.

In conservation efforts, it is often necessary to distinguish between short-term declines to relatively stable population sizes and long-term declines. The expected minimum population size does not indicate whether a particular decline is expected in the near future or at some other point within the timeframe of the analysis. Therefore, it may be necessary to evaluate the propensity of decline over a range of timeframes to help distinguish between short-term and long-term declines. Additionally, the expected minimum population size focuses on the smallest population size so it does not indicate the propensity for recovery. An alternative in this case is to calculate the expected *maximum* population size to indicate the expected recovery of an endangered species or the incidence of a pest outbreak (McCarthy, 1996).

Burgman *et al.* (1993) advocated the use of quasi-extinction curves to assess the viability of populations. Impact of management on populations can be assessed by comparing risks of decline under the influence of management to the case of an alternative. The two risk curves may be compared directly by assessing the change in the risk of decline to specified (or critical) population sizes (Ginzburg *et al.*, 1982). Alternatively, the impact of management on the risk of decline may be summarized by calculating the area between the two risk curves (Burgman *et al.*, 1993). While this provides a general index of the change in the risk of decline, which is termed added risk by Burgman *et al.* (1993), it is not immediately obvious how such an index should be interpreted. The results of this study demonstrate that the area between two risk curves is equal to the difference in the expected minimum population size.

Where researchers wish to use a single value to summarize the propensity of decline faced by a population, the expected minimum population size will often be a more useful value than the risk of extinction or the risk of decline to some other small population size. This does not imply that risks of extinction should be ignored, or that any one value can fully summarize a distribution of population sizes. Together, the two quantities (extinction risks and expected minimum population sizes) provide a good summary of a quasi-extinction curve. However, the expected minimum population size is better for indicating the propensity for decline, especially when the risk of extinction is small.

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APPENDIX

In order to derive equation (2), we substitute (1) for $Q(n)$ to obtain

$$E[n] = 1 - \int_0^1 Q(n)dn = 1 - (I_1 + I_2), \quad (\text{A1})$$

where

$$I_1 = \int_0^1 \varphi(-u + \ln n/w) dn \quad (\text{A2})$$

and

$$I_2 = \int_0^1 e^{2u \ln n/w} \varphi(u + \ln n/w) dn \quad (\text{A3})$$

Changing variables to $x = \ln n$ and integrating by parts we obtain

$$\begin{aligned} I_1 &= \int_{-\infty}^0 \varphi(-u + x/w) e^x dx \\ &= [e^x \varphi(-u + x/w)]_{-\infty}^0 - \int_{-\infty}^0 e^x \varphi'(-u + x/w) dx \\ &= \varphi(-u) - (w\sqrt{2\pi})^{-1} \int_{-\infty}^0 e^x e^{-(x/w - u)^2/2} dx \\ &= \varphi(-u) - e^{w(w+2u)/2} \varphi(-u-w), \end{aligned} \quad (\text{A4})$$

where in the last step we have completed the square in the exponent of the integrand and changed variables to express the resulting integral in terms of

$$\varphi(x) = [1/\sqrt{2\pi}] \int_{-\infty}^x e^{-t^2/2} dt \quad (\text{A5})$$

Similarly, we can write

$$\begin{aligned} I_2 &= \int_{-\infty}^0 e^{(1+2u/w)x} \varphi(u + x/w) dx \\ &= w \{ \varphi(u) - \int_{-\infty}^0 e^{(1+2u/w)x} \varphi'(u + x/w) dx \} / y \\ &= w \{ \varphi(u) - e^{wy/2} \varphi(-u-w) \} / y \end{aligned} \quad (\text{A6})$$

$$\text{where } y = w + 2u \quad (\text{A7})$$

Combining (A1), (A4) and (A6), and using the fact that

$$\varphi(x) + \varphi(-x) = 1 \quad (\text{A8})$$

we obtain the result stated in equation (2), namely

$$E(n) = 2u\varphi(u)/y + 2(u+w)e^{wy/2}(1-\varphi(u+w))/y \quad (\text{A9})$$

In the derivation above we have implicitly assumed that $y \neq 0$. When $y=2u+w=0$, i.e., $r=-\sigma^2/2$ (corresponding to so-called zero drift), one can again evaluate relevant integrals using integration by parts. Alternatively, one can set $2u=w+\varepsilon$ in equation (A9), expand in powers of ε and then proceed to the limit $\varepsilon \rightarrow 0$. In either case, one obtains

$$E(n) = 2(1+u^2)\varphi(u) + 2ue^{-u^2/2}/\sqrt{(2\pi)}, (u=-w/2) \quad (\text{A10})$$

Also, in the borderline case $r=0$ (i.e., $u=0$), (A9) becomes

$$E(n) = 2[1-\varphi(w)]e^{-w^2/2}, (u=0) \quad (\text{A11})$$

Limiting (asymptotic) values of the above results can also be obtained from the approximation

$$\varphi(x) \approx 1 - e^{-x^2/2}/[x\sqrt{(2\pi)}], \text{ as } x \rightarrow \infty \quad (\text{A12})$$

For example, when $r=0$ ($w=\sigma\sqrt{T}$, $u=0$), one obtains from (A11) and (A12)

$$E(n) \approx 2/\sigma\sqrt{(2\pi T)}, \text{ as } T \rightarrow \infty \quad (\text{A13})$$

Similarly, when $r>0$, (A8), (A9) and (A12) give

$$E(n) \approx 2u/y = 2r/(2r+\sigma^2), (r>0), \text{ as } T \rightarrow \infty \quad (\text{A14})$$

Asymptotic results can also be obtained when $r<0$. In these cases we find not surprisingly that

$$E(n) = 0, (r<0), \text{ as } T \rightarrow \infty \quad (\text{A15})$$

FIGURE LEGENDS

Fig. 1. The probability (%) of a population remaining above 1% (dotted line) and 10% (dashed line) of the initial population size for a period of 100 years versus the mean population growth rate (r) and for three different values for the standard deviation in the growth rate (σ). The expected minimum population size (solid line) is shown as a percentage of the initial population size.

Fig. 2. Quasi-extinction risk curves for three different mean population growth rates and $\sigma=0.2$. The curves show the probability of declining to or below the threshold (expressed as a percentage of the initial population size) at some time within the next 100 years. Differences in the expected minimum population size are equal to the average amount that the curves move to the left or right (towards or away from extinction).

Fig. 3. The probability (%) of a population of *Burramys parvus* remaining above 0 females (extinction, dotted line) and 5 females (dashed line) for a period of 100 years versus the changes in the population growth rate. The expected minimum population size (solid line) is shown as a percentage of the initial population size, which was 20 females.

Fig. 1

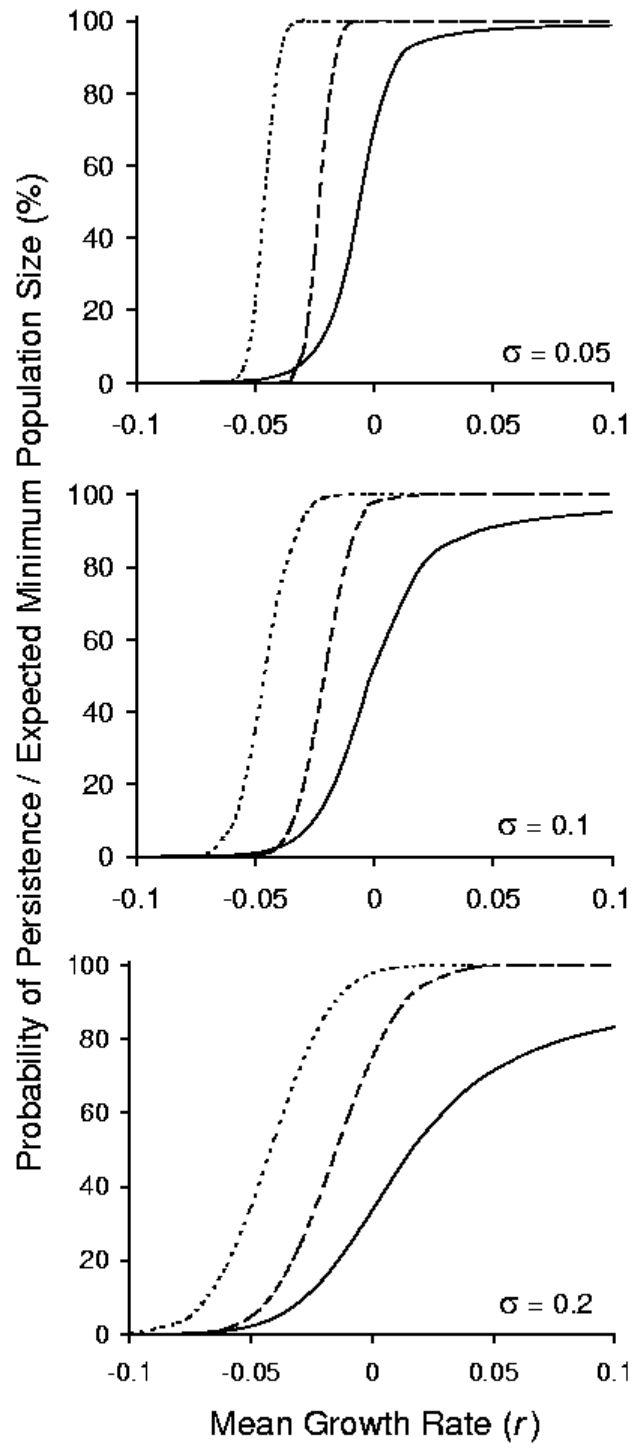


Fig. 2

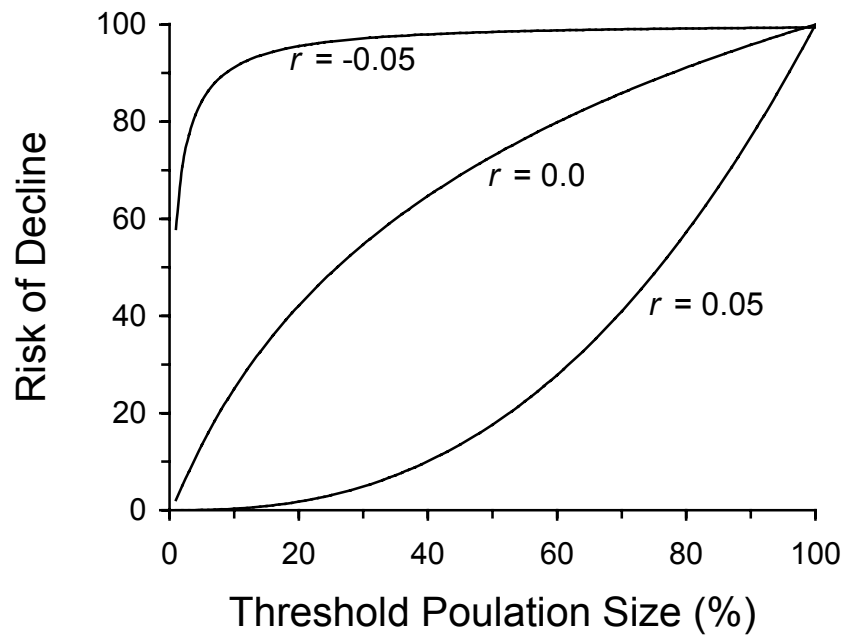


Fig. 3

