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The effect of density-dependent catastrophes on population persistence time

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Summary

1. There has been increasing recognition that catastrophes are an important factor in modelling threatened populations. However, density dependence has generally been omitted from models of threatened populations on the assumption that this omission yields conservative predictions. We explore the significance of including density-dependent catastrophes in models of threatened populations.
2. Using an analytical model, we show that density-dependent catastrophes have a significant effect on population persistence, decreasing mean persistence time at large population sizes and causing a relative increase at intermediate sizes.
3. We illustrate our results with empirical data from a disease outbreak in crabeater seals *Lobodon carcinophagus* and show that intermediate population sizes have the longest predicted persistence times.
4. The pattern we found is qualitatively different from previous results on persistence time based on density-independent models, in which persistence time increases with population size to an asymptote.
5. *Synthesis and applications.* This study has important implications for the conservation of species that may experience density-dependent catastrophes, such as disease outbreaks or starvation. Our results indicate that small and intermediate sized populations may contribute disproportionately to species persistence. Thus populations that have been dismissed as ‘marginal’ may actually be important for conservation. In addition, culling may increase the persistence of populations that experience density-dependent catastrophes.

Key-words: birth-death Markov process, disease, extinction, PVA, starvation.

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Introduction

Predicting persistence times and extinction rates for threatened populations is a central focus in conservation biology and has been one of the main tools for making important species and habitat management decisions (Boyce 1992; Burgman, Ferson & Akcakaya 1993; Beissinger & Westphal 1998; Reed *et al.* 2002). Early studies used simple exponential growth models with variation in the birth or death rates due to varying environmental conditions (Goodman 1987; MacArthur & Wilson 1967). These initial investigations predicted that persistence time increased very rapidly with popu-

lation size, reaching exceedingly long periods once a population reached a relatively small size (Shaffer 1987). These results stimulated interest in the effect of infrequent, large increases in death rates, or ‘catastrophes’, on persistence times (Ewens *et al.* 1987). Mathematical work on similar problems concerning extinction and loss of alleles due to extreme mortality events or emigration was also in progress, although it was not generally applied directly to endangered species (Brockwell, Gani & Resnick 1982; Brockwell 1985; Ewens 1989). Catastrophes can cause large decreases in mean persistence time, which can be described as a power function of the population ceiling (Lande 1993). Depending on the relative size of the catastrophes and the population growth rate, persistence times can either increase at an increasing or a decreasing rate with the population ceiling (Lande 1993; Mangel & Tier 1993). These

results have led to widespread recommendations to increase the population sizes deemed necessary to maximize persistence (Mace & Lande 1991; Mangel & Tier 1993; Meffe & Carroll 1994).

However, these general results are based on a simple treatment of catastrophes. In fact, a lack of attention to the effects of catastrophic mortality has been cited as one of the primary weakness of models of declining species (Coulson *et al.* 2001). Catastrophes are generally included in these models as either extreme variation in vital rates, driven by environmental stochasticity, or as mortality events occurring at random intervals that remove a large portion of the population (e.g. Lande 1993; Doak, Kareiva & Klepetka 1994; Marmontel, Humphrey & Oshea 1997). Empirical evidence suggests that these representations are too simple. Catastrophes are often more complex, and in particular may be caused by factors that have density-dependent feedbacks. The two factors identified by Young (1994) as the most common causes of massive die-offs, or catastrophes, in his review of large mammal die-offs were disease and starvation, both of which are likely to be density-dependent. Inclusion of density dependence in catastrophic mortality may radically change the extinction time predictions made by population models.

Density dependence has often been ignored in models of extinction risk (e.g. Inchausti & Weimerskirch 2001), based on some early modelling results demonstrating that this was a conservative assumption relative to extinction risk (Ginzburg, Ferson & Akcakaya 1990). However, recent results using a very well understood population of feral sheep have shown that extinction risk is quite sensitive to density dependence, at least for density dependence in the population growth rate (Chapman *et al.* 2001). Thus, it is unclear whether ignoring density dependence is a conservative assumption, and it probably depends on the particular system in question. To determine if density-dependent catastrophes were included in population models when appropriate, we searched for papers on the viability of species that had potentially density-dependent catastrophes in Young's (1994) review. While the importance of including density dependence may seem an obvious point, only one of the population viability analyses we

examined modelled catastrophes in this way and even this analysis did not examine its influence directly (Table 1). In fact, several analyses modelled factors that are likely to be density-dependent, such as disease mortality, as density-independent (e.g. Marmontel *et al.* 1997). This contradicts empirical evidence that both disease transmission and mortality are density-dependent in some wildlife populations (Hochachka & Dhondt 2000).

In light of their prevalence in natural systems and the potential effect on extinction risk, it is important to examine the impact that density-dependent catastrophes have on persistence time. Understanding the role that density-dependent catastrophes may play is especially pressing, given that they may qualitatively change the results of models that are often used to make decisions among management alternatives.

Catastrophes have two general characteristics: probability and intensity. The probability of a catastrophe is the chance that it will occur in an interval of time, for instance the chance of an extreme drought or a pest outbreak in a given year. Independently, one can also characterize the intensity of the catastrophe, for example how much does the 50-year drought increase the per capita death rate over the average rate. Each of the two parameters, probability of occurrence and intensity, can either be density-dependent or density-independent. This gives four possible ways for catastrophes to enter into population dynamics.

It is not difficult to imagine real examples of each of these types of feedback in natural systems. For instance, coastal dune systems in the south-eastern USA are heavily impacted by hurricanes, and small mammal populations in this habitat decline precipitously the year after hurricanes due to starvation (Swilling *et al.* 1998). While the probability of a catastrophe, i.e. a hurricane, in this case is density-independent, the resulting population declines due to starvation are probably density-dependent phenomena.

Disease outbreaks may provide an example of catastrophic events that are density-dependent in both their probability and intensity. For instance, the rate of spread of *Mycoplasma gallisepticum*, a poultry pathogen, among house finch *Carpodacus mexicanus* populations

Table 1. Catastrophes in population models for species where there is evidence for density dependence based on Young (1994)

Authors	Species	Population model	Included catastrophes	Source	Density dependent in model	Evidence for density dependence
Kokko, Lindstrom & Ranta (1997)	Seals	Difference equation, matrix	No	Not applicable	Not applicable	Yes
Song (1996)	Deer	Matrix	Yes	Drought (starvation)	No	Yes
Swart, Lawes & Perrin (1993)	Monkey	Differential equations	Yes	Not specified	No	Yes
Caughley & Gunn (1993)	Kangaroo	Difference equations	Yes	Drought (starvation)	No	Yes
Pascual, Kareiva & Hilborn (1997)	Wildebeest	Matrix, nonlinear difference equations	Yes	Drought (starvation)	Yes	Yes
Pascual & Hilborn (1995)	Wildebeest	Difference equation	Yes	Drought (starvation)	Yes	Yes
Armbruster & Lande (1993)	Elephant	Leslie matrix	Yes	Drought (starvation)	No	Yes

throughout the eastern USA depends on density, with larger populations experiencing the epizootic earlier during its regional spread (Hochachka & Dhondt 2000). In addition to density-dependent transmission, the size of the declines suffered by the infected house finch populations also depends on density, with larger populations suffering greater mortality (Hochachka & Dhondt 2000). Another case study comes from a disease outbreak that produced very high mortality in a group of nine subpopulations of crabeater seals *Lobodon carcinophagus* wintering on the ice in the Crown Prince Gustav Channel in Antarctica. In this case the probability of the disease outbreak appears to be strongly density-dependent, but the intensity less so.

Past work on catastrophes has usually assumed density-independence for both probability and intensity. We first investigate how predictions for mean persistence time change when catastrophe probability is density-dependent and intensity is independent, and then how predictions change when both are density-dependent. Initially, we explore these patterns in a general model. We then illustrate these ideas using demographic data on crabeater seals.

Methods

MODEL FORMULATION

To develop a model of density-dependent catastrophes we expanded upon a birth and death process model developed by MacArthur & Wilson (1967) and later modified to include catastrophes by Mangel & Tier (1993). Taylor & Karlin (1998) present an introduction to these methods. We assume a minimum size at which the population is extinct (the critical population size) and known values for the maximum population size, carrying capacity, and birth and death rates. Then the mean time to drop to the critical population size from any population size x , assuming the population changes by at most one individual per time step, is:

$$T(x) = 1 + B(x)T(x+1) + (1 - B(x) - D(x))T(x) + D(x)T(x-1). \quad \text{eqn 1}$$

Here $B(x)$ is the instantaneous birth rate at population size x , $D(x)$ is the instantaneous death rate at size x . This equation can be written simultaneously for all population sizes as a vector of $T(x)$'s and a matrix, called the infinitesimal generator, containing the $B(x)$'s and $D(x)$'s (Taylor & Karlin 1998). If \mathbf{T} is the vector of mean persistence times for populations from the minimum size to the carrying capacity and \mathbf{M} is the matrix of population size specific birth and death rates, Mangel & Tier (1993) show that

$$\mathbf{T} = -\mathbf{M}^{-1}. \quad \text{eqn 2}$$

This is an analytical method for calculating mean persistence times that can accommodate very complex

dynamics, including density-dependence (Mangel & Tier 1993). In most cases the matrix inversion will have to be done numerically, and there are many software packages available that can perform this operation. We used True BASIC™ (<http://www.truebasic.com>), a modern structured programming language which is interpreted into C, running on a Macintosh G3 computer.

Mangel & Tier (1993) extend this basic model to include a two part process for catastrophes, composed of the rate of occurrence for catastrophes at a given population size (size is interchangeable with density because the model assumes a constant habitat area) $C(x)$, and the intensity of the catastrophes. Given that a catastrophe occurs, we define intensity, $Q(y|x)$, as:

$$Q(y|x) = \Pr\{\text{decrease is } y \text{ individuals} \mid \text{current population size is } x\} \quad \text{for } y > 1 \quad \text{eqn 3}$$

where $Q(y|x)$ must sum to one over all possible catastrophe sizes:

$$\sum_{y=2}^x Q(y|x) = 1. \quad \text{eqn 4}$$

We depart from Mangel & Tier (1993) in ignoring catastrophes with no deaths, $Q(0|x)$, and ones that are analogous to the individual death term, $Q(1|x)$. This modification yields a matrix of population size specific rates similar to eqn 2, with the addition of catastrophe probabilities in the subdiagonal:

$$M = \begin{pmatrix} -R(x_c + 1) & B(x_c + 1) \\ D(x_c + 2) & -R(x_c + 2) \\ C(x_c + 3)Q(2|x_c + 3) & D(x_c + 3) \\ C(x_c + 4)Q(3|x_c + 4) & C(x_c + 4)Q(2|x_c + 4) \\ \dots & \dots \\ 0 & 0 & \dots \\ B(x_c + 2) & 0 & \dots \\ -R(x_c + 3) & B(x_c + 3) & \dots \\ D(x_c + 4) & -R(x_c + 4) & \dots \\ \dots & \dots & \dots \end{pmatrix} \quad \text{eqn 5}$$

Where $C(x)$ is the catastrophe rate at size x , x_c is the population size below which extinction occurs, and

$$R(x) = B(x) + D(x) + C(x) \quad \text{eqn 6}$$

is the rate of change in population size at x . This matrix can be inverted as above in eqn 2 to yield a vector of mean persistence times for all population sizes.

In order to investigate the effect of density-dependence in catastrophe probability, we chose a function for the catastrophe rate that would be flexible but would maintain a sigmoidal shape. We defined the catastrophe rate as:

$$C(x) = \left[\omega_0 + \omega_1 \left(\frac{x^\Gamma}{x^\Gamma + x_{th}^\Gamma} \right) \right] \quad \text{eqn 7}$$

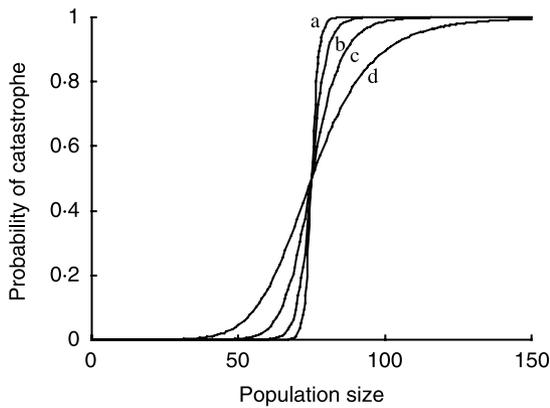


Fig. 1. Functional forms used for the density-dependent probability of catastrophe in the model. The curves represent different onsets of the probability of catastrophes, driven by values of Γ . From top to bottom the values for Γ in the figure are: a = 60, b = 30, c = 15, and d = 7.5. The density-dependent probability function is $\Pr\{\text{catastrophe}\} = \omega_1 \left(\frac{x^\Gamma}{x^\Gamma + x_{th}^\Gamma} \right)$, with $\omega_1 = 1$, and $x_{th} = 75$.

Here the rate of density-independent catastrophes is ω_0 . The rate of density-dependent catastrophes is $\omega_1 \left(\frac{x^\Gamma}{x^\Gamma + x_{th}^\Gamma} \right)$, where x is the current population size, x_{th} is the size at which the rate is $\frac{\omega_1}{2}$, and Γ is a parameter allowing modification of the strength of the density-dependence (Fig. 1). We chose this particular functional form for three reasons: (i) it agrees with the conclusion that disease outbreaks in wildlife populations generally occur when the population exceeds a threshold value (Dobson & Hudson 1995); (ii) it matches the observed pattern in the empirical data from crabeater seals that we use; and (iii) it is a relatively simple form that requires few parameters and thus is straightforward to analyse. In discussing density-dependent catastrophes we will use ω_1 , the maximum rate, to refer to a particular catastrophe rate. The actual values for $C(x)$ will be much less for most population sizes, with its value reaching ω_1 only near the maximum population size.

In the paper we will generally discuss catastrophe frequency as a probability instead of a rate for clarity, therefore we show the method for conversion from rates. This is also a necessary step for simulations, as although the rates can be represented directly as probabilities ($B(x)\Delta t + o(x)\Delta t$), these are not bounded by 1 when Δt is very close to 0 (Hilborn & Mangel 1997; p. 69). A change in population size occurs with probability:

$$\Pr\{\text{change in population size in } \Delta t\} = 1 - e^{-(B(x)+D(x)+C(x))\Delta t} \quad \text{eqn 8}$$

The probability of a particular type of change, e.g. a birth, is the product of the probability of a change (eqn 8) times the relative probability of the type of change of interest (a birth):

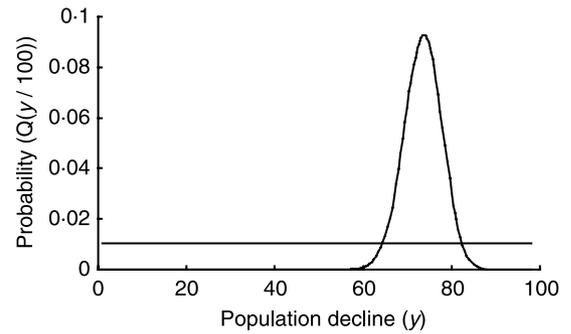


Fig. 2. Catastrophe intensity probability distributions. These are the probability mass functions for the number of individuals dying if a catastrophe occurs. The distributions shown are for populations starting at an initial size of 100 individuals. The flat line is a uniform distribution, indicating a density-independent intensity. The humped function is a binomial with parameters $\Pr\{\text{survival}\} = 0.25$ and $n = 98$, indicating a density-dependent intensity. Note that the graph only goes to 98, because for a population with a population ceiling of 100 we only allowed catastrophes that caused a decline of 2 or more individuals, resulting in a maximum of 98.

$$\Pr\{\text{birth in } \Delta t\} = \Pr\{\text{change in population size in } \Delta t\} \times \left(\frac{B(x)}{B(x) + D(x) + C(x)} \right) \quad \text{eqn 9}$$

Analogously, death and catastrophe rates can be converted to probabilities by replacing the birth rate in the numerator of the last term in eqn 9 with appropriate rate.

We modelled the intensity of catastrophes as either a uniform or binomially distributed decrease in population size (Fig. 2). For the uniform distribution, if a catastrophe occurs, all population sizes two or more less than the current size are equally likely outcomes. Although we use this as a density-independent case, the population size will have some effect on the size of the catastrophe. On average, the population after a catastrophe will be approximately half of the original population. We use the uniform distribution as our density-independent case for three reasons: (i) if the size of a catastrophe were wholly density-independent, i.e. a set value, it would either devastate the populations at small population sizes or be trivial at large sizes; (ii) it is a common distribution used in many population viability models; and (iii) in comparison with the binomial model the effect of uniformly distributed catastrophes is much less dependent on density. For the binomial model we assume all individuals are equally likely to die in a catastrophe with probability $1 - p$. The most likely reduction in the population size is $(1 - p)(x - 2)$, where x is the pre-catastrophe population size (Fig. 2). Resulting populations will be concentrated near px rather than distributed across the range of values; thus population reductions due to binomial catastrophes are more sensitive to the pre-catastrophe population size. Although it would be possible to make

the intensity of catastrophes more strictly density-dependent by allowing the survival probability to depend on density, we chose to avoid this complication to maintain comparability with the empirical example we use.

It is important to note that our model does not include environmental stochasticity, otherwise known as process error (Hilborn & Mangel 1997). To incorporate process error in a model one needs to deal with the variation in demographic rates over time, and ideally incorporate not only their variance, but also the covariance among rates. This is a complex, but solvable problem for demographic simulation models (e.g. Doak *et al.* 1994). However, incorporating process error into the type of birth-death process model we use is difficult. The primary problem is that it would be necessary to take the expectation of the inverse of the matrix of birth, death, and catastrophe rates, \mathbf{M} , across the joint distribution of the demographic rates:

$$\mathbf{T} = E_{\varepsilon}[-\mathbf{M}^{-1}(b(\varepsilon), d(\varepsilon), c(\varepsilon))] \quad \text{eqn 10}$$

Where ε denotes the process error in the birth (b), death (d) and catastrophe rates (c). It is important to be clear, introducing process error does not alter the fundamental underlying process – the population still changes by only single births or deaths and catastrophes – the values in the inverse matrix are now just an expectation across the variation in each rate.

An alternative approach for calculating equation 10 would be to discretize the joint distribution of the birth and death rates, calculate \mathbf{M} for each possible joint realization of the rates, invert each \mathbf{M} , and then take the expectation across these inverted matrices. We performed this discretized analysis assuming a symmetric beta distribution for additive process error in either the birth rate or the death rate, holding the other rate constant, to evaluate the effects of environmental stochasticity on our model results. We varied each rate in steps of 5% from –100% to +100%, yielding 20 possible realizations for either the birth or death rate. We explored the effects of this additive process error as the variance in error distribution increased up to a maximum of 0.4. To illustrate the range of this variance, at the maximum error variance of 0.4 there was a 5% chance that the observed rate would differ by 75% or more from the mean rate in any given observation.

Incorporating process error into the birth, death, and catastrophe model we used resulted in quantitative changes in our results, primarily reducing the persistence of small and intermediate sized populations. However, while there were quantitative effects, the qualitative results of our model did not change, and thus we chose to exclude environmental stochasticity from our analysis. It is important to note that the time required for calculating the expectation of the inverse matrices can be prohibitive if the number of realizations of the process error is very large.

PARAMETER VALUES

Basic demographic rates

We chose parameters based on a hypothetical species that has one offspring per individual per year in a population with annual population growth rates $\lambda = 1.01$ or $\lambda = 1.05$. We chose λ values slightly above 1 as an optimistic, but realistic conservation case. We used a birth rate of 1 per year to match our empirical example and for ease of calculation. We calculated the death rate for the species using the population growth rate and birth rate (Appendix 1). We followed the basic MacArthur & Wilson (1967) model formulation, holding these rates constant below the population ceiling, set at 100, above which $B(x) = 0$.

Catastrophe probability

We chose a range of catastrophe parameters to cover the spread of possible values. It is important to remember that these are maximum rates, and in the density-dependent case the rates will be substantially below the maximum for a portion of the range of possible population sizes. The maximum probability of catastrophe varied from 0.006 to 0.902. This is equivalent to maximum catastrophe rates between 1 every 100 and 1 every 0.1 years. We used a range of ω_1 values (seven) that allowed us to explore the effect of different intensities of density dependence, without departing from a basic sigmoidal shape that gave a maximum catastrophe probability of approximately ω_1 . The value for x_{th} was 75 in all of the analyses. In preliminary analyses, altering x_{th} had no effect on the qualitative patterns we found, thus we fixed it at this value arbitrarily. We analysed the model for each of the catastrophe rates as a density-independent rate ($\omega_0 > 0$, $\omega_1 = 0$), as a density-dependent rate ($\omega_0 = 0$, $\omega_1 > 0$) and for a selected set of combined rates ($\omega_0 > 0$, $\omega_1 > 0$). The combined density-independent and density-dependent case did not differ qualitatively from the density-dependent case, so we will not discuss these results in detail.

Catastrophe intensity

The intensity of catastrophes was constant for the uniform distribution model, with the average mortality being half of the current population size, and the populations remaining after catastrophes evenly distributed between the pre-catastrophe population size and zero. For the binomial model we used survival probabilities of 0.5, 0.25 or 0.1.

Crabeater seals Lobodon carcinophagus

In addition to these hypothetical cases, we also examined the effect of density-dependent catastrophic mortality on persistence time using field data for crabeater seals. We explore this case to illustrate our results using

field data, with the clear recognition that we do not have adequate data to fully characterize the population dynamics of this species. However, in collecting these data we discovered that there is an amazing lack of similar data on die-offs, even for relatively well-studied large mammals, making stronger empirical tests of our results difficult.

In 1956, nine subpopulations of crabeater seals wintering on the ice in the Crown Prince Gustav Channel, off Graham Island in Antarctica, experienced mass die-offs due to an outbreak of disease (Laws & Taylor 1957). We used the data from Laws & Taylor (1957) on these subpopulations to parameterize our model. The nine populations ranged in size from 50 to 2000 animals. Based on these data we set the population ceiling at 2000, and assumed an annual population growth rate $\lambda = 1.01$ or 1.05 for populations below that size. Birth rates were set at 0.5 offspring per year per female, and death rate was determined from this and the population growth rate. Empirical estimates of disease mortality across the subpopulations varied from 0% to 97% , with most populations below 400 individuals experiencing negligible disease mortality. Above 400 individuals mortality rates increased rapidly. Based on this we set the threshold for disease outbreaks (x_{th}) at 400 individuals. There was no significant trend in per capita mortality with population size above 400 individuals, so we used Laws & Taylor's (1957) mean mortality rate of 85% to estimate the individual survival probability. Thus, we assume catastrophe intensity is binomially distributed, and each seal in a population has a survival probability of 0.15 , if a catastrophe occurs. We set $\Gamma = 30$ to give a relatively rapid onset for disease outbreaks at population sizes above 400 individuals. We were unable to find data on the frequency or probability of disease outbreaks in crabeater seals, so we estimated it based on data from harbour seals *Phoca vitulina* using maximum likelihood methods (Geraci *et al.* 1982; Appendix 2). Due to the suggested prevalence of disease outbreaks in seal populations and the similarity of life histories among seals, this should be a reasonable first approximation (Young 1994). The most likely estimate for the catastrophe rate was $C(x) = 0.05$ or 1 outbreak every 20 years on average, and the upper 95% confidence limit was $C(x) = 0.115$ or an outbreak every 9 years (Appendix 2). We ran the model using both the maximum likelihood estimate and the value at the upper confidence limit.

Results

EFFECT OF DENSITY DEPENDENCE IN THE PROBABILITY OF A CATASTROPHE

Density dependence in the probability of catastrophes has a large effect on the pattern of population persistence time with increasing initial population size (Fig. 3). This effect is particularly apparent in comparison with the pattern generated by density-independent

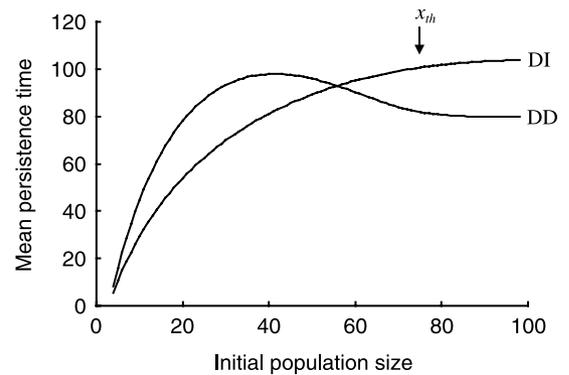


Fig. 3. Persistence time for populations with density-dependent (DD) and density-independent (DI) catastrophe probabilities. The intensity of catastrophes for both curves is density-independent. The probability of catastrophe for the density-independent case is 0.025 and the maximum probability for the density-dependent case is 1 (i.e. ω_0 and ω_1 , respectively). The population growth rate for both curves is $\lambda = 1.01$, and $x_{th} = 75$ and $\Gamma = 15$ for the density-dependent case. The population ceiling for both cases is 100 individuals.

catastrophe probabilities (Fig. 3). Three qualitative differences in the patterns are important. First, density-dependent catastrophes generate a local maximum in persistence times at small initial population sizes. Secondly, persistence times for populations with a given density-dependent catastrophe probability are equivalent to identical populations with much smaller density-independent probabilities. Thirdly, persistence times rise more rapidly at small population sizes in the density-dependent case. All of these patterns are driven by the lack of catastrophes in the density-dependent case at small population sizes and the rapid increase in their frequency at larger sizes. Simultaneously including density-independent and dependent catastrophes in the model did not qualitatively change this pattern from the density-dependent catastrophes case, thus we will not present results for cases with both types of catastrophes.

The probability of catastrophe has a large effect on population persistence time (Fig. 4). If density-dependent catastrophes are relatively rare, with a maximum rate around 1 every 100 years ($\omega_1 = 0.01$), they effect persistence time, but there is not a major qualitative difference between the patterns in the density-dependent and density-independent cases, i.e. both rise nearly monotonically toward an asymptote (Fig. 4a, top curve, Fig. 3). However, as the probability of catastrophes increases, persistence time for a given initial population size decreases rapidly (Figs 4b and 5). At these shorter persistence times the effect of density dependence in the probability of a catastrophe becomes apparent, and results in a depression in persistence time for populations initially near or above x_{th} , the threshold for density dependence (Figs 4b and 5). Comparing maximum persistence time and persistence time at the population ceiling, these depressions ranged up to 16% when $\lambda = 1.05$, and 21% when $\lambda = 1.01$

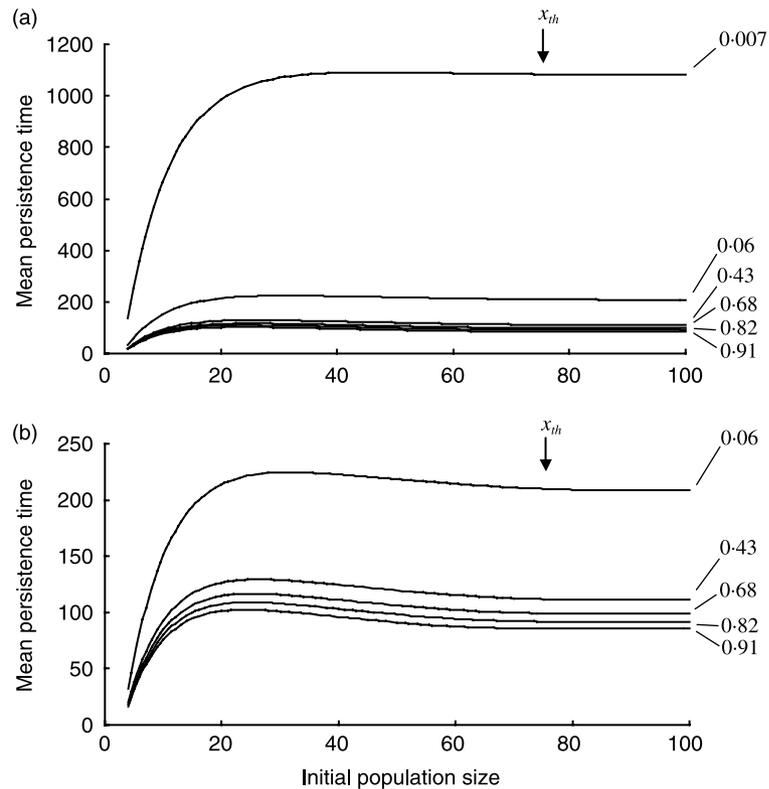


Fig. 4. Persistence time for high growth rate populations with a density-independent probability of catastrophic mortality. The intensity of catastrophes is density-independent (i.e. mortality is uniformly distributed). Each line represents a different probability of catastrophe. Panel (a) shows the results for all the analyses we conducted; panel (b) is the same, but does not include the lowest probability run. The probabilities shown in the figure have been rounded for brevity, the actual values, from top to bottom, are: 0.007, 0.059, 0.425, 0.684, 0.824 and 0.905. These correspond to average rates of: 1 catastrophe every 100 years, 1 every 10 years, 1 every year, 1 every 0.4 years, 1 every 0.2 years and 1 every 0.1 years, respectively. For these analyses the growth rate $\lambda = 1.05$, $x_{th} = 75$, and $\Gamma = 15$.

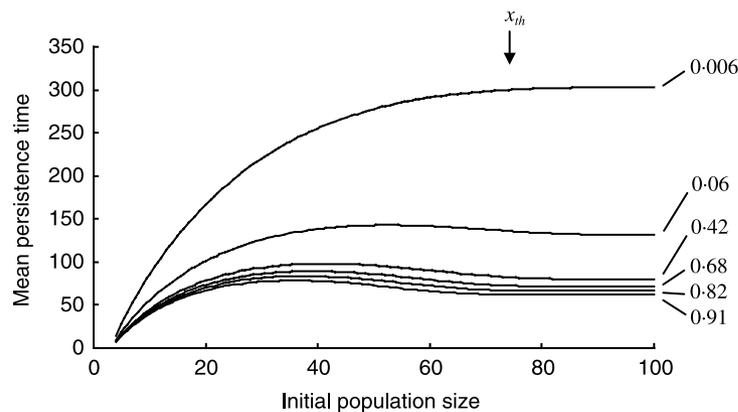


Fig. 5. Persistence time for low growth rate populations with a density-dependent probability of catastrophic mortality. The intensity of catastrophes is density-independent (i.e. mortality is uniformly distributed). Each line represents a different probability of catastrophe. The probabilities shown in the figure have been rounded for brevity, the actual values, from top to bottom, are: 0.006, 0.058, 0.419, 0.677, 0.819 and 0.902. These correspond to average rates of: 1 catastrophe every 100 years, 1 every 10 years, 1 every 1 years, 1 every 0.4 years, 1 every 0.2 years and 1 every 0.1 years, respectively. $\Gamma = 15$ and $x_{th} = 75$. The growth rate for these runs was $\lambda = 1.01$.

(Figs 4b and 5, respectively). This effect is apparent even at relatively low maximum catastrophe probabilities, e.g. $P \approx 0.06$ (Fig. 5). In fact, additional incremental increases in the maximum catastrophe probability have diminishing effects on persistence time beyond this initial pattern (Fig. 5).

EFFECT OF THE FORM OF DENSITY DEPENDENCE

As Γ (the parameter that controls the steepness of the density dependence function) increases, the effect of catastrophes becomes more pronounced (Fig. 6). As

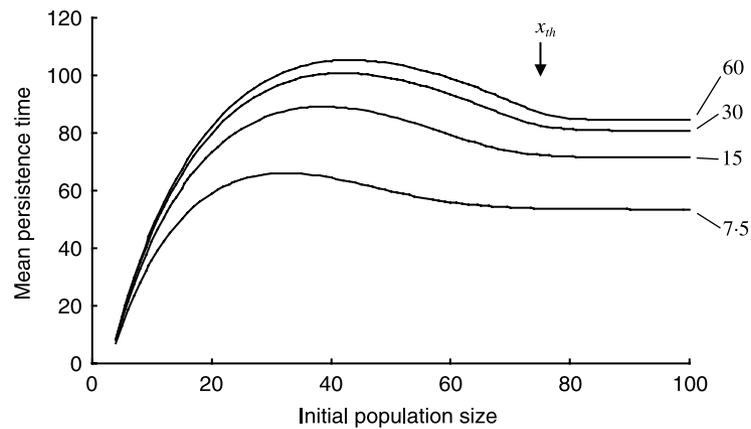


Fig. 6. Persistence times for a population with differentially sharp onsets of density-dependence in catastrophic mortality. $\Gamma = 60, 30, 15,$ and $7.5,$ moving from top to bottom. These equate to a step function, a sharp sigmoidal curve, a smooth sigmoidal curve, and, a more gentle sigmoidal curve, respectively (see Fig. 1). These times were generated from a model with density-independent catastrophe intensity, a low growth rate ($\lambda = 1.01$), $x_{th} = 75,$ and a maximum probability of catastrophe of $0.677.$

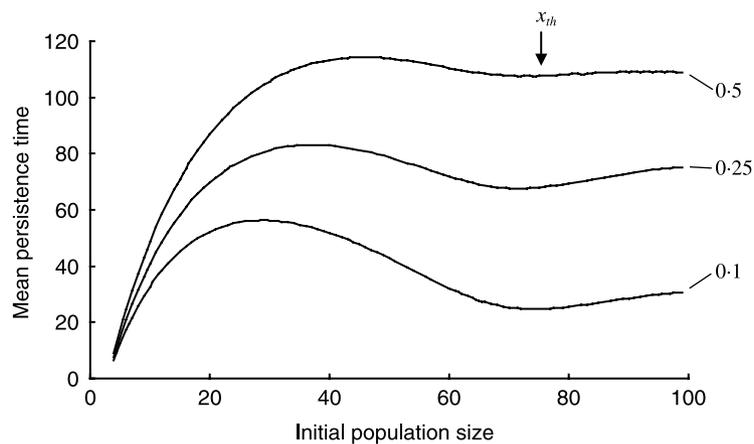


Fig. 7. Persistence times for a population with density-dependent probability and intensity of catastrophes. Each line represents a different intensity of catastrophe (equivalent to the probability an individual survives). From top to bottom the intensities are $0.5, 0.25,$ and $0.1.$ This model used the low growth rate ($\lambda = 1.01$) and a maximum catastrophe probability of $0.419.$ The density-dependence parameter, gamma, was 15 and $x_{th} = 75.$

the density dependence function becomes more step-like, the peak in persistence time at lower population sizes becomes sharper and longer relative to the subsequent trough (Fig. 6). The population size with the maximum persistence time also changes. For instance, comparing populations with a maximum catastrophe probability of approximately $0.4,$ the population with maximum persistence time moves from 32% of the population ceiling to 43% as the onset of density dependence becomes more abrupt (Fig. 6).

EFFECTS OF DENSITY-DEPENDENT CATASTROPHE PROBABILITY AND INTENSITY

When catastrophe intensity increases with density (i.e. is binomially distributed), there is a pronounced effect on persistence time (Fig. 7). The local maximum in persistence time at low population sizes is sharper and higher relative to the population ceiling relative to the density-independent intensity case (compare Figs 7

and 6, third curve from the top). As the intensity of the catastrophes increases, the differential in persistence time at intermediate population sizes becomes more pronounced. For instance, if the maximum probability of a catastrophe occurring is approximately 0.4 and the individual survival probability is 0.5 when one occurs, the predicted maximum persistence time is 5% longer than the persistence time at the population ceiling (Fig. 7, top curve). In contrast, if $P = 0.1,$ the predicted maximum is nearly twice the persistence time at the ceiling (Fig. 7, bottom curve). In addition, the range of population sizes that have persistence times close to the maximum is also more narrow for populations with more intense catastrophes (Fig. 7). Finally, if catastrophes are very intense there may be some intermediate population sizes that have particularly short persistence times (Fig. 7, bottom curve). This is driven by the catastrophe probability reaching its maximum below the population ceiling and causing populations to make sojourns into small sizes where they are susceptible

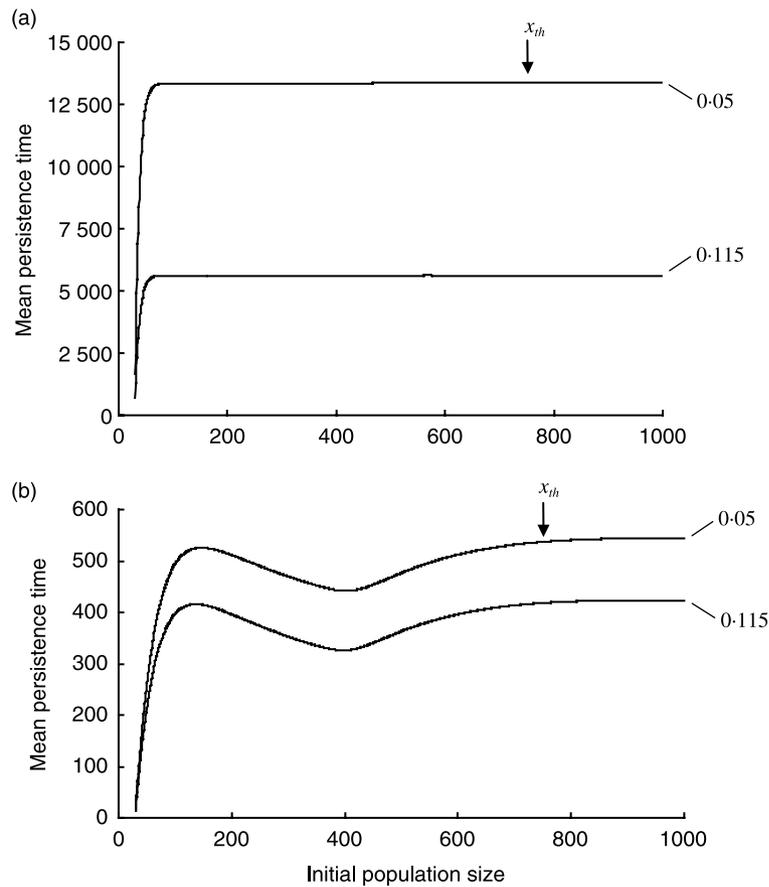


Fig. 8. Persistence times for crabeater seal populations with catastrophes, in which probability and intensity are density-dependent. Panel (a) a population with an annual per capita growth rate of 1.05; (b) one with a growth rate of 1.01. Parameters for the model are given in the methods. The top line in each figure is the persistence time using the maximum likelihood estimate of the maximum probability of catastrophe for the seals ($P = 0.05$, or every 20 years on average), the bottom line is the results using the upper 95% confidence boundary of the estimate as the maximum probability of catastrophe ($P = 0.115$ or every 9 years on average). Catastrophe rates are based on data from Laws & Taylor (1957).

to extinction due to demographic stochasticity. As the initial size increases further above x_{th} , the proportional reductions in population size due to catastrophes no longer take the population to sizes that are susceptible to extinction via demographic stochasticity.

PREDICTIONS USING DATA FOR CRABEATER SEALS

Using the density-dependent probability and intensity model, i.e. assuming that all seals in a population have an equal chance of contracting a disease and dying, we found a strong effect of catastrophic mortality on seal persistence times (Fig. 8). We investigated persistence times at two different arbitrary population growth rates ($\lambda = 1.01$ and 1.05) and two catastrophe probabilities ($P = 0.05$ and 0.115) which were estimated from empirical data. Higher growth rates led to a decreased effect of density-dependent catastrophes on persistence time (Fig. 8a). Although there was still an effect, it was negligible when scaled against the mean time to extinction (Fig. 8a). Populations with the lower growth rate showed a strong effect of density dependence in

catastrophe probability and intensity (Fig. 8b). Persistence times reached a local maximum at 147 individuals for the lower catastrophe probability, and 137 for the higher (Fig. 8b). In both cases, the predicted persistence times declined to a local minimum above this size, which was centred just below the threshold population size for catastrophes. Persistence times then rose as the initial population size increased toward the population ceiling. For example, the higher catastrophe probability case had an initial peak in persistence time of 416 years at 137 individuals, which declined to a local minimum of 326 years at 398 individuals, and finally rose to 423 years at the population ceiling (Fig. 8b). The probability of catastrophe had an effect on the predicted persistence times, giving reduced persistence times with more frequent catastrophes (Fig. 8a,b). However, there was no qualitative difference in the pattern of persistence across population size as the catastrophe frequency increased.

Discussion

Our results demonstrate that the way catastrophes are incorporated into population viability analysis (PVA)

models can make a significant difference in the predictions they give for persistence times. Most importantly, density dependence in the probability or intensity of catastrophes can produce qualitatively different outcomes when examining the effect of initial population size on mean persistence time. Given that population size and density are related, either due to aggregation by individuals or limited habitat, positive density dependence in the probability of catastrophes may make larger populations more vulnerable to extinction. Positive density dependence in the intensity of catastrophes also has a strong effect on persistence times, causing reductions at large population sizes. Together, these two factors can generate mean persistence times for large population sizes that are substantially smaller than times expected for smaller population sizes. There are a very limited number of species for which there is adequate field data to test the generality of this pattern. However, predictions based on data from disease outbreaks in crabeater seal populations indicate that real populations may follow this pattern, with greatly reduced mean persistence times at intermediate population sizes.

Our results have a number of implications. First, if density-dependent catastrophes are a significant factor in regulating populations, a population may persist longer if it is kept at a lower density. It is important to keep in mind however, that other factors such as environmental stochasticity may pose a significant threat, particularly at small and intermediate population sizes. Secondly, there may be a narrow range of population sizes, well below the population ceiling, for which populations tend to persist the longest. Thirdly, due to the more rapid rise in persistence time, very small populations affected by density-dependent catastrophes may persist longer than similar populations affected by density-independent ones.

Data from a survey of large mammals indicate that mechanisms which could cause density-dependent catastrophes, such as disease or starvation, may actually be relatively common (Young 1994). Moreover, empirical estimates of catastrophic mortality among large mammals suggest mean survival probabilities ranging from 0.10 to 0.20, within the range of values we examined (Young 1994). These data suggest that density-dependent catastrophes may be important forces in the population dynamics of many threatened species. This is particularly true for organisms that are likely to experience positively density-dependent catastrophes, as in fire susceptible systems such as chaparral or for any species affected by starvation or epidemic disease outbreaks.

One important point to note in evaluating our results is that our model does not include environmental stochasticity. Inclusion of environmental stochasticity, or process error, in a model of extinction that includes both demographic stochasticity, or sampling error, and catastrophes in an analytic framework has been elusive. Many simulation models have included all

three types of stochasticity; however, their results have generally been specific to a particular system and not intended to explore the relative importance of these factors in persistence (see References in Table 1). Our preliminary analysis indicated that incorporating process error would decrease the strength of the patterns we have shown; however, it would not change them qualitatively. The primary effect of process error appears to be in reducing the persistence of small populations, although they did still have longer mean times to extinction than larger populations for some parameter combinations. Clearly, conclusive results on the relative effects of environmental stochasticity and density-dependent catastrophes will require further development of the analytical tools available for modelling these types of systems.

There is an ongoing argument in the literature as to whether catastrophes and environmental stochasticity should be considered as separate phenomena in extinction processes, or whether catastrophes really represent an extreme case of environmental stochasticity, or process error (e.g. Lande 1993; Caughley 1994; Young 1994, 1999; Erb & Boyce 1999; Reed *et al.* 2002). In part this issue seems to be a result of the definition of catastrophes from the perspective of their effects, not the underlying mechanisms (e.g. Young 1994). This has led to the question of whether they are statistically separable from smaller variations in population size or growth rate that are presumably caused by 'normal' process error, or environmental stochasticity (e.g. Erb & Boyce 1999).

A more fruitful approach might be to define catastrophes and environmental stochasticity by the characteristics of their underlying mechanisms. For instance, in the case of the critically endangered Alabama beach mouse *Peromyscus polionotus ammobates* annual changes in population size are driven by summer rainfall which affects the seed crop on which they feed. These mice inhabit frontal dunes along the coast of the south-eastern US, and as such their habitat is subject to impacts from hurricanes moving up through the Gulf of Mexico (Swilling *et al.* 1998). These hurricanes have a variety of effects, including permanent and temporary damage to the beach substrate, flooding resulting in direct mortality and necessitating dispersal to protected areas, and destruction of the annual seed crop. Thus annual process error, or environmental stochasticity, could be equated with summer rainfall, while hurricane effects represent catastrophic events. In this case it is unclear which mechanism might result in larger magnitude changes in population size. The primary difference between the two sources of variation in population is their recurrence interval, not the magnitude of their effects (Swilling *et al.* 1998; Oli, Holler & Wooten 2001). The process error, or environmental stochasticity, is introduced every summer, while the catastrophes occur at random intervals.

One would model these two sources of population variation quite differently, and would generate

expectations for their magnitude and frequency using entirely separate data sets. This represents a much more nuanced view of environmental stochasticity and catastrophes, and potentially presents a resolution to the debate about how to separate the two sources of variation. The model we developed follows this framework, although we have chosen not to include environmental stochasticity in the version we present here.

MANAGEMENT IMPLICATIONS

Our results have several ramifications for conservation efforts. First, more detailed information on the frequency and intensity of mass die-offs may be necessary to properly manage some species. This information is difficult to obtain, particularly in cases where there are infrequent but very intense catastrophes. However, even basic information on the time period between large mortality events and some approximation of their size would be a significant step. This information could be gathered in the context of basic monitoring and should be a priority for conservation organizations and agencies.

Secondly, recommendations are often made to alter management to increase the population size of threatened species. This is particularly true if density-independent catastrophes are considered in the assessment of their dynamics due to the large increases in predicted persistence time that are obtained by increasing population size. However, if the management results in high densities, increasing population size may actually reduce persistence.

One might think that management recommendations would generally focus on increasing the amount of habitat as a means of altering population sizes, thus leaving density unaffected. However, if the proposed management involves increasing either the carrying capacity or the growth rate of a population (for instance by reducing the mortality rate, e.g. Inchausti & Weimerskirch 2001), without a concomitant increase in habitat area, densities will increase. Even in cases where population sizes are manipulated by altering available habitat, if animals aggregate for some activity such as breeding, feeding, or migration, the end result may be that densities increase with population size for at least some portion of the lifespan. For instance, pinnipeds aggregate on breeding grounds, and thus increases in population size may result in higher densities for at least short periods during the breeding season, which could have substantial effects on the dynamics as we have shown in our crabeater seal example.

Even in cases where persistence times are long for large populations, they may be much shorter at intermediate levels. This is clearly illustrated by our crabeater seal example. If a seal population is at a density of 100 individuals per unit area, and a manager charged with conserving the population has information that persistence times are much longer at levels closer to 1000, it may seem advisable to manage the

population to increase it to the higher population size. However, in making this decision one must weigh the benefits of increased persistence time at higher abundance against the danger presented by the greatly reduced persistence times predicted for intermediate population levels through which the population must move. Obviously some of the population dynamic parameters must change for this increase to occur, so it is not clear exactly what will happen at these intermediate sizes, but a reduction in persistence time is a definite possibility. One possible approach to this complex problem would be to use modelling to determine the optimal decision in the particular situation (e.g. McCarthy, Possingham & Gill 2001). This approach has a long history in harvesting models, particularly in fisheries, where similar questions have been addressed (e.g. Hanson & Ryan 1988).

Thirdly, in cases where density-dependent catastrophes are important, small populations may contribute more to persistence than had been previously thought due to the rapid rise in persistence time with population size. This argues for careful evaluation of which 'marginal' populations we are willing to sacrifice when making decisions about priorities for conservation of a species. Finally, where a high density of a threatened species does occur, it may be possible to increase the probability of persistence by culling the population. This is particularly applicable for refuges where large wildlife populations are confined or for species that aggregate. Traditionally, this has not been a management approach taken for threatened species; however, this practice is widely used to prevent population crashes for managed game species (Robinson & Bolen 1989). The idea of culling populations of threatened species represents a departure from conventional conservation measures; however, our results indicate it is an option that should be investigated further in some cases.

Although many populations of threatened species may be at levels too low to experience density-dependent mortality, various forces such as limited habitat availability, social structure, or breeding aggregations can result in unexpectedly high densities, even among sparse populations. Many conservation biologists dismiss density dependence when constructing PVAs, often citing literature that indicates that this is a conservative assumption (Ginzburg *et al.* 1990). While true in terms of the predictions for mean persistence time, neglecting density dependence is clearly not conservative with respect to the qualitative patterns in predicted persistence times. Density dependence in catastrophic mortality results in significant reductions in predicted persistence times at large population sizes and qualitatively changes the pattern of persistence time with population size. Thus, it is important to consider the possible effects of density dependence when calculating persistence times, particularly if a population is known to be subject to catastrophic mortality.

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Appendix 1

To determine the parameters for the crabeater seal populations we began by assuming an annual population growth rate, λ , an annual birth rate of 1 offspring per female, and a 1 : 1 sex ratio. From these values we constructed a death rate that gave realistic average lifetimes. If $N(t)$ is the population size at time t , b is the instantaneous birth rate and d is the instantaneous death rate:

$$\frac{dN}{dt} = (b - d)N \quad \text{eqn 1.1}$$

Thus in a population with no deaths and one birth per breeding pair

$$\lambda = \frac{N(1)}{N(0)} = e^b = \frac{3}{2} \quad \text{eqn 1.2}$$

Because $\lambda = e^r = e^{(b-d)}$ and we now know e^b we find that

$$d = -r + \ln\left(\frac{3}{2}\right) \quad \text{eqn 1.3}$$

Thus $d = 0.396$ for $\lambda = 1.01$ and 0.357 for $\lambda = 1.05$.

These rates are analogous to exponential decay rates. For these rates to be realistic they need to result in reasonable average lifespans given reasonable age specific mortality rates. Although there are many ways to partition the rates it is necessary that the possibilities at least include partitions that would be reasonable for a large mammal.

An individual with a constant death rate of 0.396 has a mean lifetime of 2.5 years, while a death rate of 0.357 yields an expected lifetime of 2.8 years. Using age-specific mortality rates for a 1 year juvenile phase between 0.85 and 0.9 and a subsequent adult mortality rate of 0.05 we obtain a similar range of expected

lifetimes, with an expected adult lifetime of 20 years. While these results do not guarantee our parameters are correct, they at least provide evidence that we are within the range of reasonable values.

Appendix 2

We calculated the rate of catastrophes based on data reported by Geraci *et al.* (1982) using maximum likelihood methods (Hilborn & Mangel 1997). Geraci *et al.* report that in 1980, 445 harbour seals of a local population of 600 died; this local group was a part of a regional metapopulation of approximately 10 000 individuals. They report similar die-offs in 1931, 1957, and 1964. We take t_i to be the time between the i^{th} and $i + 1^{\text{st}}$ catastrophe. If the catastrophe rate is constant:

$$\Pr\{t < \text{time between two catastrophes} < t + dt\} = ce^{-ct} dt + o(dt) \quad \text{eqn 2.1}$$

Given this assumption and the observed times between die-offs, the maximum likelihood estimate (MLE) for c was 0.0526. The 95% confidence interval around this estimate is $0 < c < 0.115$.

Clearly, there are other more simple methods for calculating the catastrophe rate. For instance, it could be calculated by simply dividing the number of catastrophes by the total number of years of observation. However, we chose the more formal MLE method because it gives not only an unbiased estimate of the rate but also a confidence interval. It is obvious that our confidence interval does not have enough data points behind it to be very well founded. However, given the paucity of data on catastrophes, and extinctions in general, we find it much more useful to make an educated guess about the upper bounds of the rate rather than making arbitrary decisions or avoiding exploring the possibilities all together.