



Four Facts Every Conservation Biologists Should Know about Persistence

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FOUR FACTS EVERY CONSERVATION BIOLOGIST SHOULD KNOW ABOUT PERSISTENCE¹

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The future's uncertain and the end is always near
—J. Morrison (*Roadhouse Blues*)

INTRODUCTION

In the natural world, populations or individual stocks can decrease by large amounts in short intervals of time. We refer to all such changes as “catastrophes” and include physical factors such as hurricanes, freezes, and droughts, biological factors such as epidemics or invasion by a new competitor or predator, or perturbations of the environment caused by humans. Examples of such catastrophes, across a wide range of taxa and species, abound. In the Caribbean Sea (Richards and Bohnsack 1990), several epizootics occurred in the 1980s, including a massive fish kill in the reefs (the cause of which is still unknown) and a mass mortality of sea urchin (*Diadema* spp.) in which up to 98% of the population was destroyed in many areas (Lessios 1988, Levitan 1988).

Geraci et al. (1982) report that 445 harbor seals out of a local population of 600 and a metapopulation of $\approx 10\,000$ harbor seals died in New England during an epizootic and that similar catastrophes occurred in 1931, 1957, and 1964. Harwood and Hall (1990) report a mass mortality of $\approx 18\,000$ common seals in northern Europe in 1988, of $\approx 3\,000$ Baikal seals in the former Soviet Union in 1987, of $\approx 2\,500$ (out of a population of 3000) crabeater seals in the Antarctic in 1955, and that in 1758 (in a less precise era) “multitudes” of seals died. Since the 1970s, there appears to have been an increase in the incidence of such unusual marine mammal mass mortalities throughout the world (Marine Mammal Commission 1993; some of the most recent unusual mortality events are described in this report).

The 1982–1983 El Niño event led to a 60–70% overall mortality, mainly due to starvation, of marine iguanas (Laurie and Brown 1990). The heath hen was driven extinct by a combination of catastrophes including a fire, harsh winter, heavy predation by goshawks, and

an epizootic (Simberloff 1988:497). Catastrophes, often interwoven with other kinds of environmental fluctuation, have been associated with the extinction or severe decrease in population size of the Laysan teal, the Great Auk, butterflies, reindeer (in which 5500 out of 6000 individuals were killed), and the Short-tailed Albatross (Simberloff 1988:499).

Menges (1990), in a population viability analysis of the endangered plant Furbish's lousewort, notes the importance of catastrophic events. For example, in 1983–1984, 3 out of 10 of Menges's field sites were destroyed by the abiotic catastrophe of ice scour and bank slumping. At a fourth field site, only two adult plants remained. After including catastrophes in a population viability analysis, Menges concludes: “Catastrophic mortality dominates estimates of population viability, causing the majority of extinctions when added to within-population environmental stochasticity” (1990:57). Even so, it is remarkable that there are few other examples of population viability analysis that include catastrophes (Ginzburg et al. 1990, Boyce 1992).

Young (1993) reviews the literature concerning 92 natural die-offs of large mammals and finds that the severities of the die-offs (caused by natural catastrophes such as disease or starvation) showed a relative peak at 70–90% of the population. Herbivore die-offs were often caused by starvation, carnivore die-offs by disease. He also provides examples of the numerous but nonquantitative reports of catastrophic die-offs. Thus, the results of Geraci et al. (1982) and Menges (1990) suggest that it is possible to at least approximately estimate the rate of catastrophes, and those of Young (1993) suggest that it is possible to estimate the distribution of the number of individuals killed in a catastrophe. For example, using the data in Geraci et al. (1982) leads to a maximum likelihood estimate of the rates of catastrophes of $\approx 5\%$, with a 95% confidence interval of $[0, 0.115]$. In the case of catastrophic forest fires, it may be possible to calculate the rates of catastrophes more accurately because of the scar rings left by the fires (e.g., Clark 1989).

¹ For reprints of this Special Feature, see footnote 1, p. 583.

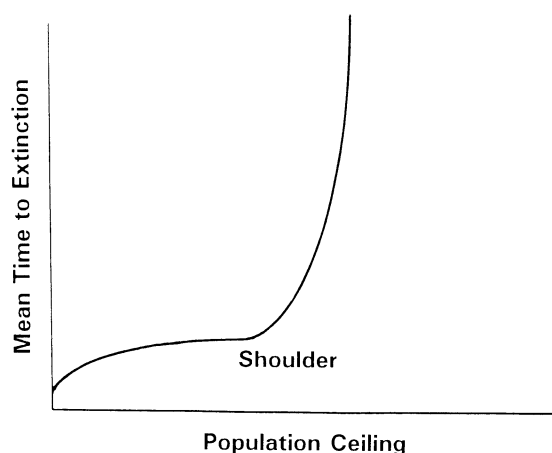


FIG. 1. The "shoulder" in the mean time until extinction based on a simple birth and death model (MacArthur and Wilson 1967). This model has a population ceiling with a constant per capita birth rate below the ceiling and constant per capita death rate (see text for more details.) The shoulder and associated extremely large persistence times is often identified with the "minimum viable population" (Soulé 1987). Here we assume that the initial value of the population is the same as the population ceiling.

Because of the mathematical difficulties, catastrophes are usually not included in birth and death models (MacArthur and Wilson 1967), which allow jumps of single individuals, or diffusion models (Leigh 1981), which are based on the assumption that the population is likely to change but only by a small amount. However, catastrophes are important and, as Menges (1990) suggests and we shall argue below, may be more important in determining persistence time than any other factor usually considered. Furthermore, the intuition developed using simple birth and death models or diffusion models can be very misleading when catastrophes are included. For example, as we show below, the "shoulder" (Fig. 1) associated with the model of MacArthur and Wilson (1967), and often used to help identify a "minimum viable population" (Soulé 1987), disappears when catastrophes are included. Even though most population viability analyses have gone beyond this simpler model (Boyce 1992), we believe that an explicit focus on catastrophes is important because it forces us to think differently about the evaluation of conservation measures.

In recent years, new methods have been developed for the analysis of population models that include catastrophes (Hanson and Tuckwell 1978, Mangel 1989, Peters and Mangel 1990, Anderson 1991, Mangel and Tier 1993a, b). Some of these methods are analytical and exact, some are analytical and approximate, and some are numerical (but based on numerical analysis, rather than Monte Carlo simulation). These new meth-

ods and the great technological advances in computing over the last 15 yr allow us to change the way that we think about persistence of populations. Measures of persistence, such as the mean time to extinction, play an important role in population viability analysis (Boyce 1992) and other applications of theory to conservation. In this note, we summarize four important facts from a theory of persistence that includes catastrophes. The results are nonintuitive and have clear implications for management and policy.

THE FACTS

Fact 1: A population can grow, on average, exponentially and without bound and still not persist

Imagine the simplest case of population growth, say $\frac{dN}{dt} = rN$, where N is population size at time t and r is the intrinsic growth rate. Given initial population size N_0 , we know that the population will grow without bound exponentially, so that $N(t) = N_0 e^{rt}$. Now suppose that this population is subject to catastrophes that occur at some rate c , so that the probability of a catastrophe in the interval between 0 and t is $1 - e^{-ct}$ and that when a catastrophe occurs, there is a probability distribution for the number of individuals who die, with mean number of deaths $m(N)$ when the population size is N . The mean rate of death due to catastrophe for population of size N is then $cm(N)$ and, on average, the population dynamics are now $\frac{dN}{dt} = rN - cm(N)$. For example, if individuals die independently with probability p , then the number of deaths has a binomial distribution with parameters N and p and the mean population dynamics are $\frac{dN}{dt} = rN - cpN$. Intuition suggests, and it can be verified (Peters and Mangel 1990), that in general if the mean death rate exceeds the birth rate, then the chance of the population persisting for long times is 0.

On the other hand, even if the birth rate exceeds the mean death rate for all values of population size, the population need not persist (Peters and Mangel 1990). Without going into the details (which can be found in Peters and Mangel 1990), the basic idea is the following. We measure persistence in this case by the probability $P(N_0)$ that the population never goes extinct (with no population ceiling), given that its initial size is N_0 . We then derive an equation that characterizes how $P(N_0)$ varies with N_0 and solve this equation. In the course of the solution, we see that if $rN < cm(N)$, then the only solution is $P(N_0) = 0$. If $rN > cm(N)$, then $P(N_0) > 0$, and can almost always be written in a form like $P(N_0) = 1 - K \exp[-H(N_0)]$, where the

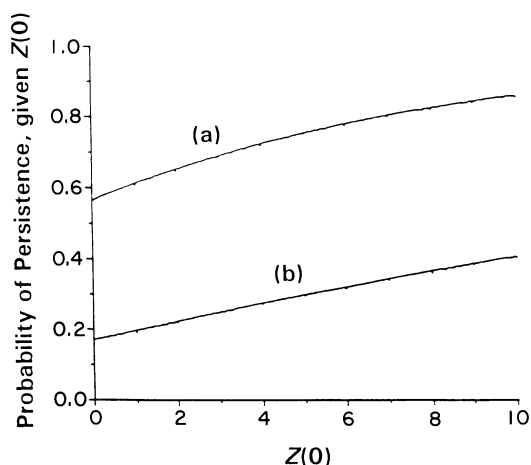


FIG. 2. An example of fact 1, that in the presence of catastrophes an exponentially growing population need not persist. We focus on the logarithm of population size, which satisfies the growth equation $\frac{dZ}{dt} = r$ with initial value $Z(0)$.

Between catastrophic events $\frac{dZ}{dt} = r$, catastrophes occur at rate c , and when a catastrophe occurs, the logarithm of population size decreases by an amount Y , following an exponential distribution with mean \bar{Y} . Parameter values for curve (a) are $b = 0.9$, $d = 0.329$, $c = 0.05$, and $\bar{Y} = 5$ and for curve (b) are $b = 0.4$, $d = 0.1$, $c = 0.05$, and $\bar{Y} = 5$. Note that $Z(0) = 5$ corresponds to ≈ 150 individuals and $Z(0) = 10$ corresponds to $\approx 22\,000$ individuals.

constant K and the function $H(N)$ depend upon the particular form of the rate of catastrophes and the distribution of deaths when a catastrophe occurs (Peters and Mangel 1990 give examples). The constant K typically involves the ratio of the mean rate of death due to catastrophe and the mean growth rate, and the function $H(N_0)$ depends upon the population dynamics and the particular form of the catastrophe distribution.

A simple, somewhat stylized example can be constructed by noting that if the population grows exponentially according to $\frac{dN}{dt} = rN$, then the logarithm of population $Z(t) = \log[N(t)]$ has a constant growth rate $\frac{dZ}{dt} = r$. We assume that catastrophes occur at rate c and that when a catastrophe occurs, the logarithm of population size decreases by an amount Y , following an exponential distribution with mean \bar{Y} , and define persistence as the probability that $Z(t)$ never falls below 0. We can use Eq. 4.12 of Peters and Mangel (1990) to obtain this probability:

$$\Pr\{\text{persistence, given } Z(0) = z_0\} = 1 - \left(\frac{c}{r}\right)\bar{Y} \exp\left[-\left(\frac{1}{\bar{Y}} - \frac{c}{r}\right)z_0\right].$$

The results (Fig. 2) show only moderate persistence for the exponentially growing population in the presence of catastrophes, caused by the potentially large and rapid decrements in population size when a catastrophe occurs.

If this exponentially growing population actually represented the average of a pure birth and death process, then we would write $r = b - d$, where b and d are the birth and death rates (see the Appendix for elaborations). It is a classical result (see Ludwig 1974 and citations therein) that even though $b > d$, not all population trajectories will lead to persistence of the population. Because of "runs of bad luck" some trajectories will lead to extinction, even though on average persistence is predicted. If $N_a(0) = n_0$ and the individual trajectories are independent, the probability of persistence is $1 - \left(\frac{d}{b}\right)^{n_0}$ if $d < b$ and is 0 otherwise. Note

that this will quickly rise to 1 as n_0 increases. For the parameter values shown in both curves of Fig. 2, the birth and death estimate of the probability of persistence reaches 1 when $Z(0) = 3$, i.e., for 20 individuals. We thus see that ignoring catastrophes greatly overestimates the persistence of the population.

Fact 2: There is a simple and direct method for the computation of persistence times that virtually all biologists can use

We shall now describe (Mangel and Tier 1993a) a very simple method that makes computation of persistence times accessible to virtually all biologists. In order to illustrate this second fact, it is easiest to consider a particular model of a population with both demographic fluctuations and environmental catastrophes (Mangel and Tier 1993a). We assume that the population can be described by a single variable $N(t)$, representing population numbers at time t and that if the current population size is n then the probability of a birth in a very small interval of time Δt is $B(n)\Delta t$ and that the probability of a single death from demographic causes in Δt is $D(n)\Delta t$. In addition, we assume that the chance that an environmental catastrophe occurs is $C(n)\Delta t$ and that when such a catastrophe occurs, the probability that y of the n individuals present die is $Q(y | n)$, so that $\sum_{y=0}^n Q(y | n) = 1$ and $m(n) = \sum_{y=0}^n nQ(y | n)$. We also assume that there is a critical population size n_{crit} below which the population is functionally extinct.

The method rests on the following simple observation. Regardless of the complexity of the density dependence in birth, death, and catastrophes, there is without a doubt a maximum value that the population can attain. This value, n_{max} , is then a population ceiling,

in the spirit of MacArthur and Wilson (1967), but differs in one extremely important respect: in virtually all previous work (reviewed in Mangel and Tier 1993b) the density dependence in the models has been trivial and the ceiling itself has introduced density dependence. Our situation is different in that we separate the ceiling and the mechanisms producing density dependence, so that there can be extremely complicated density dependence for population sizes below n_{\max} . The behavior of the population below n_{\max} will generally involve stable equilibria, one of which can be interpreted as the carrying capacity. We also expect that if the population size is near n_{\max} , it will move towards the carrying capacity. This is in contrast to the MacArthur–Wilson type models in which the population ceiling is interpreted as the carrying capacity of the population.

For example, a birth and death description for the population dynamics of the adults of the flour beetle *Tribolium* has (Peters et al. 1989) $B(n) = b_0(n + b_1) \exp(-b_2 n)$ and $D(n) = d_1 n$, where b_0 , b_1 , b_2 , and d_1 are parameters (this description excludes catastrophes). The interpretation of these functions is the following. The death rate simply increases with population size. The linear birth rate is modified in two ways. It decreases because of cannibalism on pre-adult stages. But note that $B(0) = b_0 b_1 > 0$; this represents “recruitment” into the adult stage from other stages of life history, even when there are no adults present (see Peters et al. 1989 for further interpretation). We could identify the “carrying capacity” as the positive steady state n_s satisfying $B(n_s) = D(n_s)$. The population ceiling n_{\max} should then be much greater than n_s and we see that if $n \gg n_s$, then the birth rate is exponentially small and the death rate continues to grow. The net effect will be movement towards n_s .

To measure the persistence of the population, we define the random variable $\tau(n)$ as the first time that the population size reaches or is less than n_{crit} , given that it starts at n . The first measure of population performance is the mean extinction (or persistence) time $T(n)$, which is the average value of $\tau(n)$. The mean persistence time is often involved in population viability analysis (Boyce 1992) and, as described below (in fact 4), can be used to estimate the probability of persistence over a specified interval of time, conditioned on the initial size of the population.

With the assumptions described above, $T(n)$ satisfies (MacArthur and Wilson 1967, Leigh 1981, Mangel and Tier 1993a).

$$\begin{aligned} -1 &= B(n)T(n+1) + D(n)T(n-1) \\ &\quad - [B(n) + D(n) + C(n)]T(n) \\ &\quad + C(n) \sum_{y=0}^n Q(y|n)T(n-y). \end{aligned} \quad (2)$$

The importance of the population ceiling is that we can write Eq. 2 as a matrix equation of the form

$$\mathbf{M}\mathbf{T} = -\mathbf{1}, \quad (3)$$

where the vector $\mathbf{T} = \{T(n_{\text{crit}}), T(n_{\text{crit}} + 1), \dots, T(n_{\max})\}^T$ and the vector $-\mathbf{1} = \{-1, -1, \dots, -1\}^T$. If we set $R(n) = B(n) + D(n) + C(n) - C(n)Q(0|n)$, the first few lines of \mathbf{M} are as shown below.² Eq. 3 can be solved for \mathbf{T} :

$$\mathbf{T} = -\mathbf{M}^{-1}\mathbf{1} \quad (4)$$

where \mathbf{M}^{-1} is the inverse of the matrix \mathbf{M} . Computer languages such as TRUEBASIC, MATLAB, or MATHEMATICA have built-in programs for inverting matrices. This means that once \mathbf{M} is defined (that is, after the underlying biological processes are understood), finding the persistence time for any population level is essentially a trivial computational problem and can be handled by most small computers easily. This is true for even reasonably large state spaces, as will be seen in the examples below or in Mangel and Tier (1993a).

We can study the variability of the persistence time by computing the second moment $S(n)$ of $\tau(n)$, which satisfies (Mangel and Tier 1993a)

$$\mathbf{M}\mathbf{S} = -2\mathbf{T}, \quad (5)$$

where the vector $\mathbf{S} = \{S(n)\}$. The solution of Eq. 5 is

$$\mathbf{S} = -2\mathbf{M}^{-1}\mathbf{T}, \quad (6)$$

and since we have already computed \mathbf{M}^{-1} , this requires no further complicated calculation. The variance of the extinction time for a population with initial size n , $V(n)$, is then computed component-wise using $V(n) = S(n) - T^2(n)$ and the coefficient of variation is $\text{cv}(n) = \frac{\sqrt{V(n)}}{T(n)}$. The cv gives a standard measure with which to compare the variability of extinction times for different population dynamics. The variance and cv are important statistics and often cannot be computed analytically.

In summary, fact 2 shows that (thanks to the development of powerful microcomputers and high-level computer languages) the computation of the mean and variance of extinction times can now be done in just

² The first few lines of \mathbf{M} :

$-R(n_{\text{crit}} + 1)$	$B(n_{\text{crit}} + 1)$	0	0
$D(n_{\text{crit}} + 2) + C(n_{\text{crit}} + 2)Q(1 n_{\text{crit}} + 2)$	$-R(n_{\text{crit}} + 2)$	$B(n_{\text{crit}} + 2)$	0
$C(n_{\text{crit}} + 3)Q(2 n_{\text{crit}} + 3)$	$D(n_{\text{crit}} + 3) + C(n_{\text{crit}} + 3)Q(1 n_{\text{crit}} + 3)$	$-R(n_{\text{crit}} + 3)$	$B(n_{\text{crit}} + 3)$

a few lines of computer code (although it does take some serious, biological work to get the matrix \mathbf{M} , as in the description of the flour beetle dynamics above; Peters et al. 1989). Thus, although one must still use a numerical method, it is not a Monte Carlo simulation, which may require thousands of runs to obtain reasonable estimates of the statistics on persistence time (cf. Murphy et al. 1990). We now consider the implications of this fact.

Fact 3: The shoulder of the MacArthur–Wilson model occurs with other models as well, but disappears when catastrophes are included

The model used by MacArthur and Wilson (1967) was based on the following population dynamics: No catastrophes, so that $C(n) = 0$, $B(n) = \lambda n$ for $n = 1, 2, \dots, K$ (the population ceiling), and $B(n) = 0$ for $n > K$, and $D(n) = \mu n$. Here n_{\max} has a natural definition as $n_{\max} = K + 1$. This model leads to a “shoulder” if one plots $T(K)$ as a function of K : as K increases, $T(K)$ first rises, then has a plateau, and then rises very rapidly. The value of K corresponding to the onset of this rapid rise is often used to define the minimum viable population (Fig. 1).

By using fact 2, it is possible to explore the mean persistence time for a wide variety of models involving more complicated population dynamics. Other models, with complex density dependence occurring for values of $n \ll n_{\max}$ also lead to shoulders. For example, Mangel and Tier (1993a) consider a birth–death–immigration model in which $B(n) = b_0(n + b_1) \exp(-b_2 n)$ and $D(n) = d_1 n$. A typical result (Fig. 3) is the following: for a certain set of parameters, if catastrophes are ignored the mean persistence time is the same whether $n_{\max} = 50$ or 300. However, when catastrophes are included, this is absolutely not the case and the persistence time does not plateau at small values of n_{\max} (or K in the MacArthur–Wilson model). In fact, there is a slow but steady rise in the mean persistence time as n_{\max} increases.

Fact 4: Extinction times are approximately exponentially distributed and this means that extinctions are likely

By using the numerical methods described in fact 2, Mangel and Tier (1993a) show that $\text{cv}(n_{\max}) \rightarrow 1$ as n_{\max} increases. This is consistent with the general theoretical result (Keilson 1979) that the persistence time $\tau(n)$ is exponentially distributed: $\Pr\{\tau(n) \leq t\} = 1 - \exp[-t/T(n)]$ and that the probability density for the persistence time $\tau(n)$ is $\Pr\{t \leq \tau(n) \leq t + dt\} = \frac{1}{T(n)} \exp\left(-\frac{t}{T(n)}\right) dt$. We can

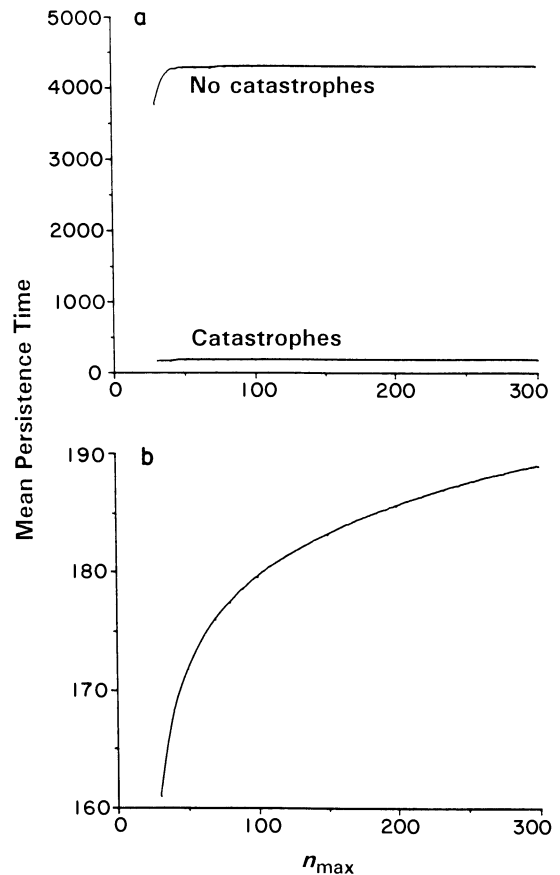


FIG. 3. Results for a model of flour beetle dynamics (from Mangel and Tier 1993a) in which if the population size is currently n , the probability of a birth in the next unit of time is $b_0(n + b_1) \exp(-b_2 n)$ and the probability of a death is $d_1 n$; these balance at $n_s = 26$ individuals, which can be identified with the carrying capacity. (a) Comparison of the mean persistence time in the absence of catastrophes with the mean persistence time when catastrophes occur. The catastrophe model has rate $C(n) = 0.05$ for all values of population size and the distribution of deaths $Q(y|n)$ is binomial with parameters n and $p = 0.5$ (see Eq. 2 and discussion leading to it). Thus, catastrophes occur at a rate of about once every 20 time units and when a catastrophe occurs, each individual has a 50% probability of death. (b) Further examination of the mean persistence time in the presence of catastrophes. Notice that the mean persistence time rises slowly with the population ceiling and that the shoulder associated with the model in the absence of catastrophes disappears.

view this density as a likelihood for $\tau(n)$ and ask what is the most likely value? The answer is that the most likely value of $\tau(n)$, regardless of the value of the mean persistence time, is 0! That is, in an “ensemble average world view,” the mean $T(n)$ is achieved by the average of lots of very rapid extinctions with some very long persistences.

This idea is best illustrated by considering individual

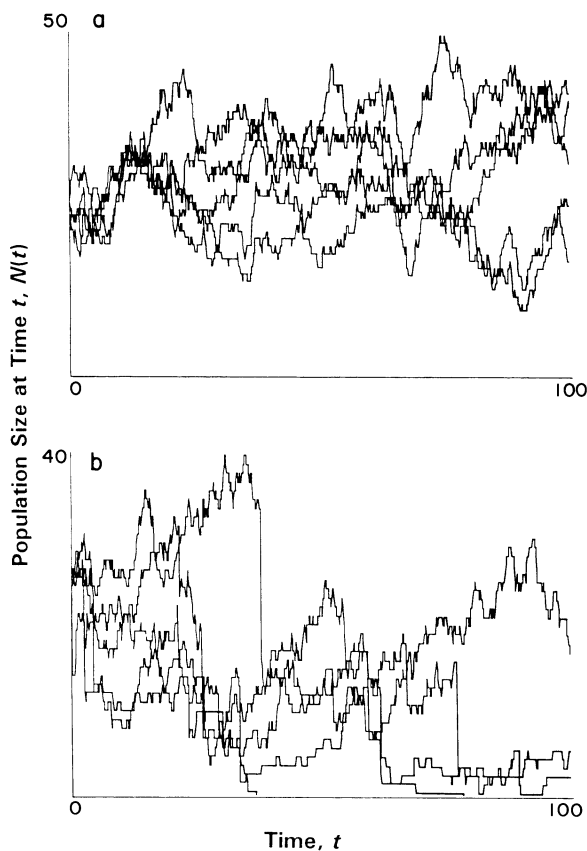


FIG. 4. Examples of population trajectories, in the absence (panel a) or presence (panel b) of catastrophes. Here we have simulated the birth and death dynamics used to generate the mean times shown in Fig. 3, and assumed no population ceiling. In the absence of catastrophes, all five trajectories persist for the 100 time units shown; however in the presence of catastrophes two of the five trajectories lead to extinction before $t = 100$, two other trajectories lead to values of population size that are low at $t = 100$, and only one of the five populations is relatively large at $t = 100$.

trajectories of populations (Fig. 4). Here we have plotted five trajectories for the birth and death dynamics of flour beetles, used to generate the persistence times in Fig. 3, with a very large population ceiling. In the absence of catastrophes (Fig. 4a), we see that all five trajectories persist for the 100 time units shown, however in the presence of catastrophes (Fig. 4b) two of the five trajectories lead to extinction before $t = 100$ (remember that the mean persistence time is ≈ 200), two other trajectories lead to values of population size that are low at $t = 100$, and only one of the five populations is relatively large at $t = 100$.

Population viability analysis often has as its goal the prediction that the population will persist for a specified amount of time, given the initial size. Our result

shows that this can be estimated through the use of an exponential distribution with mean $T(n)$, and for this reason it is important to compute $T(n)$ as accurately as possible.

THE IMPLICATIONS

We now consider some implications of these results. When making recommendations to managers, it is imperative (so as to avoid the egg on the face phenomenon) to provide the most realistic and honest assessments of the situation. The four facts listed above have many important consequences.

Even under the absolute best circumstances, the long-term persistence of populations is not guaranteed (fact 1). This suggests, for example in the consideration of reserve design, that more than one reserve, spaced apart (so that catastrophes occur independently at different reserves) is probably more effective. Perhaps we need to rethink yet again the SLOSS (single large or several small) debate concerning the structure of reserves. That is, at a local level, catastrophes are likely to make local extinctions far more common than short-term studies of environmental variability would lead us to believe. Thus, we need to consider catastrophes in the general discussion of SLOSS. For example, the discussions of corridors in conservation (Fahrig and Merriam 1985, Burkey 1989, Hobbs 1992) often ignore corridors as a means of passing catastrophic epizootics.

It is now possible to numerically compute persistence times for populations with extremely complicated dynamics, including two sexes, age structure, clutch births, etc. (fact 2). Thus, a two-pronged attack can be taken. The method described here and in Mangel and Tier (1993a) can be used to investigate, from the general theoretical perspective, how these factors alter persistence. At the same time, it is worthwhile to invest resources into the details for the determination of these processes so that it will be possible to build detailed and accurate models for particular endangered species. On the other hand, because it will generally be difficult to accurately estimate the rates of catastrophes and the distribution of deaths, this work calls into question the use of mean extinction times in the practice (vs. the theory) of conservation biology; we should begin to consider alternative measures.

Minimum viable population sizes are almost certainly much larger than those predicted based on some variant of the MacArthur–Wilson model (fact 3) or any other population viability analysis that ignores catastrophes.

Even when conserved populations are large, we should expect extinctions; they are likely events (fact 4) and we should be prepared with contingency plans when events that could lead to extinctions occur.

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APPENDIX

In this Appendix, we elaborate upon the results of the analysis shown in Fig. 2. In doing so, we use this simple example to show the logic underlying the more complex calculations in Peters and Mangel (1990). Recall that we let $Z(t) = \log[N(t)]$ denote the logarithm of population size and assume that be-

tween catastrophic events $\frac{dZ}{dt} = r$, that catastrophes occur at

rate c and that when a catastrophe occurs, the logarithm of population size decreases by an amount Y , following an ex-

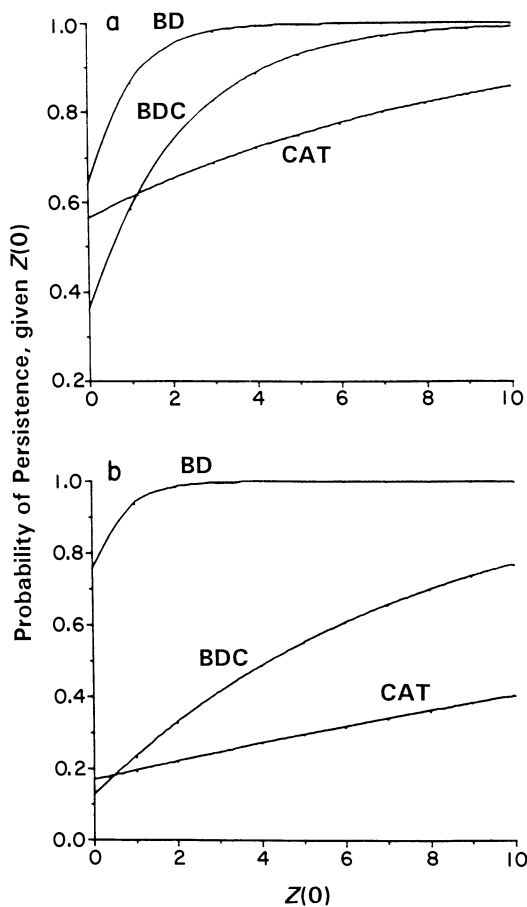


FIG. A1. The persistence of an exponentially growing population in the presence of catastrophes (curve labeled CAT) and in the birth-and-death process interpretation of the model. We focus on the logarithm of population size, which satisfies the growth equation $\frac{dZ}{dt} = r$ with initial value $Z(0)$. The curve labeled CAT is constructed using the theory of Peters and Mangel (1990) in which we assume that between catastrophic events $\frac{dZ}{dt} = r$, that catastrophes occur at rate c , and that when a catastrophe occurs, the logarithm of population size decreases by an amount \bar{Y} , following an exponential distribution with mean \bar{Y} . The curve labeled BD is constructed by assuming that $Z(t)$ is the average of a birth and death process \tilde{Z} with birth rate b and death rate d , with $r = b - d$. The curve labeled BDC is based on the assumption that in the presence of catastrophes the death rate is increased from d to $d + c\bar{Y}$. Parameter values for panel (a) are $b = 0.9$, $d = 0.329$, $c = 0.05$, and $\bar{Y} = 5$ and for panel (b) are $b = 0.4$, $d = 0.1$, $c = 0.05$, and $\bar{Y} = 5$.

ponential distribution with mean \bar{Y} . Defining persistence to mean the probability that $Z(t)$ never falls below 0 (i.e., that the population size never falls below 1), we can use Eq. 4.12 of Peters and Mangel:

$$\Pr\{\text{persistence, given } Z(0) = z_0\} = 1 - \left(\frac{c}{r}\right)\bar{Y} \exp\left[-\left(\frac{1}{\bar{Y}} - \frac{c}{r}\right)z_0\right]. \quad (\text{A.1})$$

Next, suppose that we assume that $Z(t)$ is actually the average of a birth and death process \tilde{Z} for which

$$\Pr\{\text{change in } \tilde{Z} \text{ in the next } \Delta t = 1\} = b\Delta t + o(\Delta t)$$

$$\Pr\{\text{change in } \tilde{Z} \text{ in the next } \Delta t = -1\} = d\Delta t + o(\Delta t) \quad (\text{A.2})$$

$$\Pr\{\text{no change in } \tilde{Z} \text{ in the next } \Delta t\} = 1 - b\Delta t - d\Delta t + o(\Delta t),$$

where $o(\Delta t)$ denotes terms that involve higher powers of Δt . Then if $P(z_0)$ is the probability that $Z(t)$ never falls below 0, given that $Z(0) = z_0$, we have for $z_0 \geq 1$

$$P(z_0) = bP(z_0 + 1) + (1 - b - d)P(z_0) + dP(z_0 - 1). \quad (\text{A.3})$$

That is, the probability of persisting from z_0 is the average of (a) the probability of persisting from $z_0 + 1$, given that in the next interval of time the value of \tilde{Z} changes by 1, (b) the probability of persisting from z_0 , given that in the next interval of time the value of \tilde{Z} does not change, and (c) the probability of persisting from $z_0 - 1$, given that in the next interval of time the value of \tilde{Z} changes by -1. For $z_0 = 0$ we have

$$P(0) = bP(1) + (1 - b - d)P(0). \quad (\text{A.4})$$

Setting $P(z_0) = 1 - K \exp(-Hz_0)$ in Eq. A.3 we find that H satisfies the equation

$$b + d - be^{-H} - de^H = 0. \quad (\text{A.5})$$

The solution of Eq. A.5 is $H = \log(b/d)$. Using Eq. A.4 we find that the constant K is given by

$$K = \frac{d}{b + d - be^{-H}} = \frac{d}{b}. \quad (\text{A.6})$$

Note that $K < 1$ because, in general, a population starting at $Z(0) = 0$ will have a chance of growing and thus escaping extinction. We can compare this result with the model that allows for catastrophes (the curves labeled CAT and BD in Fig. A1).

How can we include catastrophes in this model? One approach is to use the techniques of Peters and Mangel (1990) as described in the text. A simple alternative would be to increase the death rate d by the deaths associated with catastrophes. That is, we replace d by $d + c\bar{Y}$ (curve labeled BDC in Fig. A1). However, this averaging process leads to either an over- or underestimation of the probability of persistence.