



A Simple Direct Method for Finding Persistence Times of Populations and Application to Conservation Problems

Marc Mangel, Charles Tier

Proceedings of the National Academy of Sciences of the United States of America,
Volume 90, Issue 3 (Feb. 1, 1993), 1083-1086.

Your use of the JSTOR database indicates your acceptance of JSTOR's Terms and Conditions of Use. A copy of JSTOR's Terms and Conditions of Use is available at <http://www.jstor.org/about/terms.html>, by contacting JSTOR at jstor-info@umich.edu, or by calling JSTOR at (888)388-3574, (734)998-9101 or (FAX) (734)998-9113. No part of a JSTOR transmission may be copied, downloaded, stored, further transmitted, transferred, distributed, altered, or otherwise used, in any form or by any means, except: (1) one stored electronic and one paper copy of any article solely for your personal, non-commercial use, or (2) with prior written permission of JSTOR and the publisher of the article or other text.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Proceedings of the National Academy of Sciences of the United States of America is published by National Academy of Sciences. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/nas.html>.

Proceedings of the National Academy of Sciences of the United States of America
©1993 National Academy of Sciences

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2001 JSTOR

<http://www.jstor.org/>
Tue Apr 17 14:04:50 2001

A simple direct method for finding persistence times of populations and application to conservation problems

(extinction/minimum viable populations/environmental catastrophes)

MARC MANGEL AND CHARLES TIER

Center for Population Biology and Section of Zoology, University of California, Davis, CA 95616; and Department of Mathematics, Statistics, and Computer Science (M/C 249), University of Illinois, Box 4348, Chicago, IL 60680

Communicated by Robert T. Paine, October 26, 1992 (received for review August 17, 1992)

ABSTRACT The computation of persistence times of populations has become a central focus in conservation biology. We describe a simple, direct method for finding the statistics of persistence times by assuming that there is a maximum population size. Thus, even though the population dynamics may be very complex for population sizes below the maximum, it is possible to write a finite set of equations from which the mean and second moment of the persistence time can be found by using simple, algebraic methods. We apply the method to compute the mean and coefficient of variation of persistence times of populations that suffer large decrements (catastrophes). Our results show that in the presence of catastrophes, the increase in mean persistence time with large populations is not nearly as rapid as other theories suggest and that catastrophes occurring at even modest rates can considerably increase the risk of extinction.

The computation of the persistence times of populations has become a central focus in conservation biology (1). In this note, we describe an exceptionally simple, direct computational method for finding the statistics of persistence times once the important biological processes are understood.

For pedagogical ease, we consider a particular model of a population with both demographic fluctuations and environmental catastrophes (2) and assume that the population can be described by a single variable $X(t)$, representing population numbers at time t . Our results can be extended to population vectors in a conceptually direct manner (see *Discussion*).

We assume that this population can change due to single births and deaths (3, 4). If the current population size is x , then the probability of a birth in a very small interval of time Δt is $B(x)\Delta t + o(\Delta t)$, where $o(\Delta t)$ indicates higher order Δt terms, and the probability of a single death from demographic causes in Δt is $D(x)\Delta t + o(\Delta t)$. We assume that the chance that an environmental catastrophe occurs is $C(x)\Delta t + o(\Delta t)$ and that when such a catastrophe occurs, the probability that y of the x individuals present die is $Q(y|x)$, so that $\sum_{y=0}^x Q(y|x) = 1$. We also assume that there is a critical population size x_c below which the population is functionally extinct.

Our 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 x_{\max} is then a population ceiling in the spirit of MacArthur and Wilson (3) but differs in one extremely important respect. In

virtually all previous work (reviewed in ref. 2), the density dependence in the models has been trivial, and the ceiling itself has introduced density dependence. Our situation is different in that there can be extremely complicated density dependence for population sizes below x_{\max} . The behavior of the population below x_{\max} generally will involve stable equilibria, one of which can be interpreted as the carrying capacity. We also expect that if the population size is near x_{\max} , then it will decrease and move towards the carrying capacity. This is in contrast to the MacArthur–Wilson-type models in which the population ceiling is also interpreted as the carrying capacity of the population. Thus, we restrict the population size to the interval $x_c + 1$ to x_{\max} . In the model of MacArthur and Wilson, $B(x)$ vanishes if $x > x_{\max}$.

To measure the persistence of the population, we define the random variable $\tau(x)$ as the first time that the population size reaches or is less than x_c , given that it starts at x ; we shall call it the “persistence time” or “extinction time.” Our goal is to present a simple and straightforward method of computing the first and second moments of $\tau(x)$. We will use the coefficient of variation (CV) to measure the variability of persistence times.

THE METHOD

The first measure of population performance is the mean extinction time $T(x)$, where E is expectation:

$$T(x) = E\{\tau(x)\}. \quad [1]$$

With the assumptions described above, $T(x)$ satisfies the following equation (2–4):

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

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

$$\mathbf{MT} = -\mathbf{1}, \quad [3]$$

where the vector $\mathbf{T} = \{T(x_c+1), \dots, T(x_{\max})\}^T$, the matrix \mathbf{M} is defined below, and the vector $-\mathbf{1} = \{-1, -1, -1, \dots, -1\}^T$. If we set $R(x) = B(x) + D(x) + C(x) - C(x)Q(0|x)$, the first few rows of the matrix \mathbf{M} are

$-R(x_c+1)$	$B(x_c+1)$	0	0
$D(x_c+2) + C(x_c+2)Q(1 x_c+2)$	$-R(x_c+2)$	$B(x_c+2)$	0
$C(x_c+3)Q(2 x_c+3)$	$D(x_c+3) + C(x_c+3)Q(1 x_c+3)$	$-R(x_c+3)$	$B(x_c+3)$
$C(x_c+4)Q(3 x_c+4)$	$C(x_c+4)Q(2 x_c+4)$	$D(x_c+4) + C(x_c+4)Q(1 x_c+4)$	$-R(x_c+4)$

Eq. 3 can be solved for T as follows:

$$T = -M^{-1}1, \quad [4]$$

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

We can study the variability of the persistence time by computing the second moment $S(x)$ as follows:

$$S(x) = E\{\tau(x)^2\}. \quad [5]$$

Similar to the treatment for $T(x)$ in Eq. 2 above, $S(x)$ satisfies $S(x) = 0$ for $x \leq x_c$ and for $x > x_c$ as follows:

$$\begin{aligned} -2T(x) &= B(x)S(x+1) + D(x)S(x-1) \\ &\quad - [B(x) + D(x) + C(x)]S(x) \\ &\quad + C(x) \sum_{y=0}^x Q(y|x)S(x-y), \end{aligned} \quad [6]$$

so that in matrix form we have

$$MS = -2T, \quad [7]$$

where the vector $S = \{S(x)\}$. The solution of Eq. 7 is

$$S = -2M^{-1}T, \quad [8]$$

and since we have already computed M^{-1} , this requires no further complicated calculation. The variance of the extinction time for a population with initial size x , $V(x)$, is then computed component-wise by using

$$V(x) = S(x) - T^2(x), \quad [9]$$

and the coefficient of variation is

$$CV(x) = \frac{\sqrt{V(x)}}{T(x)}. \quad [10]$$

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.

EXAMPLES

To illustrate the method, we shall consider two examples. The first involves a reanalysis of the model of MacArthur and Wilson. The second involves a model of flour beetle dynamics, which has a more complicated state of dependence.

In the model of MacArthur and Wilson, $C(x) = 0$ (no catastrophes), $B(x) = \lambda x$ for $x = 1, 2, \dots, K$, and $B(x) = 0$ for $x > K$, and $D(x) = \mu x$. Here x_{\max} has a natural definition as $x_{\max} = K + 1$. A serious defect of this model (5) is that moderate values of K produce exceptionally large persistence times. For example, when $\lambda = 2.5$, $\mu = 1.82$, and $x_c = 3$ (Fig. 1, curve a), K values of 20, 30, 40, and 50 produce respectively $T(K)$ values of 90.1, 1405, 24,667, and 466,261. That is, when K increases by a factor of 2.5, $T(K)$ increases by a factor of more than 5000, or when K increases by a factor of 0.2, $T(K)$ increases by a factor of more than 20. This kind of observation has often had important policy implications in setting the size of "minimum viable populations" (1, 5).

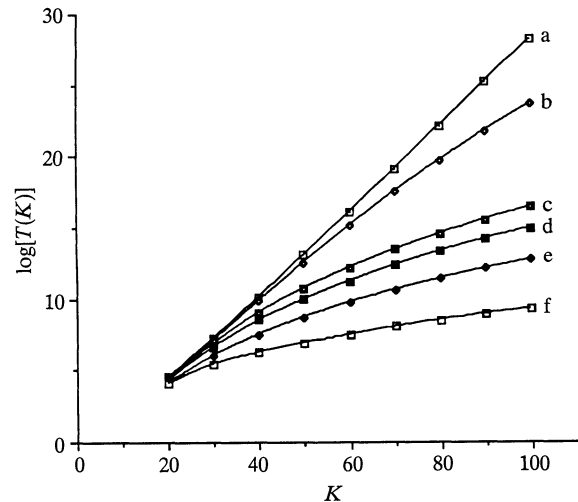


FIG. 1. Results for the MacArthur-Wilson model. Curves: a, mean extinction time $T(K)$ when catastrophes are ignored [note both the exceptionally large value of $T(K)$ and $T(K)$ continues to increase as K increases]; b-f, mean extinction time $T(K)$, with $K = x_{\max}$, when catastrophes as described in the text are included for various combinations of catastrophe rate c and probability of death p as follows: $c = 0.02$, $p = 0.25$ (b); $c = 0.01$, $p = 0.5$ (c); $c = 0.02$, $p = 0.5$ (d); $c = 0.05$, $p = 0.5$ (e); and $c = 0.02$, $p = 0.75$ (f).

We can use our method to investigate the effects of catastrophes on these exceptionally large times. For example, suppose that $C(x)$ is a constant $C(x) = c$ and that $Q(y|x)$ is a binomial distribution with parameter p . The approximate interpretation of these values is that catastrophes occur about once every $1/c$ years, and when a catastrophe occurs, individuals have independent probabilities of death of p . We then find (Fig. 1, curves b-f) considerable reduction in the mean persistence time. Including relatively rare catastrophes can reduce the mean extinction time considerably. The logarithmic scale in Fig. 1 somewhat distorts the significance of the effect of including catastrophes. To more closely study this effect, we can plot $[T(K) - T_c(K)]/T(K)$, where $T(K)$ is the mean persistence time in the absence of catastrophes and $T_c(K)$ is the mean persistence time when catastrophes are included, as a function of K (Fig. 2). This ratio is a measure

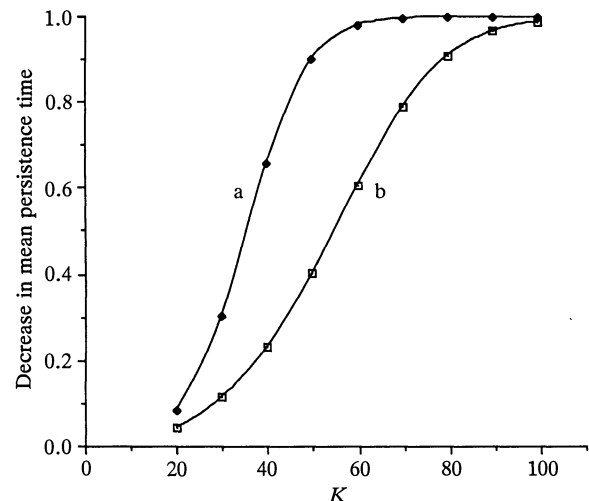


FIG. 2. The ratio $[T(K) - T_c(K)]/T(K)$, where $T(K)$ is the mean persistence time in the absence of catastrophes and $T_c(K)$ is the mean persistence time when catastrophes are included, is a measure of the decrease in the mean extinction time due to catastrophes. For curve a, the catastrophe rate $c = 0.01$ and death probability $p = 0.5$; for curve b, $c = 0.02$ and $p = 0.25$.

of the decrease in the mean extinction time due to catastrophes. For modest values of K , ignoring the presence of environmental catastrophes can overestimate the mean persistence time by 99% or more.

In the model for the population dynamics of the flour beetle *Tribolium* (6), $B(x) = b_0(x + \delta)\exp(-b_1x)$ and $D(x) = d_1x$, where the parameters can be empirically determined. For example, when $b_0 = 0.13$, $b_1 = 0.0165$, $d_1 = 0.088$, and $\delta = 1$ and in the absence of catastrophes, the birth rate and death rate balance at about $x = 26$, so that we can take $x_{\max} = 50$ and be fairly confident that the population is never likely to exceed this value. In fact, if we choose $x_{\max} = 50$ or 300, there is virtually no effect on the persistence time (Fig. 3A). However, this rapid shoulder does not persist when catastrophes are included (Fig. 3B–D). It is likely, of course, that the mean extinction time does reach a plateau even in the presence of catastrophes as x_{\max} increases, but the rise is clearly much slower. Another way of seeing this is to plot $T(x_{\max})/T(x_{\max} = 300)$ as in Fig. 4. This ratio clearly is 1 when $x_{\max} = 300$, but the figure shows that the rapid rise when catastrophes are ignored does not occur when they are included. In general, determining an appropriate choice of x_{\max} requires some amount of numerical experimentation to insure that the predictions for $T(x)$, when x is below x_{\max} , do not depend upon the choice of x_{\max} . This is easily done with a simple numerical method. For example, for the combinations of parameters in Fig. 3 B–D, the value of $T(10)$ is essentially constant as long as $x_{\max} \geq 50$.

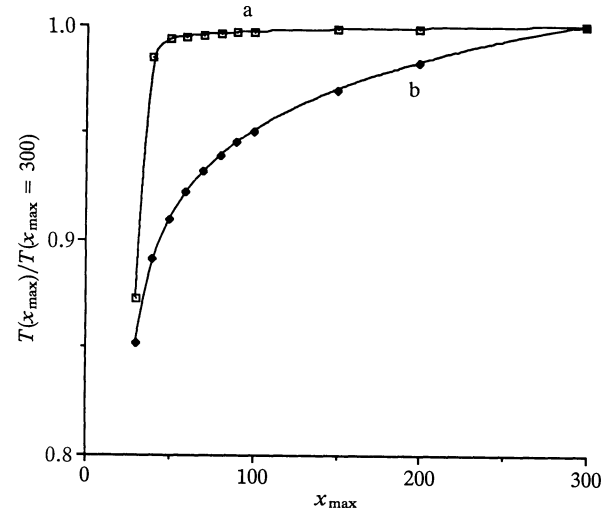


FIG. 4. By plotting the ratio $T(x_{\max})/T(x_{\max} = 300)$ (curve a) or $T_c(x_{\max})/T_c(x_{\max} = 300)$ (curve b) (for $c = 0.05$ and $p = 0.5$) for values of $x_{\max} \leq 300$, we can directly see that the relative rise in mean extinction time when catastrophes are included is much slower.

We can use Eq. 7–10 to study the coefficient of variation of the persistence time. In both cases (and for other models), we find that $CV(x)$ starts at around 2 and approaches 1 as $x \rightarrow x_{\max}$ and x_{\max} increases. This is consistent with the

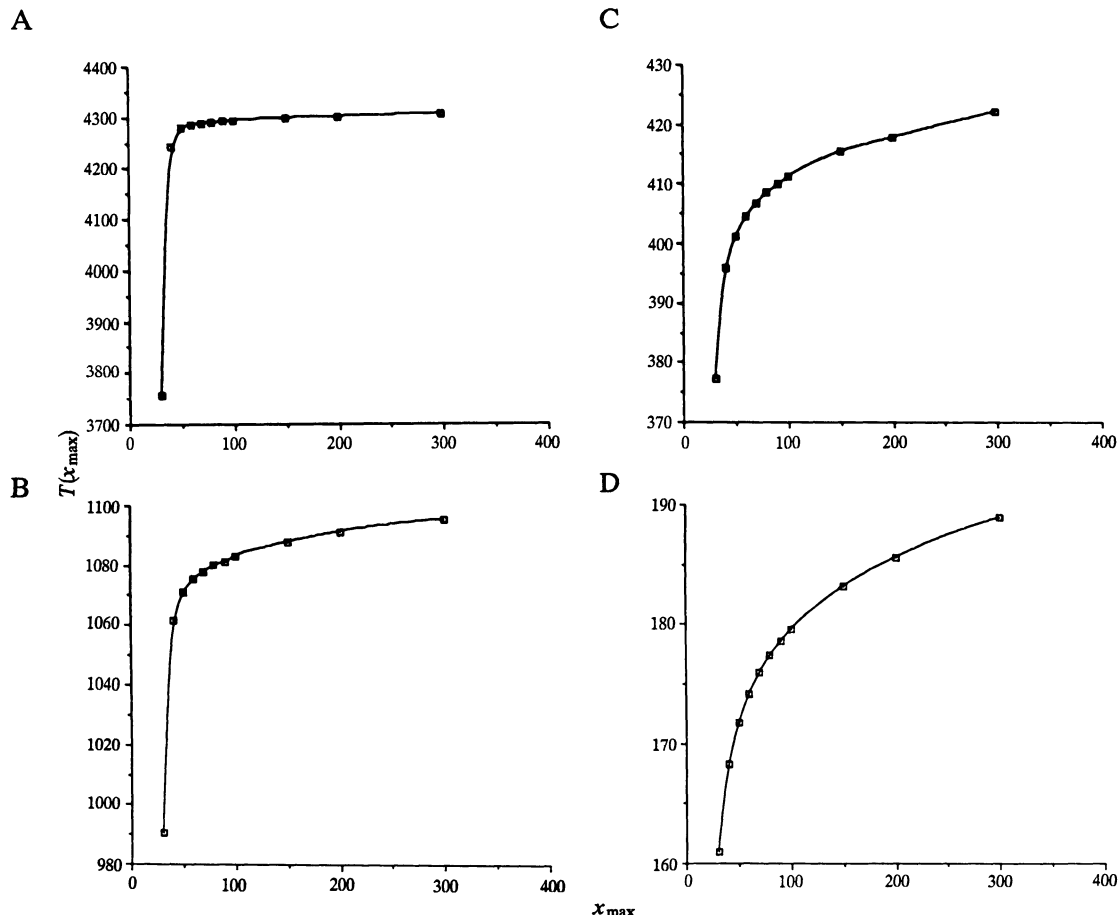


FIG. 3. Results for the flour beetle model, in which there is a stable steady state independent of maximum population size and in which the population ceiling is much larger than the stable steady state. (A) Persistence time $T(x_{\max})$ is shown as a function of the population ceiling x_{\max} when catastrophes are ignored. As with the MacArthur–Wilson model, there is a “shoulder” in the persistence time, which (for these parameters) rises rapidly for values of x_{\max} around 50. (B–D) This shoulder disappears when catastrophes are included, and, although the persistence time $T_c(x_{\max})$ increases with x_{\max} , it is >1 order of magnitude smaller than the persistence time when catastrophes are ignored. (B) Catastrophe rate $c = 0.01$ and death probability $p = 0.5$. (C) $c = 0.025$, $p = 0.5$. (D) $c = 0.05$, $p = 0.5$.

theoretical (7) and numerical (8) results that $\tau(x)$ is exponentially distributed, so that $\Pr\{\tau(x) \leq t\} = 1 - \exp[-t/T(x)]$, where \Pr is probability. It also means that the mean $T(x)$ is achieved by the averaging of many rapid extinctions and a few large ones (in fact, the most likely value for the density $\Pr\{t \leq \tau(x) \leq t + dt\} = 1/T(x)\exp[-t/T(x)]dt$ is $t = 0$).

DISCUSSION

We have provided a framework for computing the statistics of extinction times by a direct and simple method. Because of its direct nature, we are now able to explore more realistic biological descriptions for the dynamics of the population. These include factors such as immigration, emigration, multiple births (clutches), sex or age, true metapopulations, and more than one species. We can also include different types of catastrophes that occur at different rates and have different effects on the population. For example, a population might be in a physically unstable environment but also might be susceptible to a certain disease that leads to periodic epidemics. This would lead to two different types of jump terms in Eq. 2. The advantage of our approach is that the complexity of the model does not impact on it, whereas analytic methods are often strongly model dependent.

The results have a number of implications. Since it is now possible to numerically compute persistence times for populations with extremely complicated dynamics, it is worthwhile to invest resources into the determination of these dynamics. Our results show that in the presence of catastrophes, minimal viable population sizes are almost certainly

much larger than those predicted on the basis of some variant of the MacArthur–Wilson model. The properties of the CV of the extinction time show that even when conserved populations are large, we should expect extinctions; they are likely events, and we should be prepared with contingency plans when such extinctions occur. In fact, the analysis presented here calls into question the use of the mean extinction time in the practice (vs. the theory) of conservation biology and suggests that alternative measures should be developed.

We thank Peter Kareiva and an anonymous referee for helpful comments that improved presentation, Bernard Roitberg for hospitality during preparation of the manuscript, and Dorothy Scott for providing an opportunity for further collaboration. The work of M.M. was partially supported by National Science Foundation Grant OCE 90-16895; and the work of C.T., by National Science Foundation Grant DMS 89-22988.

1. Soule, M. E. (1987) *Viable Populations for Conservation* (Cambridge Univ. Press, Cambridge, U.K.).
2. Mangel, M. & Tier, C. (1993) *Theor. Popul. Biol.*, in press.
3. MacArthur, R. H. & Wilson, E. O. (1967) *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, NJ).
4. Leigh, E. G. (1981) *J. Theor. Biol.* **90**, 213–239.
5. Mangel, M. (1989) *Nat. Resource Modeling* **4**, 255–271.
6. Peters, C. S., Mangel, M. & Costantino, R. F. (1989) *Bull. Math. Biol.* **51**, 625–638.
7. Keilson, J. (1985) *Rarity and Exponentiality* (Springer, Heidelberg).
8. Goodman, D. (1987) in *Viable Populations for Conservation*, ed. Soule, M. (Cambridge Univ. Press, Cambridge, U.K.), pp. 11–34.