

Dynamics of Metapopulations with Demographic Stochasticity and Environmental Catastrophes

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Received September 20, 1991

In the first part of the paper, a method is developed for computing extinction properties of populations that are subject to demographic and environmental noise (catastrophes). The theory requires estimation of demographic birth and death rates, rates of catastrophes, and distribution of deaths when catastrophes occur. The colonization probability (chance of successful immigration), mean extinction time, and the long time conditional distribution of population size are predicted. The results can be put into algorithmic form so that workers can concentrate on developing parameters from empirical data. In the second part, the results are compared to the exact solution of a model (due to MacArthur and Wilson) without catastrophes and shown to be extremely accurate. The MacArthur–Wilson model is then extended to include environmental catastrophes. Finally, a metapopulation model with linear birth and death rates, immigration, catastrophes occurring at a rate independent of population size, and individuals dying independently is proposed. © 1993 Academic Press, Inc.

INTRODUCTION

The last decade has seen an enormous increase of interest in problems of conservation biology (Shaffer, 1981; Soule, 1987) and in questions concerning the dynamics of metapopulations (Gilpin and Hanski, 1991). Central to these problems is the computation of quantities associated with colonization by and extinction of local populations. Field data on extinctions are now appearing in the literature so that it will be soon possible to compare theories with field observations. For example, Pimm *et al.* (1988)

present a data-base of short-term survival (10's of years) of 355 populations of 100 species of British land birds. With these data, they are able to compute risk of extinction (reciprocal extinction time) as a function of population size and species characteristics such as body size. Aebischer (1986) analyzes the die-off of shag on the Isle of May, SE Scotland. This population was growing nearly exponentially until a crash in 1974–1976; the decline could be traced to an environmental disaster. Aebischer's data can be used to estimate birth and death rates.

Young (1993) gives data on more than 80 large mammal die-offs in nature, including population size before and after the catastrophe, source of the catastrophe (ranging from starvation induced by drought, winter, or other factors, through disease, predation, and habitat change), and habitat

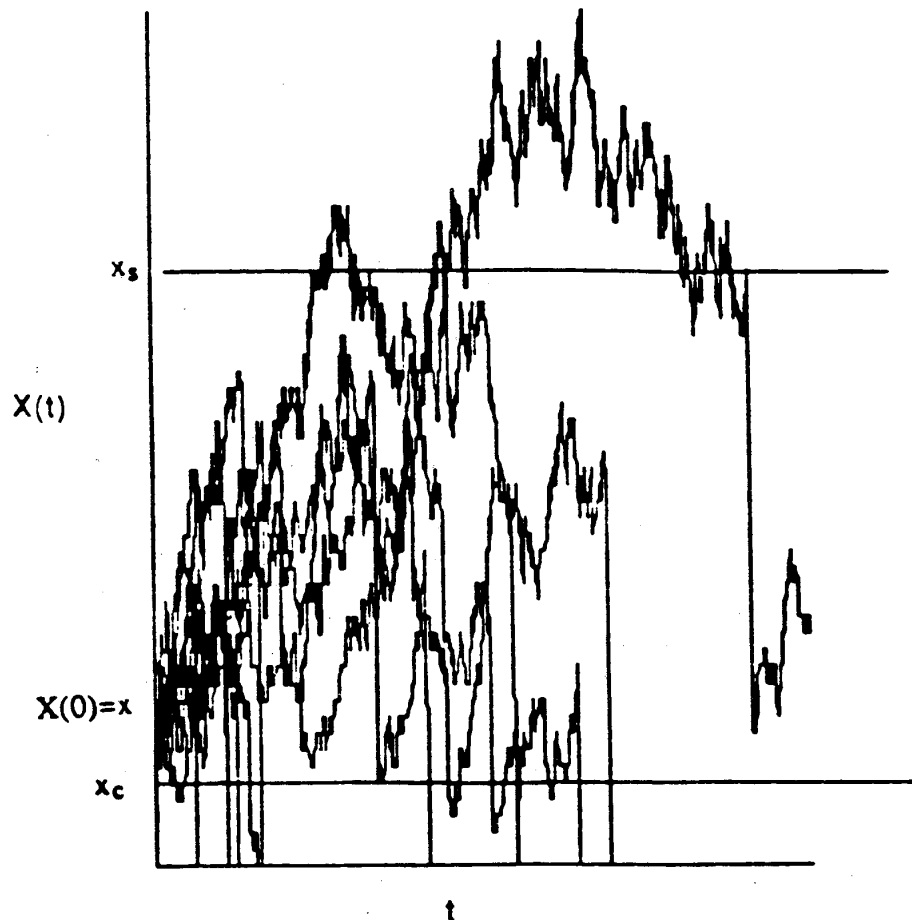


FIG. 1. A sample of 10 population trajectories, each starting at the same value of $X(0)=x$ and subject to the same birth, death, immigration, and catastrophe probabilities, but experiencing differing sample paths. Ultimately all populations go extinct. We define the immigration success probability as the chance that a population crosses the line $X(t)=x_s$ before it crosses the line $X(t)=x_c$. The mean extinction time is the average time (averaged over different population trajectories) until the population reaches $X(t)=x_c$.

distribution of the die-offs. These data can be used to estimate the population loss due to catastrophes. Dennis *et al.* (1991) show how growth and extinction parameters of endangered species can be estimated. Their data, for large mammals, could be used to estimate birth and death rates and Young's data used to estimate the rate and size of catastrophes so that a complete description of the underlying processes of birth, death, immigration, emigration and catastrophe is possible. A reasonable range for the rate of catastrophes is $0.02\text{--}0.06\text{ year}^{-1}$ (Truman Young, personal communication).

Schoener and Schoener (1983) present data showing that time to extinction of *Anolis* lizards on islands increases with vegetated area of the island. They observe that "On islands where lizards have gone extinct, populations never exceeded initial (propagule) sizes and extinction occurred in periods ranging from 5–11 days to 3 years" (cf. Fig. 1). Schoener and Spiller (1992) present data on turnover and persistence in island populations of orb spiders. To obtain these data, they surveyed about 100 islands and those islands with extant populations were recorded. Then over the next four years, extinction events were noted. In this manner, Schoener and Spiller obtained information on the fraction of populations remaining as a function of time (i.e., a measure of persistence), as a function of spider species, and frequency distributions of population size. Harrison *et al.* (1988) study the bay checkspot butterfly and argue that this population is most accurately described as a metapopulation and infer its spatial extent. Forney and Gilpin (1989) describe experiments used to determine the kind of stochasticity that occurs during the extinction of populations of *Drosophila*. Similar approaches are used by Bengtsson (1989) and Taylor (1990).

Theories to describe the survival and extinction of populations cannot be purely deterministic since extinction is often due to random or stochastic events. Three principal factors that contribute to extinction are:

1. Demographic accidents caused by uncertainties in births and deaths.
2. Nonconstant environments caused by minor fluctuations in habitat.
3. Catastrophes: declines caused by environmental disasters or mass emigrations.

The risks of demographic accidents and nonconstant environments are greatest for small populations. In contrast, catastrophes present risk to large populations which are seemingly safe from extinction. The quantitative aspects of the survival of local populations are often described by the mean time to extinction, the probability of extinction and the

probability of successful immigration and colonization of a population, given its current size (Fig. 1).

MacArthur and Wilson (1967, p. 68ff) developed a theory which only involves demographic stochasticity with linear birth and death rates. Their theory predicts enormous extinction times for modest carrying capacities and per-capita birth to death ratios only slightly larger than 1. A number of elaborations of this theory have appeared in the literature. Richter-Dyn and Goel (1972) described extensions of the basic theory of MacArthur and Wilson that included more realistic density dependent birth and death rates. They studied a number of different performance measures such as the probability density for the population, the moments of the extinction time, the probability that the population reaches a specified value before going extinct, and the mean extinction time. However, they only treated only demographic stochasticity. Hanson and Tuckwell (1978) were the first to include explicit environmental shocks. To do this, they studied a population undergoing logistic growth (i.e., without demographic stochasticity) subject to randomly occurring decrements of population due to environmental catastrophes. The population process satisfied a stochastic differential equation driven by the increment of a Poisson process. Hanson and Tuckwell obtained numerical solutions, but not analytical results. Leigh (1981) extended the MacArthur-Wilson theory to include a varying environment using a diffusion approximation and Goodman (1987a, b) extended Leigh's method of including environmental uncertainty.

Pakes *et al.* (1979) modeled a population growing deterministically and exponentially, subject to emigrations of random size at random time. Although the emigrations can be viewed as "environmental catastrophes," the model lacks demographic stochasticity (because of deterministic growth) and does not allow colonization from the metapopulation. They found that as initial population size approaches infinity, the mean extinction time grows as the logarithm of initial population size.

Murthy (1981) modeled a population growing deterministically towards a carrying capacity and subject to environmental catastrophes which occur at random times (i.e., are exponentially distributed) and lead to a random reduction in the size of the population. Trajstman (1981) extended the work of Pakes *et al.* (1979) to the case in which the population has "bounded growth," but the growth model is still deterministic. At random times the population is subject to emigrations of random size. Peters and Mangel (1990) used asymptotic methods similar to the ones in this paper to generalize the work of Pakes *et al.* (1979) and Trajstman (1981) so that the probability of extinction for any form of the deterministic growth can be considered.

Brockwell *et al.* (1983) considered a continuous, deterministically growing population subject to randomly occurring environmental

catastrophes in which the probability of a catastrophe depends upon current population size and in which case the decrements in population size are not necessarily discrete. For the case of exponential decrements in population size, they proved a theorem indicating when a stationary probability distribution for population size will exist. For special cases in the probability distribution of decrements (truncated exponential, uniform and degenerate in which the catastrophe wipes out the entire population), Brockwell *et al.* determined the stationary distribution of population size when the rate of catastrophes is constant or proportional to population size.

Brockwell (1985) modeled a linear birth and death process and assumed that the probability of a catastrophe is proportional to the current population size and that its size has fixed probability independent of the current population size. Brockwell determined the generating function (z -transform) for the distribution of the time to extinction (Brockwell, 1985, Eq. 2.9) and the generating function for the probability of ultimate extinction, given that initial population size. The mean extinction time is shown to grow logarithmically for large initial populations. This is the closest to our work, but Brockwell's results only apply for the specific forms of birth and death rates, whereas ours does not have such a limitation.

Lande and Orzack (1988) used a diffusion model to study the extinction dynamics of populations in a fluctuating environment. Bartoszyński *et al.* (1989) modeled a linear birth and death process in which catastrophes occur at a rate independent of population size and in which each individual has equal chance of death during a catastrophe. In this case, the probability distribution of deaths in a catastrophe is binomial. They derived the partial differential-difference equation for the generating function of population size. This equation is not easily solved, so Bartoszyński *et al.* were only able to prove general properties about the generating function or provide simulation results.

A key observation from this brief review of work relating to extinction of populations is that if environmental catastrophes are included in the basic MacArthur-Wilson model, the extinction times should no longer be enormous. Instead extinction times should grow slowly with initial population size (Fig. 2). The intuitive reason is that environmental catastrophes can reduce a population by large amounts in short times; this keeps extinction times bounded. Although this has previously been recognized by some of the authors whose work was described above, until now we have lacked a method for computing extinction times in the presence of catastrophes. Our goal is to develop a method for computing extinction measures for a population incorporating demographic stochasticity and environmental catastrophes. Our approximations are accurate, easy to

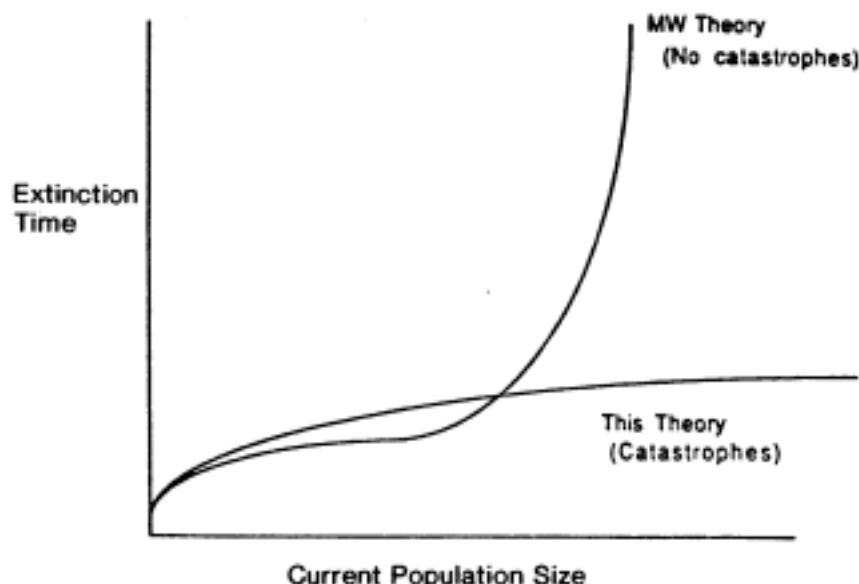


FIG. 2. The theory of extinction times in the absence of environmental catastrophes (due to MacArthur and Wilson; labeled by MW) leads to two qualitatively strong predictions. The first is a "shoulder" or point of inflection, i.e., a population size at which the extinction time begins to rise rapidly. This is often called the Minimum Viable Population. The second is enormously large extinction times for modest population sizes. On the other hand, in the presence of catastrophes, the shoulder and the enormously large times both disappear. In this paper, we show how to calculate the limiting value of the extinction time, as population size increases.

compute and valid for realistic parameter ranges. Since this area of population biology is actually being used in policy decisions (Shaffer and Samson, 1985; Burgman and Neet, 1989; Murphy, 1989; Estes, 1991; Soule, 1991), the best possible models and computational methods are essential.

In Part I of this paper, we describe an analytical theory for the computation of extinction properties of populations. Elsewhere (Mangel and Tier, 1993), we describe a purely numerical procedure for the computation of these properties of populations. The difficulty in the purely numerical solution of Eq. (10) is that it is not a closed system of equations (because of the

$$B(x) T(x+1)$$

term). Consequently, the numerical method requires additional assumptions, as described in Mangel and Tier (1993). The analytical methods used in the present paper are based on the use of asymptotic methods in stochastic processes. We show how to compute the mean extinction time and the probability of successful colonization for models with realistic birth and death rates and environmental catastrophes. Our results are put into algorithmic form using symbolic and numeric computation so that they can

be employed by field workers. For simplicity of presentation, we focus on cases in which the probability that a catastrophe occurs is independent of population size, but our method can be generalized easily. However, throughout we assume that the distribution of deaths depends upon population size.

In Part II, we illustrate our method on several examples. First, we compare our approximate extinction measures with the exact solutions of the MacArthur-Wilson (1967) model. We find that the approximations are quite accurate. Next, we include environmental catastrophes in the MacArthur-Wilson model. We find that a considerable reduction in persistence time occurs when catastrophes with modest rates and intensities are included. Finally, we describe a specific model for colonization and extinction (the linear-birth-death-immigration-catastrophe model) that is an alternative to the usual " r and K " logistic models which have dominated thinking in conservation biology. We explain how the alternate model may be more appropriate for many common situations in which density dependence is less of a regulating factor for population size than immigration and death through catastrophe. Although the two models which we use for examples involve either linear population dynamics or extremely simple nonlinearities (as the model of MacArthur and Wilson), the methods we present here are fully general and applicable to any form of nonlinear population dynamics.

I. A GENERAL THEORY FOR THE COMPUTATION OF EXTINCTION AND COLONIZATION PROPERTIES OF METAPOPULATIONS

We envision a metapopulation consisting of a large number of smaller, local populations (Fig. 3) and potential, but currently empty, habitats. Within a local population, demographic processes involve birth, death, immigration and emigration. In a short interval of time, these result in only unit changes in population size. In addition, a local population may experience a "catastrophe" in which a large number of individuals either emigrate or die. We concentrate on the dynamics of one of these local populations.

The population is described by a single variable $X(t)$, representing population size at time t . Let ΔX denote the change in population from t to $t + \Delta t$, so that $\Delta X = X(t + \Delta t) - X(t)$. We want to describe the dynamics of the population, taking both demographic processes and potential catastrophes into account.

First consider demographic processes. When Δt is sufficiently small only one birth or death can occur during the interval of length Δt . Given that

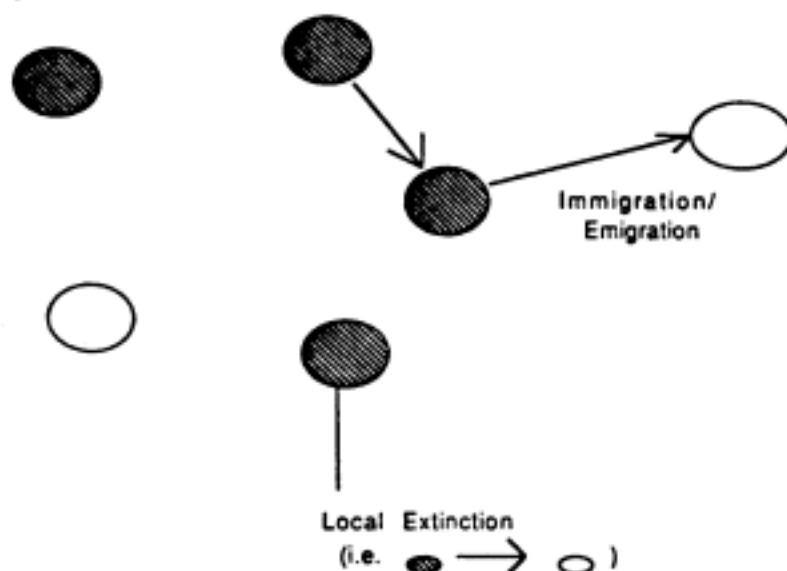


FIG. 3. A "metapopulation" consists of a number of local populations (filled ellipses) and potential, but currently empty, habitats. Within a local population, demographic processes involve birth, death, immigration and emigration. In addition, a local population can suffer a "catastrophe" and go extinct. We concentrate on the dynamics of one of these local populations.

$X(t) = x$, we assume that, in the absence of a catastrophe, the probability of a birth is given by

$$\begin{aligned} \Pr\{\Delta X = 1 \mid X(t) = x, \text{ no catastrophe in the next } \Delta t\} \\ &= R(x, \Delta t) \\ &= [B(x)/(B(x) + D(x))](1 - \exp(- (B(x) + D(x)) \Delta t)). \end{aligned} \quad (1)$$

The probability of a single death from demographic causes is

$$\begin{aligned} \Pr\{\Delta X = -1 \mid X(t) = x, \text{ no catastrophe in the next } \Delta t\} \\ &= L(x, \Delta t) \\ &= [D(x)/(B(x) + D(x))](1 - \exp(- (B(x) + D(x)) \Delta t)). \end{aligned} \quad (2)$$

Finally, the probability of no change in population size from demographic causes is

$$\begin{aligned} \Pr\{\Delta X = 0 \mid X(t) = x, \text{ no catastrophe in the next } \Delta t\} \\ &= \exp(- (B(x) + D(x)) \Delta t). \end{aligned} \quad (3)$$

In these equations, $B(x)$ corresponds to the unit increase in population in Δt from birth or immigration and $D(x)$ corresponds to the unit decrease in

population from death or emigration. These could be considered the "usual" or "typical" demographic parameters.

Equations (1)–(3) are written using exponentials because in this form they are directly usable in Monte Carlo simulations for arbitrary choices of $B(x)$, $D(x)$, and Δt . To analyze the limit as $\Delta t \rightarrow 0$, we expand the exponentials. If $o(\Delta t)$ denotes terms such that $o(\Delta t)/\Delta t \rightarrow 0$ as $\Delta t \rightarrow 0$, we find

$$\Pr\{\Delta X = 1 | X(t) = x, \text{ no catastrophe}\} = B(x) \Delta t + o(\Delta t),$$

$$\Pr\{\Delta X = -1 | X(t) = x, \text{ no catastrophe}\} = D(x) \Delta t + o(\Delta t),$$

$$\Pr\{\Delta X = 0 | X(t) = x, \text{ no catastrophe}\} = 1 - (B(x) + D(x)) \Delta t + o(\Delta t).$$

These equations, however, hold only for infinitesimally small Δt , and workers interested in simulating population processes should not use them, but should use (1)–(3) instead.

A catastrophe is assumed to always be detrimental. To fully describe environmental catastrophes, we must specify the rate of catastrophes and the distribution of deaths. Let $C(x)$ denote the rate of catastrophes when the population size is $X(t) = x$, in that

$$\Pr\{\text{catastrophe occurs in the next } \Delta t | X(t) = x\} = 1 - \exp(-C(x) \Delta t).$$

Physical catastrophes may have $C(x) = C$, independent of population size, but biological catastrophes such as epidemics may strongly depend upon population size (Harwood and Hall, 1990). If a catastrophe occurs when the population size is $X(t) = x$, we assume that y individuals die with probability $Q(y|x)$; this allows for density dependence in the deaths due to catastrophes. The normalization condition on the number of deaths is $\sum_{y=0}^{\infty} Q(y|x) = 1$. (For simplicity, $y=0$ is allowed, but is not likely.) In summary, the probability of y deaths from a catastrophe is given by

$$\begin{aligned} \Pr\{\Delta X = -y | X(t) = x\} \\ = J(x, y, \Delta t) = Q(y|x)(1 - \exp(-C(x) \Delta t)). \end{aligned} \quad (4)$$

As described above, $Q(y|x)$ and $C(x)$ describe not only deaths from catastrophe, but include multiple or group emigration.

If $m_1(x)$ is the mean of the catastrophe distribution $Q(y|x)$, the mean change of the population will be

$$E\{\Delta X | X(t) = x\} = [B(x) - D(x) - C(x) m_1(x)] \Delta t + o(\Delta t). \quad (5)$$

This suggests considering the "average" population dynamics, for a continuous approximation x_{av} , described by

$$\frac{dx_{av}}{dt} = B(x_{av}) - D(x_{av}) - C(x_{av}) m_1(x_{av}). \quad (6)$$

We assume the average population dynamics, given by (6), has a steady state x_s , which is much larger than 1 individual; usually $x_s \geq 10$ will be sufficient for our methods to provide accurate numerical results. Alternatively, x_s is the value of population size such that $E\{\Delta X | X(t) = x_s\} = 0$. The assumption that $x_s \gg 1$ is important for our analysis and will be met for nearly all interesting and practical conservation problems. In addition, we assume that $B(x)$, $D(x)$ and $Q(y|x)$ vary slowly with x , meaning that a small change in x (e.g., 1 individual) produces only a small change in $B(x)$, $D(x)$, and $Q(y|x)$, i.e., their first differences with respect to x are $O(1/x_s)$. Thus we assume that these functions are of the form $B(x/x_s)$, $D(x/x_s)$ and $Q(y|x/x_s)$. The birth and death parameters can be determined by standard demographic methods. For example, Peters *et al.* (1989) have explicitly analyzed the dynamics of the flour beetle *Tribolium* using a birth and death formulation in which $B(x) = r(x + \delta) \exp(-\alpha x)$ and $D(x) = \omega x$, where r , δ , α , and ω are parameters that could be experimentally determined. Knowledge about the rate of catastrophes $C(x)$ and the distribution of deaths from catastrophes $Q(y|x)$ is more limited, but is becoming less so. In this paper, we use the simplest assumption is that $C(x) = C$, a constant. This means that the occurrence of a catastrophe is independent of population size. This would correspond, for example, to a physical environmental catastrophe. The function $Q(y|x)$ can be determined from knowledge of the distribution of deaths when a catastrophe occurs.

We assume that extinction corresponds to a critical value of population size x_c , i.e., the population is classified as extinct if $X(t) \leq x_c$ (Fig. 1). Since we are interested in studying properties related to the first extinction of the population, we consider a process with population sizes less than or equal to x_c as absorbing points. We adopt the following conservative criterion for the definition of x_c by noting that if $B(0) > 0$ then "immigration" can occur to the local population. In case of immigration, the local population becomes extinct only temporarily, until the next immigrant arrives but this does not have to be accounted for in our model. This can be actual physical immigration to the population, as in the case of a general metapopulation, or immigration from one stage of the life cycle (e.g., pupae) to the stage that is described by $X(t)$ (e.g., adult) (Peters *et al.*, 1990). Thus, we can choose $x_c = 1$ if $B(0) = 0$, since a single individual cannot find a mate, or $x_c = 0$ if $B(0) > 0$. One could, of course, set x_c higher than these values to study the case in which the population falls below some predetermined critical value.

Colonization and Extinction Measures

We are interested in two measures of population performance. When a population starts at some initial value $X(0) = x$, it will grow and decline according to the dynamics described in the previous section and, ultimately, will reach extinction, although this may only be temporary if immigration occurs (e.g., Fig. 1). The *immigration success* or *colonization probability* is the chance that an immigrating module establishes itself before extinction. This is the probability that the local population crosses x_s (defined below (6)) before it crosses x_c , as a function of initial population size $X(0) = x$. Denoting this probability by $V(x)$, we have

$$V(x) = \Pr\{X(t) \geq x_s \text{ before it falls to or below } x_c, \text{ given that } X(0) = x\}. \quad (7)$$

Since a population starting at $X(0) \geq x_s$ always exceeds or equals x_s before it falls to or below x_c , we have $V(x) = 1$ if $x \geq x_s$. Similarly, $V(x) = 0$ for $x \leq x_c$.

Our second measure of performance is the (arithmetic) *mean extinction time*, which is the average of the first time that the population falls to or below x_c , given that it starts at initial size $X(0) = x$. Symbolically, we write

$$T(x) = E\{\text{smallest } t \text{ such that } X(t) \leq x_c | X(0) = x\}. \quad (8)$$

Since a population starting with $x \leq x_c$ has already fallen below this critical values, we have $T(x) = 0$ for $x \leq x_c$.

The key quantity is $T(x)$, and thus we derive the equation that it satisfies. To do this, assume that $X(t) = x$, and consider an interval of time Δt sufficiently small that only one of three mutually exclusive events occurs: (i) no change in population, (ii) no catastrophe but a birth or death, or (iii) a catastrophe. Incorporating these and using the law of total probability gives the result

$$\begin{aligned} T(x) = & \Delta t + (\exp(-(B(x) + D(x)) \Delta t) \exp(-C(x) \Delta t) T(x) \\ & + (1 - \exp(-(B(x) + D(x)) \Delta t)) \exp(-C(x) \Delta t) \\ & \times [R(x, \Delta t) T(x+1) + L(x, \Delta t) T(x-1)] \\ & + \exp(-(B(x) + D(x)) \Delta t) (1 - \exp(-C(x) \Delta t)) \\ & \times \sum_{y=0}^{x-x_c} J(x, y, \Delta t) T(x-y). \end{aligned} \quad (9)$$

The terms on the right hand side of (9) correspond to the following: the interval of time that the population survives, regardless of what happens at

the end of Δt ; the probability that no population change occurs in this Δt times the mean extinction time from population size x , the probability that no catastrophe occurs but that a birth or death does occur times the mean extinction time from the new population size ($x+1$ with probability $R(x, \Delta t)$ or $x-1$ with probability $L(x, \Delta t)$), and the probability that a catastrophe occurs times the mean extinction time from the new population size ($x-y$ with probability $J(x, y, \Delta t)$).

We now expand all of the quantities on the right hand side of (9) in powers of Δt , cancel $T(x)$ from both sides, collect terms in powers of Δt , divide by Δt and let $\Delta t \rightarrow 0$ to obtain (the same procedure as in MacArthur and Wilson, 1967, or Leigh, 1981)

$$\begin{aligned} -1 = & B(x) T(x+1) + D(x) T(x-1) - (B(x) + D(x) + C(x)) T(x) \\ & + C(x) \sum_{y=0}^{x-x_c} Q(y|x) T(x-y). \end{aligned} \quad (10)$$

A similar procedure shows that $V(x)$ satisfies an equation analogous to (10), with the left hand side replaced by 0. In our construction of $T(x)$, we determine $V(x)$. Higher moments of the extinction time can be found by solving equations analogous to (10) in which the right hand side describes the x -dependence of the j th moment of the extinction time and the -1 on the left hand side is replaced by the $(j-1)$ th moment of the extinction time.

Determination of the Extinction Time

We now present a thorough derivation of the method for calculating of the mean extinction time and emphasize the algorithmic nature of our approach. (An excellent reference on the methods that we use is Bender and Orszag, 1978.) We begin by measuring population size as a fraction of x_s defined from (6). Thus, let

$$n = x/x_s \quad \text{or} \quad x = x_s n.$$

As population size ranges from 0 to x_s , n ranges from 0 to 1. Furthermore, when the population changes by 1 individual, the scaled population size changes by $1/x_s$, which we assume is small. It is the smallness of this change which our method of analysis exploits. Similarly define $n_c = x_c/x_s$. Using the assumption that $B(x)$ and $D(x)$ are slowly varying in x , we define $b(n) = B(x_s n)$ and $d(n) = D(x_s n)$. For simplicity of presentation, we assume that the rate of catastrophes (but not the distribution of deaths) is independent of population size and is thus a constant C ; for consistency of notation we set $c = C$ and $q(s|n) = Q(s|x_s n)$. By using this scaling, the

steady state of the "average" dynamics is now $n = 1$. Defining $t(n) = T(x_s, n)$, Eq. (10) becomes

$$-1 = b(n) t \left(n + \frac{1}{x_s} \right) + d(n) t \left(n - \frac{1}{x_s} \right) - (b(n) + d(n) + c) t(n) + c \sum_{s=0}^{\infty} q(s|n) t \left(n - \frac{s}{x_s} \right). \quad (11)$$

Equation (11) is the fundamental equation for our analysis. We have extended the upper limit in the summation to ∞ , since $t(n) = 0$ if $n < n_c$.

Since $x_s \gg 1$ by our earlier assumption, we begin by considering the limit in which $x_s \rightarrow \infty$. In that case, there is a non-zero probability of ultimate persistence (Peters and Mangel, 1990), which means that the mean extinction time approaches infinity. Thus, we conclude

$$t(n) \rightarrow \infty \quad \text{as} \quad x_s \rightarrow \infty. \quad (12)$$

To determine the value of $t(n)$, we assume that it has the form

$$t(n) = P(x_s) u(n), \quad (13)$$

where $0 \leq u(n) \leq 1$ and $P(x_s) \rightarrow \infty$ as $x_s \rightarrow \infty$. We understand that (13) defines the constant P and the bounded function $u(n)$, both of which must be determined.

Assuming that $P(x_s) \gg 1$, we substitute (13) into (11) and use the result that $1/P(x_s) \sim 0$ to obtain

$$0 \sim b(n) u \left(n + \frac{1}{x_s} \right) + d(n) u \left(n - \frac{1}{x_s} \right) - (b(n) + d(n) + c) u(n) + c \sum_{s=0}^{\infty} q(s|n) u \left(n - \frac{s}{x_s} \right). \quad (14)$$

We begin by assuming that $u(n)$ can be represented by the power series

$$u(n) = u_0(n) + (1/x_s) u_1(n) + (1/x_s)^2 u_2(n) + \dots,$$

which we substitute (14). We then expand in powers of $(1/x_s)$ and collect terms according to those powers to find that the leading term is

$$[b(n) - d(n) - cm_1(n)] du_0/dn = 0.$$

Since the coefficient of the derivative is not zero in the interval $0 < n < 1$, we conclude that $du_0/dn = 0$ and that $u_0(n)$ is a constant, which we set to be 1 because of the normalization following (13). However, this is only true

if n is bounded away from n_c since $u_0 = 1$ fails to satisfy the condition $t(n_c) = 0$, $n \leq n_c$. However, we already see that the extinction time does not rise without bound, because of catastrophe reductions in population size, and is approximated by

$$t(n) \sim P(x_s) \quad n \gg n_c.$$

We have thus captured the generally well known phenomenon of colonization and extinction: if a propagule establishes itself from small size, it does so very rapidly. Once established, the mean extinction time is much larger than the time to establishment.

Knowing that $u(n)$ is a constant when $n \gg n_c$, however, leaves two major obstacles. First, what is the extinction time when the population size is small? Second, what is the value of the constant $P(x_s)$? We know that at the critical value of population size, the extinction time is 0 and we know that it rises to $P(x_s)$ as described above. This means that there is a "boundary layer" (cf. Bender and Orszag, 1978) near the critical value. To find $u(n)$ when the population size is small, i.e., $n - n_c$ is close to zero, we introduce a scaled discrete variable k that measures deviations from n_c :

$$k = (n - n_c)x_s. \quad (15)$$

This choice of scaling returns us to the original variable, except that we shall now assume that the values of k of interest are such that the birth, death, rates catastrophe and the catastrophe distributions can be treated as constants, with their values determined by the values at n_c . We thus "freeze" the coefficients at $n = n_c$ and denote $b_c = b(n_c)$, $d_c = d(n_c)$, and $q_c(s) = q(s|n_c)$ and let $U(k)$ denote the solution of (14) in this new variable with the frozen coefficients. We then find that to leading order in $1/n_c$

$$0 = b_c U(k+1) + d_c U(k-1) - (b_c + d_c + c) U(k) + c \sum_{s=0}^k q_c(s) U(k-s).$$

The simplification is that we now have a difference equation with constant coefficients which can be solved by the method of generating functions or "z-transforms" (e.g., Caswell, 1989, p. 96 ff).

For an arbitrary function $f(k)$, the z-transform $\hat{f}(z)$ is defined by

$$\hat{f}(z) = \sum_{k=0}^{\infty} f(k) z^k, \quad (16)$$

where $0 < z < 1$. The key results that we will need are (i) the z-transform of

a convolution is the product of the z -transforms and (ii) the so-called final value theorem of z -transforms, which states that

$$\lim_{z \rightarrow 1} (1 - z) \hat{f}(z) = f(\infty). \quad (17)$$

This result links limiting behavior of the original function and of its transform.

The transform of $U(k)$ will be denoted by $\hat{U}(z)$. To find it, first note that $U(0) = 0$ (i.e., when $n = n_c$ the extinction time is 0), and then multiply the equation for $U(k)$ by z^k and sum over k to obtain

$$\begin{aligned} 0 = & b_c \sum_{k=0}^{\infty} z^k U(k+1) + d_c \sum_{k=0}^{\infty} z^k U(k-1) \\ & - [b_c + d_c + c] \sum_{k=0}^{\infty} z^k U(k) + c \sum_{k=0}^{\infty} z^k \sum_{s=0}^k q_c(s) U(k-s). \end{aligned}$$

The last term is a convolution (Caswell, 1989) so that we obtain

$$\begin{aligned} 0 = & b_c (1/z) \sum_{k=1}^{\infty} z^{k+1} U(k+1) + d_c z \sum_{k=1}^{\infty} z^{k-1} U(k-1) \\ & - [b_c + d_c + c] \hat{U} + c \hat{U} \hat{q}_c, \end{aligned}$$

where \hat{q}_c is the z -transform of $q_c(s)$. Note that the first sum on the right hand side of the above equation is the same as $(b_c/z)[\hat{U} - U(1)z]$ and that the second sum on the right hand side is exactly \hat{U} (since $U(0) = 0$) so that we obtain

$$0 = (b_c/z)(\hat{U} - U(1)z) + d_c z \hat{U} - [b_c + d_c + c] \hat{U} + c \hat{U} \hat{q}_c.$$

Solving for \hat{U} gives

$$\hat{U} = b_c U(1) z / (b_c + d_c z^2 - (b_c + d_c + c) z + c z \hat{q}_c). \quad (18)$$

Since $U(1)$ appears, and it is not yet known, the construction is not complete. To find $U(1)$ we must perform "asymptotic matching" by recognizing that as j increases, $U(j)$ should approach the same value as solution $u(x)$, which is $u(x) \sim 1$ valid away from x_c . We then use the final value theorem on (18) to compute the limit of $U(j)$ and then using L'Hopital's rule, we find

$$U(1) = (b_c - d_c - c m_1) / b_c \quad (19)$$

so that

$$\hat{U} = [b_c - d_c - cm_1] z / [b_c + d_c z^2 - (b_c + d_c + c) z + czq_c]. \quad (20)$$

We have thus constructed the z -transform of U for small population sizes which turns out to be uniformly valid over the entire state space.

Since $U(n_c) = 0$ and $U(n) \rightarrow 1$ as $n \rightarrow \infty$, we have determined the colonization probability during the construction of $U(n)$. That is,

$$V(x) = U(x/x_s).$$

In order to proceed with computations, one must find $U(n)$ from the z -transform. The development of symbolic manipulation packages has made this particularly easy. For example, a partial fraction inversion algorithm is available in the symbolic manipulation language MAPLE (Char *et al.*, 1988). In particular, the most recent version of MAPLE (V) contains internal functions "ztrans" and "invztrans" for computing and inverting z -transforms.

Next, we must determine the constant $P(x_s)$. To do so, we adapt a method used by Knessl *et al.* (1984) and Matkowsky *et al.* (1984) to our problem. The idea is develop an auxiliary formula to determine $P(x_s)$ that involves the solution of a simpler equation. The method rests on the use of the adjoint equation (Courant and Hilbert, 1962) and the procedure goes as follows. We first multiply (11) by an unknown function $W(x)$ and sum from $x_c + 1$ to ∞ . Next we shift the differences from $T(x)$ to $W(x)$ and interchange the order of the summations. This yields the discrete analog of the Lagrange identity in differential equations (Courant and Hilbert, 1962). Knessl *et al.* (1984) and Matkowsky *et al.* (1984) show that the appropriate choice of $W(x)$ is the solution of adjoint equation

$$\begin{aligned} 0 = & B(x-1) W(x-1) + D(x+1) W(x+1) - (B(x) + D(x) + C(x)) W(x) \\ & + \sum_{y=1}^{\infty} C(x+y) Q(y|x+y) W(x+y). \end{aligned} \quad (21)$$

The use of the adjoint equation insures that when the procedure described above is followed and the appropriate boundary conditions are applied, most of the terms in the sum cancel and we obtain

$$B(x_c) W(x_c) T(x_c + 1) = \sum_{x=x_c+1}^{\infty} W(x).$$

Now using the fact that

$$T(x) \sim P(x_s) V(x),$$

we find that

$$P(x_s) = \sum_{x=x_c+1}^{\infty} W(x)/[B(x_c) W(x_c) V(x_c+1)]. \quad (22)$$

We are left with the simpler problem of constructing $W(x)$ which satisfies the same equation as the stationary density of population size but without boundary conditions. For the process which is stopped after first extinction, the only possible stationary solution is 0. In that case, we refer to $W(x)$ as the conditional density of the population for populations that are not yet extinct. This describes the long-time behavior of population size before extinction. If reintroduction occurs and proper boundary conditions are used then $W(x)$ would be the true stationary density of population size. We can easily determine $W(x)$ numerically if the state space is bounded. Alternatively, we can construct an approximation to $W(x)$ using the asymptotic method described in the Appendix. In either case, once we have determined $W(x)$, the extinction time $T(x)$ is given by

$$T(x) = V(x) \sum_{x=x_c+1}^{\infty} W(x)/[B(x_c) W(x_c) V(x_c+1)]. \quad (23)$$

Using the approximate construction in the Appendix, we find that $W(x)$ is given by

$$W(x) \sim g(x/x_s) \exp(-\psi(x/x_s)x_s), \quad (24)$$

where ψ and g are solutions of the ordinary differential equations (in which ' denotes a derivative)

$$b(n) e^{\psi'(n)} + d(n) e^{-\psi'(n)} + c \sum_{s=0}^{\infty} q(s|n) e^{-s\psi'(n)} = b(n) + d(n) + c \quad (25)$$

and

$$\mathcal{A}(n) g'(n) = \mathcal{B}(n) g(n)$$

$$\begin{aligned} \mathcal{A}(n) &= d(n) e^{-\psi'(n)} - b(n) e^{\psi'(n)} + c \sum_{s=0}^{\infty} q(s|n) s e^{-s\psi'(n)} \\ \mathcal{B}(n) &= b'(n) e^{\psi'(n)} - d'(n) e^{-\psi'(n)} - c \sum_{s=0}^{\infty} \frac{\partial}{\partial n} [q(s|n)] s e^{-s\psi'(n)} \\ &\quad + (1/2) \psi''(n) \\ &\quad \times \left\{ b(n) e^{\psi'(n)} + d(n) e^{-\psi'(n)} + c \sum_{s=0}^{\infty} s^2 q(s|n) e^{-s\psi'(n)} \right\}. \end{aligned} \quad (26)$$

Equations (23)–(26) embody the main theoretical result. A further simplification can be obtained by asymptotically expanding the summation in (23) when x_s is large. This is described in the Appendix.

Algorithm

The theoretical results of the previous section can be summarized in the following computational algorithm.

1. Model $B(x)$, $D(x)$, C , and $Q(y|x)$. This is the essential biological analysis. Identify the large parameter x_s using the average equation (6) or the value of x where the distribution of the population size is peaked. It is important that between x_c and x_s there should be no other rest points of (6).
2. Scale the equation (10) for $T(x)$ to get (11) and define functions b , d , q , and c . The slowly varying assumption can be verified by requiring that all coefficients in (11) are of the same order.
3. Construct $V(x) = U(x/x_s)$ where the z -transform of U satisfies (20).
4. Find $W(x)$ by constructing g and ψ using (25) and (26). This gives the conditional distribution of populations that have survived. The mean and variance of the size of surviving populations can then be computed directly from $W(x)$.
5. Find $P(x_s)$ using (22). This is the maximum possible extinction time. This requires computing $\sum_{x=x_c+1}^{\infty} W(x)$.
6. Find $T(x) \sim P(x_s) V(x)$. This is the mean extinction time from initial population size $X(0) = x$.

Each of steps 3–6 can be easily implemented using a symbolic manipulation package, such as MAPLE (Char *et al.*, 1988) or Mathematica, eliminating the need for tedious calculation.

II. APPLICATIONS

MacArthur–Wilson Model with No Catastrophes

First, we consider the model of MacArthur and Wilson (1967). Since the exact solution for the mean extinction time is available, we are able to demonstrate the accuracy of our approximations. The model only

involves demographic stochasticity and no environmental catastrophes so that $C=0$. The population undergoes exponential growth up to a population ceiling of K beyond which the birth rate is zero. Thus, in our notation,

$$B(x) = \begin{cases} \lambda x & \text{if } x \leq K \\ 0 & \text{if } x > K \end{cases} \quad (27)$$

$$D(x) = \mu x,$$

where we assume that $\lambda > \mu$. In addition, we assume that extinction occurs at x_c . If the initial population size is less than or equal to $K+1$ then the state space for the model is $\{x_c, \dots, K+1\}$. The exact solution for the mean extinction time is

$$\begin{aligned} T(x) &= T(x_c + 1) \sum_{j=0}^{x-1} \left(\frac{\mu}{\lambda}\right)^j \\ &\quad - \sum_{j=1}^{x-x_c-1} \frac{1}{(x_c + j)\lambda} \sum_{l=0}^{x-x_c-1-j} \left(\frac{\mu}{\lambda}\right)^l, \quad x_c < x \leq K, \\ T(x_c + 1) &= \sum_{j=x_c+1}^{K+1} \frac{1}{j\lambda} \left(\frac{\lambda}{\mu}\right)^{j-x_c}. \end{aligned}$$

Our approximate method can be applied directly to this model if we let the population ceiling K play the role of the large parameter x_s in our analysis. We trace through the steps of the algorithm.

1. For this example the model is given so no biological measurements are needed and we use K as the large parameter.

2. Because of the special form of the equation the slowly varying assumption is automatically satisfied if we simply replace x by Kn and divide by K so that

$$b(n) = \begin{cases} \lambda n & \text{if } n \leq 1 \\ 0 & \text{if } n > 1 \end{cases}$$

$$d(n) = \mu n.$$

The values of λ and μ should be of the same order of magnitude (as they are, see MacArthur and Wilson, 1967).

3. From (18), the z -transform of U is

$$\hat{U} = \frac{(\lambda - \mu)z}{\mu z^2 - (\lambda - \mu)z + \lambda}$$

and computing its inverse, we find that

$$V(x) = 1 - \left(\frac{\mu}{\lambda}\right)^{x - x_c}.$$

4. The conditional density can be found directly (Ludwig, 1974) and is

$$W(x) = \frac{1}{x} \left(\frac{\lambda}{\mu}\right)^x \quad x = x_c, \dots, K+1.$$

5. For this example, we use the discrete Lagrange identity to find that

$$P(x_s) = \sum_{x=x_c+1}^{K+1} \frac{1}{x} \left(\frac{\lambda}{\mu}\right)^{x - x_c} / (\lambda - \mu).$$

6. We thus obtain the approximate result

$$T(x) \sim P(x_s) V(x) \sim P(x_s) \left[1 - \left(\frac{\mu}{\lambda}\right)^{x - x_c} \right]. \quad (28)$$

Ludwig (1978) derived an asymptotic expression for $T(1)$ when $x_c = 0$ and K is large. If we set $x_c = 0$ and expand the sum in $P(x_s)$ for large K we find that

$$\sum_{x=1}^{K+1} \frac{1}{x} \left(\frac{\lambda}{\mu}\right)^x \sim \frac{\lambda}{(K+1)(\lambda - \mu)} \left(\frac{\lambda}{\mu}\right)^{K+1}.$$

Using this approximation in (28) we find that the leading term in $T(1)$ is

$$T(1) \sim \frac{1}{(K+1)(\lambda - \mu)} \left(\frac{\lambda}{\mu}\right)^{K+1},$$

which agrees with Ludwig's result. Hence, our method indeed produces the leading term in the asymptotic expansion for the mean extinction time.

To illustrate the numerical accuracy of the approximation, we compare our approximation with the exact solution (Fig. 4).

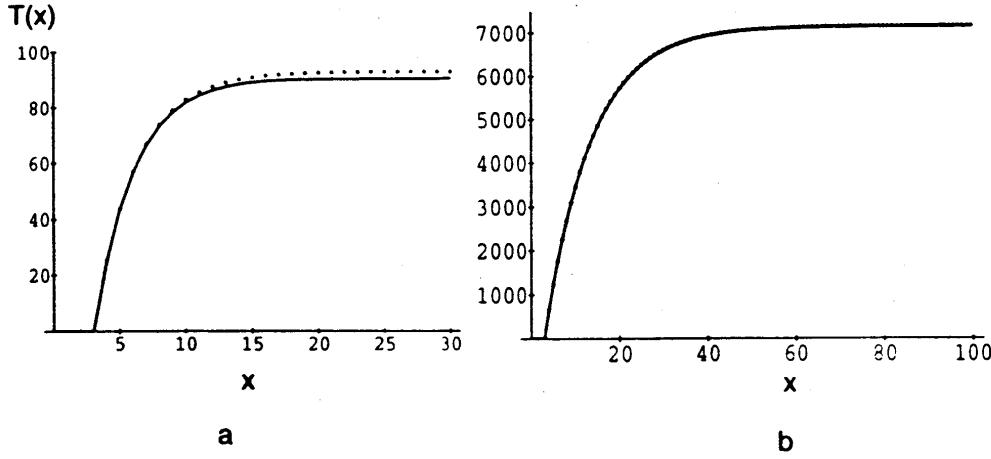


FIG. 4. The mean extinction time $T(x)$ as a function of the initial population size x for the MacArthur–Wilson model with no catastrophes. The exact solution (solid) and our approximation (dotted) when (a) $\lambda = 2.5$, $\mu = 1.82$, $x_c = 3$, $K = 20$, or (b) $K = 100$ are shown. The asymptotic solution is extremely accurate, even when K is only 20.

MacArthur–Wilson Model with Catastrophes

We now extend the MacArthur–Wilson model considered in the previous example to include catastrophes. We assume the birth and death rates are given by (27) and that the rate of catastrophes is a constant C . The distribution of the size of the catastrophes is the exponential distribution

$$Q(y|x) = (1 - \rho)\rho^y, \quad (29)$$

where ρ is a parameter. The mean catastrophe size is $\rho/(1 - \rho)$ and the z -transform of Q is $\hat{q} = (1 - \rho)/(1 - z\rho)$. In addition, extinction occurs when the population size falls below $x_c + 1$. We now use our algorithm to construct $T(x)$.

1. Again we assume the model is known. The scaling parameter is K , the population ceiling. For this model, the rest point x_s is unstable and we require that x_s be outside $(x_c, K + 1)$. Otherwise it must be accounted for (see Peter and Mangel, 1990).

2. We introduce the scaling $n = x/K$, define $c = C/K$ and obtain the scaled equation (11). All parameters should be the same order.

3. The z -transform of U is can easily be computed from (20) using MAPLE as

$$\hat{U} = \frac{1}{1 - z} - \frac{b_c(1 - \rho - \rho z + \rho^2 z) + c\rho^2 z}{(1 - \rho)[d_c \rho z^2 - (c\rho + b_c \rho + d_c)z - b_c]},$$

where $b_c = \lambda x_c$ and $d_c = \mu x_c$. For specific values of the parameters, the inverse of \hat{U} can be found and leads to a formula for $V(x)$ of the form

$$V(x) = 1 - k_1 r_1^{x-x_c} - k_2 r_2^{x-x_c},$$

where the k_i are constants. A general formula can be obtained but it is quite complicated.

4. The conditional density $W(x)$ can be found by the approximation (24). The function ψ is determined by (25) which for this example is

$$\lambda n e^{\psi'} + \mu n e^{-\psi'} - (\lambda n + \mu n + c) + c \frac{1 - \rho}{1 - \rho e^{-\psi'}} = 0.$$

This is a cubic in $\exp(-\psi')$ which has a solution $e^{-\psi'} = 1$ or $\psi' = 0$. We choose the solution of the remaining quadratic equation as the one that reduces to the exact solution in the previous example when $c = 0$ and hence

$$\psi(n) = - \int_{n_c}^n \ln \left[\frac{(\mu + \rho\lambda)s + \rho c + \sqrt{((\mu + \rho\lambda)s + \rho c)^2 - 4\rho\mu\lambda s^2}}{2\rho\mu s} \right] ds.$$

Similarly, g can be found using (26) which leads to

$$g(n) = e^{\int_{n_c}^n (\mathcal{B}(s)/\mathcal{A}(s)) ds}, \quad (30)$$

where \mathcal{A} and \mathcal{B} are defined in (26). The resulting integrals can easily be computed numerically. We have chosen $w(n_c) = 1$. Alternatively, we can compute a numerical approximation to W using (21) directly as we do in the below example.

5. The constant $P(x_s)$ is computed using (22) where the function $W(x)$ is computed using the previous step.

6. An approximation to the mean extinction time is

$$T(x) \sim P(x_s) [1 - k_1 r_1^{x-x_c} - k_2 r_2^{x-x_c}].$$

We illustrate our results and hence the effects of catastrophes in the MacArthur–Wilson model. In Table I, we use the above algorithm to compute the mean extinction time for different values of the catastrophe rate c and the mean number killed per catastrophe. The sensitivity of the mean extinction time to the mean number of deaths per catastrophes is illustrated. We have also compared our approximation to the mean extinction time to a numerical solution of Eq. (10), which is feasible since the state space is bounded. Clearly, our approximation is quite accurate.

TABLE I

Comparison of Approximate $T(K)$ and Numerical Result
when $c = 0.01$, $\lambda = 2.5$, $\mu = 1.82$, $K = 30$, and $x_c = 3$

Mean deaths/catastrophe	Approximate $T(K)$	Numerical
0	1408	1404
0.75	1398	1392
1.0	1394	1387
4.0	1162	1144
9.0	568	546

A Metapopulation Model

For the final example, we consider a model of a metapopulation including stochastic births and deaths, immigration and catastrophes. In particular, we assume linear birth (with immigration) and death rates, and catastrophes independent of population size. The underlying thematic principle for this model is that density dependent population regulation (as in the logistic equation) may not be nearly as important for metapopulation dynamics as the processes of immigration and environmental catastrophe.

Our assumption about the demographic processes is that

$$\begin{aligned} B(x) &= B_0 + B_1 x \\ D(x) &= D_1 x. \end{aligned} \tag{31}$$

The choice that B_0 is non-zero corresponds to immigration from an outside "pool," consistent with the concept of a metapopulation. As described above, D_1 can be viewed as having components composed of death and emigration. Karlson and Levitan (1990) describe a situation in which this model is clearly appropriate. Pulliam (1991) describes a broader class of "sink models."

As in the previous example, we assume that the rate of catastrophes is a constant C and that the distribution of the number of deaths per catastrophe is (29). The mean number of deaths is $\rho/(1-\rho)$. In this model, we allow the population size to take value in $\{x_c, x_c + 1, \dots\}$, i.e., there is no population ceiling as in the previous model. Without the ceiling, the state-space is now unbounded which makes direct numerical solution of $T(x)$ more difficult. However, our method can be applied without difficulty.

1. Again the model is given and we now determine x_s . If x_{av} denotes the mean population dynamics as defined by (6), then

$$\frac{dx_{av}}{dt} = B_0 + B_1 x_{av} - D_1 x_{av} - C \frac{\rho}{1-\rho}. \quad (32)$$

since $dx_{av}/dt = 0$ at x_s , we find

$$x_s = \frac{B_0 - C(\rho/(1-\rho))}{D_1 - B_1}. \quad (33)$$

This steady state is stable if

$$D_1 > B_1 \quad \text{and} \quad B_0 > C \frac{\rho}{1-\rho},$$

which we assume to be true. That is, on average, per capita death rate exceeds per capita birth rate and immigration rate exceeds the mean rate of deaths due to catastrophes. These assumptions could apply to a local population which is part of a metapopulation but which is unable to sustain itself without immigration. One example of such a population appears to be the elephant seals *Mirounga angustirostris* on Año Nuevo (California) mainland (B. Le Bouef, personal communication). Observation of such a population may provide (through the immigration rate) information on the general state of the entire metapopulation.

2. The slowly varying assumption means that $C(\rho/(1-\rho))$ and $B_0 \gg D_1$ and B_1 so that the processes of catastrophic extinction and immigration dominate the per capita death and birth rates. Thus, we define

$$b(n) = b_0 + B_1 n$$

$$d(n) = D_1 n,$$

where

$$b_0 = \frac{B_0}{x_s}, \quad c = \frac{C}{x_s}.$$

Since the parameter x_s plays the role of a "deterministic steady state," and all of the parameters of the model enter into (33), we see that there are many different ways in which the same population size x_s can be achieved. For example, as intuition suggests, when per capita birth rate is high (i.e., B_1 is only slightly less than D_1), then populations can achieve a large value of x_s with relatively low immigration rates (B_0). On the other hand, when per capita per rates are low relative to per capita death rates, large immigration rates are required to achieve a large value of x_s .

3. As described below Eq. (20), the colonization probability is determined by inverting

$$\hat{U} = \frac{1}{1-z} - \frac{b_c(1-\rho-\rho z+\rho^2 z)+c\rho^2 z}{(1-\rho)[d_c\rho z^2-(c\rho+b_c\rho+d_c)z-b_c]},$$

where $b_c = b_0 + B_1 x_c$ and $d_c = D_1 x_c$. The probability of successful colonization by a propagule of the smallest size is

$$V(x_c + 1) = \frac{b_0 - c\rho/(1-\rho)}{b_0}.$$

Thus the probability of successful immigration is independent of B_1 and D_1 and, in this case, depends solely on the relative values of the immigration rate and the mean rate of deaths due to catastrophes. Hence the colonization probability, in this model, is independent of demographic processes. Some intuition about the result is that on average, the birth rate is lower than death rate in this model so that a successful colonization must be "driven" by immigration rates that exceed catastrophic declines.

4. The conditional density $W(x)$ is again found using the approximation (24). As in the previous example, (25) can be reduced to a quadratic equation for $\exp(-\psi'(n))$. Only one root of the quadratic equation insures that $\psi(n)$ has a minimum at $n=1$ (i.e., at $x=x_s$). To determine $\psi(n)$, we solved (25) for $\psi'(n)$ and integrate to find

$$\psi(n) = - \int_{n_c}^n \ln \left[\frac{d(s) + \rho b(s) + \rho c - \sqrt{(d(s) + \rho b(s) + \rho c)^2 - 4\rho b(s) d(s)}}{2\rho d(s)} \right] ds.$$

This expression is then integrated numerically. The solution of (26) is again given by (30). We can use $W(x)$ to determine how the incidence function (Hanski, 1992) of populations depends upon the various parameters characterizing birth, death, immigration, and catastrophe.

5. and 6. The extinction time for an established population is found from (23) and is of the form

$$T(x) \sim P(x_s)[1 - k_1 r_1^{x-x_c} - k_2 r_2^{x-x_c}],$$

where the constants k_i and r_i are functions of the parameters characterizing birth, death, catastrophe, and immigration.

In Tables II and III, we illustrate the above results. The most striking feature of the results is the stabilizing effect of immigration on the mean

extinction time when catastrophes are infrequent ($c = 0.01$). The mean extinction time is not greatly effected by the increase in the mean number of deaths per catastrophes. The catastrophe rate is increased by a factor of 10 for the data in Table III. Here increasing the mean number of deaths per catastrophe decreases the mean extinction time to a greater extent than in the previous example.

TABLE II

Approximate $T(K)$ when $c = 0.01$, $B_0 = 10$,
 $B_1 = 1.9$, $D_1 = 2.2$, and $x_c = 10$

Mean deaths/catastrophe	Approximate $T(K)$
0	29.8
0.75	29.7
1.0	29.7
4.0	29.3
9.0	28.7
12.0	28.3

TABLE III

Approximate $T(K)$ when $c = 0.1$, $B_0 = 10$,
 $B_1 = 1.9$, $D_1 = 2.2$, and $x_c = 10$

Mean deaths/catastrophe	Approximate $T(K)$
0	29.8
0.75	29.1
1.0	28.3
4.0	25.7
9.0	21.6

DISCUSSION

Most readers are probably familiar with the story about the person who is looking for keys under the lamppost because that is where the light is, rather than that is where the keys were dropped. The story is not as humorous if a seriously injured individual is on the ground and needs to be taken to the hospital. We believe that this is the situation with the theoretical tools used in conservation biology: while it is wonderful to work with models that have exact solutions, we should not let mathematical expediency overrule biological considerations.

The model of MacArthur and Wilson has dominated the conceptual development of conservation biology. This model predicts a shoulder in extinction time as population ceiling K increases (this has lead to a focus

on “Minimum Viable Populations”) and extremely large extinction times for modest values of K . The MacArthur–Wilson model has a particular advantage because exact solutions can be found. In general, when an arbitrary population ceiling is imposed (as in the MacArthur–Wilson model), simpler techniques can be employed (also see Talent, 1990; and Mangel and Tier, 1993). Our work has confirmed previous theoretical proof that when modestly sized environmental catastrophes are included in the MacArthur–Wilson model, the enormous extinction times disappear. We, however, also provide a method for computing the appropriate extinction times. In addition, our methods apply to cases in which there is no arbitrary population ceiling and to cases in which the biological parameters are determined not for mathematical convenience but for realistic description.

We have additionally proposed a model of population regulation that involves immigration, birth, death, and catastrophe. Such regulatory mechanisms may have wide application, as in the marine system described by Karlson and Levitan (1990) and the terrestrial system described by Schoener and Spiller (1992). Extensions of our work will include detailed comparisons of the theory with these kinds of field systems and elaboration of the theory by including the state of a number of populations simultaneously. Although some of the technical details change, the conceptual foundations are exactly the same. Finally, by developing a method that can be described in algorithmic fashion, we make the technique accessible to a range of colleagues.

APPENDIX

Approximation to $W(x)$

We now give details on the derivation of $W(x)$. In order to find $W(x)$ that satisfies (21), reintroduce the scaled variable $n = x/x_s$ and assume that $w(n) = W(x)$. In terms of the scaled variable, $w(n)$ satisfies

$$0 = b(n - 1/x_s) w(n - 1/x_s) + d(n + 1/x_s) w(n + 1/x_s) - (b(n) + d(n) + c) w(n) + c \sum_{s=0}^{\infty} q(s|n + s/x_s) w(n + s/x_s). \quad (\text{A.1})$$

Again, following Knessl *et al.* (1984) and Matkowsky *et al.* (1984), we assume that $w(n)$ has a solution of the form

$$w(n) = g(n) \exp(-\psi(n)x_s), \quad (\text{A.2})$$

where $g(x)$ and $\psi(x)$ are to be determined. To do this, first substitute (A.2) into (A.1), giving

$$\begin{aligned} 0 = & b(n-1)/x_s) g(n-1/x_s) \exp(-\psi(n-1/x_s)x_s) \\ & + d(n+1/x_s) g(n+1/x_s) \exp(-\psi(n+1/x_s)x_s) \\ & - (b(n) + d(n) + c) g(n) \exp(-\psi(n)x_s) \\ & + c \sum_{s=0}^{\infty} q(s|n+s/x_s) g(n+s/x_s) \exp(-\psi(n+s/x_s)x_s). \end{aligned}$$

This equation is expanded in powers of $1/x_s$ and coefficients of various powers of $1/x_s$ are set equal to zero. This produces a nonlinear equation, called the eikonal equation, for ψ and a linear equation, called the transport equation, for $g(n)$. The eikonal equation is

$$b(n) e^{\psi'(n)} + d(n) e^{-\psi'(n)} + c \sum_{s=1}^{\infty} q(s|n) e^{-s\psi'(n)} = b(n) + d(n) + c. \quad (\text{A.3})$$

We have already encountered this equation (Eq. (25)) in the text. The function $g(n)$ satisfies

$$\begin{aligned} g'(n) & \left[d(n) e^{-\psi'(n)} - b(n) e^{\psi'(n)} + c \sum_{s=0}^{\infty} q(s|n) s e^{-s\psi'(n)} \right] \\ & = g(n) \left[b'(n) e^{\psi'(n)} - d'(n) e^{-\psi'(n)} - c \sum_{s=0}^{\infty} \frac{\partial}{\partial n} [q(s|n)] s e^{-s\psi'(n)} \right. \\ & \quad \left. + (1/2) \psi''(n) \left\{ b(n) e^{\psi'(n)} + d(n) e^{-\psi'(n)} + c \sum_{s=0}^{\infty} s^2 q(s|n) e^{-s\psi'(n)} \right\} \right], \end{aligned} \quad (\text{A.4})$$

which is Eq. (26) of the text. The solution of this equation is (30). The eikonal equation may have an analytical solution for $\psi'(n)$, which can then be integrated pointwise. The function $g(n)$ can be represented as the exponential of an integral.

Approximation for $\sum W$

It is possible to further simplify the formula for $P(x_s)$ by asymptotically expanding the sum in the numerator. We consider the situation where x_s is a rest point of (6). Since $w(n) = w(x/x_s)$, this sum can be written as

$$S = \sum_{x=x_c}^{\infty} w(x/x_s) = x_s \left[\sum_{x=x_c}^{\infty} w(x/x_c)(1/x_s) \right]. \quad (\text{A.5})$$

The summation inside the [] in (A.5) is, in the limit as $x_s \rightarrow \infty$, the integral of $w(z)$ from 0 to ∞ . Thus

$$S \sim x_s \int_0^\infty w(z) dz = x_s \int_0^\infty g(z) \exp(-\psi(z) x_s) dz. \quad (\text{A.6})$$

Assuming that $\psi(z)$ has its minimum at a point z_r , we apply Laplace's method (Bender and Orszag, 1978) to the integral in (A.6) to obtain

$$S \sim x_s g(z_r) \exp(-\psi(z_r) x_s) \int_{-\infty}^\infty \exp(-\psi''(z_r)(z - z_r)^2 x_s/2) dz. \quad (\text{A.7})$$

Changing variables to evaluate the integral gives

$$S \sim x_s g(z_r) \exp(-\psi(z_r) x_s) [2\pi/x_s \psi''(z_r)]^{1/2}. \quad (\text{A.8})$$

Hence

$$\sum_{x=x_c}^\infty W(x) \sim g(z_r) \exp(-\psi(z_r) x_s) [2\pi x_s / \psi''(z_r)]^{1/2}. \quad (\text{A.9})$$

ACKNOWLEDGMENTS

The work of MM was supported by NSF Grants BSR 86-1073, 91-17603, and OCE 91-16895; that of CT by NSF Grant DMS 89-22988. We also thank Joel Keizer, Director of the Institute for Theoretical Dynamics at UC Davis, for support that allowed this collaboration to blossom. We thank D. Ludwig, T. Schoener, D. Spiller, T. Young, and three anonymous reviewers for comments on previous versions of the paper and T. Schoener and D. Spiller for conversations about linking their work and this theory. MM especially thanks P. E. Bradshaw for many illuminating conversations.

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