Population growth with randomly distributed jumps*

Floyd B. Hanson[1], **Henry C. Tuckwell**[2]

[1]Department of Mathematics, Statistics, and Computer Science (M/C 249), University of Illinois at Chicago, 851 S. Morgan, Chicago, IL 60607-7045, USA
e-mail: hanson@uic.edu
[2]Epidemiologie et Sciences de l'Information, Universite Paris 6 (INSERM U444), Faculte de Medecine St Antoine, 27 rue Chaligny, 75571 Paris Cedex 12, FRANCE
e-mail: tuckwell@b3e.jussieu.fr

Received 21 June 1996; received in revised form 17 February 1997

Abstract. The growth of populations with continuous deterministic and random jump components is treated. Three special models in which random jumps occur at the time of events of a Poisson process and admit formal explicit solutions are considered: A) Logistic growth with random disasters having exponentially distributed amplitudes; B) Logistic growth with random disasters causing the removal of a uniformly distributed fraction of the population size; and C) Exponential decay with sudden increases (bonanzas) in the population and with each increase being an exponentially distributed fraction of the current population. Asymptotic and numerical methods are employed to determine the mean extinction time for the population, qualitatively and quantitatively. For Model A, this time becomes exponentially large as the carrying capacity becomes much larger than the mean disaster size. Implications for colonizing species for Model A are discussed. For Model B and C, the practical notion of a small, but positive, effective extinction level is chosen, and in these cases the expected extinction time rises rapidly with population size, yet at less than an exponentially large order.

Key words: Population extinction – Randomly distributed jumps – Bonanzas – Disasters

1 Introduction

We are interested in determining the time to extinction of a population which is subjected to randomly occurring disasters when these disasters have a continuous distribution of sizes. In the time intervals between disasters the population evolves deterministically.

Previously we have analyzed population growth which is logistic and suffers dis-

*This paper is to appear in *J. Math. Biol. (1997) 35: 001-019.*

asters at the times of occurrence of events in a simple Poisson process. In the first case [12], the disasters were of constant size. In a subsequent investigation [13], the disasters were density independent in the sense that they were a constant multiple of the current population size. In both cases the expected time to extinction satisfied a singular differential-difference equation. These equations were solved by the method of steps modified by a singular decomposition for the equations associated with biological extinction. This singular decomposition was rigorously analyzed in [8] within the framework of a general discrete jump model. It was shown that the singular decomposition makes the singularities removable by transforming the original singular boundary value problem to two nonsingular problems, so that numerical procedures were well conditioned. The extinction time grew exponentially with the carrying capacity of the environment.

Hanson and co-workers [22, 23, 9, 10] have applied this Poisson disaster model to the optimal harvesting in an uncertain environment with a focus on fisheries applications. In [22], Ryan and Hanson treated the problem of exponential growth in the presence of random disasters and bonanzas. In [23], they considered a logistically growing population with density independent (i.e., linear in population size) random disasters. Optimal harvesting in the presence of density dependent (i.e., nonlinear in amplitude) disasters is studied in [10]. A multispecies model of a Lake Michigan predator-prey system was presented and computationally analyzed in [9] using fishery catch data for alewives undergoing occasional massive mortalities to estimate disaster parameters.

In most previously studied stochastic population models it was assumed that populations change size continuously, as for example in diffusion processes. Tuckwell and Koziol [27] have reviewed the logistic model with diffusion type noise, and have also modeled a stochastic logistic process with dispersal according to either Bose-Einstein or Maxwell-Boltzmann statistics.

However, all real populations experience catastrophic disasters or bountiful bonanzas of various magnitudes, ranging in size from very small to large. Adverse phenomena can have many causes: floods, tsunami, sea level changes, earthquakes, volcanoes, impacts of extraterrestrial objects, plate tectonics, climate changes, famines, predation, competition, war, fires, accidents, infectious diseases and storms or other adverse weather effects. Examples of favorable effects are bumper harvests, destruction of predators, destruction of competitors, sudden abundance of prey or other food, sudden availability of colonizable patches, favorable ocean currents and beneficial weather.

Flessa [6] lists several contrasting interpretations of the fossil record for the cause or causes of mass extinctions that occurred at the Cretaceous-Tertiary boundary. Jablonski [15] discusses the plausibility of many potential causes of mass extinctions.

Ludwig et al.[16] strongly emphasize the importance of uncertainty and how it can mask overexploitation effects, leading to unwise exploitation policies, especially those based upon sustainable yield theory.

Previously, Tsurui and Osaki [25] have treated the first passage time to exceed a certain threshold in the case of exponentially distributed, but positive Poisson amplitudes (i.e., bonanzas exponentially distributed in both time and amplitude) in a background of deterministic exponential decay. Mangel and Tier [17, 18] derive a birth and death model with catastrophes, presenting solution by both asymptotic and numerical methods. In [17], they emphasize a simple direct method to compute persistence times for birth and death models with catastrophes. Pakes et al. [20] modeled the problem of mass emigration of an exponentially growing population with randomly distributed emigration occurring according to a population size dependent jump process. In a related paper, Trajstman [24] formulated the problem of growth with emigration more succinctly as a nonstationary compound Poisson process superimposed upon a linear bounded deterministic component. Brockwell el al. [4] treat the births, immigration and catastrophes as discrete state-space Markov models using distributions that result in explicit solutions, with comparisons to simple *semi-stochastic* continuous state-space linear models. In a subsequent paper [5], they treat catastrophes in continuous state-space in the present of upward growth according to a compound Poisson process with an arbitrary distribution of the upward jumps using the methods of their discrete state-space paper [4]. Brockwell [3] presents another variation on the emigration (catastrophe or disaster) model using a birth, death and catastrophe process, while also treating a corresponding jump diffusion (stochastic diffusion with Poisson distributed disasters) model. Bartoszynski et al. [1] analyze disaster and bonanza models based upon Markov branching processes that include the birth, death and population size independent Poisson disaster or bonanza processes.

An element of realism is introduced if multiple disasters or bonanzas are incorporated in deterministic models of population growth. Models will be examined for a population which grows logistically except when it undergoes sudden changes at times of events of a Poisson process and whose sizes are random with continuous distributions. Three special cases are presented in Sect. 3 in which formal explicit solutions for the extinction time are obtained. In the first case disasters occur whose magnitude is exponentially distributed, but is independent of the population size. Also, the asymptotic behavior is given for large values of the limiting population size. In the second case the disaster size is density independent (i.e. proportional to the population size) and uniformly distributed. Asymptotic solutions are given for large initial population size. In the third case the exponentially distributed, density-independent bonanza is treated.

2 The general models

A population that starts out at size $N(0) = x$ and grows logistically to $N(t)$ at time t satisfies the deterministic process, $dN(t)/dt = F(N(t))$, in the absence of stochastic effects.

If the population, instead, grows deterministically only between jumps in population size which arrive at the times of events of a Poisson process and with a magnitude that is continuously distributed, then the growth of the population satisfies the following stochastic differential equation,

$$dN(t) = F(N(t))dt + \int_{-\infty}^{\infty} J(N(t), u)\mathcal{P}[du, dt], \quad N(0) = x \quad \in (a, b]. \tag{2.1}$$

Here $\mathcal{P}$ is a Poisson random measure (Gihman and Skorohod [7]). The symbol $\mathcal{P}[du, dt]$ counts the number of jumps of a compound Poisson process with amplitudes $J(x, u)$ generated in the mark interval $(u, u + du)$ during the time interval $(t, t + dt)$, while $\int_{-\infty}^{\infty} \mathcal{P}[du, dt]$ is the number of jumps in $(t, t + dt)$. The mean rate of arrival of jumps with amplitudes in $(u, u + du)$ is $\mathrm{E}[\mathcal{P}[du, dt]] = \phi(u)du\ dt$. Thus, the total jump rate is $\lambda = \int_{-\infty}^{\infty} \phi(u)du > 0$, $\phi(u)/\lambda$ is the probability density function for the marks u. The expected jump size conditioned on the population size at t is $\mathrm{E}[J(N(t), u)|N(t) = x] = \int_{-\infty}^{\infty} \phi(u)J(x, u)du/\lambda$.

In our first paper [12], the special case of a downward jump with fixed magnitude ε, $\phi(u) = \lambda\delta(u - \varepsilon)$, $J(N, u) = -u$, $F(N) = rN(1 - N/K)$ was treated, and

$$dN(t) = rN(t)\,(1 - N(t)/K)\,dt - \varepsilon d\Pi(t; \lambda), \tag{2.2}$$

where $\Pi(t; \lambda)$ is a simple Poisson process with rate parameter λ, r is the intrinsic per capita rate of increase, K is the carrying capacity of the environment, $N(0) \in (0, K]$ and $\varepsilon > 0$. The Poisson random integral in (2.1) is replaced by $-\varepsilon d\Pi(t; \lambda)$.

In [13] we considered the particular choices $\phi(u) = \lambda\delta(u - \varepsilon)$, $J(N, u) = -Nu$ and $F(N) = rN(1 - N/K)$ so that

$$dN(t) = rN(t)\,(1 - N(t)/K)\,dt - \varepsilon N(t)d\Pi(t; \lambda), \tag{2.3}$$

where $N(0) \in (\Delta, K]$ for some $0 < \Delta < K$ and $0 < \varepsilon < 1$. The case $\varepsilon \geq 1$ is trivial, since the first jump leads to certain extinction. Note that in this case the single mark $u = \varepsilon$ is the proportion lost in this density independent disaster, whereas in the previous case the mark represents the absolute amount lost in a population size independent disaster. The choice of a positive *effective extinction level* Δ permits the population to go extinct in finite time in analogy with the discrete population case where extinction occurs when the population gets below reproducing pair, rather then zero or below.

In the above models, the quantity of immediate interest is the extinction or persistence time of the population size on some interval (a, b). Let

$$T_{\mathrm{ext}}(x) = \inf_t\{N(t) \notin (a, b) \mid N(0) = x \in (a, b)\} \tag{2.4}$$

be the random variable denoting this persistence time and its expectation be $T(x) = \mathrm{E}[T_{\mathrm{ext}}(x)]$.

For the model of equation (2.1) with $F(N)$ appropriate for logistic growth, this quantity satisfies the integro-differential equation [26]

$$F(x)T'(x) + \int_{-\infty}^{\infty} T(x + J(x, u))\phi(u)du - \lambda T(x) = -1, \tag{2.5}$$

when x is in (a, b). The choice of the minimum population a depends on the choice of the drift $F(x)$ and the jump size $J(x, u)$. In those cases where the value zero is attainable, $a = 0$ is chosen to identify extinction with the passage of the population size to zero or below. If zero is not attainable in a finite time, then for practical considerations an effective extinction should be defined as the first passage to some small positive population size $a = \Delta$.

2.1 Boundary conditions

The general boundary condition for the integro-differential equation (2.5) is that $T(x) = 0$ for $x \leq a$ or $x \geq b$. This is a simple consequence of the fact that the first exit time from (a, b) is zero if the process starts outside that interval.

In addition to the above boundary condition, the integro-differential equation is solved subject to the constraints that $T(x)$ be bounded and continuous in its domain, deriving natural boundary conditions in each special case where appropriate.

3 Special examples

The integro-differential equation (2.5) can be reduced to quadratures in special cases.

3.1 Model A: logistic growth with exponentially distributed, N-independent disasters

For a population that has a limited environment, a logistic model with fixed carrying capacity serves as a simple deterministic, continuous model. However, it is unrealistic to expect a population to increase continuously without being interrupted by occasional disasters of various magnitudes. We will assume, in accordance with intuition, that large disasters occur less frequently than small ones. Hence we choose an exponential distribution for the magnitude of the downward jumps. Thus we choose

$$F(x) = rx\left(1 - x/K\right), \quad J(x, u) = -u, \quad \text{and} \quad \phi(u) = \begin{cases} \lambda/m e^{-u/m}, & u \geq 0 \\ 0, & \text{otherwise} \end{cases}, \tag{3.1}$$

where $r > 0$ and $K > 0$, so that the drift is logistic and the amplitude of the disasters is independent of population size. The conditional mean jump amplitude is $\mathrm{E}[J(N(t), u)|N(t) = x] = m$ and the conditional variance is $\mathrm{Var}[J(N(t), u)|N(t) = x] = m^2$. Choosing $a = 0$ and $b = +\infty$, (2.5) becomes

$$rx\left(1 - x/K\right) T'(x) + \frac{\lambda}{m} \int_0^{\infty} e^{-u/m} T(x - u) du - \lambda T(x) = -1. \tag{3.2}$$

Applying the general boundary condition and changing variables in the integrand,

$$\left[rx\left(1 - x/K\right) T'(x) - \lambda T(x) + 1\right] e^{x/m} + \frac{\lambda}{m} \int_0^{x} e^{v/m} T(v) dv = 0. \tag{3.3}$$

A *natural boundary condition* at extinction follows from taking the limit $x \to 0^+$ in (3.3) which yields $T(0^+) = 1/\lambda$. This condition means that sufficiently small populations would go extinct at the first disaster. Note that $T(0^+)$ bounded implies that $T'(x)$ is less than order $1/x$ as $x \to 0^+$.

A single differentiation in x converts the integro-differential equation (3.3) to a first order ordinary differential equation in $T'(x)$,

$$mrx\,(1 - x/K)\,T''(x) + [rx\,(1 - x/K) + mr\,(1 - 2x/K) - m\lambda]\,T'(x) = -1. \quad (3.4)$$

The first integral of (3.4) yields

$$\lambda T'(x) = x^{q-1}(K - x)^{-q-1}e^{-x/m}\left[C_1 + q\frac{K}{m}\int_x^K e^{z/m}z^{-q}(K - z)^q dz\right], \quad (3.5)$$

where $q \equiv \lambda/r$ is the *bio-disaster growth ratio* defined in our previous papers [12, 13]. The parameter q is the ratio of the deterministic return (e-folding) time, $1/r$, to the expected waiting time, $1/\lambda$, between disasters.

The constant, C_1, of integration in (3.5) must be zero when $q > 0$ ($\lambda > 0$ and $r > 0$), because $T'(x)$ must be less than order $1/(K - x)$ for $T(x)$ to be bounded as $x \to K^-$. Thus, $\lambda T'(K^-) = q/((q + 1)m)$ is a second natural condition. Another integration with this natural condition converts (3.5) into closed form:

$$\lambda T(x) = 1 + \frac{qK}{m}\int_0^x e^{-y/m}y^{q-1}(K - y)^{-q-1}\int_y^K e^{z/m}z^{-q}(K - z)^q dz dy. \quad (3.6)$$

It is important to note that this formal solution has been obtained from the singular functional differential equation (3.3) using natural boundary conditions that are deduced from (3.3) and boundedness. No externally imposed Dirichlet conditions have been or can be imposed, assuming $q > 0$.

The second order differential equation (3.4) for mean first exit time $T(x)$ has an interesting interpretation as arising from a stochastic diffusion. This equation would govern the first passage time for a diffusion process governed by the Itô stochastic differential equation

$$\begin{aligned} d\widetilde{N}(t) \;=\; & \left[r\widetilde{N}(t)\left(1 - \widetilde{N}(t)/K\right) + mr\left(1 - 2\widetilde{N}(t)/K\right) - m\lambda\right] dt \\ & + \sqrt{2mr\widetilde{N}(t)\left(1 - \widetilde{N}(t)/K\right)}\,dW(t), \end{aligned} \quad (3.7)$$

where $W(t)$ is the Wiener or Gaussian process. The diffusion coefficient, $2mr\widetilde{N}(1 - \widetilde{N}/K)$, is proportional to the logistic growth function. The drift in the square bracket of (3.7) is basically the logistic growth perturbed by the mean jump rate, $-m\lambda$, and by the derivative of the diffusion coefficient. The boundary conditions as a set are natural for the original expected extinction time of the exponentially distributed disaster model.

There appears to be no simpler form for (3.6) in terms of elementary functions. When K is very large compared to the mean jump size m, the double integral in (3.6) can be simplified asymptotically by a 2-dimensional extension of Laplace's method [11]. The method relies on the fact that the dominant contribution of the exponentials in the double integral occurs at the maximum of the exponent of the integrand at $(y, z) = (0, K)$. Expanding the integrals about this maximum and extending the limits of integration of the inner integral to infinity and retaining the outer integral limits to preserve the uniform validity at $x = 0$,

$$\begin{aligned} \lambda T(x) \;\; \sim \;\; & 1 + q\Gamma(q+1)R^{-2q}e^{R}\left[1 + \frac{q(q+1)}{R}(1 + \frac{(q+1)(q+2)}{2R}) \right. \\ & \left. + \mathcal{O}\left(\frac{1}{R^3}\right)\right]\left[\left(1 + \frac{q(q+1)}{R} + \frac{q(q+1)^2(q+2)}{2R^2}\right)\gamma\left(q, \frac{x}{m}\right) \right. \\ - & \left. \frac{(q+1)}{R}\left(1 + \frac{(q+2)(q+1+x/m)}{2R}\right)\left(\frac{x}{m}\right)^q e^{-x/m} + \mathcal{O}\left(\frac{1}{R^3}\right)\right] \end{aligned} \tag{3.8}$$

as $R \equiv K/m \to \infty$, where $\Gamma(q)$ is the gamma function and $\gamma(q, x)$ is the incomplete gamma function. The approximation (3.8) is uniformly valid when $x = 0^+$ because $\gamma(q, 0) = 0$. In (3.8), only the first three exponentially large terms with exponent R have been retained. When $x = K^-$ and $\gamma(q, R) \sim \Gamma(q)$, the approximation (3.8) simplifies to

$$\lambda T(K^-) \sim 1 + \Gamma^2(q+1)R^{-2q}e^{R}\left[1 + \frac{2q(q+1)}{R}\left(1 + \frac{(q+1)^2}{R}\right) + \mathcal{O}\left(\frac{1}{R^3}\right)\right] \tag{3.9}$$

as $R \equiv K/m \to \infty$. The simplified asymptotic approximation (3.9) indicates that $\lambda T(K^-)$ will be exponentially large when R is large, i.e., its behavior is exponentially dominated by the factor, $\exp(R)$, when the carrying capacity K is a large multiple of the mean disaster amplitude m. There is also a weaker, algebraic dependence on the bio-disaster growth parameter q due to the factor R^{-2q}. The approximation, (3.8) or (3.9), should be useful for very large R.

Extinction according to this model is certain, but the population will persist for extremely long times, provided x/m and R are sufficiently large. It is well known that almost all species that have ever existed have become extinct. Raup [21] gives a summary of mean species duration times for many fossil groups, the range being between one and eleven million years.

In contrast, small values of x are of interest in studying the relative dangers in going extinct from a small number of colonizers. Very close to the extinction level, as $x/m \to 0^+$ and using (3.6), the composite dependence is found

$$\lambda T(x) \sim 1 + \begin{cases} \dfrac{q}{(q-1)}\dfrac{x}{m}, & q > 1 \\ -\frac{x}{m}\ln\left(\frac{x}{me}\right), & q = 1 \\ R\left(\frac{x}{K}\right)^q \int_0^1 z^{-q}(1-z)^q e^{Rz}dz, & 0 < q < 1 \end{cases}, \tag{3.10}$$

due to the singularities in the z-integral. Approximation (3.10) implies that when the bio-disaster growth ratio q is less than one, $\lambda T(x)$ will increase most rapidly; in fact, with a vertical asymptote as $x/m \to 0^+$ and also with exponential dependence on R when R is large. When q is greater than one the increase in x is only linear in x. Hence $q < 1$ or $r > \lambda$ is advantageous to the colonizing population, because very long persistence time will be most probable for a relatively small initial population size.

The same singular features of the solution (3.6) that limit the usefulness of the asymptotic approximation (3.8) also hinder the numerical approximation of (3.6) for general values of q and moderate values of R. We here first isolate the singular powers containing q and approximate only the nonsingular terms. Let $u(x) = x/(K-x)$ when $x < K/2$ and $v(x) = (K-x)/x = 1/u$ when $x > K/2$, so that (3.6) is transformed to a more manageable form:

$$\lambda T(x) = \begin{cases} 1 + qRe^R \int_0^{u(x)} U^{q-1} A(U) \\ \qquad \times \left[\int_0^1 V^q B(V) dV + e^{-R/2} \int_U^1 W^{-q} C(W) dW\right] dU, & x \le \frac{K}{2} \\ \lambda T\left(\frac{K}{2}\right) + qRe^{R/2} \int_{v(x)}^1 V^{-q-1} D(V) \int_0^V W^q B(W) dW dV, & x \ge \frac{K}{2} \end{cases} \tag{3.11}$$

where $A(u) = \exp(-Ru/(1+u))$, $B(u) = A(u)/(1+u)^2$, $D(u) = \exp(-R/2)/A(u)$, and $C(u) = D(u)/(1+u)^2$. The relatively nice functions A, B, C, and D are approximated by linear interpolation with sufficient accuracy using parabolically spaced nodes and the remaining integrals can be done exactly, because their integrals contain only powers, some singular.

Some numerical results using (3.11) for *Model A* with $\lambda T(x)$ are given in the semilog plot of Fig. 1. Here, K has the value 10, while $q = 0.5$, 1.0 and 2.0. These values of q are just representative of the three distinct asymptotic cases, which are $0 < q < 1$, $q = 1$ and $q > 1$. Taking into account the logarithmic scale, it can be seen that the differences between the values of $\lambda T(x)$ are large at small and moderate values of x, for various values of q. The curves for $q = 0.5$ (the smallest bio-disaster growth ratio considered) rise very sharply away from $x = 0^+$ in comparison with the curve for $q = 2.0$. Note the tremendous advantage that populations with large per capita growth rates r have because their mean persistence times are the longest and are achieved with a small colonization effort. Another qualitative biological implication of the results is that the population can reach nearly maximal persistence outside of a sufficiently small neighborhood of extinction, but strong colonization properties are critical within this neighborhood.

In Fig. 2, the asymptotic (3.10) and numeric (3.11) approximations to the exact solution for the expected extinction time are compared in terms of the percent relative difference. The difference is quite small for values of the bio-disaster ratio of $q = 0.5$ and 1.0, but quite large for $q = 2.0$, reaching about 30% for small, colonization level, population sizes. Thus, for small population sizes and higher bio-disaster growth ra-

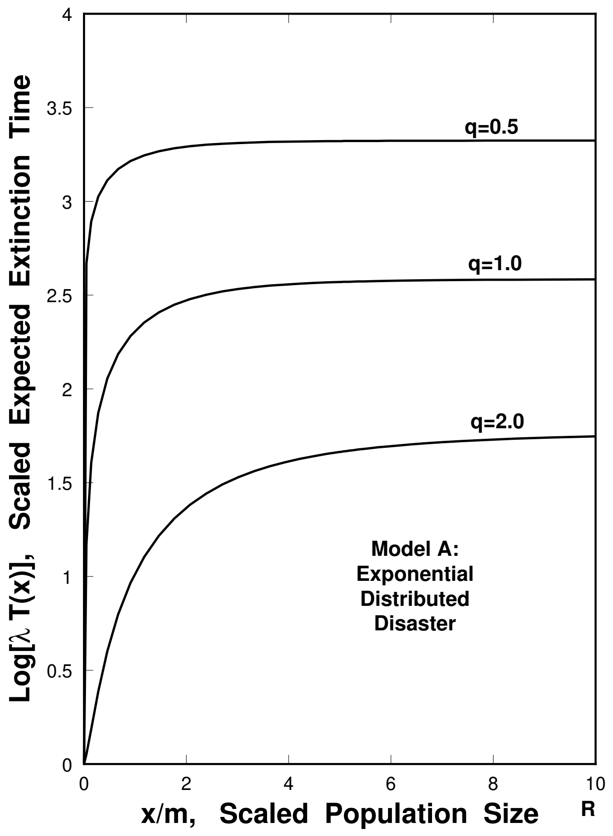

Figure 1: Logarithm of the scaled, expected extinction time, $\log\{\lambda T(x)\}$, for *Model A* with exponentially distributed, size independent disasters as a function of the initial population size, x, for several values of the bio-disaster growth ratio, $q = 0.5, 1.0, 2.0$

tios, the asymptotic approximation significantly underestimates the extinction time, and so overestimates the danger of extinction.

3.2 Model B: density independent disasters with uniformly distributed jump size

When the effect of a disaster is proportional to population size the disaster is said to be *density independent*, because the relative disaster size is independent of N. The density independent disaster is usually due to abiotic causes which affect the population as a whole, whereas biological causes due to species interactions, such as epizootics, may lead to nonlinear or other density independent disasters [9]. For convenience, the size of the disaster per unit population size is assumed to be uniformly distributed on $(0, 1)$. Note that any disaster greater than the population size has the same effect as a disaster wiping out the whole population. An example of possible density independent disasters with uniform distribution is the occasional massive

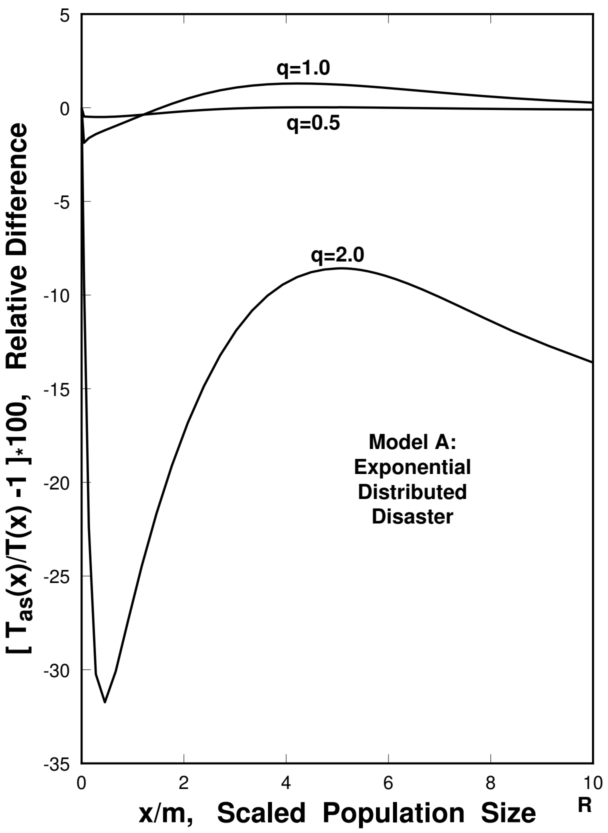

Figure 2: The percent relative difference between the asymptotic and numerical approximations to expected extinction time, $(T_{\rm as}(x)/T(x) - 1) * 100$, for *Model A* with exponentially distributed, N-independent disasters as a function of the initial population size, x, for several values of the bio-disaster growth ratio, $q = 0.5, 1.0, 2.0$

die-offs of alewives in Lake Michigan, but in [9] only a simple Poisson disaster in a multi-species bioeconomic model is used due to limited field data.

Hence,

$$J(x,u) = -xu, \quad F(x) = rx\,(1 - x/K) \quad \text{and} \quad \phi(u) = \begin{cases} \lambda, & 0 < u < 1 \\ 0, & \text{otherwise} \end{cases} . \tag{3.12}$$

The conditional mean jump size is $\mathrm{E}[J(N(t),u)|N(t) = x] = -x/2$ with conditional variance $\mathrm{Var}[J(N(t),u)|N(t) = x] = x^2/12$. Since the disaster gets small with the population size, ideal extinction at $x = 0^+$ will take an infinite amount of time. Therefore, let $a = \varDelta > 0$ be the *effective extinction size*, the lowest viable population size, in analogy with a discrete population being extinct when there is less than one mating pair. The expected extinction time equation (2.5) with general boundary condition reduces to

$$rx\,(1-x/K)\,T'(x)+\lambda\int_0^{1-\Delta/x}T(x-ux)du-\lambda T(x)=-1 \qquad (3.13)$$

on (Δ, K). The effective extinction boundary condition for (3.13) does not have the simple form as the extinction natural boundary condition of *Model A*, but instead has a mixed condition, $r\Delta(1-\Delta/K)T'(\Delta^+)=\lambda T(\Delta^+)-1$, which arises because (3.13) is not singular at $x=\Delta^+>0$.

As in the prior case, the integro-differential equation can be converted to a first order differential equation in $T'(x)$ similar to the stochastic diffusion-like expected extinction time equation (3.4) for *Model A*. Transforming x out of the integrand, multiplying by x and differentiating,

$$rx^2\,(1-x/K)\,T''(x)+\left[\left(rx^2\,(1-x/K)\right)'-\lambda x\right]T'(x)=-1. \qquad (3.14)$$

Otherwise, the two integrations with $T(K^-)$ bounded work the same as before and

$$\begin{aligned}\lambda T(x)=1 \quad &+\quad \Delta^{q-1}(K-\Delta)^{-q}\int_\Delta^K z^{-q}(K-z)^q dz\\ &+\quad qK\int_\Delta^x y^{q-2}(K-y)^{-q-1}\int_y^K z^{-q}(K-z)^q dzdy \qquad (3.15)\end{aligned}$$

is the formal result. For numerical purposes, (3.15) can be transformed to isolate potential troublesome arbitrary powers related to the disaster growth ratio q as in *Model A* to the more manageable form:

$$\lambda T(x)=\begin{cases}1+u^{q-1}(\Delta)\;A(\Delta)\left[\int_{u(\Delta)}^1\;U^{-q}B(U)dU+\int_0^1V^qB(V)dV\right], \\ \quad x=\Delta^+\\ \lambda T(\Delta^+)+q\int_{u(\Delta)}^{u(x)}U^{q-2}A(U)\left[\int_U^1W^{-q}+\int_0^1W^q\right]B(W)dWdU, \\ \quad \Delta<x\le K/2\\ \lambda T(K/2)+q\int_{v(x)}^1V^{-q-1}A(V)dV\int_0^V W^qB(W)dWdV, \\ \quad K/2<x\le K\end{cases} \qquad (3.16)$$

but with new definitions, $A(u)=1+u$ and $B(u)=1/(1+u)^2$.

For large carrying capacity K relative to the effective extinction level Δ, the formal solution (3.15) has the asymptotic simplification as follows,

$$\lambda T(x) \sim \begin{cases} \dfrac{1}{1-q}\left[\left(\frac{K}{\Delta}\right)^{1-q} - q\left(\frac{K}{x}\right)^{1-q} - q\ln\left(\frac{ex}{\Delta}\right)\right] + \mathcal{O}(1), \\ \qquad 0 < q < 1,\ x \geq \Delta \\ \left[\frac{1}{2}\ln\left(\dfrac{K^2}{\Delta x}\right) - 1\right]\ln\left(\frac{x}{\Delta}\right) + \ln\left(\frac{K}{\Delta}\right), \\ \qquad q = 1,\ x \geq \Delta \\ \dfrac{q}{q-1}\ln\left(\frac{ex}{\Delta}\right) + \mathcal{O}(1), \\ \qquad q > 1,\ x \geq \Delta \end{cases}, \tag{3.17}$$

as $K/\Delta \to \infty$. This result has been obtained by a somewhat different method through simply factoring out the most dominant parts of the integrals in (3.15). The non-exponential integrands lack the sharp maxima needed to apply Laplace's method. The approximation (3.17) indicates that expected persistence time grows algebraically or logarithmically as $K/\Delta \to \infty$, while in *Model A* the asymptotic growth is exponential in $R \equiv K/m$.

The numerical results for *Model B*, using similar techniques to those employed in *Model A*, are exhibited in Fig. 3 for $q = 0.5, 1.0$ and 2.0. Again, the advantage for a population described by *Model B* occurs when q is less than unity, but it is less pronounced than in *Model A*. Figure 4 shows the relative difference between the asymptotic approximation and the numerical computation for *Model B* for the same set of bio-disaster values. The asymptotic approximation is reasonable for the case $q = 1.0$, as long as the initial population size is not near extinction, somewhat less reasonable for $q = 2.0$, and very bad for $q = 0.5$. The qualitative biological implications of the results are similar to those of *Model A*, because sufficiently far away from extinction, nearly maximal persistence is achieved. Due to a combination of the uniformity of the disaster amplitude distribution (the larger disasters are just as likely as the smaller ones) and the density independent property of the disaster amplitudes (the larger disasters can be comparable in size to the population size N), the nearly maximal persistence times are not exponentially large, but are only algebraic-logarithmically large.

3.3 Model C: exponentially distributed, N-independent bonanza

Some populations such as scrub oaks, sea palms, according to Paine [19], benefit from disasters to other species because such disasters provide open patches which are bonanzas for them as colonizing species. In the absence of the availability of these patches these populations decline in numbers. Hence, let the decline be a linear decaying function, $F(x) = -rx$.

Model C is also motivated by the simple model of certain fish stocks that remain at low levels most of the time, but have occasional bonanzas in recruitment. Hennemuth et al. [14] offer examples from the North Atlantic fisheries. The term, $-rx$, corresponds to the usual assumption that adult fish populations decay exponentially between recruitments (Beverton and Holt [2]). A model of optimal harvesting in the presence of discrete bonanzas is given by Ryan and Hanson [22].

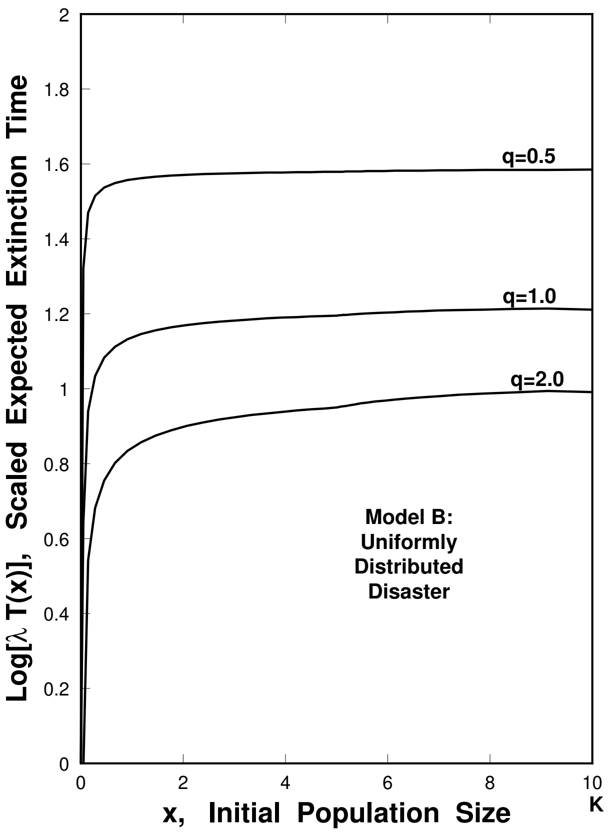

Figure 3: Logarithm of the scaled, expected extinction time, $\log\{\lambda T(x)\}$, for *Model B* of uniformly distributed, density independent disasters as a function of the initial population size, x, for several values of the bio-disaster growth ratio, $q = 0.5, 1.0, 2.0$

In this model, a *bonanza* causes a rapid upsurge in the population size. However, it is assumed that the benefits of the upsurge are limited by an amount $K - x$ so that the upsurged population size will not exceed some limit K. Hence, the jump size is

$$J(x, u) = \begin{cases} u, & u \in (0, K - x) \\ 0, & u \notin (0, K - x) \end{cases}, \tag{3.18}$$

and the distribution is exponential as in *Model A*. The conditional mean jump size is $\mathrm{E}[J(N(t), u)|N(t) = x] = m[1 - (1 + \xi)\exp(-\xi)] \in [0, m)$, where $\xi \equiv (K - x)/m$, and the conditional variance is $\mathrm{Var}[J(N(t), u)|N(t) = x] = m^2[1 - \xi^2 \exp(-\xi) - (1 + \xi)^2 \exp(-2\xi)] \in [0, m^2)$.

In this case, zero cannot be reached in a finite time, since zero can only approached like $O(\exp(-rt))$, so a minimum population size $a = \Delta$ is selected.

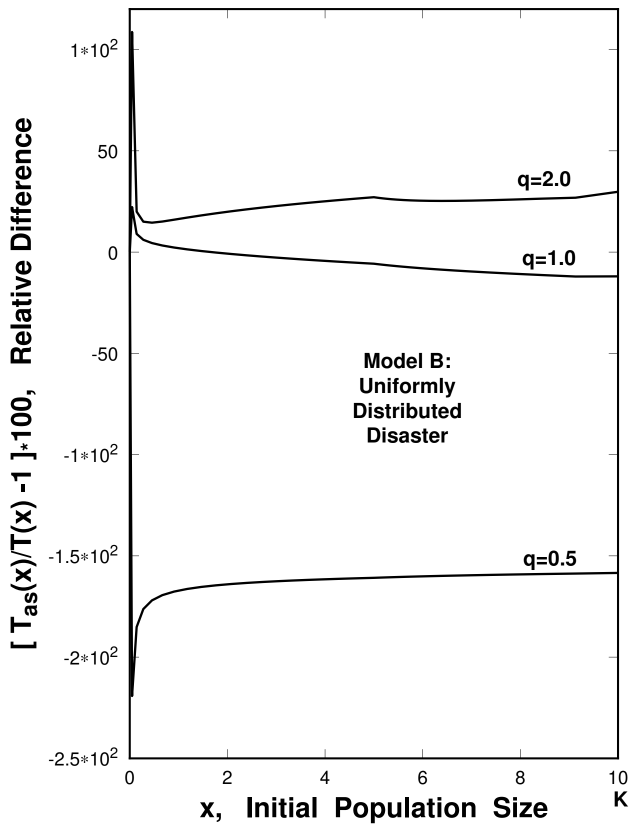

Figure 4: The percent relative difference between the asymptotic and numerical approximations to expected extinction time, $(T_{\rm as}(x)/T(x) - 1) * 100$, for *Model B* with exponentially distributed, N-independent disasters as a function of the initial population size, x, for several values of the bio-disaster growth ratio, $q = 0.5, 1.0, 2.0$

The equation governing the mean persistence time reduces to

$$\begin{aligned} -rxT'(x) &+ \frac{\lambda}{m}\int_0^{K-x} e^{-u/m} T(x+u)du \\ &+\frac{\lambda}{m}T(x)\int_{K-x}^{\infty} e^{-u/m}du - \lambda T(x) = -1, \end{aligned} \tag{3.19}$$

provided x is in $(\Delta, K]$.

As with *Models A* and *B*, Equation (3.19) may be converted by differentiation to a first order ODE for $T'(x)$ in the form like that for a stochastic diffusion,

$$mrxT''(x) + \left[-r(x-m) + \lambda m\left(1 - \exp\left(-\frac{(K-x)}{m}\right)\right)\right]T'(x) = -1. \tag{3.20}$$

The general boundary condition and the fact that at $x = \Delta^+$ the population will drift below the effective extinction level Δ with rate $-r$ before the first upsurge with probability one imply the initial condition, $T(\Delta^+) = 0$. In addition, allowing $x \to K^-$ in (3.19) yields the nonsingular, final condition, $T'(K^-) = 1/(rK)$. The solution of (3.20) from quadratures is

$$\lambda T(x) = qR^q e^{-R} \int_{\Delta/m}^{x/m} \frac{e^y y^{-1-q}}{h(y)} \left[1 + R^{-q} e^R \int_y^R e^{-z} z^q h(z) dz dy \right], \tag{3.21}$$

where the variables of integration have been scaled by the mean jump amplitude m, $R \equiv K/m$, $q \equiv \lambda/r$ is now the *bio-bonanza ratio*, and $h(x) = \exp[qe^{-R}\int_x^R (e^t/t)dt]$ is the integrating factor for (3.20).

For the numerical evaluation of multiple integral form of the solution (3.21), a multiple integral modification of the standard Simpson's rule is used to achieve sufficient accuracy. The principal multiple integration modification arises in the double integral,

$$\begin{aligned} \int_{x_{j-1}}^{x_j} G(y) \int_y^{x_n} H(z) dz dy \quad \simeq \quad & \frac{x_j - x_{j-1}}{6} \left((G_{j-1} + 4G_{j-0.5} + G_j) \int_{x_j}^{x_n} H(z) dz \right. \\ & \left. + G_{j-1} \int_{x_{j-1}}^{x_j} H(z) dz + 4G_{j-0.5} \int_{x_{j-1}}^{x_{j-0.5}} H(z) dz \right), \end{aligned} \tag{3.22}$$

where $G_j \equiv G(x_j)$ for $j = 0$ to n. For the last inner integral, modification of the standard Simpson's rule by using the same parabolic approximation over the half-subinterval $(x_{j-1}, x_{j-0.5})$ with compatible accuracy of standard Simpson's, i.e.,

$$\int_{x_{j-1}}^{x_{j-0.5}} H(z) dz \simeq \frac{x_j - x_{j-1}}{24} \left(5H_{j-1} + 8H_{j-.05} - H_j \right), \tag{3.23}$$

although the extra accuracy of Simpson's rule for cubics must be sacrificed. Hence, using the combined full and half-interval Simpson's rule yields a numerical method for the double integrals with quadratic accuracy. Similarly, the full solution (3.21) can be approximated as triple and double integrals similar to the double integral case.

As $R \to \infty$, a simple asymptotic approximation does not appear to work, in spite of the appearance of the exponentially small factor e^{-R} and exponentially large factor e^R in (3.21), which are cancelled out nonuniformly by exponentials in the integrands.

Some examples of the numerical results obtained for *Model C* are shown in Fig. 5, just scaled by the disaster rate λ and not in logarithm form, in contrast to figures for the previous models. Here, $K = 10$, $m = 1$ and $\Delta = 1$, so that $R = 10$ and $\Delta/m = 1$. The *bio-bonanza growth ratio*, $q \equiv \lambda/r$, has the values $q = 0.5, 1.0$ and 2.0 for the curves starting from the bottom to top, respectively. Apparently, q should be greater than one for a population to attain reasonable extinction time levels, i.e., so that the bonanzas more than compensate for the deterministic exponential decay.

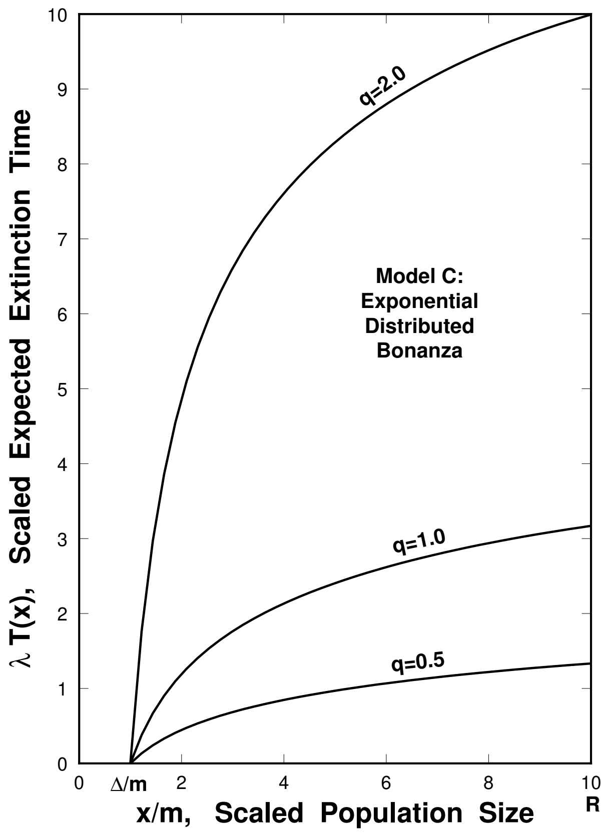

Figure 5: Scaled, expected extinction time, $\lambda T(x)$, for *Model C* with exponentially distributed, N-independent bonanzas as a function of the initial population size, x, for several values of the bio-disaster growth ratio, $q = 0.5, 1.0, 2.0$

The qualitative biological implications of the results are somewhat similar to those of *Models A* and *B*, considering that the results of *Model C* are not presented in logarithmic form, in that, away from effective extinction, extinction times take on larger values, though less dramatically than the former models. *Model C* is quite different from the other models in terms of the roles played by deterministic and stochastic processes, because extinction is caused by exponential deterministic decay to an effective extinction (true extinction to zero population is not attainable), while persistence is strengthened by random bonanzas.

Note that the expected extinction time is an increasing function of the bio-bonanza ratio in Fig. 5 for *Model C*, but it is a decreasing function of the bio-disaster ratio in the disaster examples of Fig. 1 for *Model A* and Fig. 3 for *Model B*, since the bonanza is beneficial while the disaster is adverse to the population.

Even though the relative carrying capacity $R = 10$, the curves do not exhibit near horizontal asymptotes as the relative population size x/m approaches R, confirming the difficulty in finding an asymptotic behavior for large R.

4 Conclusions

Two models of growth with randomly occurring disasters and one model of decay with randomly occurring bonanzas have been presented for which the equations reduce to first order ordinary differential equations as in Eqs. (3.4), (3.14), and (3.20). These equations would correspond to the expected extinction time for a stochastic diffusion with drift, except that the boundary conditions, natural or otherwise, as a set do not correspond to the usual diffusion.

Due to the nature of the reduced equation, the expected extinction time can be further reduced to quadratures, i. e., to a formal solution in terms of explicit integrals. The reduction to quadratures still leaves nontrivial explicit integrals, so special numerical techniques have been used in each case, adapted to some critical form of the integrals for better conditioning.

For *Models A* and *B*, which included disasters, the expected extinction time $T(x)$ quickly levels off outside of a neighborhood of extinction or effective extinction, but the fast growth near extinction is exponential for the exponential distributed disaster of *Model A*, but algebraic-logarithmic for the uniformly distributed disaster of *Model B*. For the exponentially distributed bonanza case of *Model C*, the growth with respect to scaled, initial population size x is much more varied in dependence. Also, the expected extinction time is an decreasing function of the bio-disaster ratio $q = \lambda/r$ in the disaster models, but an increasing function of the bio-bonanza ratio $q = \lambda/r$ in the bonanza model.

In all the models, the common qualitative biological implication of the results is that sufficiently far away from the colonizing important neighborhood of extinction or effective extinction, the larger persistence times are achieved. However, the quantitative levels of the persistence times varies considerably for the three models. The size and distribution of the random disasters undoubtedly provides the difference between *Models B* and *A*, with more dangerous and larger disasters being more likely for *Model B*. *Model C* is quite different from the other two models, in that the deterministic process makes the population tend toward extinction, while the stochastic process make it tend away from extinction, the opposite tendencies in contrast to the other two models.

In the case of the models with disasters, *A* and *B*, asymptotic simplifications have been found useful for particular ranges of the bio-disaster ratio, away from extinction. The asymptotic results are useful in determining the qualitative behavior of the expected extinction time. Asymptotic simplification was not fruitful for the third, bonanza model, *Model C*.

Acknowledgements. This research supported in part by National Science Foundation Grants DMS 91-02343, 93-01107 and 96-26692 at the University of Illinois at Chicago. We performed part of this research in the Department of Biomathematics at the University of California at Los Angeles and in the Department of Mathematics at Monash University. We thank two reviewers for their constructive criticisms which led to a more concise paper.

References

1. Bartoszynski, R., Bühler, Chan, W., Pearl, D. K.: Population processes under the influence of disasters occurring independently of population size. J. Math. Biol. **27**, 167-178 (1989)

2. Beverton, R. J. H., Holt, S. J.: On the dynamics of exploited fish populations. Fisheries investigations, series II, vol. 19. London: Ministry of Agriculture, 1957

3. Brockwell, P. J.: The extinction time of a birth, death and catastrophe process and of a related diffusion model. Adv. Appl. Probab. **17**, 42-52 (1985)

4. Brockwell, P. J., Gani, J., Resnick, S. I.: Birth, immigration and catastrophe processes. Adv. Appl. Probab. **14**, 709-731 (1982)

5. Brockwell, P. J., Gani, J. M., Resnick, S. I.: Catastrophe processes with continuous state-space. Austral. J. Statist. **25**, 208-226 (1983)

6. Flessa, K. W.: The "facts" of mass extinctions. In: V. L. Sharpton, P. D. Ward: Global catastrophes in earth history (Special Paper 247, pp. 1-7) Boulder: Geological Society of America 1990

7. Gihman, I. I., Skorohod, A. V.: Stochastic differential equations. New York: Springer 1972

8. Hanson, F. B.: Analysis of a singular functional differential equation that arises from stochastic modeling of population growth. J. Math. Anal. Applic. **96**, 405-419 (1983)

9. Hanson, F. B.: Bioeconomic model of the Lake Michigan alewife fishery. Can. J. Fish. Aquat. Sci. **44**, suppl. 2, pp. 298-305 (1987)

10. Hanson, F. B., Ryan, D.: Optimal harvesting with density dependent random effects, Natural Resource Modeling **2**, 439-455 (1988)

11. Hanson, F. B., Tier, C.: A stochastic model of tumor growth. Math. Biosci. **61**, 73-100 (1982)

12. Hanson, F. B., Tuckwell, H. C.: Persistence times of populations with large random fluctuations. Theor. Popul. Biol. **14**, 46-61 (1978)

13. Hanson, F. B., Tuckwell, H. C.: Logistic growth with random density independent disasters. Theor. Popul. Biol. **19**, 1-18 (1981)

14. Hennemuth, R. C., Palmer, J. E., Brown, B. E.: A statistical description of recruitment in eighteen selected fish stocks. J. Northw. Atl. Fish. Sci. **1**, 101-111 (1980)

15. Jablonski, D.: Causes and consequences of mass extinctions: A comparative approach. In: D. K. Elliot: Dynamics of extinction (pp. 183-229) New York: Wiley 1986

16. Ludwig, D., Hilborn, R., Walters, C.: Uncertainty, resource exploitation, and conservation: Lessons from history. Science **260**, 17 & 36 (1993)

17. Mangel, M., Tier, C.: A simple, direct method for finding persistence times of populations and application to conservation problems. Proc. Nat. Acad. Sci. USA **90**, 1-28 (1993)

18. Mangel, M., Tier, C.: Dynamics of metapopulations with demographic stochasticity and environmental catastrophes. Theor. Popul. Biol. **44**, 1-31 (1993)

19. Paine, R. T.: Disaster, catastrophe, and local persistence of the sea palm *Postelsia palmaeformis*. Science **205**, 685-686 (1979)

20. Pakes, A. G., Trajstman, A. C., Brockwell, P. J.: A stochastic model for a replicating population subjected to mass emigration due to population pressure. Math. Biosci. **45**, 137-157 (1979)

21. Raup, D. M.: Extinction: Bad genes or bad luck?. Acta Geologica Hispanica, Concept and Method in Paleontology **16**, 25-33 (1981)

22. Ryan, D., Hanson, F. B.: Optimal harvesting with exponential growth in an environment with random disasters and bonanzas. Math. Biosci. **74**, 37-57 (1985)

23. Ryan, D., Hanson, F. B.: Optimal harvesting of a logistic population in an environment with stochastic jumps. J. Math. Biol. **24**, 259-277 (1986)

24. Trajstman, A. C.: A bounded growth population subjected to emigrations due to population pressure. J. Appl. Probab. **18**, 571-581 (1981)

25. Tsurui, A., Osaki, S.: On a first-passage problem for a cumulative process with exponential decay. Stoch. Processes Applic. **4**, 79-88 (1976)

26. Tuckwell, H. C.: On the first exit time problem for temporally homogeneous Markov processes. J. Appl. Prob. **13**, 39-48 (1976)

27. Tuckwell, H. C., Koziol, J. A.: Logistic population growth under random dispersal. Bulletin Math. Biol. **49**, 495-506, 1987.