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## RISKS OF POPULATION EXTINCTION FROM DEMOGRAPHIC AND ENVIRONMENTAL STOCHASTICITY AND RANDOM CATASTROPHES

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*Abstract.*—Stochastic factors affecting the demography of a single population are analyzed to determine the relative risks of extinction from demographic stochasticity, environmental stochasticity, and random catastrophes. Relative risks are assessed by comparing asymptotic scaling relationships describing how the average time to extinction,  $T$ , increases with the carrying capacity of a population,  $K$ , under each stochastic factor alone. Stochastic factors are added to a simple model of exponential growth up to  $K$ . A critical parameter affecting the extinction dynamics is  $\bar{r}$ , the long-run growth rate of a population below  $K$ , including stochastic factors. If  $\bar{r}$  is positive, with demographic stochasticity  $T$  increases asymptotically as a nearly exponential function of  $K$ , and with either environmental stochasticity or random catastrophes  $T$  increases asymptotically as a power of  $K$ . If  $\bar{r}$  is negative, under any stochastic demographic factor,  $T$  increases asymptotically with the logarithm of  $K$ . Thus, for sufficiently large populations, the risk of extinction from demographic stochasticity is less important than that from either environmental stochasticity or random catastrophes. The relative risks of extinction from environmental stochasticity and random catastrophes depend on the mean and environmental variance of population growth rate, and the magnitude and frequency of catastrophes. Contrary to previous assertions in the literature, a population of modest size subject to environmental stochasticity or random catastrophes can persist for a long time, if  $\bar{r}$  is substantially positive.

Understanding the risks of extinction affecting single populations is important in both pure and applied ecology, in the development of models of more complex, spatially distributed populations, and in the formulation of effective conservation plans for threatened and endangered species (Soulé and Simberloff 1986; Lande 1988; Karieva 1990; Gilpin and Hanski 1991).

In an important article, Shaffer (1981) suggested that stochastic demographic and genetic factors determine the minimum size of a viable population, which can be defined in terms of the probability of extinction within a specified time (e.g., a 95% probability of persistence for 100 yr, or a 99% probability of persistence for 1,000 yr). Ginzburg et al. (1982) advocated the use of stochastic demographic models as a basis for risk assessment in environmental impact statements. Concepts and methods of stochastic population modeling play an integral part in population viability analysis (Gilpin and Soulé 1986; Burgman et al. 1993).

Shaffer (1981, 1987) discussed three stochastic demographic factors that are the subject of the present article. First, *demographic stochasticity* is caused by chance realizations of individual probabilities of death and reproduction in a finite

population. Because independent individual events tend to average out in large populations, demographic stochasticity is most important in small populations. Second, *environmental stochasticity* arises from a nearly continuous series of small or moderate perturbations that similarly affect the birth and death rates of all individuals (within each age or stage class) in a population (May 1974). In contrast to demographic stochasticity, environmental stochasticity is important in both large and small populations. Finally, *catastrophes* are large environmental perturbations that produce sudden major reductions in population size. Like environmental stochasticity, catastrophes are important in populations of all sizes.

Based on models of stochastic population growth and simple scaling arguments concerning the average time until extinction of a population due to each of these factors acting alone, Shaffer (1987) attempted to deduce their relative importance.

It is well-known that under demographic stochasticity alone (in a constant environment) the average time to extinction increases almost exponentially with carrying capacity (MacArthur and Wilson 1967; Richter-Dyn and Goel 1972; Leigh 1981; Gabriel and Bürger 1992). Ludwig (1976) and formulas in Leigh (1981) and Tier and Hanson (1981) show that, under density-dependent population growth in a random environment, the mean time to extinction is a power function of the carrying capacity. In contrast, Goodman (1987*a*, 1987*b*) claimed that because of environmental stochasticity alone the average time to extinction always increases less than linearly with carrying capacity. Ewens et al. (1987) developed a density-independent catastrophe model and concluded that the average time to extinction increases only logarithmically with initial population size. From the qualitative scaling relationships in Goodman (1987*a*, 1987*b*) and Ewens et al. (1987), Shaffer (1987) concluded that random catastrophes are more important than environmental stochasticity, which is more important than demographic stochasticity in determining average persistence times of populations. Later authors presented the same conclusions (Pimm and Gilpin 1989; Soulé and Kohm 1989; Hedrick and Miller 1992).

The relative importance of demographic and environmental stochasticity and random catastrophes discussed by Shaffer (1987) is intuitively appealing and eventually may be supported by empirical evidence. However, I demonstrate in this article, as shown by previous results of Ludwig (1976), Leigh (1981), and Tier and Hanson (1981), that Goodman's (1987*a*, 1987*b*) somewhat less than linear scaling of average extinction time with carrying capacity under environmental stochasticity is incorrect. I also show that the logarithmic scaling of average extinction time with initial population size under random catastrophes found by Ewens et al. (1987) does not generalize to density-dependent population growth.

I develop analytical models showing that curves of average persistence time as a function of population size may be concave or convex under the influence of either environmental stochasticity or random catastrophes, and I show that no general theoretical statement can be made concerning the relative risks of population extinction from these two stochastic factors. When the long-run growth rate of a population is negative, regardless of whether the cause is deterministic or stochastic, the average extinction time scales logarithmically with initial population size, as suggested by Ludwig (1976) and Brockwell (1985). To demonstrate

these assertions, I analyze the mean time to extinction in a simple model of density-dependent growth of a population subject to different demographic risks.

#### DETERMINISTIC MODEL

To facilitate the analysis of stochastic factors affecting population growth, I introduce a simple deterministic model of density-dependent growth of a population without age structure. The population size,  $N$ , has a constant per capita growth rate,  $r$ , except at the carrying capacity (or ceiling),  $K$ , where growth ceases:

$$\frac{dN}{dt} = \begin{cases} rN & \text{for } 1 < N < K \\ 0 & \text{for } N = K. \end{cases} \quad (1)$$

For an initial population size  $N_0$  between one and  $K$ , the population grows exponentially with time  $t$  as  $N(t) = N_0 e^{rt}$ . If  $r$  is positive, population growth continues until  $K$  is reached. This simple model of exponential growth up to a carrying capacity was analyzed by MacArthur and Wilson (1967), Leigh (1981), and Goodman (1987*a*, 1987*b*) in their investigations of demographic and environmental stochasticity.

If  $r$  is negative, the population declines to extinction, which is defined to occur at a population size of  $N = 1$  individual. For a population initially at carrying capacity,  $N_0 = K$ , the time until extinction,  $-(\ln K)/r$ , then depends on the natural logarithm of the initial size. In the following sections we will see that a roughly logarithmic dependence of extinction time on initial population size carries over to stochastic models.

#### DIFFUSION THEORY FOR STOCHASTIC MODELS

Demographic and environmental stochasticity, involving a nearly continual series of small or moderate perturbations of the population numbers, can be accurately modeled as a diffusion process, provided that the mean absolute growth rate per unit time is small,  $|\bar{r}| \ll 1$  (Keiding 1975; Leigh 1981). For populations with discrete generations this condition implies a low growth rate per generation. For populations with overlapping generations that reproduce at discrete times, the condition is less restrictive, requiring only a low growth rate per reproductive interval (if mortality and reproductive rates are independent of age).

Diffusion theory can then be employed to calculate the mean time to extinction of the population (Karlín and Taylor 1981, chap. 15). A diffusion process is completely described by its infinitesimal moments and by the behavior of sample paths at the boundaries. For a population of size  $N$ , the infinitesimal mean and variance,  $\mu(N)$  and  $\sigma^2(N)$ , give, respectively, the expected change and the variance of the change in population size per unit time. Starting from a given initial size,  $N_0$ , the mean time to extinction, denoted as  $T \equiv T(N_0)$ , is the solution of

$$\frac{1}{2} \sigma^2(N_0) \frac{d^2 T}{dN_0^2} + \mu(N_0) \frac{dT}{dN_0} = -1, \quad (2)$$

with the boundary conditions  $T(1) = 0$  and a reflecting boundary at  $K$ . A reflecting boundary condition with density-independent population growth was employed by MacArthur and Wilson (1967), Leigh (1981), and Goodman (1987*b*). The same result can be obtained more simply by regarding equation (1) as the limit of a continuum of models with weaker forms of density dependence (see, e.g., Richter-Dyn and Goel 1972). We can then use the general solution to equation (2) in Karlin and Taylor (1981) to show that

$$T(N_0) = 2 \int_1^{N_0} e^{-G(z)} \int_z^K \frac{e^{G(y)}}{\sigma^2(y)} dy dz, \quad (3)$$

where

$$G(y) = 2 \int^y \frac{\mu(N)}{\sigma^2(N)} dN.$$

This formula differs slightly from that of Ludwig (1976, eq. [3.12]) and Leigh (1981, eq. [8]) because they defined extinction as occurring at a population size of  $N = 0$  instead of 1, and we have incorporated the fact that  $N$  cannot exceed  $K$  in equation (1).

For populations subject to demographic or environmental stochasticity, with positive long-run growth rates and a sufficiently large initial size, Richter-Dyn and Goel (1972) and Leigh (1981) showed that the average time to extinction is nearly independent of the initial population size. A similar conclusion holds for populations subject to random catastrophes (see Appendix formula [A15a]). This occurs because such a population is most likely to grow quickly toward carrying capacity and to spend a long time fluctuating near  $K$  before stochastic factors finally cause extinction. The persistence of an established population with a positive long-run growth rate can thus be accurately described by its average time to extinction starting from carrying capacity.

We therefore follow Shaffer (1987) in considering the extinction dynamics of density-dependent populations that start at carrying capacity. Formula (3) will be used to evaluate the influence of demographic and environmental stochasticity on population persistence and to compare the results for populations with positive or negative long-run growth rates to those of earlier authors.

#### DEMOGRAPHIC STOCHASTICITY

In a finite population, the per capita growth rate,  $r$ , is subject to random variation due to independent chances of individual mortality and reproduction. Thus, for a population of size  $N$ ,  $r$  is a random variable with mean  $\bar{r}$  and variance  $V_1/N$  per unit time, with no autocorrelation. The parameter  $V_1$  is the variance in individual fitness per unit time (Keiding 1975; Leigh 1981; Goodman 1987*a*, 1987*b*). The growth rate of a population at a particular time,  $r$ , is the mean Malthusian fitness of individuals in the population (Crow and Kimura 1970, chap. 1), and its variance follows the standard statistical formula for the sampling variance of a mean (i.e., individual variance divided by population size). The long-run growth rate of a population subject to demographic stochasticity is simply  $\bar{r} = \bar{r}$ .

Assuming that the continuous-time model in equation (1) represents an approximation to an actual population that reproduces at discrete time intervals, the Ito stochastic calculus is appropriate to obtain the infinitesimal mean and variance of the diffusion process (Turelli 1977; Karlin and Taylor 1981, chap. 15.14), which are

$$\mu(N) = \bar{r}N \quad \text{and} \quad \sigma^2(N) = V_1N. \tag{4}$$

For populations initially at carrying capacity,  $N_0 = K$ , the average time to extinction, from formula (3), is

$$T(K) = \frac{1}{\bar{r}} \int_1^K \frac{e^{a(N-1)}}{N} dN - \frac{\ln K}{\bar{r}}, \tag{5a}$$

where  $a = 2r/V_1$ . Leigh (1981, pp. 220–221) derived a similar formula, assuming  $V_1 = 1$ . Figure 1 illustrates the average extinction time as a function of carrying capacity for populations with different mean growth rates.

Asymptotic scaling relationships for the average extinction time with increasing carrying capacity can be derived from formula (5a) in cases where  $\bar{r}$  is positive, zero, or negative. For positive  $\bar{r}$ , the integral in formula (5a) can be approximated by expanding  $1/N$  in a Taylor series around  $1/K$  (as in Leigh 1981), and if  $aK \gg 1$ , we can retain only the first two terms in the series to find

$$T(K) \approx \frac{e^{a(K-1)} - 1}{\bar{r}aK} \left( 1 + \frac{1}{aK} \right) \quad \text{for } aK \gg 1. \tag{5b}$$

The dominant term is proportional to  $e^{aK}/K$ . This nearly exponential scaling of average extinction time is qualitatively consistent with previous results (MacArthur and Wilson 1967; Richter-Dyn and Goel 1972; Leigh 1981; Goodman 1987*b*; Gabriel and Bürger 1992).

For  $\bar{r} = 0$ , equation (5a) reduces to a nearly linear dependence of average extinction time on carrying capacity,  $T(K) = 2(K - 1 - \ln K)/V_1$ , in close agreement with the linear relationship derived by Leigh (1981).

For negative  $\bar{r}$ , when  $-aK \gg 1$  the integral in equation (5a) approaches a constant that involves the exponential integral,  $E_1(-a) = \int_{-a}^{\infty} z^{-1}e^{-z}dz$  (tabulated in Abramowitz and Stegun 1972),

$$T(K) \approx \frac{-\ln K + e^{-a}E_1(-a)}{\bar{r}} \quad \text{for } -aK \gg 1 \tag{5c}$$

With a negative average (or long-run) growth in a population under demographic stochasticity, the dominant term in the asymptotic scaling of average extinction time is proportional to the logarithm of carrying capacity, as in a population undergoing a deterministic decline.

ENVIRONMENTAL STOCHASTICITY

We model the effects of a changing environment by allowing the population growth rate to fluctuate with time as a stationary time series with mean growth

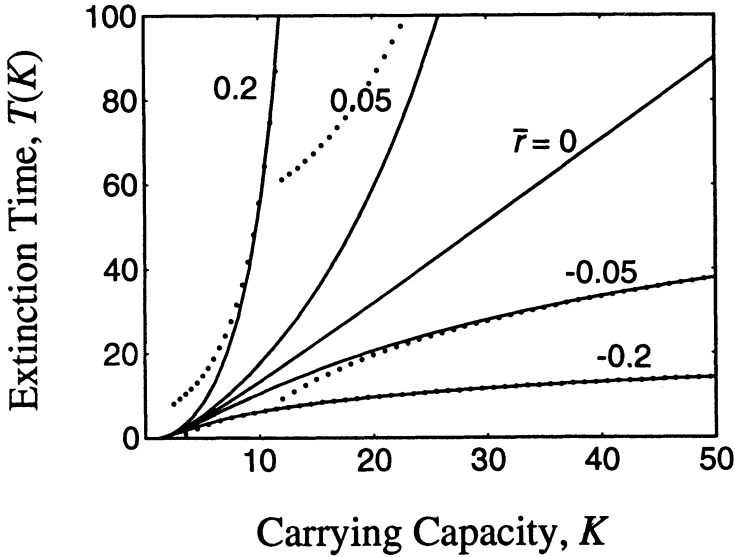


FIG. 1.—Average time to extinction under demographic stochasticity for a population initially at carrying capacity. Each curve represents a different value of the mean population growth rate,  $\bar{r}$ . The sampling variance in fitness per individual per unit time due to demographic stochasticity is  $V_1 = 1$ . Solid lines show the diffusion approximation (eq. [5a]), and dotted lines give asymptotic approximations (eqq. [5b], [5c]).

rate  $\bar{r}$ , environmental variance  $V_e$ , and no autocorrelation. Again assuming that equation (1) approximates a population reproducing at discrete intervals, we can use diffusion theory to analyze the process. The infinitesimal mean and variance of the diffusion process are

$$\mu(N) = \bar{r}N \quad \text{and} \quad \sigma^2(N) = V_e N^2. \tag{6}$$

Transformation of the diffusion process to a logarithmic scale would yield the transformed infinitesimal mean and variance as  $\bar{r} - V_e/2$  and  $V_e$ , respectively, in the domain  $0 < \ln N < \ln K$  (Karlin and Taylor 1981, chap. 15.3). The expected value of the logarithm of population size then changes according to

$$E[\ln N(t)] = \ln N_0 + (\bar{r} - V_e/2)t \tag{7}$$

in the density-independent region. For this reason, the quantity  $\bar{r} = \bar{r} - V_e/2$ , termed the long-run growth rate, can be considered as a stochastic analogue of  $r$  in the deterministic model (see Tuljapurkar 1982; Lande and Orzack 1988). Discounting the mean growth rate because of random environmental fluctuations is explained by Lewontin and Cohen (1969) in terms of the finite rate of increase,  $e^r$ , the arithmetic mean of which determines the expected population size, whereas the smaller geometric mean determines the dynamics of extinction. For the diffusion approximation in equation (6), the logarithm of the expected population size is  $\ln E[N(t)] = \ln N_0 + \bar{r}t$  in the density-independent region, in contrast to equation (7).

From formula (3), the average time to extinction with environmental stochasticity is

$$T(K) = \frac{2}{V_e c} \left( \frac{K^c - 1}{c} - \ln K \right), \quad (8a)$$

in which  $c = 2\bar{r}/V_e - 1 = (2/V_e)\bar{r}$ . Figure 2 shows how the mean extinction time increases with carrying capacity for different values of  $c$ .

With a positive long-run growth rate, the average time to extinction scales asymptotically as a power function of the carrying capacity,

$$T(K) \approx 2K^c/(V_e c^2) \quad \text{for } c \ln K \gg 1. \quad (8b)$$

Ludwig (1976) showed for logistic population growth in a random environment that the asymptotic scaling of  $T(K)$  is proportional to  $K^c$ . Formulas in Leigh (1981) and Tier and Hanson (1981) are also in agreement with this scaling of mean extinction time.

Goodman (1987*b*) derived a compatible result but assumed, inappropriately for environmental stochasticity, that  $\bar{r} < V_e/2$ , which implies a negative long-run growth rate for the population ( $c < 0$ ) and a less than linear scaling described below. Contrary to Goodman (1987*a*, 1987*b*), in a population subject to environmental stochasticity the average time to extinction can increase faster than linearly with carrying capacity. In formula (8b),  $T(K)$  is linear when  $c = 1$ , curves downward when  $c < 1$ , and curves upward when  $c > 1$ . The scaling of average extinction time with carrying capacity is determined by the ratio of the mean growth rate to its variance and has positive curvature when  $\bar{r}/V_e > 1$ . This only requires that the growth rate have a mean larger than its environmental variance.

If the long-run growth rate is zero ( $\bar{r} = 0$  or  $c = 0$ ), the average time to extinction depends on the square of the logarithm of carrying capacity,  $T(K) = (\ln K)^2/V_e$ . Goodman (1987*b*) derived this formula, but under the incorrect condition  $\bar{r} = 0$  instead of  $\bar{r} = 0$ . When the mean growth rate is zero ( $\bar{r} = 0$  or  $c = -1$ ), the long-run growth rate is negative,  $\bar{r} = -V_e/2$ , and the average time to extinction is nearly proportional to the logarithm of the carrying capacity.

With a negative long-run growth rate in a population with environmental stochasticity,

$$T(K) \approx \frac{-\ln K - 1/c}{\bar{r}} \quad \text{for } -c \ln K \gg 1, \quad (8c)$$

the dominant term in the average time to extinction is proportional to the logarithm of carrying capacity, in agreement with Ludwig (1976).

#### RANDOM CATASTROPHES

Large, infrequent perturbations such as sudden catastrophes must be modeled differently than with diffusion processes such as those used above to describe demographic and environmental stochasticity. Hanson and Tuckwell (1981) introduced a population-dynamic model in which catastrophes reduce the population



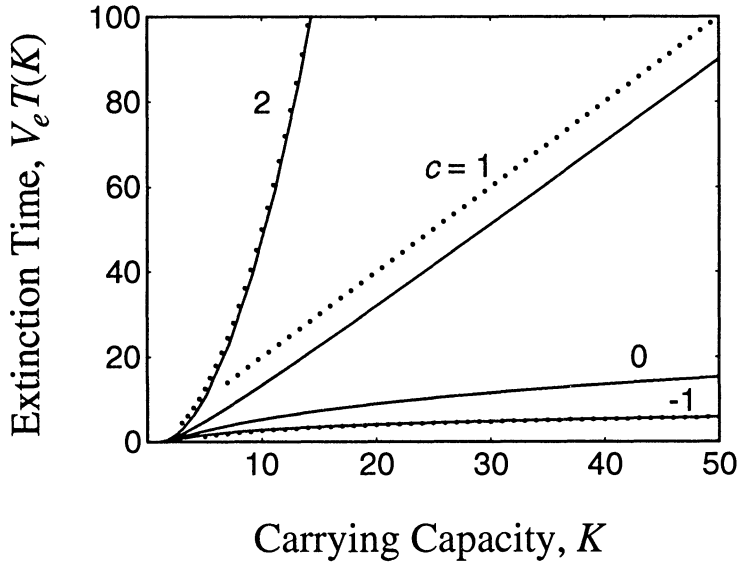


FIG. 2.—Average time to extinction under environmental stochasticity for a population initially at carrying capacity. The mean and variance of the population growth rate caused by a fluctuating environment are  $\bar{r}$  and  $V_e$ . Each curve corresponds to a different value of  $c = 2\bar{r}/V_e - 1$ . Solid lines display the diffusion approximation (eq. [8a]), and dotted lines are asymptotic approximations (eqq. [8b], [8c]).

by a fixed proportion at random times. In their model the population grows deterministically between catastrophes with a logistic form of density dependence. They were unable to derive a complete analytical solution but presented numerical results for some parameter values. Ewens et al. (1987) analyzed a similar model of catastrophes in a population with no density regulation. Here I show that, by modifying Hanson and Tuckwell's model to incorporate the form of density dependence in equation (1), an analytical solution can be obtained for the average time to extinction of a population subject to random catastrophes.

Each catastrophe is assumed to reduce instantaneously the population by a proportion  $\delta$ , that is, a population of size  $N$  just prior to a catastrophe is reduced to size  $(1 - \delta)N$  just after the catastrophe. Catastrophes occur as a Poisson process with rate parameter  $\lambda$ , so that the waiting time for a catastrophe has an exponential distribution,  $\lambda^{-1}e^{-\lambda t}$  with mean  $1/\lambda$ , and the probability of  $i$  catastrophes occurring in a time interval of length  $t$  is  $(\lambda t)^i e^{-\lambda t}/i!$  for  $i = 0, 1, 2, \dots$ . Between catastrophes the population grows at the constant per capita rate,  $r$ , until the carrying capacity,  $K$ , is reached (eq. [1]) or a catastrophe occurs.

It is easiest to analyze this model in terms of the natural logarithm of population size,  $n = \ln N$ . Then from an initial value of  $n_0 = \ln N_0$ ,  $n$  grows linearly with time at the constant rate  $r$ ,  $n(t) = n_0 + rt$ , until it reaches  $k = \ln K$  or a catastrophe strikes. Each catastrophe now reduces  $n$  by an additive amount,  $\epsilon = -\ln(1 - \delta)$ . Extinction occurs at  $n = \ln 1 = 0$ . This type of process, with additive downward jumps of constant magnitude happening at random times, was studied

by Hanson and Tuckwell (1978). Starting from  $n_0$ , the average time until extinction, denoted as  $T(n_0)$ , obeys a differential-difference equation,

$$r \frac{dT(n_0)}{dn_0} - \lambda T(n_0) + \lambda T(n_0 - \epsilon) = -1 \tag{9}$$

for  $0 < n_0 \leq k$ , with  $T(n_0) = 0$  for  $n_0 \leq 0$ . The boundary condition differs depending on whether  $r$  is positive or negative. For  $r > 0$ , the appropriate boundary condition is  $T(k) - T(k - \epsilon) = 1/\lambda$  because the expected time to move from the stable point  $k$  to  $k - \epsilon$  is the expected waiting time until the next catastrophe,  $1/\lambda$ . Then  $T(n_0)$  is discontinuous at the extinction boundary,  $n = 0$ , because starting from an infinitesimally small value,  $0^+$ , the population will grow and persist until a (series of) catastrophe(s) causes its extinction. When  $r$  is positive, the boundary condition at  $T(k)$  therefore determines  $T(0^+)$  (Hanson and Tuckwell 1978). When  $r$  is negative, the appropriate boundary condition is  $T(0^+) = 0$ .

Exact analytical solutions of equation (9) can be obtained using Laplace transforms (Churchill 1958; Bellman and Cooke 1963), as shown in the Appendix. The exact solutions are so complex as to be uninformative, except in facilitating the construction of graphs as in figure 3. Asymptotic analysis, also given in the Appendix, produces approximate formulas that are more readily interpretable. An important parameter in both the exact and approximate solutions is the ratio of the catastrophe rate times catastrophe size to the population growth rate between catastrophes,  $\gamma = \lambda\epsilon/r$ . This parameter is closely related to the long-run growth rate of the population including catastrophes,  $\bar{r} = r - \lambda\epsilon$ . Another important parameter is the number of catastrophes from carrying capacity to extinction in the absence of population growth,  $k/\epsilon$ .

Figure 3 depicts average times to extinction as a function of  $k/\epsilon$ . It can be seen for  $\bar{r} > 0$  (or  $0 < \gamma < 1$ ) that  $\ln(\lambda T(k))$  increases asymptotically as a linear function of  $k/\epsilon$ , so that  $\lambda T(k)$  increases exponentially with  $k/\epsilon$ . For  $\bar{r} < 0$  (or  $0 > \gamma > 1$ ), figure 3 (*bottom*) shows the asymptotic linear dependence of average extinction time on  $k/\epsilon$ .

For  $\gamma > 0$ , the asymptotic solution is

$$\lambda T(k) \approx \frac{\gamma}{1 - \gamma} \left( \frac{e^{\beta k/\epsilon} - 1}{\beta} - \frac{k}{\epsilon} \right) + O(1), \tag{10a}$$

in which  $\beta$  is the solution of the transcendental equation  $\beta/(e^\beta - 1) = \gamma$ , and  $O(1)$  is a constant of order 1.

When the long-run growth rate of the population is positive,  $0 < \gamma < 1$ , then  $\beta$  is positive and the exponential term dominates in equation (10a). In this case  $\beta$  gives the asymptotic slope of the lines in figure 3 (*top*). Because  $k = \ln K$ ,  $T(k)$  is asymptotically proportional to  $K^{\beta/\epsilon}$ . The average time to extinction thus scales in proportion to a power of the carrying capacity and increases faster than linearly with  $K$  when  $\beta > \epsilon$ . For example, if each catastrophe reduces the population to  $e^{-2} = 13.5\%$  of its size just prior to the catastrophe, so that the catastrophe size on the logarithmic scale is  $\epsilon = -\ln(e^{-2}) = 2$ , then  $\beta > 2$  when  $\gamma < 0.313$  or  $\lambda/r < 0.157$ . Thus, the average time to extinction for a population subject to

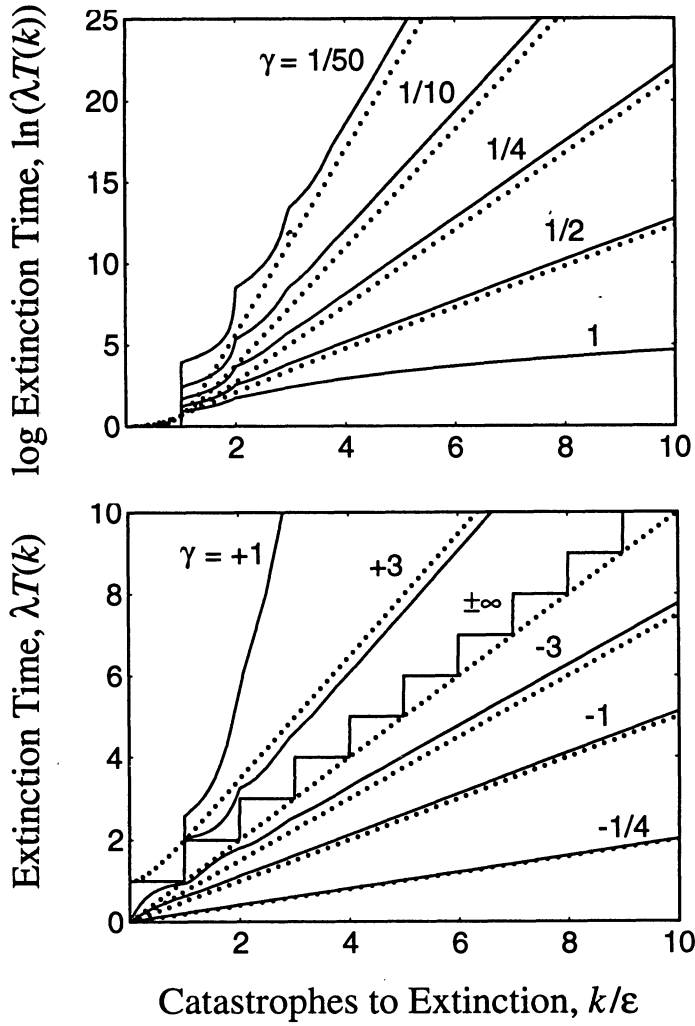


FIG. 3.—Average time to extinction under random catastrophes for a population initially at carrying capacity,  $K = e^k$ . Different curves correspond to the given values of  $\gamma = \lambda\epsilon/r$  in which  $\lambda$  is the catastrophe rate,  $\epsilon$  is the catastrophe size on the logarithmic scale, and  $r$  is the growth rate of the population between catastrophes. In both graphs the *abscissa* gives the number of catastrophes from carrying capacity to extinction for a population with  $r = 0$  (or  $\gamma = \pm\infty$ ). *Top*, double logarithmic plot for positive long-run growth rates,  $r - \lambda\epsilon > 0$  (or  $0 < \gamma < 1$ ). *Bottom*, semilogarithmic plot for negative long-run growth rates,  $r - \lambda\epsilon < 0$  (or  $0 > \gamma > 1$ ). *Solid lines* are exact solutions (Appendix), and *dotted lines* give asymptotic approximations (for  $\gamma > 0$ , eq. [10a] with  $O(1) = 1$ , and for  $\gamma < 0$ , eq. [10c]).

infrequent catastrophes can easily increase much faster than linearly with carrying capacity.

When  $\gamma > 1$ , the long-run growth rate is negative, and  $\beta$  is negative. In this case the exponential term in equation (10a) is negligible if  $-\beta k/\epsilon > 2$ , and the asymptotic solution becomes

$$\lambda T(k) \approx \frac{-\gamma}{1-\gamma} \left( \frac{k}{\epsilon} + \frac{1}{\beta} \right) + O(1). \quad (10b)$$

When  $\gamma < 0$ , the long-run growth rate is again negative, and the asymptotic solution is simply

$$\lambda T(k) \approx \frac{-\gamma}{1-\gamma} \left( \frac{k}{\epsilon} \right). \quad (10c)$$

Thus, when the long-run growth rate is negative in a population subject to random catastrophes,  $0 > \gamma > 1$ , asymptotic formulas for the average extinction time are dominated by a linear function of  $k$ , which is a logarithmic function of carrying capacity,  $T(k) \approx -(\ln K)/\bar{r}$ , as under demographic or environmental stochasticity (eqq. [5c], [8c]).

#### DISCUSSION

The average time to extinction of a population, starting from carrying capacity  $K$ , follows different scaling laws in response to demographic stochasticity, environmental stochasticity, or random catastrophes. When the long-run growth rate of the population is positive, the scaling relationships are as follows. With demographic stochasticity the per capita growth rate fluctuates because of sampling effects caused by finite population size. The average time to extinction increases almost exponentially with carrying capacity, in proportion to  $e^{aK}/K$ , where  $a = 2\bar{r}/V_1$ , in which  $\bar{r}$  and  $V_1$  are, respectively, the mean Malthusian fitness and its variance among individuals. The nearly exponential scaling of mean time to extinction with increasing  $K$  under demographic stochasticity alone is consistent with results of previous authors (MacArthur and Wilson 1967; Richter-Dyn and Goel 1972; Leigh 1981; Gabriel and Bürger 1992).

Under environmental stochasticity the per capita growth rate fluctuates with temporal changes in the environment. The average extinction time scales as a power of the carrying capacity, proportional to  $K^c$ , where  $c = 2r/V_e - 1$ , in which  $\bar{r}$  and  $V_e$  are, respectively, the mean and environmental variance in  $r$ . The average extinction time therefore scales faster or slower than linearly with  $K$ , depending on whether  $\bar{r}/V_e$  is greater than or less than one. Positive (upward) curvature of the scaling relationship only requires that  $\bar{r} > V_e$ . Formulas in Leigh (1981) and Tier and Hanson (1981) are consistent with the scaling of mean extinction time as a power function of  $K$  under environmental stochasticity.

Goodman's (1987b) formulas are also consistent with this scaling law, but he claimed that with environmental stochasticity the average extinction time always scales less than linearly with carrying capacity ( $c < 1$ ), which implies that only

extremely large populations are likely to persist for long periods in a fluctuating environment. Goodman's erroneous conclusion traces to an inappropriate analogy between environmental stochasticity and the classical birth-death model of demographic stochasticity and his assumption that  $\bar{r} < V_e/2$ , which implies that the long-run growth rate of the population,  $\bar{r} - V_e/2$ , is negative. If this assumption were generally valid, few, if any, species would exist today.

It is nevertheless true that, in sufficiently large populations, environmental stochasticity poses a greater risk of extinction than demographic stochasticity. This conclusion follows intuitively from the fact that the importance of demographic stochasticity in causing fluctuations in population growth rate,  $r$ , is inversely proportional to population size, whereas fluctuations in  $r$  caused by environmental stochasticity may be independent of population size. In the present models with a positive long-run growth rate, the average time to extinction under demographic stochasticity, proportional to  $e^{aK}/K$ , increases with  $K$  faster than that under environmental stochasticity, proportional to  $K^c = e^{c \ln K}$ , regardless of the constants of proportionality or the values of  $a$  and  $c$ . If the per capita growth rate has a mean larger than its variance ( $\bar{r} > V_e$  or  $c > 1$ ), the average persistence time under environmental stochasticity may be extremely long, even for populations of modest size.

Under random catastrophes, the long-run growth rate of the population,  $r - \lambda\epsilon$ , is positive when the growth rate between catastrophes,  $r$ , exceeds the catastrophe rate,  $\lambda$ , multiplied by the catastrophe size on the natural logarithmic scale,  $\epsilon$ . In this case, the average time to extinction scales in proportion to  $K^{\beta/\epsilon}$ , where  $\beta$  is the solution of an equation involving  $\gamma = \lambda\epsilon/r$  (see eq. [10a]). This scaling is more than linear when the exponent is greater than one, or  $\beta > \epsilon$ . The average persistence time of a population subject to infrequent catastrophes can easily increase much faster than linearly with carrying capacity. Consequently, a population of modest size may persist for a long time in the presence of random catastrophes, if its long-run growth rate is positive. This analytical conclusion confirms previous numerical results obtained by Hanson and Tuckwell (1981) for a population with logistic growth subject to random catastrophes.

Because average persistence times scale as power functions of carrying capacity under both environmental stochasticity and random catastrophes, no general statement can be made about which is more important in large populations. Their relative importance depends on the values of several parameters in addition to carrying capacity, which in the present models are the mean and environmental variance of per capita growth rate and the magnitude and frequency of catastrophes. The similarity of the scaling laws for extinction risks under environmental stochasticity and random catastrophes makes intuitive sense when catastrophes are viewed as extreme manifestations of a fluctuating environment.

In the random catastrophe model analyzed by Ewens et al. (1987) the logarithmic scaling of average persistence time with population size is a consequence of their assumption that the long-run growth rate of the population is negative. This assumption was necessary in their density-independent model in order for eventual extinction to be a certain event. With density dependence, as in the present catastrophe model or that of Hanson and Tuckwell (1981), eventual extinction is

certain even for a population with a positive long-run growth rate below carrying capacity.

The present analysis demonstrates that Goodman (1987*a*, 1987*b*), Ewens et al. (1987), and Shaffer (1987) seriously overestimated the risks of population extinction from environmental stochasticity and random catastrophes, as did Soulé and Kohm (1989), Pimm and Gilpin (1989), and Hedrick and Miller (1992). Prevailing views regarding the persistence of populations under environmental stochasticity or random catastrophes have been too pessimistic, at least for populations with a positive long-run growth rate. Empirical evidence may ultimately accumulate to indicate that random catastrophes pose a greater risk of population extinction than does environmental stochasticity. The only general statement supported by existing theory is that in sufficiently large populations demographic stochasticity is a less important cause of extinctions than either environmental stochasticity or random catastrophes.

Unfortunately, for many species threatened with extinction, long-run growth rates of populations are near zero or negative. For populations with a negative long-run growth rate, regardless of the stochastic factors involved, the average time to extinction scales with the natural logarithm of the carrying capacity, divided by the long-run rate of population decline, as previously noted by Ludwig (1976) and Brockwell (1985) for different forms of stochasticity and density dependence. Thus, a large initial size does little to extend the average lifetime of a population with a negative long-run growth rate.

The present results are based on a simple model of density-independent population growth below carrying capacity. They are, however, in qualitative agreement with analytical results of Ludwig (1976), Leigh (1981), and Tier and Hanson (1981) for demographic and environmental stochasticity and numerical results of Hanson and Tuckwell (1981) for random catastrophes, under the logistic model of density dependence. This concordance suggests that the qualitative scaling relationships and relative risks of extinction described here are likely to be general and robust properties of the dynamics of single-population models.

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#### APPENDIX

##### ANALYSIS OF RANDOM CATASTROPHES

Solution of the random catastrophe model is simplified by the transformations  $x = n_0/\epsilon$  and  $\tau(x) = \lambda T(n_0)$ , so that the catastrophe size becomes one and the mean time to extinction is scaled in units of the mean waiting time between catastrophes. Equation (9) becomes

$$\frac{d\tau(x)}{dx} - \gamma\tau(x) + \gamma\tau(x-1) = -\gamma \quad \text{for } 0 < x < k/\epsilon, \quad (\text{A1})$$

with  $\tau(x) = 0$  for  $x \leq 0$ . The parameter  $\gamma = \lambda\epsilon/r$  gives the ratio of the magnitude of the expected rate of change of  $n$  from catastrophes to the population growth rate between catastrophes. For  $\gamma \geq 0$  the boundary condition is  $\tau(k/\epsilon) - \tau(k/\epsilon - 1) = 1$ , whereas for  $\gamma < 0$  the boundary condition is  $\tau(0^+) = 0$ .

EXACT SOLUTION USING LAPLACE TRANSFORM

Denote the Laplace transform of  $\tau(x)$  as  $\bar{\tau}(s) = \int_0^\infty e^{-sx}\tau(x)dx$ , where  $s$  is a complex variable. Applying the Laplace transform to equation (A1) using the tables in Churchill (1958) yields

$$\bar{\tau}(s) = \frac{-\gamma/s + \tau(0^+)}{s - \gamma(1 - e^{-s})}. \tag{A2}$$

The denominator can be expanded as a power series in  $(\gamma/s)(1 - e^{-s})$ , and  $(1 - e^{-s})^m$  can be expanded using the binomial theorem, which gives

$$\bar{\tau}(s) = \frac{-\gamma/s + \tau(0^+)}{s} \sum_{m=0}^\infty \left(\frac{\gamma}{s}\right)^m \sum_{j=0}^m \binom{m}{j} (-1)^j e^{-js}. \tag{A3}$$

The inverse Laplace transform of  $s^{-m-1}e^{-js}$  is  $U(x - j)(x - j)^m/m!$ , where  $U(x - j)$  is the unit step function, which is zero for  $x < j$  and one for  $x > j$ . Taking the inverse Laplace transform of equation (A3) and interchanging the order of summation, we have

$$\tau(x) = \sum_{j=0}^\infty \frac{(-1)^j}{j!} \{-\gamma\Sigma_A(x) + \tau(0^+)\Sigma_B(x)\} U(x - j), \tag{A4}$$

where

$$\begin{aligned} \Sigma_B(x) &= \sum_{m=j}^\infty \frac{\gamma^m}{(m - j)!} (x - j)^m \\ &= \gamma^j(x - j)^j e^{\gamma(x-j)} \end{aligned}$$

and

$$\begin{aligned} \Sigma_A(x) &= \sum_{m=j}^\infty \frac{\gamma^m}{(m - j)!} \frac{(x - j)^{m+1}}{m + 1} \\ &= \int_j^x \Sigma_B(x) dx \\ &= (-1)^j j! \gamma^{-1} \left\{ -1 + e^{\gamma(x-j)} \sum_{i=0}^j \frac{(-\gamma)^i (x - j)^i}{i!} \right\}. \end{aligned}$$

Substituting the final forms of these summations back into equation (A4), the solution is

$$\tau(x) = [x] + 1 + A(x) + \tau(0^+)B(x), \tag{A5}$$

in which  $[x]$  is the integer part of  $x$ , for example,  $[e] = 2$ , and

$$A(x) = - \sum_{j=0}^{[x]} e^{\gamma(x-j)} \sum_{i=0}^j \frac{(-\gamma)^i (x - j)^i}{i!} \tag{A6}$$

$$B(x) = \sum_{j=0}^{[x]} \frac{(-\gamma)^j (x - j)^j}{j!} e^{\gamma(x-j)}. \tag{A7}$$

When  $\gamma$  is negative, the boundary condition at  $x = 0^+$  causes the last term in equation (A5) to vanish, whereas when  $\gamma$  is positive, the boundary condition at  $x = k/\epsilon$  determines the initial value

$$\tau(0^+) = \frac{-A(k/\epsilon) + A(k/\epsilon - 1)}{B(k/\epsilon) - B(k/\epsilon - 1)}. \tag{A8}$$

The average times to extinction for a population starting at carrying capacity, with  $\gamma$  positive, negative, or zero, are as follows. For  $0 < \gamma < +\infty$ ,

$$\lambda T(k) = [k/\epsilon] + 1 + A(k/\epsilon) + \tau(0^+)B(k/\epsilon). \tag{A9a}$$

For  $-\infty < \gamma < 0$ ,

$$\lambda T(k) = [k/\epsilon] + 1 + A(k/\epsilon). \tag{A9b}$$

For  $\gamma = \pm \infty$  (or  $r = 0$ ), equation (A1) reduces to a difference equation with the solution

$$\lambda T(k) = [k/\epsilon] + 1. \tag{A9c}$$

A high degree of precision is required for numerical evaluation of the exact solutions. Figure 3 was computed with 100 significant digits to evaluate the summations, using Mathematica (Wolfram 1991).

APPROXIMATE SOLUTION BY ASYMPTOTIC METHODS

Figure 3 indicates that the asymptotic form of  $\tau(k/\epsilon)$  is exponential for a positive long-run growth rate,  $r - \lambda\epsilon > 0$ , and linear for a negative long-run growth rate,  $r - \lambda\epsilon < 0$ . To obtain the asymptotic behavior of  $\tau(k/\epsilon)$  with increasing  $k/\epsilon$ , we must first derive the asymptotic form of  $\tau(x)$  with increasing  $x$  for a fixed value of  $k/\epsilon$ . We try a solution to equation (A1) of the form

$$\tau(x) \approx \alpha e^{-\beta x} + ax + b, \tag{A10}$$

where  $\alpha$ ,  $\beta$ ,  $a$ , and  $b$  are constants to be determined. Substituting formula (A10) into equation (A1) gives

$$-\alpha\{\beta - \gamma(e^\beta - 1)\}e^{-\beta x} + a(1 - \gamma) = -\gamma. \tag{A11}$$

Validity of the solution for all  $0 < x < k/\epsilon$  requires that

$$\beta = \gamma(e^\beta - 1) \quad \text{and} \quad a = -\gamma/(1 - \gamma). \tag{A12}$$

This transcendental equation for  $\beta$  admits a real solution only if  $\gamma \geq 0$ . If  $\gamma < 0$ , then we must set  $\alpha = 0$ , and equation (A10) becomes linear. The boundary condition for  $\gamma \geq 0$ , along with equation (A12), determines the constant

$$\alpha = \frac{-\gamma}{(1 - \gamma)\beta} e^{\beta k/\epsilon} \quad \text{for } \gamma > 0. \tag{A13}$$

The last constant can be determined with a small error by requiring (somewhat arbitrarily) for a population with  $\gamma > 0$  and  $k/\epsilon = 0^+$  that  $\tau(0^+) = O(1)$ , which is a constant of order 1, giving

$$b = -\alpha + O(1). \tag{A14}$$

Thus, for  $\gamma > 0$  the mean time to extinction starting from  $x$  is

$$\tau(x) \approx \frac{\gamma}{1 - \gamma} \left\{ e^{\beta k/\epsilon} \left( \frac{1 - e^{-\beta x}}{\beta} \right) - x \right\} + O(1). \tag{A15a}$$

Note that  $\gamma = 1$  is a singular point for the asymptotic solution, which separates two domains of behavior. For  $0 < \gamma < 1$ ,  $\beta$  is positive and the exponential terms dominate for sufficiently large  $x$ . The mean extinction time is then almost independent of the initial



population size (provided that  $\beta x \gg 1$ ) and nearly equal to that starting at the carrying capacity,

$$\tau(k/\epsilon) \approx \frac{\gamma}{1-\gamma} \left( \frac{e^{\beta k/\epsilon} - 1}{\beta} - \frac{k}{\epsilon} \right) + O(1). \quad (\text{A15b})$$

For  $\gamma > 1$ ,  $\beta$  is negative and the linear terms in equation (A15a) dominate when  $-\beta x \gg 1$ ,

$$\tau(k/\epsilon) \approx \frac{-\gamma}{1-\gamma} \left( \frac{k}{\epsilon} + \frac{1}{\beta} \right) + O(1). \quad (\text{A16a})$$

For  $\gamma < 0$ ,  $\alpha = 0$  in equation (A11), and the final constant can be determined with a small error by requiring for a population with  $k/\epsilon = 0^+$  that  $\tau(0^+) = 0$  (since  $r$  is negative), giving  $b = 0$ , and

$$\tau(x) \approx \frac{-\gamma}{1-\gamma} x. \quad (\text{A16b})$$

Thus, when  $0 > \gamma > 1$ , the asymptotic form of the mean extinction time is linear for large  $k/\epsilon$ .

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