

Persistence Times of Populations with Large Random Fluctuations

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The growth of populations which undergo large random fluctuations can be modelled with stochastic differential equations involving Poisson processes. The problem of determining the persistence time is that of finding the time of first passage to some small critical population size. We consider in detail a simple model of logistic growth with additive Poisson disasters of fixed magnitude. The expectation and variability of the persistence time are obtained as solutions of singular differential-difference equations. The dependence of the persistence time of a colonizing species on the parameters of the model is discussed. The model may also be viewed as random harvesting with fixed quotas and a comparison is made between the mean extinction time and those for deterministic models.

INTRODUCTION

Our main purpose here is to illustrate a method of studying the persistence of populations which undergo large fluctuations due to a randomly varying environment. Such fluctuations may be in the form of natural disasters such as those caused by severe weather, floods, fire, disease, food supply devastation by pests, and excessive harvesting or hunting. Large increases, due to favorable climatic conditions for food production or reproduction, sudden influx of immigrants, and decrease in predation, may also occur.

Some of the motivation for considering the theory of such population growth processes comes from field data such as those relating to eruptions and crashes in ungulate populations. Examples are provided by Scheffer (1951) and Klein

(1968), who analysed reindeer fluctuations, and by Mech (1966), who reported a study on moose numbers. The reindeer introduced onto certain Alaskan islands initially underwent a rapid rise in numbers with a subsequent sudden decline. The latter was due not only to overbrowsing and poor physical condition of the animals but also to a severe winter with heavy snow and extreme cold which accentuated the crash. A similar sequence of events was experienced by a moose population on Isle Royale but in this case overbrowsing was accompanied by a spruce budworm infestation and subsequently by a fire. Further examples of populations with sudden decrements are cited in Holling's (1973) review of the catastrophic changes in fish stocks.

These kinds of phenomena are often complex and it is very likely that both deterministic and stochastic components contribute to the observed fluctuations. We will focus on the effects of possibly large random fluctuations when they are superimposed upon deterministic growth. Since models with more than one component are somewhat mathematically intractable when random effects are introduced, we will restrict our attention to single species models.

Previous models for growth in random environments have usually been either of the unrestricted branching process type (e.g., Athreya and Karlin, 1971; Kaplan *et al.*, 1975) or diffusion processes (for many examples and references, see Goel and Richter-Dyn, 1974; May, 1975; Ludwig, 1975; Levandowsky and White, 1977). The trajectories of diffusion processes are continuous and large changes in short times are usually unlikely so that it seems they are inadequate to describe population growth when large fluctuations tend to be the rule rather than the exception.

We will consider one of a class of models in which the sample paths of the population size may have finite jump discontinuities, representing sudden changes in its value. The general model, which may have deterministic, diffusion, and jump components, can be written as the stochastic differential equation of a continuous time, continuous state space Markov process (Gihman and Skorohod, 1972). The persistence time (extinction time) is studied as the time of first passage to some critically small value (possibly zero) of the population size. We will analyse a simple model in which disasters of fixed magnitude occur randomly. The effects of density-independent fluctuations are the subject of another report (Hanson and Tuckwell, 1977).

2. A SIMPLE MODEL OF POPULATION GROWTH WITH RANDOM DISASTERS

As we have seen above, many populations undergo large fluctuations in their numbers in relatively short times. In this section we present a simple model with deterministic and random components.

In order to make the random process $N(t)$, which represents the population size (in numbers or biomass), a Markov process we will assume that disasters

arrive randomly according to a Poisson process. Disasters when they occur, will be assumed to lead to decreases in $N(t)$ of constant magnitude. Between disasters the growth will be assumed logistic.

The symbol $\Pi(\lambda; t)$ will be used to denote a temporally homogeneous Poisson process at time t with rate parameter λ . Assuming this process is initially zero we have, therefore,

$$\Pr\{\Pi(\lambda; t) = k\} = (\lambda t)^k e^{-\lambda t}/k!, \quad k = 0, 1, 2, \dots, \quad (1)$$

and this process has jump discontinuities of magnitude $+1$. Just as it is convenient to use a shorthand notation for stochastic differentials involving a Wiener process, we will use the abbreviation $d\Pi(\lambda; t)$ to represent an infinitesimal increment of a Poisson process. Such an increment has the properties

$$E[d\Pi(\lambda; t)] = \lambda dt, \quad \text{VAR}[d\Pi(\lambda; t)] = \lambda dt \quad (2)$$

and the same probability law as given in (1) with t replaced by dt . Note that a Poisson process has independent increments.

A reasonable model for deterministic growth is provided by the logistic equation

$$dN/dt = rN(1 - N/K), \quad (3)$$

where r (assumed positive) is the net intrinsic growth rate and K is the carrying capacity of the habitat. We assume that in the absence of disasters the population evolves according to this equation. Suppose now that disasters occur according to the Poisson process $\Pi(\lambda; t)$ and that each disaster depletes the population size by ϵ . That is, if a disaster occurs at t_1 we have the jump

$$N(t_1^+) - N(t_1^-) = -\epsilon. \quad (4)$$

Typical sample paths for the model are shown in Fig. 1, both those illustrated having initial value $N(0) = x$. The upper path hovers near the carrying capacity.

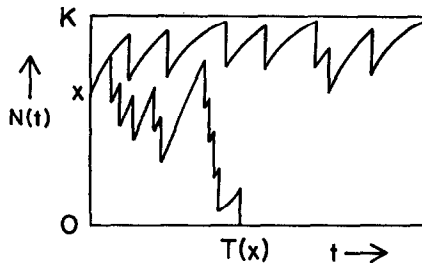


FIG. 1. Two typical trajectories of the population size described by the model equation (5).

The population trajectory depicted by the lower path becomes rapidly extinct at $N = 0$. Note that the population size can never reach K but it can reach zero in a finite time. Hence the extinction time is here taken as the time at which $N(t)$ first reaches zero.

This simple model incorporates only a few of the realities of population growth. Richer models, with density-dependent or -independent terms in the random component, can be expected to have a wider application. Nevertheless, an alternate view of the model, which adds to its interest, is that of randomly harvesting a population whose size is $N(t)$ at a mean rate λ under fixed quotas ϵ .

A description of the model is afforded by the stochastic differential equation

$$dN(t) = rN(t) \left(1 - \frac{N(t)}{K} \right) dt - \epsilon d\Pi(\lambda; t), \quad \epsilon > 0, \quad (5)$$

with $N(0) = x$ and $0 < x < K$. We seek the random variable $T(x)$ which is the time at which $N(t)$ first escapes from the interval $(0, K)$. That is, the length of time that $N(t)$ persists on $(0, K)$, or the extinction time, is

$$T(x) = \inf\{t \mid N(t) \notin (0, K) \mid N(0) = x \in (0, K)\}. \quad (6)$$

Since $N(t)$ cannot escape from $(0, K)$ through K , an exit from this interval implies extinction for the population.

The theory of first exit times for Markov processes whose sample paths may have discontinuities has been investigated by Chuang (1970), Gihman and Skorohod (1972), and Tuckwell (1976). The results of these authors can be used to study the extinction time for the model described by (5). The probability $P(x)$ that $N(t)$ leaves $(0, K)$ in a finite time, given that $N(0) = x$, satisfies the differential-difference equation

$$rx \left(1 - \frac{x}{K} \right) \frac{dP}{dx} + \lambda[P(x - \epsilon) - P(x)] = 0, \quad 0 < x < K, \quad (7)$$

with the boundary condition $P(x) = 1$ if $x \notin (0, K)$. This condition arises because if $N(t)$ starts outside $(0, K)$ then escape is certain. Since $P(x) = 1$ is the solution of (7), $T(x)$ must have finite moments.

The first moment, $E[T(x)]$, which we denote by $F(x)$, satisfies the equation

$$rx \left(1 - \frac{x}{K} \right) \frac{dF}{dx} + \lambda[F(x - \epsilon) - F(x)] = -1, \quad 0 < x < K, \quad (8)$$

with boundary condition $F(x) = 0$ for $x \notin (0, K)$ because if $N(t)$ starts outside $(0, K)$ the expected exit time is zero. The function $F(x)$ is continuous on $(0, K)$ because the deterministic growth is continuous. Another constraint is that $F(x)$ must be bounded on $[0, K]$.

We will also be interested in determining the variability of the extinction time. The second moment, $E[T^2(x)]$, which we denote by $S(x)$, satisfies

$$rx \left(1 - \frac{x}{K}\right) \frac{dS}{dx} + \lambda[S(x - \epsilon) - S(x)] = -2F(x), \quad 0 < x < K, \quad (9)$$

with the same boundary conditions and constraints as $F(x)$.

Scaling

The differential-difference equation governing the expected extinction time for the population in this simple model can be scaled into the form

$$f'(y) = \frac{\gamma k}{y(k - y)} [f(y) - f(y - 1) - 1], \quad (10)$$

so that the new jump size is conveniently one. The change of variable $y = x/\epsilon$ scales x by the jump size and $f(y) = \lambda F(x)$ scales $F(x)$ by the expected waiting time, $1/\lambda$, for one disaster. This introduces the two parameters $\gamma = \lambda/r$ and $k = K/\epsilon$ which appear in (10). The second of these, the ratio of carrying capacity to the magnitude of each disaster, is the number of disasters which would annihilate the population if $N(0) = K$ and $r = 0$ (pure Poisson process).

The parameter γ is the ratio of the disaster rate to the net intrinsic growth rate. In analogy to the bionomic growth ratio (the ratio of discount rate to r , Clark (1976)) γ might be called the "biodisaster-growth ratio." This ratio has interpretations in terms of parameters and concepts introduced in previous works on ecological strategies. For example, the characteristic return time, T_R , is the time it takes for the population size to return to $1/e$ of a small perturbation from equilibrium (May *et al.*, 1974). For the logistic $T_R = 1/r$ (though the return time all the way to equilibrium is infinite). The mean time between disasters in the present model is $1/\lambda$ and this may be considered as the length of time T_H that the habitat remains favorable, especially if the magnitude of ϵ is comparable to K . Thus γ is roughly equivalent to T_R/T_H . Since the generation time may be considered inversely proportional to r , γ also has a meaning similar to the ratio τ/T_H of Southwood *et al.* (1974), τ being the generation time. These authors related various values of τ/T_H to the notions of r - and K -selection introduced by MacArthur and Wilson (1967).

A further interpretation of γ may also be made in terms of these concepts but it seems necessary to simultaneously take into account the value of k which measures the relative magnitude of the population loss with respect to the carrying capacity. A population with large r , would be a successful strategist if λ were large (hence making γ of order unity) only if k were large; but with large r , γ could also be small and a persisting population could tolerate smaller values of k . A population might appear as a K -strategist, independently of r and λ providing $\epsilon \ll K$.

According to Pianka (1970) the r -strategist is correlated with, among other things, high r and a variable or unpredictable environment. However, Stubbs (1977) has noted, using the classification of temporary and permanent habitat animals for r - and K -selection, that some overlap exists between these groups with respect to reproductive rate. She also notes that few animals fit these extremes exactly. It may happen that changes in the environment could place the K -selector in a more unpredictable situation, as is the case of the whooping crane (Miller and Botkin, 1974). As alluded to in the last paragraph, the notions of r - and K -selection would need refining in closely examined populations.

3. METHOD OF SOLUTION

The differential-difference equation (10) can be converted to an ordinary differential equation on any interval of unit length when the solution is known on the previous interval of unit length. The equation is singular at both extinction ($y = 0$) and carrying capacity ($y = k$), so that the intervals $(0, 1)$ and $(k - 1, k)$ must be treated specially.

On $(0, 1)$ the boundary condition gives $f(y - 1) = 0$, so Eq. (10) has the solution

$$f(y) = 1 + c_1/\mu(y), \quad 0 < y < 1, \quad (11)$$

where $\mu(y) = ((k - y)/y)^\gamma$ is the integrating factor. The natural boundary condition $f = 1$ as $y \rightarrow 0^+$ is satisfied. This solution, along with continuity, provides the initial condition for the next subinterval $(1, 2)$. The constant of integration c_1 , must be determined in the last subinterval $(k - 1, k)$ by requiring $f(y)$ to be bounded as $y \rightarrow k^-$. Boundedness of f at carrying capacity implies the natural boundary condition $f(k^-) = f(k^- - 1) + 1$. It is noted that unless c_1 is chosen precisely, according to the boundedness condition, the approximation will be unbounded at $y = k^-$.

For $k = 2$ and certain values of γ , analytic solutions of (10) can be obtained. Thus when $\gamma = \frac{1}{2}$, the constant c_1 can be determined exactly in terms of elliptic functions. In the interval $1 < y < 2$,

$$f(y) = 2 + c_1 I(y)/\mu(y), \quad (12)$$

where

$$I(y) = \frac{2}{3}[F(\phi(y), \hat{k}) - E(\phi(y), \hat{k})] + \frac{\mu(y)}{\mu(y-1)},$$

$$c_1 = 1/[1 - \frac{2}{3}(K(\hat{k}) - E(\hat{k}))] \simeq 2.705,$$

$$\phi(y) = \arcsin \left(\left(\frac{2(2-y)}{3-y} \right)^{1/2} \right),$$

with $\hat{k} = 3^{1/2}/2$, and where $K(\hat{k})$, $E(\hat{k})$, $F(\phi, \hat{k})$, and $E(\phi, \hat{k})$ are elliptic functions (Gradshteyn and Ryzhik, 1963).

For larger values of k we have solved (10) by numerical methods. The integration can be started with $f(y)$ for $0 < y < 1$ as given by (11). The singular behaviour of f near k can be circumvented by introducing the decomposition

$$f(y) = P_1(y) + (Q_1(y) + f_1(y) + c_1 f_2(y))/\mu(y), \quad (13)$$

which explicitly exhibits the singular behaviour of $f(y)$ as $y \rightarrow k^-$ and makes the computation of c_1 a better-posed numerical problem. Here P_1 is a step function corresponding to the expectation of the extinction time for the pure Poisson process and Q_1 is a step function which forces $f_1(y)$ and $f_2(y)$ to be continuous on $(0, k)$. Since the integrating factor appears explicitly in the denominator of (13), f_1 and f_2 will also be bounded as $y \rightarrow k^-$. The functions f_1 and f_2 satisfy equations which are not as singular as (10) and no constants of integration arise in their calculation. Thus c_1 can be determined as the limit of bounded functions rather than as the limit involving unbounded functions which arise in the absence of the above decomposition. In fact, c_1 is determined by requiring that the coefficient of $1/\mu(y)$ vanish as $y \rightarrow k^-$ in order that $f(y)$ be bounded at k^- . Thus

$$c_1 = -(Q_1(k^-) + f_1(k^-))/f_2(k^-).$$

Similar methods were employed to determine the second moment $S(x)$. For further details of the numerical scheme see Hanson (1978).

4. RESULTS AND DISCUSSION

The expectation of the extinction time was calculated using the numerical methods outlined in the last section for values of $\gamma = \lambda/r = 0.5, 1, \text{ and } 2$. In Figs. 2, 3, and 4 we show $\lambda F(x)$, the scaled mean extinction time, plotted against x/ϵ for values of $k = K/\epsilon = 2, 6, \text{ and } 10$, respectively. (The quantity k , the scaled carrying capacity, will be referred to as the carrying capacity in the following.) For reference, in these figures, the expected extinction time for $\gamma = \infty$, corresponding to the case of pure Poisson jumps, is also displayed ($\lambda F(x) = j$ for $j - 1 \leq x/\epsilon < j$, $j = 1$ to k). Note that in all cases $\lambda F(x)$ has a discontinuity at extinction and carrying capacity because of the boundary condition $F(x) = 0$ for x outside the interval $(0, K)$.

When $k = 2$, a disaster wipes out up to half the carrying capacity, and the expected extinction times shown for this case (Fig. 2) do not differ significantly in magnitude from those for the pure Poisson process. The reason is that only a few disasters in a relatively short time interval will often lead to extinction.

The effect of the logistic drift is to make $\lambda F(x)$ continuous at $x/\epsilon = 1$. The deviation from the Poisson case becomes greater the smaller the value of γ , as the frequency of disasters, λ , diminishes relative to the growth rate r .

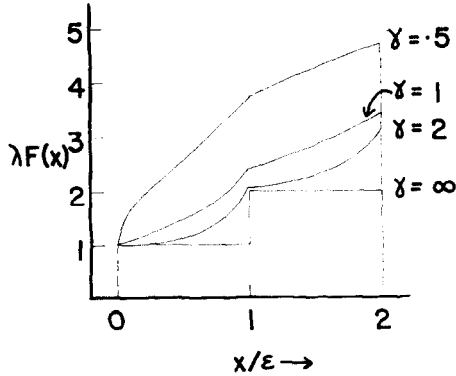


FIG. 2. Expected extinction times in units of the mean time between disasters versus the ratio, x/ϵ , of initial population size to the magnitude of each disaster for $k = K/\epsilon = 2$. The four results are for the different values of the parameter $\gamma = \lambda/r$.

Very noticeable in Fig. 2 is the difference in concavity of $\lambda F(x)$ near $x/\epsilon = 0$ for the various γ . Here, and actually independent of the carrying capacity, the concavity is downward for $0 < \gamma < 1$ and upward for $\gamma \geq 1$. Hence, when $\gamma \geq 1$ a population which attains a size near zero faces an extremely rapid extinction, on average, in comparison with a population whose biodisaster-growth ratio is < 1 . This can be looked upon as a stochastic counterpart of the Allee effect (Allee, 1931) and is particularly prominent on the curve for $k = 2$ and $\gamma = 2$ in Fig. 2.

Turning to the results for larger values of the carrying capacity (Figs. 3 and 4) there emerges an interesting qualitative dependence of the shape of $\lambda F(x)$ on γ . For both $k = 6$ and $k = 10$ and for all values of γ we have considered,

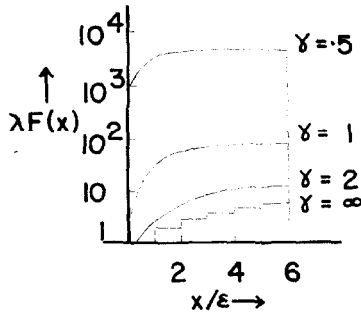


FIG. 3. As in Fig. 2 but with $k = 6$.

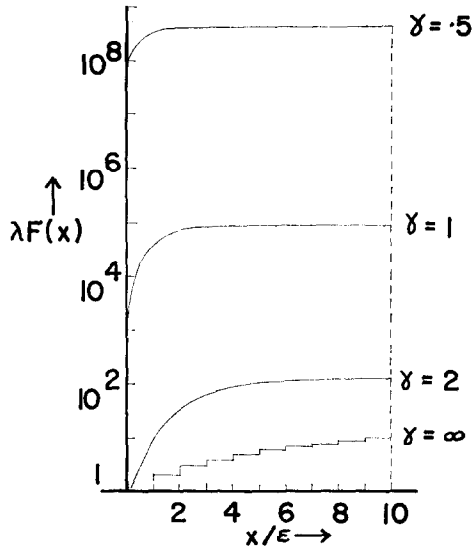


FIG. 4. As in Fig. 2 but with $k = 10$.

a plateau occurs towards the carrying capacity. For $\gamma = 0.5$ the plateaus extend over most of the domain of initial population sizes. If a population is on one of these plateaus, several disasters may occur (even in a relatively short time) and not significantly alter its expected persistence time. A population in this situation might be said to have high resilience (Holling, 1973) in that it is able to rebound after large fluctuations. Here, however, the sensitivity of the mean extinction time, to changes in x , is used as a measure of resilience rather than the probability of extinction as suggested by Holling, since the probability of extinction is 1 in our model. (Such small variations in $\lambda F(x)$ could possibly be related to r - or K -strategies, but we will defer an elaboration on this point until we report the results for density-independent disasters (Hanson and Tuckwell, 1978)).

The plateaus are less extensive for larger γ (e.g., $\gamma = 2$) with comparatively more variation in $F(x)$ with x . Even for intermediate population sizes ($x/\epsilon \simeq 0.5$) a disaster will shift the population size to a value with a much lower expected extinction time. In this case the habitat would be very unstable.

The expected extinction time increases dramatically as the carrying capacity increases. From the numerical results $f(k)$ behaves approximately as $\exp(k/\gamma)$, or faster. Thus, although the model exhibits certain extinction, this will take an extremely long time when the carrying capacity is large for moderate values of γ . For example, when k is only 10 and $\gamma = 1$, the population will have survived, on average, through 10^5 disasters, approximately, for $x > 2\epsilon$.

We may ask how a colonizing population's extinction time depends on the carrying capacity. For this we consider an initial population size $x = K/10$.

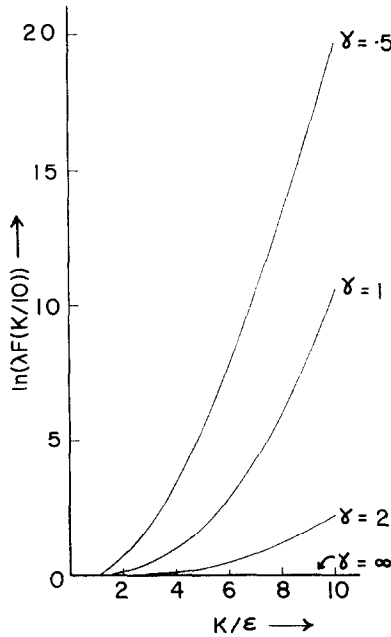


FIG. 5. Dependence of the persistence time of a colonizing species, taken here to be a population with initial size of one-tenth the carrying capacity K , on the parameter $k = K/\epsilon$.

In Fig. 5, $\ln F(K/10)$ is plotted versus $k = K/\epsilon$. It can be seen that the advantage, in the sense of a longer persistence time, grows significantly as k increases, for smaller values of γ . The mean persistence time for our colonizers with $\gamma = 0.5$ grows in an exponential fashion as k increases whereas when $\gamma = 2$ relatively little increase occurs as k increases from 2 to 10. The higher values of γ appear to characterize the less successful colonizers by virtue of their smaller extinction times. We note that this fits another of the purported correlates of an r -strategist (Pianka, 1970) in that the population is kept well below carrying capacity and must frequently recolonize.

To examine the variability of the persistence time we have calculated its coefficient of variation

$$CV_{T(x)} = \frac{\sigma_T}{\mu_T} = \frac{(S(x) - F^2(x))^{1/2}}{F(x)}, \quad (14)$$

as a function of the initial population size. The results for $k = 2, 6$ and 10 are shown in Figs. 6, 7, and 8, respectively, for values of the biodisaster-growth ratio, $\gamma, = 0.5, 1,$ and 2 . Also shown in these figures are the coefficients of variation for the pure Poisson jump process with $CV = 1/j^{1/2}, j - 1 < x/\epsilon \leq j$. When $k = 2$ the CV remains of the same order of magnitude as the Poisson

result for all the values of γ shown in Fig. 6. The discontinuity in the Poisson result has a strong influence when the drift is present in the growth process because as $\gamma \rightarrow \infty$ the CV for our model must asymptote towards the Poisson limit. This accommodation of the discontinuities resembles the nonuniform approximation of discontinuous signals by truncated Fourier series (Gibbs phenomenon).

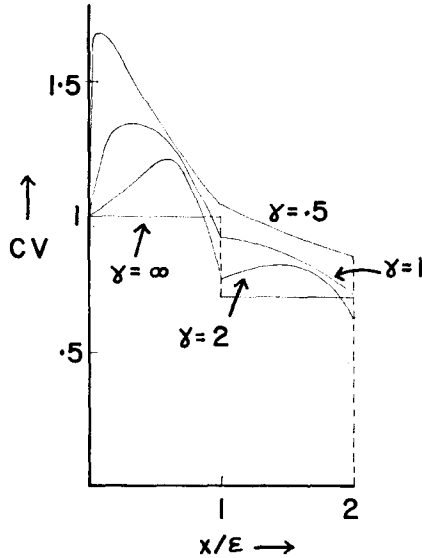


FIG. 6. Coefficient of variation of the extinction time versus initial population size for various values of the "biodisaster-growth ratio," γ , when $k = 2$.

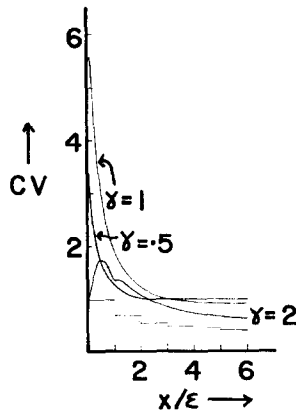


FIG. 7. As in Fig. 6, but with $k = 6$.

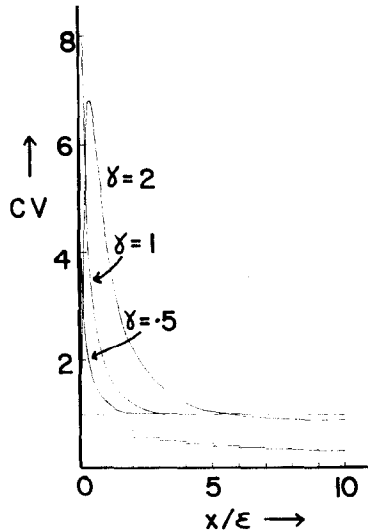


FIG. 8. As in Fig. 6, but with $k = 10$.

The greatest change in the coefficient of variation takes place when the population is just one disaster away from extinction ($0 < x/\epsilon < 1$). The population size at which this greatest change occurs becomes closer to zero as the biodisaster-growth ratio decreases. This is because an escape (temporary) away from small population sizes is more probable when γ is small.

Near carrying capacity, however, the CV has relatively little change in value, especially for $k \geq 6$. For small γ the Poisson disasters do not dominate the behaviour of the population size. The mean and the standard deviation both become infinite and the CV approaches unity. This behaviour of the CV is even more pronounced for larger carrying capacities. For example, when $k = 10$ and $\gamma = 0.5$, the CV of the persistence time is very close to 1 for $1 < x/\epsilon < 10$. Again, in all cases, at the other extreme, when γ is very large, the CV approaches a value closer to the Poisson case ($\gamma = \infty$).

5. APPLICATION AS A RANDOM HARVESTING MODEL

As suggested in Section 2, the model described by (5) can also be considered as a simple stochastic model for harvesting at fixed quotas. Since the expectation of $\epsilon d\Pi(\lambda; t)$ is $\epsilon\lambda dt$, a possible deterministic analog of (5) would be

$$d\bar{N}/dt = r\bar{N}(1 - \bar{N}/K) - H, \quad (15)$$

where $H = \epsilon\lambda$ is the constant harvesting rate. Another deterministic analog would consist of the harvesting of fixed amounts ϵ at fixed intervals $1/\lambda$, but

for the present we are interested in comparing the results for the stochastic model with known results for deterministic constant rate harvesting.

The model described by (15) is one of those studied by Brauer and Sanchez (1975). Its equilibrium solutions have the property that harvesting at $H = H_{\text{MSY}} = rK/4$ when $\bar{N}(0) = K/4$ results in a maximum sustainable yield (MSY). This MSY equilibrium is semistable in that extinction occurs for either $\bar{N}(0) < K/2$ or $H > H_{\text{MSY}}$, but a stable equilibrium is approached when $K/2 < \bar{N}(0) < K$ and $H < H_{\text{MSY}}$. Beddington and May (1977) reported deterministic recovery times for small perturbations from the stable equilibria when $H < H_{\text{MSY}}$, while Brauer and Sanchez (1975) reported the deterministic extinction times for $H > H_{\text{MSY}}$. Extinction takes an infinite time when $H < H_{\text{MSY}}$ and $\bar{N}(0) < K/2$.

Brauer and Sanchez applied their analysis of the model described by (15) to the harvesting of sandhill cranes, which was studied earlier by Miller and Botkin (1974), using a more complicated many-parameter model with age structure. Using parameter values deduced from Miller and Botkin's data, Brauer and Sanchez calculated extinction times comparable to those obtained by Miller and Botkin. In Fig. 9 mean extinction times for the present model are compared, as a function of H (which is $\epsilon\lambda$ in our case), with both Miller and Botkin's and Brauer and Sanchez's deterministic results.

Miller and Botkin estimated that the carrying capacity of the sandhill cranes was $K = 194,600$ and their data indicate that H_{MSY} is approximately 4400 per year. (Note that Brauer and Sanchez originally used an estimate of 4800 per year for H_{MSY} . However, when their results are recomputed using the value 4400/year, there is improved agreement with Miller and Botkin's result especially near the critical value, H_{MSY}). For the stochastic model, prescribed values of K and r are not sufficient to fix the extinction time as a single-valued function of the harvest rate $H = \epsilon\lambda$. Either ϵ or λ have to be chosen or estimated. The principal purpose in this section is to compare the present stochastic results with the deterministic results of Brauer and Sanchez and to give an indication of the variation of the stochastic extinction times.

The stochastic results in Fig. 9 are for $\gamma = 0.5$ and 2. These data have the same source as those of Figs. 2, 3, and 4 with additional calculations to complete the curves. Using assigned parameter values for $k = K/\epsilon$ and $\gamma = \lambda/r$, the above estimates for K and r and computed nondimensional extinction times $f(k) = \lambda F(K)$, the dimensional extinction times $F(K)$ (in years), and the harvest rate $H = \epsilon\lambda$ (in 1/years) are computed. For example, from Fig. 3 with $k = 6$ and $\gamma = 2$, $f(k) \simeq 13.6$ so that $\epsilon = K/k \simeq 32,400$, $\lambda = \gamma r \simeq 0.18/\text{year}$, $H = \epsilon\lambda \simeq 5,900/\text{year}$, and the extinction time is $F(K) = f(k)/\lambda \simeq 76$ years. For fixed γ as in the graph, as H decreases toward zero, ϵ also decreases, but $k = K/\epsilon$ increases so that extinction takes longer as H gets smaller, since there are many more steps to extinction. The jump in $F(K)$ for $\gamma = 0.5$ occurs at $k = 1$ and is due to the transition from the case of a single jump to extinction

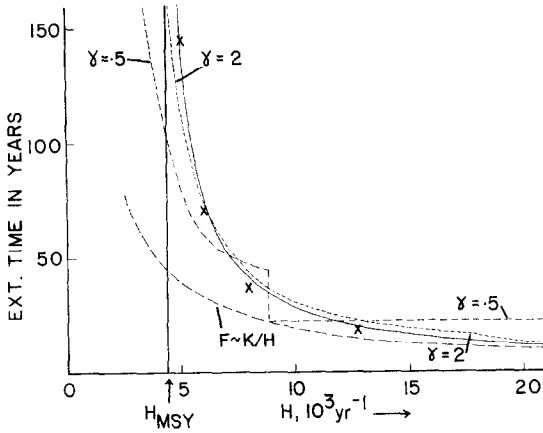


FIG. 9. Extinction time (expected value for the stochastic model) versus harvest rate H . The crosses denote the data of Miller and Botkin (1974) for Sandhill Crane. The solid curve is after Brauer and Sanchez (1975), whereas the dashed lines give the results for the present model with $\gamma = 0.5, 2$, and ∞ (Poisson limit). Further explanation is given in the text.

to the case where more than one jump is required. The jump for $\gamma = 2$ at $k = 1$ is not in the range of Fig. 9. The values $\gamma = 0.5$ and $\gamma = 2$ give extinction time values similar to those of Brauer and Sanchez except below H_{MSY} . The value $\gamma = 0.5$ represents a harvest rate half that of the intrinsic growth rate, while $\gamma = 2$ represents twice the growth rate.

The effective harvest frequencies for the sandhill cranes may be much higher than the values indicated by $\gamma = 0.5$ or 2. Miller and Botkin state that most harvesting or hunting occurs during the fall migration, which might indicate that $\lambda \simeq 1$ or $\gamma \simeq 11.1$. They also assume that the harvest is independent of the population size. However, the assumption of exponential waiting times for harvesting implied by the underlying Poisson process probably would not be a very good assumption when applied to this type of harvesting; but neither is the constant harvest rate assumption in the deterministic models. If we overlook these drawbacks, for very large frequencies λ or large γ , the expected extinction time can be approximated by the Poisson limit,

$$F(K) \simeq k/\lambda = K/H. \quad (16)$$

This is, in fact, the number of harvests in the carrying capacity in absence of deterministic growth (i.e., also the $r \rightarrow 0^+$ limit) and is plotted in Fig. 9. This approximation is nonuniform in ϵ and λ and must be viewed with caution for large λ and small H , since if λ is large, ϵ must be small to make H small. Small ϵ , then implies large $k = K/\epsilon$ and correspondingly large extinction

times. More harvests are required for extinction than are predicted by (16). Thus for $\gamma \simeq 11.1/\text{year}$ and $H \simeq 10,000/\text{year}$, $F \simeq 19.4$ years, and $\epsilon = 10,000$.

It can be seen that for harvest rates greater than H_{MSY} , the mean extinction times for the random harvesting model do not differ significantly from those for either of the deterministic models. In contrast, for $H < H_{\text{MSY}}$ the stochastic model predicts finite, though usually very large, mean extinction times, whereas the deterministic models predict no extinction if $\bar{N}(0) > K/2$ or extinction in an infinite time for $N(0) < K/2$. We consider the random model's prediction of a finite mean extinction time under these conditions is a more realistic one, since harvesting could never be purely deterministic.

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