

## Logistic Growth with Random Density Independent Disasters

FLOYD B. HANSON

*Department of Mathematics, University of Illinois at Chicago Circle,  
Chicago, Illinois 60680*

AND

HENRY C. TUCKWELL\*

*Department of Biomathematics, University of California, Los Angeles, California 90024*

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A stochastic differential equation for a discontinuous Markov process is employed to model the magnitude of a population which grows logistically between disasters which are proportional to the current population size (density independent disasters). The expected persistence or extinction time satisfies a singular differential-difference equation. When the number of disasters, in the absence of recovery, between carrying capacity and extinction is two, analytical expressions are found for the mean persistence time. A comparison is made with the previously studied case of decrements of constant magnitude. When the two problems are suitably normalized, the mean survival times are quite different for the two models, especially in a critical range of initial population sizes near extinction. The expected survival time of a colonizing species is discussed quantitatively in terms of the parameters of the model. Insight into the nature of the probability density of the survival time is obtained by means of computer simulations. The densities resemble gamma densities and long tails appear when the disasters are density independent, implying a small change of long term survival. When the number of consecutive disasters which take the population from carrying capacity to extinction is large, a singular decomposition is employed to solve the differential-difference equation for the mean persistence time. The results are discussed in terms of population strategies in hazardous environments.

### INTRODUCTION

In this paper we will consider a model for population growth which is deterministic between randomly occurring disasters. A disaster, when it occurs, removes a given fraction of the population. This type of disaster

\* New address: Department of Mathematics, Monash University, Clayton, Victoria, 3168, Australia.

model should give a more realistic description of population growth than the constant size disaster model in our previous investigation (Hanson and Tuckwell, 1978). We will find that a population's persistence time is radically increased for a critical range of initial population sizes near extinction in comparison to the case where a disaster removes a constant number of individuals.

Population trajectories often exhibit large random fluctuations. This indicates that population growth models with continuous sample paths (see, for example, Goel and Richter-Dyn, 1974 or May, 1975) may not provide an adequate representation of the underlying dynamical processes. An example of a trajectory with large fluctuations is shown in Fig. 1A. The population number is given in thousands for moose on Isle Royale in Lake Superior after an initial immigration to this habitat around 1905 (Mech, 1966). Various disasters beset this population after it achieved its maximum around 1930, including overgrazing and further damage to its food supply by spruce budworm and by fire in 1936. The growth curve of a population of reindeer on the Pribilof Islands in Fig. 1B shows an almost deterministic growth between 1910 and 1938 followed by some abrupt crashes of various magnitudes (Scheffer, 1951). One of the crashes was attributed to overgrazing and another to a severe winter in 1940. The data of Fig. 1C show fluctuations in sheep numbers (in millions) for New South Wales between 1860 and 1972. The magnitude of the decrements shows considerable variability. An interesting deterministic model for this

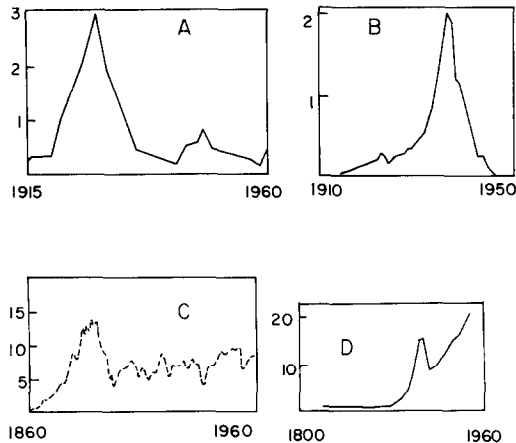


FIG. 1. Population trajectories which exhibit large fluctuations in relatively short times. A. Moose numbers on Isle Royale (Mech, 1966). B. Reindeer population sizes on the Pribilof Islands (Scheffer, 1951). C. Sheep numbers in western New South Wales (Caughley, 1976). D. North Atlantic gannet colonies off southwest Britain (Krebs, 1972). Units of population sizes are thousands except in C where the unit is a million.

population was put forth by Caughly (1976), but random effects, which surely are present, were ignored. A final field example is shown in Fig. 1D, where the number (in thousands) of North Atlantic gannet is plotted from 1820 to 1950 (see Krebs, 1972).

The models we will consider consist of deterministic growth with random fluctuations. We do not claim that the temporal evolution of the populations in the above examples is described completely by the models but that certain features of the growth processes of these populations will be represented.

In this paper we will investigate the following special case of logistic growth with density independent disasters:

$$\begin{aligned}
 dN(t) &= rN(t)(1 - N(t)/K) dt - \varepsilon N(t) d\Pi(t; \lambda), \\
 N(0) &= x, \quad 0 < \varepsilon < 1, \quad r > 0.
 \end{aligned}
 \tag{1}$$

That is, we have disasters occurring at times of events in a single Poisson process,  $\Pi(t; \lambda)$ , with rate parameter  $\lambda$ . The increment of this process in a time interval of length,  $dt$ , has the expectation

$$E[d\Pi(t; \lambda)] = \lambda dt \tag{2}$$

and variance

$$\text{VAR}[d\Pi(t; \lambda)] = \lambda dt. \tag{3}$$

If a disaster occurs at time  $t$ , then

$$N(t^+) - N(t^-) = -\varepsilon N(t^-), \tag{4}$$

whereas between disasters,  $N(t)$  grows logistically. An idea of how  $N(t)$  evolves can be obtained by the examination of Fig. 2, where some selected sample paths are sketched.

If we assume that the initial population size,  $x$ , is between 0 and  $K$  with  $0 < \varepsilon < 1$ , it is apparent that  $N(t)$  satisfying (1) will remain confined to the

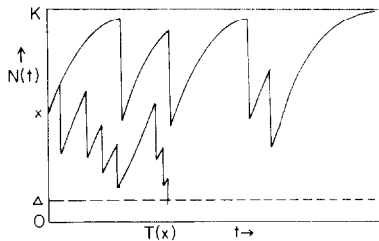


FIG. 2. Possible sample paths for the model with logistic population growth and large density independent decrements described by the stochastic differential equation (1). The initial population size is  $x$  and the extinction time is  $T(x)$ .

interval  $(0, K)$  for all time.  $K$  is unattainable in finite time because this is an asymptote for the logistic growth process. The value zero is inaccessible because the smaller  $N(t)$  gets, the smaller the population loss will be when a disaster strikes. Even in the absence of the logistic recovery the population would drop to  $(1 - \varepsilon)^n x$  after  $n$  disasters. Note, however, that if  $\varepsilon \geq 1$ , just one event in  $\Pi(t; \lambda)$  will annihilate the population, so that the persistence time would be an exponentially distributed random variable, as is the waiting time for the first event in a Poisson process.

For the model described by (1), zero is unattainable in a finite time and extinction can be defined as the event that  $N(t)$  reaches zero. Since we are interested in the persistence of a population when (1) is the governing equation, we must, for this model, define "effective extinction" as the passage of  $N(t)$  to some small value  $\Delta \in (0, K)$ , with  $x > \Delta$ . If, for example,  $N(t)$  is the continuous approximation to the number of individuals, then clearly when  $N(t)$  drops below one individual the population is not only "effectively extinct" but extinct in the true sense. The effective extinction level might also be thought of as corresponding to the case of critical depensation (see, for instance, Clark, 1976), where once the population drops below a certain level, it can never recover. Reproduction can become practically impossible for small population sizes. When  $\Delta \in (0, K)$ , the population will become effectively extinct after one disaster whenever  $\varepsilon \geq (1 - \Delta/K)$ , since then  $(1 - \varepsilon)x \leq (\Delta/K)x < \Delta$ ; i.e., any disaster knocks the population down below  $\Delta$ .

Let  $F(x)$  be the expectation of the random variable

$$T(x) = \inf_t [t \mid N(t) \notin (\Delta, K); N(0) = x \in (\Delta, K)],$$

which we consider to be the effective extinction time or persistence time of the population with initial value  $x$ . From Gihman and Skorohod (1972), and also Tuckwell (1976), we find that  $F(x)$  satisfies the following functional differential equation

$$rx(1 - x/K)F'(x) + \lambda[F((1 - \varepsilon)x) - F(x)] = -1, \quad x \in (\Delta, K). \quad (5)$$

$F(x)$ , in addition, satisfies the boundary condition that  $F(x) = 0$  when  $x \notin (\Delta, K)$  and  $F(x)$  is continuous on  $(\Delta, K)$ . In particular, we will seek a solution of (5) for which  $F$  is bounded everywhere.

The most simple case is that in which there is only one jump to extinction. This occurs when  $\varepsilon \geq 1 - \Delta/K$ , so that  $(1 - \varepsilon)x \leq \Delta$ ,  $F((1 - \varepsilon)x) = 0$  and boundedness requires that  $F(x) = 1/\lambda$  when  $x \in (\Delta, K)$ . The multiple jump or disaster cases will be considered in the next and later sections.

In the case previously considered by Hanson and Tuckwell (1978), an application was made to the problem of harvesting under fixed quotas according to a Poisson process. The model we will consider in detail below

can also be viewed as a harvesting model where the catch is proportional to the population size. A deterministic analog is the Schaefer model (Clark, 1976),

$$d\bar{N}/dt = r\bar{N}(t)(1 - \bar{N}(t)/K) - qE\bar{N}(t),$$

where  $qE$  is the effective harvesting effort. The effective effort should more generally have a stochastic component with  $\lambda\varepsilon$  corresponding to  $qE$ .

## 2. THE ANALYTIC METHOD

The method of analysis of the functional differential equation (5) is illustrated for the case in which the Poisson process requires exactly two jumps to reach "effective extinction" at  $\Delta$  starting from  $K$ . Hence we assume that  $K(1 - \varepsilon)^2 = \Delta$  or that  $\varepsilon = 1 - \sqrt{\Delta/K}$ . The equation can be solved by the "method of steps" (see, for example, El'sgol'ts and Norkin, 1973), in which we successively integrate on the first step from the initial point  $x_0 = \Delta$  to the geometric mean  $x_1 = \sqrt{\Delta K} = \Delta/(1 - \varepsilon)$  and then on the second step from  $x_1$  to the final point  $x_2 = K$ . On the first step,  $F((1 - \varepsilon)x) = 0$  since  $(1 - \varepsilon)x \leq \Delta$  and since the boundary condition requires zero expected extinction time when outside the interval of interest,  $(\Delta, K)$ . The functional differential equation becomes an ordinary differential equation,

$$rx(1 - x/K)F'(x) - \lambda F(x) = -1, \quad x \in (\Delta, x_1). \quad (6)$$

The solution is

$$\lambda F(x) = 1 + C/u(x), \quad x \in (\Delta, x_1), \quad (7)$$

where the integrating factor is given by

$$u(x) = (K/x - 1)^2.$$

The parameter  $\gamma = \lambda/r$  is the ratio of the disaster rate to the net intrinsic rate of growth and in Hanson and Tuckwell (1978)  $\gamma$  was called the "biodisaster-growth ratio." This parameter may also be thought of as the ratio of typical growth time,  $1/r$ , to the stable habitat time,  $1/\lambda$ . The constant of integration,  $C$ , cannot be determined on the first step,  $(\Delta, x_1)$ , and must be saved to satisfy the boundedness condition at  $x = K^-$ . An important feature that distinguishes Eq. (5) from other functional differential equations or differential-difference equations is that it is singular at its final end point,  $K$ , and hence its treatment is very different from the standard treatment of nonsingular cases.

On the second step,  $x \in (x_1, K)$ ,  $\lambda F((1 - \varepsilon)x)$  is known through (7) when evaluated at the functional argument,  $((1 - \varepsilon)x)$ . Upon substitution,  $F(x)$  again satisfies an ordinary differential equation,

$$(u(x)(\lambda F(x) - 2))' = Cu'(x)/u((1 - \varepsilon)x). \quad (8)$$

Continuity requires that the initial condition at  $x_1$  come from (7). One integration then gives the solution,

$$\lambda F(x) = 2 + [-u(x_1) + C(1 - I(x))]/u(x), \quad x \in (x_1, K), \quad (9)$$

where

$$I(x) = - \int_{x_1}^x dz u'(z)/u((1 - \varepsilon)z). \quad (10)$$

Since  $u(K^-) = 0$  and since we seek a bounded  $F$ , the coefficient of  $1/u(x)$  in (9) must vanish, so that

$$C = u(x_1)/(1 - I(K)),$$

and the solution to (5) is completely determined, once  $I(x)$  is evaluated.

Results for various values of  $\gamma$  are shown in Fig. 3 with  $K = 10$  and  $\Delta = 1$ . As expected, the extinction times are monotonically increasing functions of the initial population size. The expected extinction time,  $\lambda F(x)$ , decreases with  $\gamma$  and hence increases with  $r$  but decreases with  $\lambda$ . For large  $\gamma$ , e.g.,

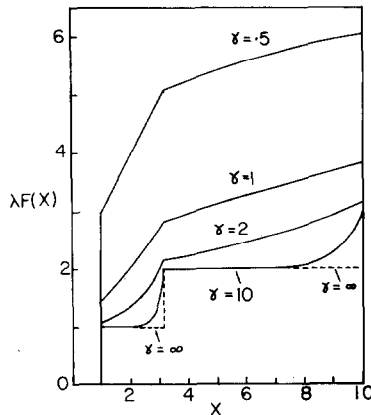


FIG. 3. Expected survival times of populations with density independent disasters (Eq. (1)) plotted against initial population size. These are analytic results; the number of consecutive disasters from carrying capacity to extinction level is two. The quantity  $\gamma$  is the biodisaster-growth ratio defined in the text,  $\Delta = 1$ ,  $K = 10$ ,  $\varepsilon = 0.683$  and the unit is the average time between disasters.

$\gamma = 10$ , the expected extinction time is close to the discontinuous pure Poisson limit ( $\gamma = \infty$ ). One may think of the larger  $\gamma$  values (e.g.,  $\gamma \geq 1$  or  $r \leq \lambda$ ) as corresponding to the “temporary habitat animals” and the smaller  $\gamma$  values (e.g.,  $\gamma < 1$  or  $r > \lambda$ ) as corresponding to the “permanent habitat animals” (Stubbs, 1977). The version of the terms *r*-strategist or *K*-strategist as used by Southwood *et al.* (1974) can also be used but Stubb’s use of the terms “temporary” and “permanent” seems more appropriate for models based on the logistic plus random environmental effects rather than on the logistic model alone. The temporary habitat animal is forced to reinvade to compensate for its small extinction time.

The results can also be viewed from the perspective of the colonizer, entering a habitat which no other members of the species occupy. This point of view is exhibited by plotting  $\lambda F(\Delta^+)$  versus the relative disaster rate,  $\epsilon$ , in Fig. 4. Both increasing  $\epsilon$  and increasing  $\gamma$  have an effect of decreasing the expected extinction time. This effect can be simply motivated by examining the conditional expectation of  $dN$ ,

$$E[dN | N(t) = n] = rn(1 - n/K) dt - \epsilon n \lambda dt.$$

In this form the effective intrinsic growth rate is  $r^* = r(1 - \gamma\epsilon)$ . Hence, increasing  $\gamma$  or  $\epsilon$  has the same qualitative effect of decreasing  $r$  with a corresponding decrease in  $\lambda F(\Delta^+)$ . The quantitative effect of  $\gamma$  and  $\epsilon$  will be discussed later. In fact, the linear or density independent disaster can be

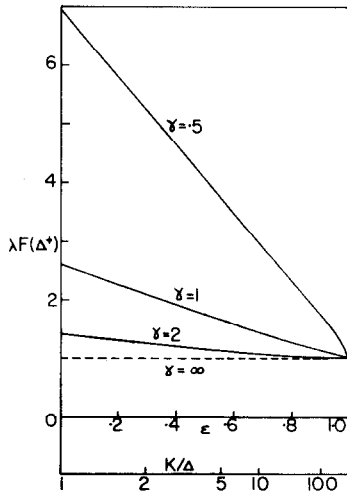


FIG. 4. Calculated mean persistence times for colonizing populations, defined as those whose initial numbers border on the persistence level. At fixed values of  $\gamma$  we show the dependence on the parameter  $\epsilon$  which is the fraction of the population removed by a disaster when it strikes. These are analytic results with two consecutive disasters from carrying capacity to extinction.

viewed as a disaster which principally modifies  $r$ , since  $r$  is the coefficient of the density independent term in the logistic growth model. For fixed  $\gamma$ , the expected extinction time varies almost linearly with  $\varepsilon$ , with the more drastic changes occurring for the smaller values of  $\gamma$ . This may indicate that more frequent small disasters may be less harmful in terms of  $\lambda F(\Delta^+)$  than less frequent larger disasters with the same value of the product  $\gamma\varepsilon$ . When  $\gamma = 2$ ,  $\lambda F(\Delta^+)$  changes very little with  $\varepsilon$  from its maximum value near unity. This can be cast as a characteristic of a "fugitive species" (see MacArthur and Wilson, 1967) that are well adapted to temporary or fast-changing habitats.

It is instructive to compare the solution of (6) for the density independent disasters with that of the corresponding constant disasters, which is the special case considered in Hanson and Tuckwell (1978),

$$dN_c(t) = rN_c(t)(1 - N_c(t)/K) dt - \varepsilon_c d\Pi(t; \lambda), \quad N_c(0) = x, \quad (11)$$

where the constant size is denoted by  $\varepsilon_c$ . This model is now reconsidered on the interval  $(\Delta, K)$  in order that a maximum number of variables will be the same for the two compared models. An important difference between this constant disaster model and the linear or density independent disaster model is that extinction in finite time is possible when  $\Delta = 0$  for (11) while it is not possible for (1). For the constant disaster model, the restriction to two jumps from  $K$  to  $\Delta$  requires that  $K - 2\varepsilon_c = \Delta$  or that  $\varepsilon_c = (K - \Delta)/2$ . The corresponding equation for the expected extinction time,  $\lambda F_c(x)$ , is the differential-difference equation,

$$rx(1 - x/K)F'_c(x) + \lambda[F_c(x - \varepsilon_c) - F_c(x)] = -1, \quad x \in (\Delta, K), \quad (12)$$

with the same constraints as those associated with (5).

The method of solution of Eq. (12) is similar to that for  $\lambda F(x)$  except for the choice of steps, which become  $(\Delta, x_c)$  and  $(x_c, K)$ , where  $x_c = (\Delta + K)/2 = \Delta + \varepsilon_c$  is the arithmetic mean of  $\Delta$  and  $K$ . The solution is given by

$$\begin{aligned} \lambda F_c(x) &= 1 + k/u(x), & \Delta < x \leq x_c, \\ &= 2 + [-u(x_c) + k(1 - I_c(x))]/u(x), & x_c \leq x < K, \end{aligned} \quad (13)$$

where

$$I_c(x) = - \int_{x_c}^x dz u'(z)/u(z - \varepsilon_c). \quad (14)$$

Boundedness of  $\lambda F_c(x)$  at  $x = K^-$  requires that the constant of integration be

$$k = u(x_c)/(1 - I_c(K)). \quad (15)$$

In order to make the comparison of the two models specific, we set  $\gamma = 1$ , in which case an explicit solution is found for the linear disaster:

$$\begin{aligned}\lambda F(x) &= 1 + \frac{(K - x_1)x}{x_1(K - x)} \Big/ [1 - I(K)], & \Delta < x \leq x_1, \\ &= 2 + \frac{(K - x_1)x}{x_1(K - x)} \ln \left( \frac{K^2 - x_1x}{(K - x_1)x} \right) \Big/ [1 - I(K)], & x_1 \leq x < K,\end{aligned}\tag{16}$$

where

$$I(K) = \frac{x_1}{K} \ln \left( \frac{K + x_1}{x_1} \right),$$

and for the constant disaster:

$$\begin{aligned}\lambda F_c(x) &= 1 + \frac{x}{x_c} \frac{K - x_c}{K - x} \Big/ [1 - I_c(K)], & \Delta < x \leq x_c, \\ &= 2 + \frac{x}{x_c} \frac{K - x_c}{K - x} [I_c(K) - I_c(x)] / [1 - I_c(K)], & x_c \leq x < K,\end{aligned}\tag{17}$$

where

$$I_c(K) = \frac{K^2}{(2K - x_c)^2} \ln \left( \frac{2K}{x_c} \right) - \frac{(K - x_c)^2}{x_c(2K - x_c)}$$

and

$$\begin{aligned}I_c(K) - I_c(x) &= \frac{K^2}{(2K - x_c)^2} \ln \left( 1 - \frac{(2K - x_c)(K - x)}{(K - x_c)x} \right) - \frac{(K - x_c)(K - x)}{(2K - x_c)x}.\end{aligned}$$

In Figs. 5A and 5B, the solutions given in (16) and (17) are plotted against the initial population size with  $\Delta = 1$  and with  $K = 10$  and 100, respectively. Our first observation is that for all four solutions shown in Figs. 5A and 5B, the magnitude of  $\lambda F(x)$  is markedly greater than that of  $\lambda F_c(x)$  between  $\Delta$  and  $x_c$ , independent of the magnitude of  $K$ . In fact, in Fig. 5B when  $x = x_1$  and  $K = 100$ ,  $\lambda F(x)$  is about twice  $\lambda F_c(x)$ . Further,  $\lambda F_c(x)$  is less than  $\lambda F(x)$  for all  $x$  except near  $K$  when  $K$  is large. Generally, the population with disasters proportional to its magnitude tends to persist longer because the closer its size gets to  $\Delta$ , the smaller are the decrements and the greater the effect of the recovery due to deterministic growth.

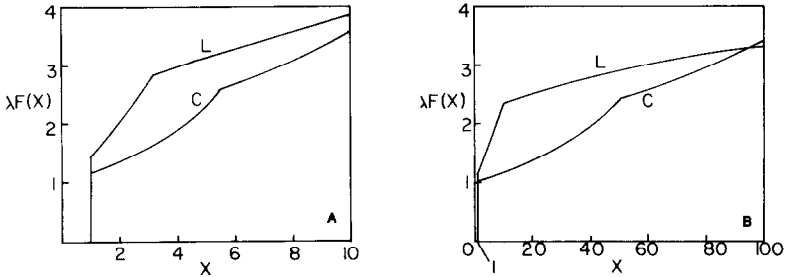


FIG. 5. (A) Mean extinction times for the models with density independent or linear (L) disasters and with disasters of constant magnitude (C). The normalization is that two disasters without recovery take the population to extinction from carrying capacity. The initial population level is  $x$ ,  $K/\Delta = 10$ ,  $\gamma = 1$  and the results are obtained analytically for both models. (B) As in (A) except with a ratio  $K/\Delta = 100$ .

However, the reason that the mean persistence times do not differ much near  $K$ , whether the disasters are of constant size or proportional to population size, seems to be the dominance of the fact that the "effective extinction point,"  $\Delta = 1$ , is at least two disasters away from carrying capacity.

It is also apparent that for fixed  $x$ ,  $\lambda F(x)$  and  $\lambda F_c(x)$  are monotonically decreasing functions of  $K$  for fixed  $\gamma$  and a fixed number of jumps between carrying capacity and extinction. Mathematically, this can be readily explained by considering at fixed  $N$  and  $N_c$  the ratios of the logistic and Poisson contributions to the first infinitesimal moment of the processes described by (1) and (11). We have for these ratios, in the case of  $n$  jumps from  $K$  to  $\Delta$ ,

$$R = [rN(1 - N/K)]/[\lambda \varepsilon N] = (K - N)/[\gamma K(1 - (\Delta/K)^{1/n})], \quad (18)$$

$$R_c = [rN_c(1 - N_c/K)]/[\lambda \varepsilon_c] = 2^n N_c(K - N_c)/[\gamma K(K - \Delta)]. \quad (19)$$

Since  $\partial R/\partial K$  and  $\partial R_c/\partial K$  are both negative, the strength of the recovery component relative to the decremental component is a decreasing function of  $K$  in both cases.

### 3. COMPUTER SIMULATIONS

In the preceding section we found the expected extinction time for the two models described by the stochastic differential equations (1) and (11), for certain values of the parameters. In our previous paper we also determined the second moment and hence the coefficient of variation of  $T(x)$  for the model with disasters of constant magnitude. The second moment of  $T(x)$ ,

which is designated  $S(x)$ , can be found by solving the functional differential equation

$$rx(1 - x/K) S'(x) + \lambda[S((1 - \varepsilon)x) - S(x)] = -2F(x), \quad (20)$$

where  $S(x)$  is subject to the same constraints as for  $F(x)$ . Similar equations can be written down for the higher moments of  $T(x)$  but rather than seeking to obtain a description of this random variable via its moments, we sought to gain insight into the nature of its probability density function. We have not yet found this density analytically and so have therefore decided to investigate its nature in a preliminary fashion by studying the results of computer simulations.

One of the main interests is to compare the densities of the persistence times when disasters are constant as opposed to the case where the magnitude of each disaster is proportional to the population size. Since the two processes described by the stochastic equations (1) and (11) differ qualitatively in that  $N=0$  is accessible in one case but not in the other, a suitable "normalizing" situation had to be devised in order to make a meaningful comparison. We therefore chose "extinction" to be the attainment of the population level  $N=1$  in both cases. The critical population sizes for the density independent disaster model (1) were set at  $K$  or  $\sqrt{K}$ , with  $\varepsilon = 1 - 1/\sqrt{K}$ . For Eq. (11) the initial population levels were either  $K$  or  $(K+1)/2$  with  $\varepsilon_c = (K-1)/2$ . Thus for both models, the initial values of the processes are such that the occurrence of either one or two disasters would lead to extinction as defined above. In these simulations we set  $r = \lambda = 1$  and employed the values of  $K = 2, 10, \text{ and } 100$ . For each set of parameters and initial values, 5000 sample paths were followed to "extinction." The histograms for the extinction times for the 12 simulation studies are shown in Figs. 6A to L, where  $K$  increases from left to right.

The top and second rows of histograms are for density independent and constant disasters, respectively, when the initial population size is just one disaster away from extinction. The lower two rows of densities have initial population levels at carrying capacity. The sample means and variances of the persistence times are given in Table I along with the exact calculated means. The latter, of course, provided useful checks of the accuracy of the simulation studies.

It can be seen that the densities of the extinction time, for both models, when  $K=2$  and  $K=10$ , resemble gamma densities of fairly low order. The results are not unlike those for the waiting times for the generation of nerve impulses in Markov models (Tuckwell, 1978). When the initial population size is  $K$ , the extinction times are, for  $K=100$ , approximately normal random variables, which is the case for higher order gamma variates.

These simulations do not exhibit very much qualitative difference in the

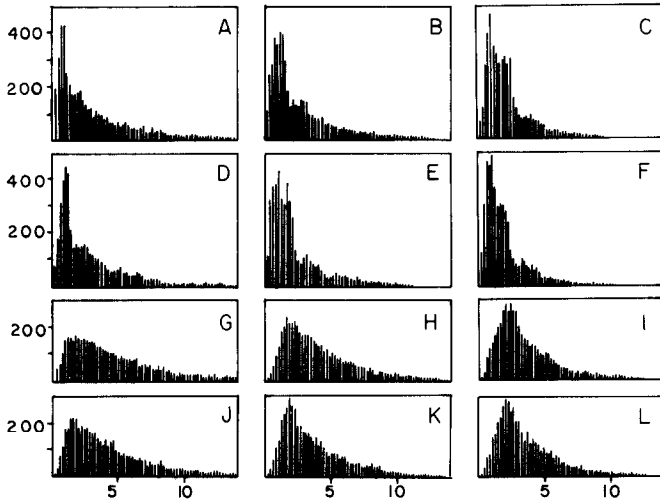


FIG. 6. Histograms of the extinction times derived from the computer simulations. For the first column,  $K = 2$ ; for the second,  $K = 10$ ; and for the third,  $K = 100$ . In each case the number of disasters is two between carrying capacity and extinction in the absence of recovery. Each histogram is for 5000 extinctions. In A-C the simulations are for density independent disasters (Eq. (1)) with  $N(0) = \sqrt{K}$ ; D-F, constant disasters (Eq. (11)) with  $N(0) = (K + 1)/2$ ; G-I, density independent disasters with  $N(0) = K$ ; and J-L, constant disasters with  $N(0) = K$ .

TABLE I  
Extinction Time Obtained from the Simulation Studies<sup>a</sup>

$K$		Equation (1) $N(0) = \sqrt{K}$	Equation (11) $N_c(0) = (K + 1)/2$	Equation (1) $N(0) = K$	Equation (11) $N_c(0) = K$
2	$\mu_T$	3.65	3.28	4.65	4.28
	$\mu'_T$	3.39	3.10	4.99	4.32
	$\sigma_T'^2$	13.13	10.78	16.05	12.11
10	$\mu_T$	2.82	2.56	3.82	3.56
	$\mu'_T$	2.73	2.26	4.07	3.72
	$\sigma_T'^2$	7.64	5.17	9.08	7.16
100	$\mu_T$	2.32	2.41	3.32	3.41
	$\mu'_T$	2.32	2.08	3.43	3.50
	$\sigma_T'^2$	4.10	4.19	5.62	6.06

<sup>a</sup> Sample means  $\mu'_T$  and sample variances  $\sigma_T'^2$  for various initial values for the two models described by the stochastic differential equations (1) and (11) of the text. Exact calculated means  $\mu_T$  are also given.

densities of the extinction times of the two ways in which the disasters may affect the population size. The reason is that an important feature of this comparison of simulations is that in each pair of cases the number of disasters in absence of recovery from  $N(0)$  or  $N_c(0)$  to  $A$  is the same even though  $N(0)$  and  $N_c(0)$  might differ. In most of the cases studies, the persistence times of populations with density independent disasters tend to be greater than those with disasters of fixed magnitudes. This was borne out in five of the six comparisons. The mean and the variance of the extinction time were greater in the constant disaster case for the simulations with  $K = 100$  and initial population size  $K$ . That this was not due simply to sampling error is confirmed by the fact that the exact calculated means were in the same relation to one another as the sample means.

One characteristic difference for the two models is that the densities in the case of density independent disasters have longer tails than the corresponding densities obtained in the constant disaster simulations. The implication is that when the magnitudes of the disasters which beset a population are proportional to the population size, the population has a small chance of persisting for an exceedingly large number of generations. This is easy to understand because of the possibility of rebound from small levels due to the almost Malthusian recovery there and the fact that at such levels a disaster can eliminate a much smaller number of individuals when the disasters are proportional to  $N$  than when they are of constant magnitude. We see that the probability mass of the extinction time is, for the constant disaster case, more concentrated near the origin, as reflected by the higher modal values (see Figs. 6A–L).

For both models the modes of the extinction times tend to increase as  $K$  increases but the tails of the corresponding densities shorten to such an extent that the mean and standard deviation nevertheless decrease. It seems reasonably safe to conclude that the densities in all 12 cases are unimodal even though histograms for initial values that are one disaster from extinction tended to exhibit secondary peaks. The latter are probably artifactual. The unimodality of first passage times for Markov processes has been remarked upon by other authors (Keilson and Ross, 1975).

#### 4. ANALYSIS FOR LARGER STEPS

When the number of disasters in absence of logistic recovery (which we shall call “steps”) from carrying capacity to effective extinction is greater than two, then multiple integrals arise whose order can be as great as the number of steps, minus one, from effective extinction. Though an explicit solution can be formally written in terms of these multiple integrals, the

explicit calculation of their integrals is prohibitive even for integral values of  $\gamma$ . Numerical integration of the functional differential equation for  $\lambda F(x)$  becomes practical and necessary. A straightforward numerical solution has its pitfalls since the unknown constant of integration  $C$  has to be carried along to the singular, final boundary at  $K$ . In addition,  $\lambda F(x)$  is extremely sensitive to the value of  $C$  chosen since there is only one value that will make  $\lambda F(x)$  bounded.

In order to make the numerical problem better posed a singular decomposition into fundamental functions, which have nicer properties, was introduced in Hanson and Tuckwell (1978) for the constant disaster model with the details given in Hanson (1981). The motivation for this decomposition comes from the form of the solution for two or more steps and is given by

$$\lambda F(x) = P(y) + [F_1(y) + Q(y) + CF_2(y)]/U(y), \quad (21)$$

where the independent variable,  $x = Ky$ , has been scaled by  $K$  and  $U(y) = u(x)$ .  $P(y)$  is the pure Poisson component of the solution which takes the value  $P(y) = j$  on the steps  $(y_{j-1}, y_j)$  for  $j = 1$  to the total number of Poisson steps  $m$ . The scaled initial point is  $y_0 = \Delta/K$ , the final point is  $y_m = 1$  and  $y_j = (\Delta/K)/(1 - \varepsilon)^j$  for  $j = 1$  to  $m - 1$ . For exactly  $m$  Poisson steps in  $(\Delta, K)$ ,  $(1 - \varepsilon)^m K = \Delta$ , otherwise nonintegral values of  $m$  are determined from the inequality:  $\Delta/(1 - \varepsilon)^{m-1} < K \leq \Delta/(1 - \varepsilon)^m$ .  $F_1$  and  $F_2$  are the fundamental continuous components of the decomposition with  $F_2/U$  being the only term multiplied by the constant of integration,  $C$ .  $Q(y)$  is a secondary step function such that  $Q/U$  exactly cancels out the jump in the Poisson step function  $P(y)$  to make the resultant solution  $\lambda F(x)$  continuous. This continuity condition requires that

$$\begin{aligned} Q(y) &= 0, & y &\in (y_0, y_1) \\ &= Q((1 - \varepsilon)y) - U(y_{j-1}), & y &\in (y_{j-1}, y_j) \text{ for } j = 2 \text{ to } m. \end{aligned}$$

Finally, the functional differential equations for  $F_1$  and  $F_2$  are found by substituting the decomposition (21) into Eq. (5) to obtain

$$\frac{dF_2}{dU}(y) = \left(\frac{F_2}{U}\right)((1 - \varepsilon)y) \quad \text{on } (y_1, 1), \quad (22)$$

with  $F_2(y) = 1$  initially on  $(y_0, y_1)$  and

$$\frac{dF_1}{dU}(y) = \left(\frac{F_1 + Q}{U}\right)((1 - \varepsilon)y) \quad \text{on } (y_1, 1), \quad (23)$$

with  $F_1(y) = 0$  initially on  $(y_0, y_1)$ . Note that the derivatives are written in terms of  $U = U(y)$  to show that the right-hand sides could be written entirely

in terms of what is known from the prior step. In addition to the simplification offered in this form, note that the coefficient of  $F_1((1 - \epsilon)x)$  and  $F_2((1 - \epsilon)x)$  on the right is  $1/U((1 - \epsilon)y)$ , which is easily shown to be bounded by  $U(\epsilon)$ . Since the coefficient in the functional differential equation is bounded, this means that the solutions  $F_1$  and  $F_2$  must also be bounded (El'sgolt's and Nor'kin, 1973). Also,  $(1/F_2(y))$  is an increasing function of  $(U(\Delta) - U(y))$ , so that  $F_2 > 0$ . Then boundary requirement that  $F(K^-)$  be bounded implies that the constant of integration is given in the general case by

$$C = - \left( \frac{F_1 - Q}{F_2} \right) (1^-). \tag{24}$$

In summary, Eq. (24) expresses  $C$  in terms of bounded functions  $F_1(y)$  and  $F_2(y)$  known entirely from their initial value problems and not from the more difficult boundary value problem satisfied by  $F(x)$ .

### 5. RESULTS AND DISCUSSION

The expected extinction times,  $\lambda F(x)$ , given in Fig. 7 for  $m = 6$  steps or jumps,  $K = 10$  and  $\Delta = 1$ , are typical of the cases with a large number of steps. The extinction times can be expected to be extremely large with very little variation with the initial population size  $x$ , when  $\gamma$  is small, e.g.,  $\gamma = 0.5$ . For species with small  $\gamma$ , the habitat appears permanent relative to an intrinsic growth time proportional  $1/r$ . As  $\gamma$  increases, i.e., as the habitat

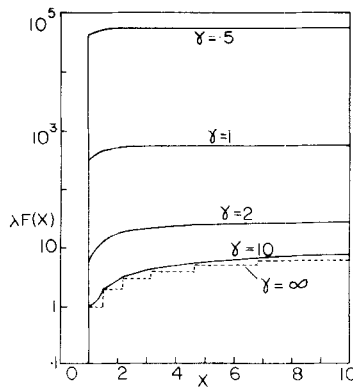


FIG. 7. Expected persistence times for the density independent disaster model as calculated from Eq. (5) as functions of the initial population size for various values of the biodisaster-growth ratio  $\gamma$ . The carrying capacity is 10 units, the extinction level 1 unit and the disasters are such that six in succession would extinguish the population from carrying capacity if there were no logistic recovery. The dashed line is for zero growth rate.

becomes less favorable or more temporary because of the greater frequency of disasters as measured relative to the intrinsic growth rate  $r$ , the expected persistence time is drastically reduced, while the variation with population size becomes more noticeable. For large values of  $\gamma$ , e.g.,  $\gamma = 10.0$ ,  $\lambda F(x)$  roughly forms an envelope for the discontinuous pure Poisson limit,  $\gamma \rightarrow +\infty$ , with  $F(x)$  less than 10 times the disaster waiting time  $1/\lambda$  at carrying capacity and essentially  $1/\lambda$  at effective extinction. The large values of  $\gamma$  correspond to the temporary habitat species that must develop other means such as a fugitive or recolonizing strategy to adapt to its harsh environment in order to persist in the large.

In Figs. 8A and B the persistence of a colonizing cohort starting at  $x = \Delta^+$  is examined in more detail as a function of the number of Poisson steps to extinction. In Fig. 8A the relative carrying capacity,  $K/\Delta$ , is held fixed at 10 so that the variation in the number of steps  $m$  and the relative disaster rate are coupled through

$$\varepsilon = 1 - (\Delta/K)^{1/m}. \quad (25)$$

Hence  $\varepsilon$  decreases as  $m$  increases. As the number of Poisson steps to extinction increases from one to six, the persistence time increases more than it would if, by a simple exponential and for  $m > 6$ , the increase is just about exponential. Using relation (25), the large  $m$  behavior can be translated to mean that as  $\varepsilon$  decreases toward zero the effect in increasing  $\lambda F(\Delta^+)$  is just about exponential with the exponent proportional to  $1/\varepsilon$ . The effect increases as  $\gamma$  decreases. Hence the effects of the number of steps  $m$  and  $\gamma$  are very great when  $K/\Delta$  is fixed. In Fig. 8B,  $\varepsilon$  is held at 0.05, to show the variation of  $m$  as it is coupled to the relative carrying capacity,  $K/\Delta$ , according to (25). The increase in the expected extinction time is approximately exponential, at least for  $\gamma > 2$ , with  $m$ , but only algebraic with  $K/\Delta$ . Hence Figs. 8A and 8B indicate that the effect on increasing  $\lambda F(x)$  is much greater when  $\varepsilon$  decreases toward zero than when the relative carrying capacity  $K/\Delta$  increases. Also the effect of increasing  $m$  is much less for the higher values of  $\gamma$  than it is for the smaller of  $\gamma$  and this is especially true for fixed  $\varepsilon$  as in Fig. 8B. The larger values of  $\gamma$  are indicative of the temporary habitat species that must continually recolonize its patch or perhaps adapt to a fugitive strategy in order to survive as a species. However, for fixed  $K/\Delta$ , with either large  $\gamma$  or  $\varepsilon$  near  $1^-$ , it can appear that the species under question is a temporary habitat species. Conversely, for fixed  $K/\Delta$ , the smaller values of  $\gamma$  or the smaller values of  $\varepsilon$  will give the appearance of a permanent habitat species. This is in contrast to the single parameter,  $\tau/H$ , used by Southwood *et al.* (1974) to classify  $r$ -strategists and  $K$ -strategists, where  $\tau$  represents the generation time (the discrete analog to  $1/r$  in our continuous deterministic component) and  $H$  represents the time the habitat remains favorable (the

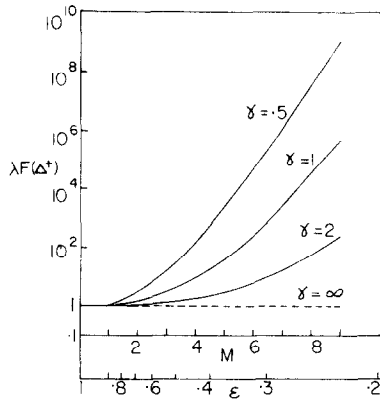


FIG. 8A. Persistence of colonizing cohort subjected to density independent disasters. The expected extinction time  $\lambda F(\Delta^+)$  is shown as a function of the number of steps  $M$  from  $K$  to  $\Delta$ , for various  $\gamma$  at fixed  $K/\Delta = 10$ . The quantities  $M$  and  $\epsilon$  are related through Eq. (25).

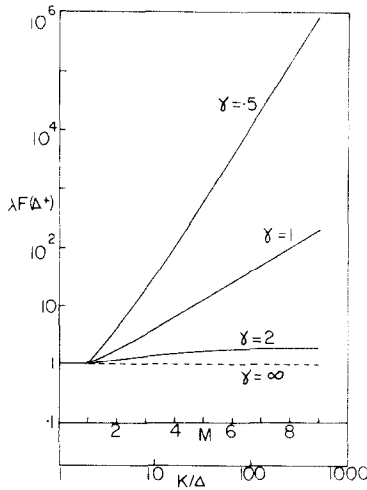


FIG. 8B. Dependence of  $\lambda F(\Delta^+)$  on  $M$  for various  $\gamma$  with  $\epsilon$  fixed at 0.5. The variation with  $K/\Delta$  follows from Eq. (25).

analog of our  $1/\lambda$ ). Their single parameter thus corresponds to our  $\gamma$ , the  $K$ -strategist corresponds to parameter values  $\tau/H$  small compared to 1 (i.e., roughly the permanent habitat animal in terms of small  $\gamma$  alone) and the  $r$ -strategist corresponds to  $\tau/H \simeq 1$  (i.e., the temporary habitat animal). According to our model, the relative size of the disaster,  $\epsilon$ , is also very important for classification purposes and there is no corresponding parameter used by Southwood *et al.* (1974).

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