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Survival of Small Populations under Demographic Stochasticity

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We estimate the mean time to extinction of small populations in an environment with constant carrying capacity but under stochastic demography. In particular, we investigate the interaction of stochastic variation in fecundity and sex ratio under several different schemes of density dependent population growth regimes. The methods used include Markov chain theory, Monte Carlo simulations, and numerical simulations based on Markov chain theory. We find a strongly enhanced extinction risk if stochasticity in sex ratio and fluctuating population size act simultaneously as compared to the case where each mechanism acts alone. The distribution of extinction times deviates slightly from a geometric one, in particular for short extinction times. We also find that whether maximization of intrinsic growth rate decreases the risk of extinction or not depends strongly on the population regulation mechanism. If the population growth regime reduces populations above the carrying capacity to a size below the carrying capacity for large r (overshooting) then the extinction risk increases if the growth rate deviates from an optimal r-value.

1. INTRODUCTION

A detailed understanding of the processes leading to population extinction is helpful for many questions in population biology, such as life history evolution, success of colonizing species, or management problems of endangered species and zoo populations. One can try to separate the

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reasons for extinction into (i) demographic processes, such as random fluctuations in birth and death rates and sex ratio, (ii) seasonal and other changes of the environment including predation and competition, (iii) catastrophes such as disease outbreaks, and (iv) genetic problems, such as accumulation of deleterious mutations or loss of adaptive variation. To judge the relative importance of these processes, one has to study not only each process separately but also their possible interactions.

An early mathematical theory of extinction was developed by Feller (1939) who treated population growth by stochastic birth and death processes. His basic model has been used, analyzed, and extended by MacArthur and Wilson (1967), Richter-Dyn and Goel (1972), Leigh (1981), Wright and Hubbell (1983), Goodman (1987), and others. This approach has been very fruitful for studies of the relative influence of a variable environment compared with stochastic demography. Its advantages and shortcomings for applications to real populations have been discussed in detail by Goodman (1987). Despite considerable mathematical effort, analytical approximations of extinction times are available only for very special population regulation mechanisms and for a restricted range of parameters. Especially for very small populations, the estimates are not reliable. Other approaches to the influence of environmental fluctuations (e.g. Strebel, 1985, or Mode and Jacobson, 1987a, b) have not been more successesful in providing analytical estimates of extinction times in small populations.

To treat populations with age structure is even more complicated. Lande and Orzack (1988) handled extinction dynamics in a fluctuating environment for density independent population growth by applying diffusion approximations to results of age structured population models of Cohen (1977) and Tuljapurkar (1982).

Astonishingly, there has not been any attempt to study in detail the influence of random fluctuations in sex ratio—probably because it is thought to be important only in very small populations. Even in comprehensive overview articles (e.g., Tuljapurkar, 1989) the sex ratio problem is neglected. Because the motivation for the present study was to have a good reference point to estimate the risk coming from genetic influences, especially from slightly deleterious mutations (see Gabriel *et al.*, 1991, and Lynch and Gabriel, 1990), we were led to include sex ratio fluctuations.

In this study we consider the extinction of small populations under different levels of demographic stochasticity and for various kinds of commonly used density dependent population growth regimes, but we do not extend the analysis to more complicated forms like "hump with tail maps," as in Milton and Bélair (1990). We restrict the analysis to constant environments, but we include random fluctuations in the sex ratio and their interaction with stochastic fecundity and survival.

2. Models

All models investigated in this paper assume a finite population with discrete generations, one or two sexes, no age structure, and no genetics. They are purely demographic and include density dependent population growth, stochasticity of actual population size, and stochastic variation of the sex ratio.

The basic density dependent relation is of the form

$$N(t+1) = F(N(t)), \tag{1}$$

where $N(t)$ is the population size at time t, $t = 0, 1, 2, \ldots$. We consider the following explicit expressions for $F(N)$:

$$F(N) = e^r N(1 + aN)^{-\beta}, \tag{1a}$$

$$F(N) = N \exp(r(1 - N/K)), \tag{1b}$$

$$F(N) = \begin{cases} N(1 + \rho(1 - N/K)), & \text{if} \quad N \leqslant K(\rho + 1)/\rho \\ 0, & \text{otherwise} \end{cases} \tag{1c}$$

(compare May and Oster, 1976, or May, 1981).

In Eqs. (1a) to (1c) the "multiplicative growth factor" for $N \to 0$ is given by the relation

$$F(N)/N = 1 + \rho = e^r, \tag{2}$$

where r corresponds to the "intrinsic growth rate". For Eq. (1a) $K = (e^{r/\beta} - 1)/a$ is the "carrying capacity," which satisfies $F(K) = K$. If $r = 0$ (or $\rho = 0$) then Eqs. (1a) to (1c) reduce to $F(N) = N$, i.e., no population regulation occurs. In the following we always assume $\beta > 0$, $r > 0$, and $\rho > 0$.

In this paper we consider a scale of five kinds of density dependent population growth regimes, labelled as PG-regimes 1 to 5, according to the following convention:

PG-regime 1: F given by Eq. (1a) with $\beta = 0.5$;

PG-regime 2: F given by Eq. (1a) with $\beta = 1$ (this is the classical Verhulst model);

PG-regime 3: F given by Eq. (1a) with $\beta = 2$;

PG-regime 4: F given by Eq. (1b);

PG-regime 5: F given by Eq. (1c).

The deterministic dynamics of these population growth regimes is quite different, in particular for large growth rates r and ρ. Under PG-regimes 1 and 2 population size always converges monotonically to K, whereas for

PG-regime 3 damped oscillations may occur for large r. In PG-regimes 4 and 5 "overshooting" of population size is larger than in PG-regime 3 and damped oscillations periodic orbits, chaos, and extinction occur for r and ρ increasing from two upwards. Indeed, the above PG-regimes lie on a scale with increasing strength of population regulation, because for fixed r, K, and N we have

$$\begin{aligned}\lim_{\beta\to\infty} & e^r N(1+aN)^{-\beta} \\ &= Ne^r \lim_{\beta\to\infty}\left(1+\frac{N}{K}(e^{r/\beta}-1)\right)^{-\beta} \\ &= Ne^r \lim_{\beta\to\infty}\left(1+\frac{Nr}{K\beta}\right)^{-\beta} = N\exp\left(r\left(1-\frac{N}{K}\right)\right).\end{aligned}$$

Thus the density dependent relation (1a) converges to (1b) as $\beta\to\infty$. In the limit $\beta\to 0$ we receive a model without population regulation, i.e., $F(N)=N$. For basic properties of these deterministic models the reader is referred to May and Oster (1976) or May (1981).

We now describe a sequence of stochastic models that includes various combinations of the effects of stochasticity of population regulation and sex ratio. The underlying population regulation mechanism may be one of the five regimes introduced above.

2.1. *Pure Sex-Ratio Variation (PS-Model)*

The simplest model including variation in sex ratio is obtained by assuming that the population dies out only because there are either no females or no males. Otherwise, the population size is assumed to be constant and equal to K. This means that one male and one female are sufficient to regenerate a full population of K individuals. Thus

$$N(t+1)=\begin{cases}0, & \text{if in generation } t \text{ there are either} \\ & \text{no females or no males} \\ K, & \text{otherwise.}\end{cases} \tag{3}$$

The probability that either no females or no males are produced is assumed to be $2\times(\frac{1}{2})^K$ (binomial distribution). This leads to a Markov chain model with three states, say 0 (no females and no males), 1 (no females or (exclusive) no males) and 2 (at least one female and one male). Transition probabilities are given by $p_{00}=p_{10}=1$, $p_{01}=p_{02}=p_{11}=p_{12}=p_{20}=0$, $p_{21}=(\frac{1}{2})^{K-1}$ and $p_{22}=1-(\frac{1}{2})^{K-1}$. We will call this the PS-model in the sequel.

2.2. *No Sex but Stochastic Population Regulation (NS-Model)*

The first step to introduce stochasticity into the deterministic population regulation model is to assume that the expected value of the population size of the next generation is given by Eq. (1), but the actual population size varies according to some probability distribution. This may be interpreted, for example, as stochastic variation of fecundity. To be definite, we assume that population size $N(t+1)$ follows a Poisson distribution (see Discussion) with expected value

$$\lambda(t+1) = F(N(t)), \tag{4}$$

where $N(t)$ denotes the actual population size in generation t and F is given by (1a), (1b), or (1c). Mathematically, this leads to a (time-homogeneous) Markov chain model with $N = 0, 1, 2, \ldots$ as possible states. It is a branching process if and only if there is no population regulation, i.e., if $F(N) = N$. Throughout, this model will be labelled as the NS-model.

This, as well as all other models, was analysed using two different methods. The first method was to simulate the resulting stochastic process directly on a computer (Monte Carlo simulation, cf. Section 3). The second method was to consider the corresponding Markov chain model. For basic properties of Markov chain models the reader is referred to Ewens (1979) and Kemeny *et al.* (1976). The transition matrix $P = [p_{ik}]_{i,k=0}^{\infty}$ for the NS-model is given by

$$p_{ik} = \text{Prob}[N(t+1) = k \mid N(t) = i] = e^{-\lambda_i} \frac{\lambda_i^k}{k!}, \tag{5}$$

where $\lambda_0 = 0$, and $\lambda_i = F(i)$ for $i \geqslant 1$. It should be noted that, due to the conventions $0^0 = 1$ and $0! = 1$, $p_{00} = 1$ and $p_{0k} = 0$ for $k \geqslant 1$. This model has one absorbing state $i = 0$, which corresponds to population extinction. It can be shown mathematically that extinction occurs with probability one for all three choices (1a)–(1c) of F (see Appendix AII).

From the transition matrix it is possible to derive a system of linear equations for the mean extinction times and in principle the whole distribution of extinction times may be computed (cf. Ewens, 1979). In cases (1a) and (1b) this sytem of linear equations is infinite, whereas in case (1c) it can be reduced to a finite one. These systems can be solved numerically and, for certain limiting cases, analytic estimates can be derived. More details are given in Section 3 and in the Appendix.

The NS-model may also be viewed as a good approximation to a model with even sex ratio. The only difference in such a model would be that one would have to choose the even non-negative integers as the state space and not all non-negative integers.

2.3. *Stochastic Sex Ratio and Stochastic Population Regulation (SS-Model)*

To combine the pure sex-ratio model and the NS-model, the population size N and the number of females N_f have to be traced. We assume that population size $N(t+1)$ depends on the number of females $N_f(t)$ in generation t and on the population size $N(t)$ in generation t according to

$$\text{Prob}[N(t+1)=k \mid N(t)=i, N_f(t)=j] = e^{-\lambda_{ij}} \frac{\lambda_{ij}^k}{k!}. \tag{6}$$

Here, λ_{ij} is the expected value of the population size $N(t+1)$, given $N(t)=i$ and $N_f(t)=j$, and again it is supposed that the actual population size follows a Poisson distribution. λ_{ij} is assumed to be of the form

$$\lambda_{ij} = \varphi(i, j)\, F(i), \qquad \text{for} \quad 0 \leqslant j \leqslant i, \tag{7}$$

where $F(i)$ describes population regulation and $\varphi(i, j)$ is a factor describing productivity of females as a function of population size and sex ratio j/i. In the present paper we assume that $\varphi(i, j)$ is given by

$$\varphi(i, j) = \begin{cases} 0, & \text{if} \quad j=0 \text{ or } j=i \\ 2j/i, & \text{otherwise,} \end{cases} \tag{8}$$

that is, $\lambda_{i(i/2)} = F(i)$ if the sex ratio is even and $\lambda_{ij} \to 0$ as the fraction of females j/i tends to zero. The sex ratio is assumed to follow a binomial distribution with both sexes having equal probability, i.e.,

$$\text{Prob}[N_f(t+1)=l \mid N(t+1)=k] = \binom{k}{l} 2^{-k}, \qquad 0 \leqslant l \leqslant k. \tag{9}$$

Equations (6) to (9) lead to a well defined model which is a bivariate Markov chain with state space $\{(i, j): i=0, 1, 2, \ldots \text{ and } 0 \leqslant j \leqslant i\}$. Here i is the population size and j the number of females. The transition matrix is given by

$$\begin{aligned} p_{ij,kl} &= \text{Prob}[N(t+1)=k, N_f(t+1)=l \mid N(t)=i, N_f(t)=j] \\ &= e^{-\lambda_{ij}} \frac{\lambda_{ij}^k}{k!} \binom{k}{l} 2^{-k}. \end{aligned} \tag{10}$$

This model is labelled the SS-model. Note that $p_{ij,00}=1$ if $j=0$ or $j=i$ and $p_{ij,kl}=0$ if $k \geqslant 1$ and $j=0$ or $j=i$. An interesting special case is the following.

2.4. *Female Independent Stochastic Population Regulation (FI-Model)*

Suppose, as in the pure sex-ratio model, that one female and one male are sufficient to generate a full population but with size determined as in the NS-model. If there are either no males or no females then extinction occurs in the next generation. This amounts to using (7) and (10) but to choosing

$$\varphi(i, j) = 1, \qquad \text{if} \quad 1 \leqslant j < i. \tag{11}$$

It follows that $\lambda_{ij} = \lambda_i = F(i)$ for $1 \leqslant j < i$. Thus, the population size is independent of the number of females N_f, except for $N_f = 0$ or $N_f = N$, and the transition probabilities are given by

$$\begin{aligned} p_{ij.kl} &= e^{-\lambda_i} \frac{\lambda_i^k}{k!} \binom{k}{l} 2^{-k}, && 0 \leqslant j \leqslant i \\ p_{ij.00} &= 1, && j = 0 \text{ or } j = i \\ p_{ij.kl} &= 0, && k \geqslant 1 \text{ and } j = 0 \text{ or } j = i. \end{aligned} \tag{12}$$

Thus, the FI-model is somewhat intermediate between the NS- and the SS-model.

3. Results

The main purposes of this paper are to investigate the mean times to extinction and the distributions of extinction times for the stochastic models in combination with the various population growth regimes and to study the relative importance of the stochastic processes for the extinction of small populations.

We used Monte Carlo simulations and numerical methods based on Markov chain theory to calculate extinction times. Both methods are independent of each other so that we could check the results and ensure that the computer programs functioned correctly. The numerical methods are described in the Appendix. The Monte Carlo simulation is straightforward. Taking the SS-model as an example, the population size and the number of females are known in any generation so that the expected number of offspring can be calculated according to the chosen population regulation. The actual offspring number, which equals the population size of the next generation, is drawn from a Poisson distribution. Then sex determination of offspring is performed with equal probability for males and females. Population extinction occurs if the number of offspring is zero either because (randomly) no offspring survive or because in the previous genera-

tion only males or only females have been produced. Technically, the limiting factor for our Monte Carlo simulations is CPU-time if the mean extinction time becomes large; with the numerical methods the available memory can become too small to guarantee numerical convergence. The programs are written in FORTRAN using routines from the NAG- and IMSL-libraries. They are available on request.

In the following we present the data concerning the extinction times and their distribution for various combinations of the density-dependent population growth regimes 1 to 5 with the stochastic models PS, NS, FI, and SS, as introduced in Section 2.

3.1. *The Verhulst Model for Various Levels of Stochasticity*

Figure 1 gives the mean time to extinction depending on the growth rate r and the carrying capacity K for PG-regime 2 in combination with the stochastic models PS, NS, FI, and SS. The populations are assumed to consist of K individuals, initially. The initial sex ratio is one, although this is of importance only for the SS-model. The line always indicates the mean time to extinction without density-dependent population regulation due to pure sex-ratio variation (PS-model). Trivially, this line is the same in all four figures because there is no dependence on r. It follows from the transition matrix (see Section 2.1) that the expected extinction time for the PS-model is $2^{K-1}+1$ (see also Eq. (19) below).

The other symbols in Fig. 1 represent the mean extinction times for the other stochastic models. The risk of extinction increases with the level of stochasticity: the NS-model always gives the largest mean extinction time, the SS-model the smallest and the FI-model is intermediate. For very small growth rates ($r=0.1$) these three extinction times are close, which implies that the mean extinction time is mainly determined by the risk of having no offspring and that the additional risk due to sex-ratio variation is relatively small. This is already indicated by the much larger extinction times for the pure sex-ratio model. These relations change drastically with increasing growth rate r. For $r=1$ the risk of extinction for the NS-model (with no sex-ratio variation but stochastic population regulation) is already slightly lower than that for the PS-model. Moreover, under stochastic density-dependent population growth, the addition of sex-ratio fluctuations (SS-model) increases the extinction risk by several orders of magnitude relative to the NS-model. For $r=2$ the risk of producing no offspring becomes negligible compared to the risk due to sex-ratio variation, even for very small carrying capacities.

The dependence on r levels off very rapidly for larger r-values, so that the difference between $r=2$ and the limit as r goes to infinity is not visible. As may be seen from Fig. 1, the mean extinction time increases approximately exponentially with K for large r. In fact, it is easy to

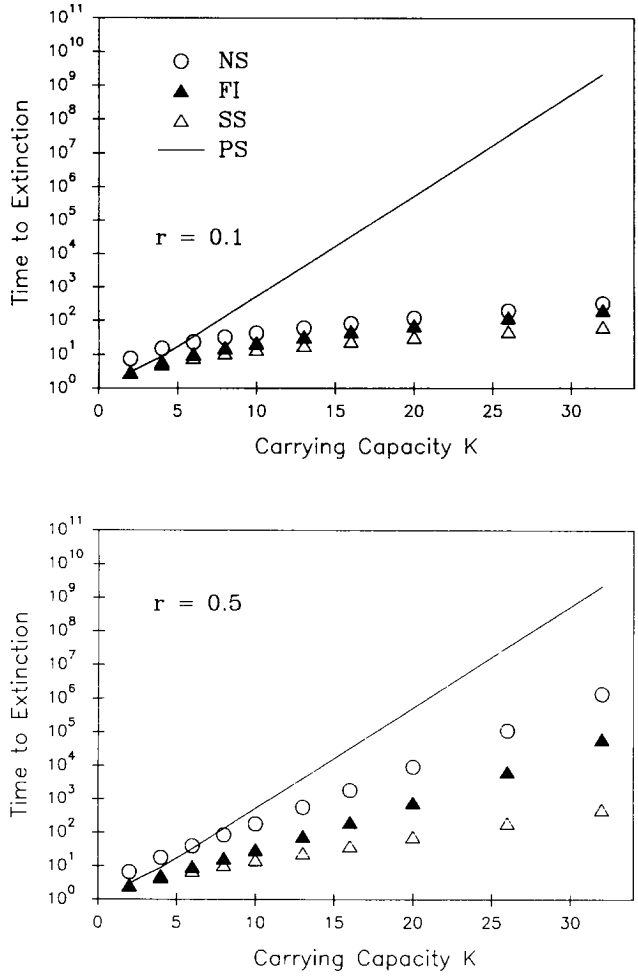


FIG. 1. Extinction under various levels of stochasticity. Mean times to extinction (in number of generations) are calculated depending on carrying capacity for population growth regime 2 (the classical Verhulst model). The lines and the symbols refer to the stochastic models; PS = pure sex ratio; NS = asexual but stochastic population regulation; FI = female independent population regulation; SS = stochastic sex ratio and stochastic population regulation (for details see Section 2). The panels differ in the intrinsic growth rate r (measured per generation). (a) $r = 0.1$; (b) $r = 0.5$; (c) $r = 1$; (d) $r = 2$.

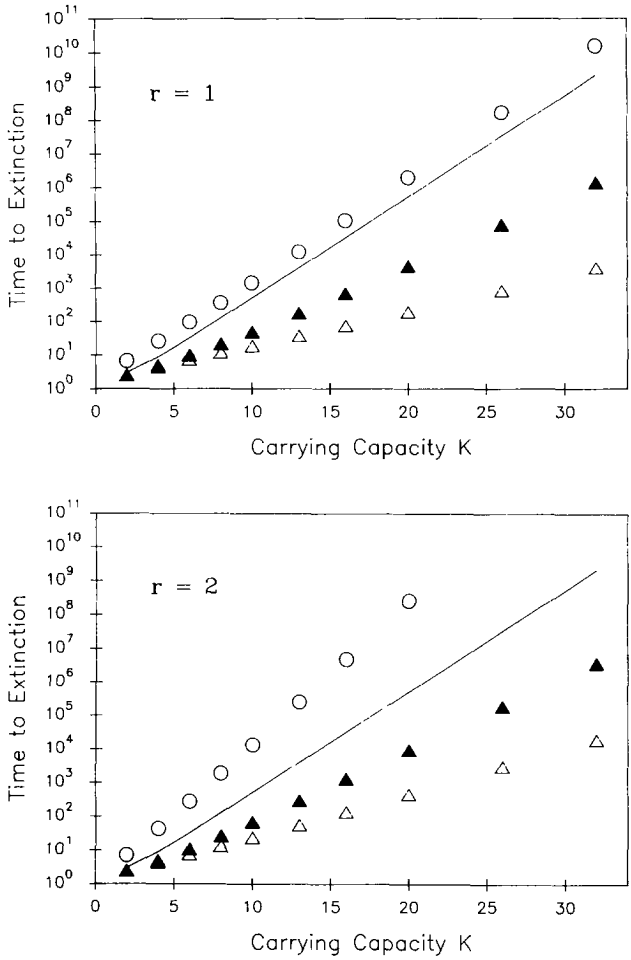


FIG. 1—*Continued*

calculate the mean extinction time for the limiting case $r \to \infty$ for the NS- and the FI-model. First note from Eq. (1a) with $\beta = 1$ that $r \to \infty$ implies $\lambda_i \to K$ uniformly for all $i \geqslant 1$. Therefore, in the NS-model the transition probabilities p_{ik} converge uniformly in i to p_{Kk} as $r \to \infty$. This shows that in the limiting case $r \to \infty$, all states $i \geqslant 1$ may be identified with, say, $i = K$, so that a Markov chain with two states 0 and K is obtained. Its transition matrix is given by

$$P = \begin{pmatrix} 1 & 0 \\ e^{-K} & 1 - e^{-K} \end{pmatrix}. \tag{13}$$

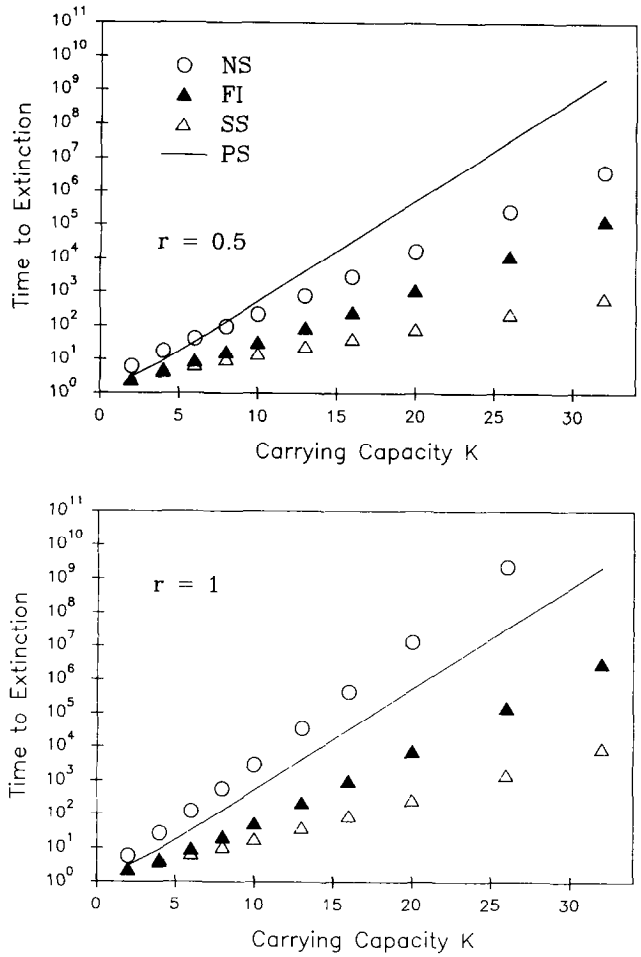


FIG. 2. Same as Fig. 1 but for population growth regime 4 and for the intrinsic growth rates (a) $r=0.5$; (b) $r=1$; (c) $r=2$; (d) $r=5$.

It follows that the mean extinction time and its variance are given by

$$t_K(r=\infty)=e^K \qquad \text{and} \qquad \sigma_K^2(r=\infty)=e^{2K}-e^K, \tag{14}$$

respectively (compare Appendix AI). Hence, the coefficient of variation is $\sigma_K/t_K=\sqrt{1-e^{-K}}$.

A similar reasoning for the FI-model yields (in the limit $r\to\infty$) a Markov chain with three states, namely (i) $N=0$, (ii) $N=K$ and $N_f=0$ or $N_f=N$, (iii) $N=K$ and $1\leqslant N_f\leqslant K-1$, and

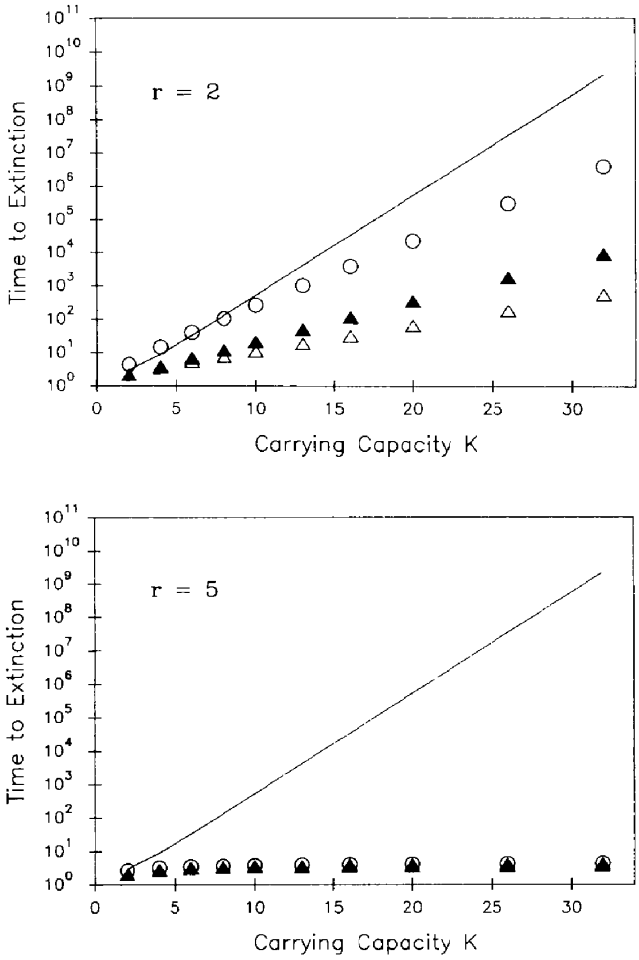


FIG. 2—*Continued*

$$P = \begin{pmatrix} 1 & 0 & 0 \\ 1 & 0 & 0 \\ e^{-K} & 2e^{-K/2} - 2e^{-K} & 1 + e^{-K} - 2e^{K/2} \end{pmatrix} \tag{15}$$

as the transition matrix. Thus the mean extinction time is

$$t_K(r = \infty) = \frac{e^K - 1}{2e^{K/2} - 1} + 1 \approx \frac{1}{2} e^{K/2} \tag{16}$$

and the coefficient of variation is $\sqrt{1-2e^{-K/2}+8e^{-K}}$. These values agree best with our simulated values for large r.

3.2. *The Exponential Model for Various Levels of Stochasticity*

The deterministic population growth regimes 4 and 5 have received a lot of attention in theoretical ecology, in particular because they exhibit very complicated dynamics (see May, 1981). PG-regime 4 has been used to model populations that are regulated by epidemics at high densities. As we have seen in Section 2, it is also the limit of the population growth regimes (1a) for $\beta \to \infty$. Figure 2 displays the mean extinction time as a function of K for the stochastic models PS, NS, FI, and SS under PG-regime 4 for different growth rates r. For $r=0.1$ (not shown) and $r=0.5$ there is almost no difference between PG-regimes 2 and 4. For $r=1$ the populations resist extinction longer under PG-regime 4. This is in accordance with Fig. 3 (see next section) from which we expect a decrease of the extinction time for further increased r. For $r=2$ the extinction times in the present case are already below the corresponding values for $r=0.5$. When $r=5$ we see a very high extinction risk caused by the high probability of no surviving offspring. In this case, the additional risk from sex-ratio variation is very small. In the limit $r \to \infty$ the mean time to extinction for PG-regimes 4 and 5 can be calculated analytically, since from Eqs. (1b) and (1c) one obtains in both cases $F(0)=0$, $F(K)=K$, $F(N)=0$ for $N>K$ and $F(F(N))=0$ for $0<N<K$, as $r \to \infty$. The corresponding mean extinction time is then

$$t_K(r=\infty)=2+\left(K+\cdots+\frac{K^K}{K!}-1\right)\Big/\left(e^K-\frac{K^K}{K!}\right). \tag{17}$$

This is almost independent of K and it follows that for all $K \geqslant 2$ the estimate $2.5 \leqslant t_K(r=\infty) \leqslant 3$ holds and that $\lim_{K\to\infty} t_K(r=\infty)=2.5$.

A continuous time version of the logistic model (PG-regime 5) was investigated by Leigh (1981), among other models. He derived an approximation for the mean extinction time if the population fluctuates with average change $M(N)\,dt=N(r-aN)\,dt$ in time dt and variance $V(N)=N$. He found that for small r and large N the mean time to extinction is almost independent of N and approximately equal to $t_K \approx \sqrt{\pi/K}(1+1/2rK)\,r^{-3/2}e^{rK}$. This is a very good approximation to our results as long as r is small ($r \approx 0.1$) but breaks down for $r \geqslant 0.5$.

3.3. *How Extinction Time Depends on the Population Growth Regulation*

Figure 3a is based on the stochastic model NS (no sex). It compares the mean times until extinction for the population growth regimes 1–5 at

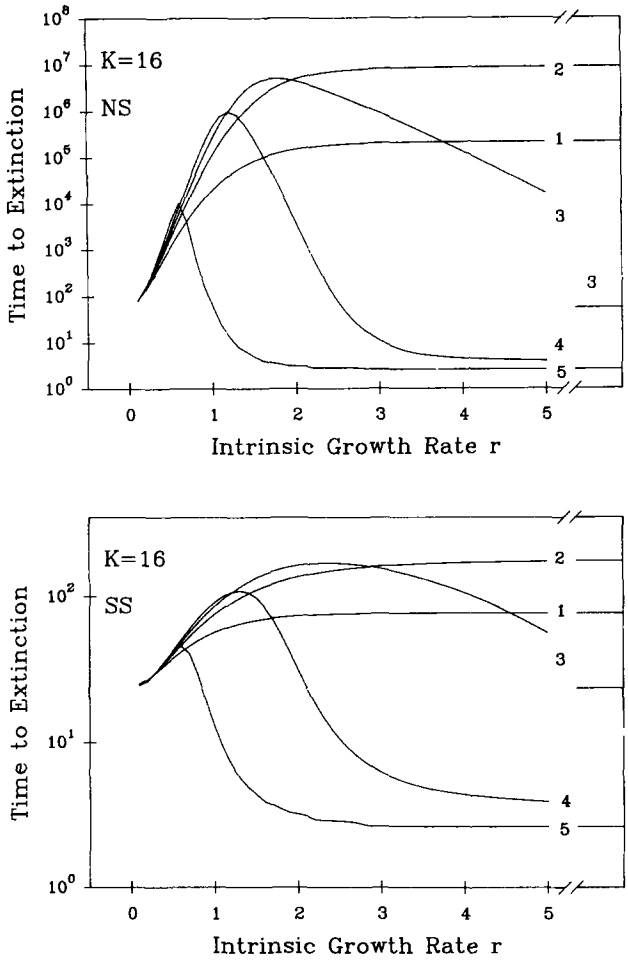


FIG. 3. Extinction under various population growth regimes. Mean times to extinction are calculated depending on intrinsic rate of increase r, $0.1 \leqslant r \leqslant 5$, for various population growth regimes which are indicated by the numbers in the figures (see Section 2). On the right hand side the limits for r to infinity are indicated. Population growth regimes 4 and 5 have the same limit. The carrying capacity is $K = 16$. The stochastic models are (a) the NS-model and (b) the SS-model.

carrying capacity $K = 16$. The initial population size is K. The lines at the right hand side of the figure indicate the limiting values as r goes to infinity. For the Verhulst model this is e^K (see (14)). For PG-regime 1 we obtain from Eq. (1a) that $F(N) = \sqrt{KN}$ as $r \to \infty$, and for PG-regime 3 we get $F(N) = K^2/N$. Note that the latter implies $F(F(N)) = N$. For these limiting cases the mean times to extinction can be calculated numerically, as

described in the Appendix. For PG-regimes 4 and 5 the limit can be calculated from Eq. (17). For $K = 16$ this gives 2.628.

At low r, all population models give similar results. For $r = 2$ the extinction times of the Verhulst model are already close to the limit, thus supporting the earlier statement that the r-dependence levels off at such intermediate r-values. β-values below 1 (PG-regime 1) lead to qualitatively similar behavior but the extinction time converges to a lower limit at high r. For β-values above 1 (PG-regime 3) the behavior is qualitatively different. After reaching a maximum, the extinction time decreases with further increasing r and converges to a value five orders of magnitude below the maximum. This results from the overshooting population regulation. For $\beta > 1$ and r sufficiently large, the expected population size for generation $t + 1$ is above K if the actual population size $N(t)$ is less than K and, vice versa. As r increases overshooting becomes more pronounced and drives populations to lower population sizes.

PG-regimes 4 and 5 show qualitatively similar behavior but reach their maxima earlier and decrease rapidly for moderate r values. PG-regimes 4 and 5 converge to the same value for high r, but regime 5 reaches its maximal extinction time for $r < 1$ and reaches its limit for r slightly less than 3. The somewhat irregular curve for PG-regime 5 results from the complex dynamics (cf. May, 1981). The values for the mean extinction time are, in this case, solutions of a system of finitely many linear equations (see Appendix, Eq. (A5)) and, therefore, exact.

We should also point out that in Fig. 3 mean extinction times are plotted only for $r \geqslant 0.1$. As r becomes very small the mean extinction time begins to increase. For $r = 0$ a kind of random walk model is obtained and it can be shown that extinction still occurs with probability one, but the mean time to extinction is infinite (Michael Moody, personal communication).

Figure 3b shows essentially the same dependencies as Fig. 3a but uses the SS-model. The initial sex ratio is always one. The results are qualitatively similar to the NS-model but extinction times are much smaller and the maximum values are reached at slightly higher r-values. The limits for $r \to \infty$ have been calculated numerically.

3.4. *Influence of the Initial Conditions*

All previous results are calculated under the assumption that the population starts at carrying capacity K. To check the generality of these results and to get further insight into the dynamics responsible for the extinction process, we now investigate the influence of the initial conditions for the various population growth regimes.

Generally, the extinction times can vary strongly with changing r as may be seen from Fig. 3. To facilitate the comparison we consider relative

extinction times obtained by normalizing with the corresponding extinction time of the population starting at carrying capacity K.

Figure 4 is based on the NS-model. Figure 4a demonstrates that for PG-regime 2 the extinction time depends only weakly on the intial population size, except for very low growth rates. For $r = 0.1$, $K = 16$, and initial population size $N(t = 0) = 1$, the time to extinction is less than a quarter of the extinction time of a population starting at carrying capacity. When $r = 1$, which is still a low growth rate (r is measured in time units of generations, therefore $r = 1$ means 2.72 surviving offspring per individual as long as population density is far from K), the maximal influence of the starting conditions is less than 20%. For initial values larger than the carrying capacity ($N(t = 0) > K$) there is even less variation in extinction time. The influence of the initial conditions becomes negligible with further increasing r.

The corresponding figures for the population growth regimes 1 and 3 (not shown) are very similar. This might be surprising in light of the different behavior of regime 3 for high r-values. However, the population dynamics leading to extinction seems to be largely unaffected by the initial value.

In contrast to the PG-regimes 1–3, the results for the PG-regimes 4 and 5 depend strongly on the initial values. The extinction time of the exponential regime 4 (Fig. 4b) varies with the initial value in a similar manner to PG-regimes 1–3 for small r. At high r-values it reaches a maximum when starting at K. For initial values below $0.6 \times K$, the extinction time is half the maximal value. This behavior results from the strong population regulation: if the initial population size is far below K, it will grow in the next generation to values far above K. In the following generation it is then exposed to a high probability of producing no offspring because the expected number of offspring is much smaller than 1. Increasing the initial value not too far above K gives the population a reasonable chance of staying near K, but for sufficiently high initial values the population goes extinct in the next generation almost certainly. PG-regime 5 with its discontinuous population regulation (the population goes extinct next generation if it is above $Ke^r/(e^r - 1)$) shows an even stronger dependence on the initial values (Fig. 4c), but for low r-values the population regulation is smooth enough to generate the same response to initial conditions as PG-regimes 1-4.

For the FI-model the dependence of the mean extinction times on the initial condition follows the same patterns we have seen in the NS-model, since the extinction time is independent of the sex ratio, as long as initially at least one male and one female are present (compare Appendix AV). For the SS-model the mean extinction time also depends on the initial sex-ratio. In all our simulations presented here this ratio was assumed to be one.

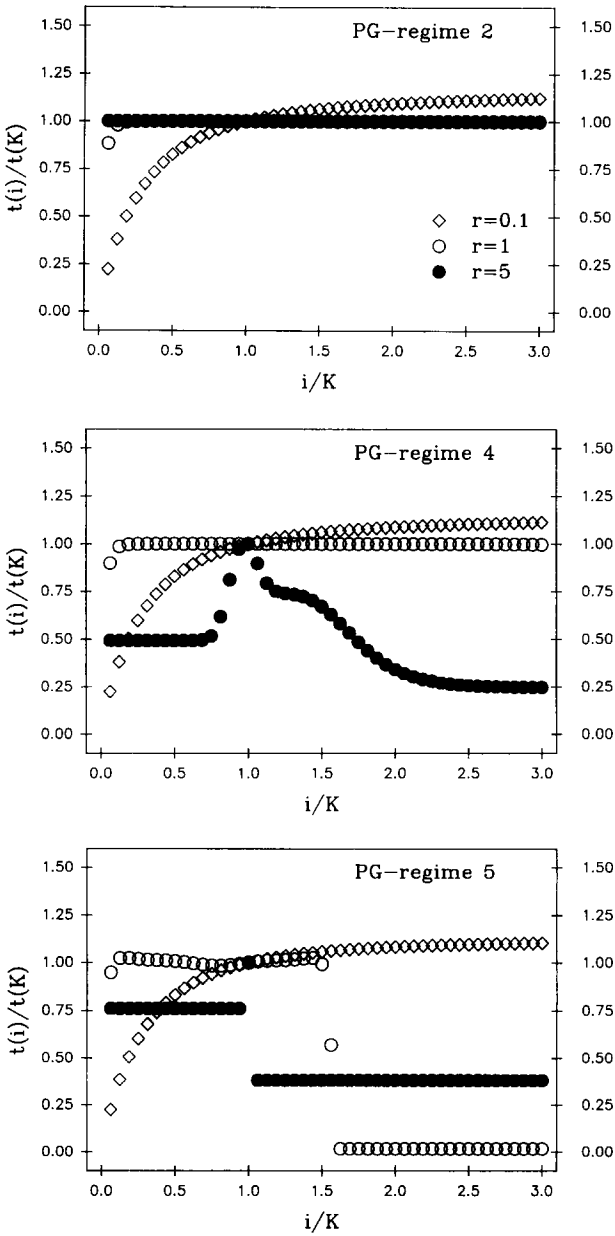


FIG. 4. Influence of initial population size. The mean extinction time $t(i)$ of populations with initial size i is normalized by the mean extinction time $t(K)$ of populations starting at carrying capacity (y-axis: $t(i)/t(K)$). The initial size i of a population is given relative to carrying capacity (x-axis: i/K). The symbols refer to the intrinsic growth rates $r=0.1$, 1, and 5. The stochastic model NS has been used. The population growth regimes are 2, 4, and 5 in (a), (b) and (c), respectively.

With this assumption the dependence on the initial population size is again similar to the NS-model. A deviation from an even initial sex ratio leads to a slightly higher extinction time if initially more females are present, and to a considerably lower extinction time as the number of females decreases to 1.

3.5. *The Distribution of Extinction Times*

The distribution of extinction times can be calculated easily if population size is constant and if extinction is solely due to sex-ratio fluctuation (PS-model). The probability that K offspring are all male or all female is $1/2^{K-1}$. If initially ($n=0$) the population consists of $K \geqslant 2$ individuals (not all female or all male), the probability that the population dies out in generation n is

$$p_n = \begin{cases} 0, & \text{for} \quad n = 0, 1 \\ \left(1 - \dfrac{1}{2^{K-1}}\right)^{n-2} \dfrac{1}{2^{K-1}}, & \text{for} \quad n \geqslant 2, \end{cases} \tag{18}$$

because extinction occurs in generation n, if in generation $n-1$ all individuals are of the same sex while in all previous $n-2$ generations individuals of both sexes were present. Equation (18) shows that extinction times are geometrically distributed up to a shift of two units in n and that the mean extinction time and its variance are

$$t_K = 2^{K-1} + 1 \qquad \text{and} \qquad \sigma_K^2 = 2^{K-1}(2^{K-1} - 1), \tag{19}$$

respectively. The coefficient of variation is therefore $\sigma_K/t_K = \sqrt{1 - 1/2^{K-1}}/(1 + 1/2^{K-1}) \approx 1 - 3/2^K$ which is approximately 1 even for small K.

Under density dependent population regulation there is, in general, no simple expression for the distribution of extinction times. However, for the NS-model and the limiting case $r \to \infty$ we obtain from the transition matrix (13) that the probability to die out in generation n is

$$p_n = e^{-K}(1 - e^{-K})^{n-1}. \tag{20}$$

Therefore, the mean extinction time is e^K (compare Eq. (14)). In general, if the conditional probability w to die out in generation n (under the condition of survival until generation $n-1$) is independent of the actual generation number then a geometric distribution of extinction time results with $p_n = w(1-w)^{n-1}$ for $n \geqslant 1$ and $p_0 = 0$. If w is small this geometric distribution can be approximated by the exponential distribution $we^{-w(x-1)}$ for $x \geqslant 1$ with expected value $1/w + 1$.

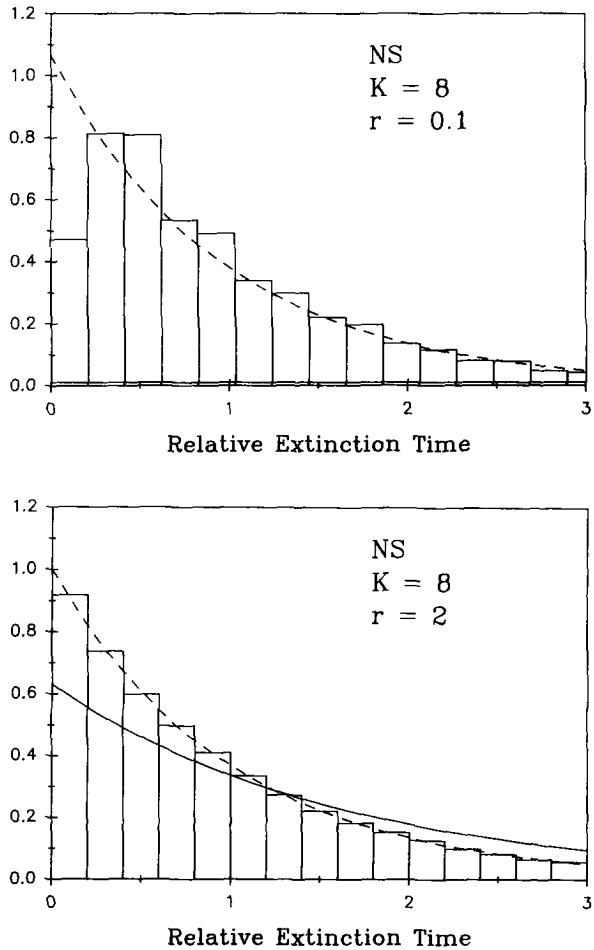
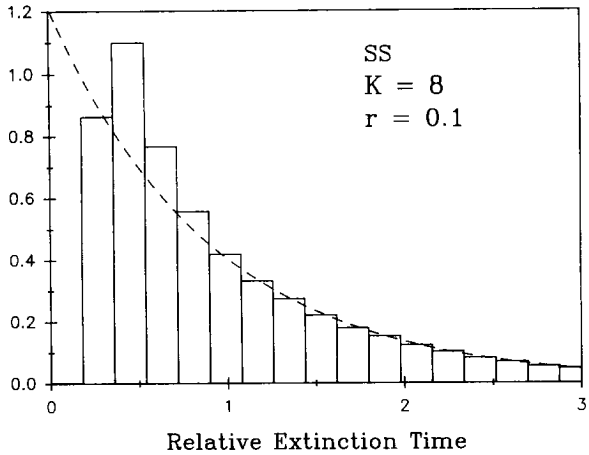


FIG. 5. Distribution of extinction times. The extinction times are given relative to their mean value so that the value 1 corresponds to the mean time of extinction. The frequencies are normalized so that they estimate the probability density function. The dashed line gives an exponential distribution with the same mean. The solid lines in (a) and (b) represent an exponential distribution with mean e^K (the $r \to \infty$ limit), scaled so that t_K again corresponds to 1. This distribution is not shown in (c) and (d) because it coincides almost with the abscissa. All panels are calculated for a carrying of $K = 8$ with PG-regime 2. For each distribution 10^5 simulations have been performed. The r-values, the type of stochastic model (NS or SS), the mean time to extinction t_K, and the length l of the intervals in the histograms, measured in number of generations, are (a) $r = 0.1$, NS, $t_K = 31.46$, $l = 6.5$; (b) $r = 2$, NS, $t_K = 1878$, $l = 376$; (c) $r = 0.1$, SS, $t_K = 11.13$, $l = 2$; (d) $r = 2$, SS, $t_K = 13.40$, $l = 2$.



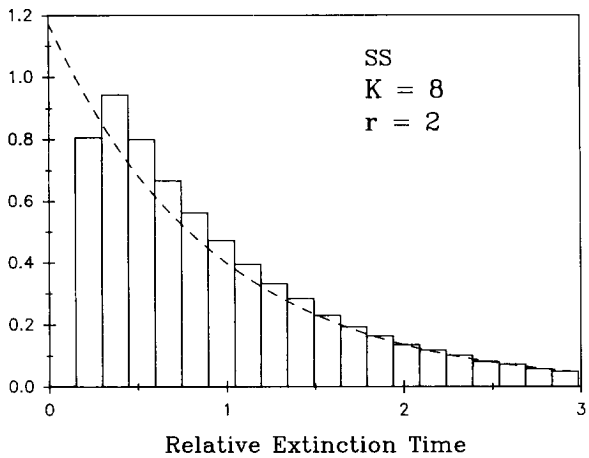


FIG. 5—*Continued*

Figure 5 gives some typical distributions of relative extinction time for PG-regime 2 at r values 0.1 and 2 with the stochastic models NS and SS. In all of these subfigures the extinction times are scaled so that the value 1 corresponds to the mean extinction time t_K for this parameter combination. The dashed lines represent the exponential distributions, with corresponding mean t_K, after scaling. To facilitate comparison of Fig. 5a and 5b, whose means are very different, we included also an (appropriately scaled) exponential distribution (solid line) with mean e^K, corresponding to the limit $r \to \infty$.

The observed distributions deviate from a geometric (exponential) distribution with the same mean. This has also been observed by Goodman (1987) for his model. He suggests that the model has a short "memory" of prior population sizes. Thinking of this as a demographic "drag," the slight deficiency at the shorter extinction times is accounted for by the relative improbability of going extinct more rapidly than the drag will permit.

In Fig. 5a, 5c, and 5d the extinction risk in the first generations is reduced compared to a geometric distribution with the same mean. The form of the distribution depends on the initial condition, unless r is large. The geometric distribution (dashed line) would be obtained if the extinction probabilities were constant and equal to $1/t_K$. If actual population size is $N(t)$, its probability of going extinct within the next generation is (from Eq. (5)) $e^{-N(t)}$. Except for the first generation, the population size can be anywhere in its state space. Therefore, the distribution of extinction times depends on the relative contributions from all possible states $N(t) > 0$. If the average of these conditional extinction probabilities is $1/t_K$, independent of generation number, then we expect a geometric distribution. But this cannot be true as long as the probabilities are influenced by the initial conditions. If, for example, the population starts at K, the extinction probability is $e^{-K} < 1/t_K$. Typically, a population that becomes extinct has decreased by random processes in several steps to a low size, at which point its extinction risk is high. Moreover, for low r it is likely that a population remains small once it is small. Thus, if $N(t)$ is sufficiently small we have $e^{-N(t)} > 1/t_K$. If such small populations make the main contribution to extinction at generation t, then we get a higher frequency of extinct populations than expected from the geometric distribution.

This verbal argument explains the hump in Fig. 5a. As observed from Fig. 5a and 5b, the deviation from a geometric distribution is much more pronounced for small r-values. Generally, the influence of starting conditions is larger if the population regulation is weaker; i.e., for smaller r we expect a stronger deviation from a geometric distribution. For large r (strong population regulation) the conditional probability of extinction is quite independent of the actual population size, because the expected population size in the next generation will always be near the capacity K. This can also be inferred from Fig. 4 which shows that for large r the mean extinction time is almost independent of the initial population size.

In the SS-model, the probability of going extinct in the first generation is again e^{-K} (compare Eq. (6)). Since in the SS-model the mean extinction time is shorter than in the corresponding NS-model a larger deviation from the geometric distribution (dashed line) occurs (see Figs. 5c, d). (Since the minimum time to extinction is two generations in the PS-model and one generation in the SS-model, these offsets become visible if the expected extinction time is very small. This causes additional deviations from the

pure geometric distribution.) The details of the distributions of extinction time are of course highly dependent on the dynamics of the population regulation.

4. Discussion

To cover the range of what is thought to be ecologically relevant (see Hassel *et al.*, 1976), we selected five different types of density dependent population regulation regimes. All these models are of course too simple to describe real populations, but are helpful to gain insight into selected processes. We did not make separate assumptions about birth and death processes but assumed that the expected size of the next generation is a function of carrying capacity, growth rate, and the size of the present generation. With discrete non-overlapping generations, the number of offspring produced is, therefore, equal to the number of newborns surviving until reproduction. Even for a species with small variation in clutch size, the distribution of surviving offspring will then be well approximated by a Poisson distribution. This has also been assumed by other authors (e.g., Maynard Smith, 1989; Bell, 1988). The reader may also note that if the number of offspring per individual follows a Poisson distribution then the total number of offspring follows a Poisson distribution.

Most restrictive is the assumption that intrinsic growth rate and carrying capacity remain constant over time. Except in some captive populations such conditions are hardly satisfied in real populations. Nevertheless, the extinction times presented in our study are not irrelevant because our estimates are minimal extinction risks coming from unavoidable sources —of course assuming that the applied density dependent population regulation is a suitable model of reality. Including the variability of the environment and considering genetical problems would lead to higher risks of extinction (cf. Lynch and Gabriel, 1990).

For weak density dependent population regulation, the risk of extinction is reduced by an increased intrinsic growth rate. A large r, however, is not always beneficial to the population: if the density dependent population regulation reduces population size to small numbers immediately after the population becomes larger than its carrying capacity (as in PG-regimes 3, 4, and 5), the risk of extinction can increase if r becomes larger than an optimal value (see Fig. 3). This raises an interesting question on the evolution of high fecundity or, more generally, on maximizing individual fitness. Because of the individual advantage, higher fecundity (or higher r on the individual level) would become fixed after a short time in a local population, but this might be countered by the higher risk of extinction of this population via group selection. In such a case, maximization of individual fitness is disadvantageous and it would be interesting to study how the

evolutionary stable strategy depends on the interaction between local populations via migration.

Almost all of our results show that the extinction time increases exponentially with carrying capacity. This is already known from other models (e.g., MacArthur and Wilson, 1967) but the rate of increase presented in this study is much smaller especially if the risk by sex ratio is included. The risk due to sex-ratio variation alone is relevant only at very small population size, but it becomes important via interaction with stochastically changing population size. To emphasize the importance of the risk by sex ratio, we point out that already at $K=20$ and the moderate growth rate $r=2$ (measured per generation) the time to extinction is six orders of magnitude higher without sex. Therefore, in cases when one could believe that the extinction risk due to variation in offspring number is negligible compared to other risks, there might still be a substantial risk if sex-ratio variation occurs.

Conservation biologists often prefer to calculate extinction risks within a given timespan. Such risk analysis can also be performed with our model results. Especially if the intrinsic growth rate is not too small, good approximate risks can be easily calculated by integration over the geometric (or exponential) distribution for the appropriate time interval using our numerical or analytical results on mean extinction time.

Appendix

(AI) For absorbing Markov chains with discrete state space $I=\{0, 1, 2, ..., n\}$ or $I=\{0, 1, 2, ...\}$ and a single absorbing state, labelled 0, the mean times t_i to absorption, or extinction times ($i \in I$, $i \neq 0$, the initial state), are the unique minimum non-negative solutions of the following system of linear equations:

$$t_i = \sum_{k \geqslant 1} p_{ik} t_k + 1, \qquad i \geqslant 1.$$

Here p_{ik} denotes the transition probability $i \to k$ (cf. Ewens, 1979 or Kemeny *et al.*, 1976). Using the vector and matrix notations $t=(t_1, t_2, ...)^{\mathrm{T}}$ (column vector of mean extinction times), $Q=[p_{ij}]_{i,j \geqslant 1}$ (the transition matrix with the 0-row and 0-column omitted), and $u=(1, 1, ...)^{\mathrm{T}}$, the above equation for the mean absorption times can be written as

$$(I-Q)t=u. \tag{A1}$$

Of course, I is the identity matrix.

If the process starts at i let t_{ij} denote the mean number of generations the process spends in j before absorption. Moreover, let $T = [t_{ij}]_{i,j \geqslant 1}$. Then it is well known (Ewens, 1979; Kemeny *et al.*, 1976) that

$$(I - Q)T = I \tag{A2}$$

holds and

$$t_i = \sum_{j \geqslant 1} t_{ij}. \tag{A3}$$

The variance of the extinction time may be calculated as

$$\sigma_i^2 = 2 \sum_{j \geqslant 1} t_{ij} t_j - t_i - t_i^2 \tag{A4}$$

(cf. Ewens, 1979) and in principle all higher moments can be derived. All the Markov chain models treated in this paper are absorbing and have 0 as the unique absorbing state (see below).

The numerical method that was mentioned in Section 2 for determining the extinction times and their variances is, in principle, based on the numerical evaluation of Eqs. (A1), (A2), and (A4) with p_{ik} chosen according to the particular model. However, all three systems are infinite dimensional because the state space is infinite due to the choice of the Poisson distribution. Therefore, careful numerical approximations are necessary.

(AII) Here we consider the asexual NS-model with stochastic population regulation. We first show that the population dies out with probability one in finite time. We consider the matrices P, Q, I, etc. as linear operators on the space l^∞ of bounded sequences $x = (x_1, x_2, \ldots)$ with norm $\|x\| = \sup_i |x_i|$. Then the norm of such an operator is given by $\|P\| = \sup_i \sum_j |p_{ij}|$. Since P is stochastic we have $\|P\| = 1$. Now we assume that the population growth function F satisfies either Eq. (1a) with $\beta \geqslant 1$ or (1b) or (1c), as in PG-regimes 2 to 5. Then $F(N)$ is bounded above, i.e., there is some $b > 0$ such that $F(N) \leqslant b$ holds for all $N \geqslant 1$. The constant b depends only on the parameters r, a, β, K, and ρ. Hence, in the notation of Section 2 $\lambda_i \leqslant b$ holds for all i. It follows from Eq. (12) that $p_{i0} = e^{-\lambda_i} \geqslant e^{-b}$ for all $i \geqslant 1$. Therefore, $\|Q\| \leqslant 1 - e^{-b}$ holds and the matrix $I - Q$ is invertible and satisfies the estimate $\|(I - Q)^{-1}\| \leqslant e^b$. Thus the solution vector t of Eq. (A1) is uniquely determined in l^∞. It follows that the mean extinction times t_i are uniformly bounded, as may be seen in Fig. 3.

Now we consider numerical questions. If F is given by the logistic equation (1c) then the Markov chain model can be reduced to a finite one, as follows. If $N(t) \geqslant K(\rho + 1)/\rho$ then $N(t+1) = 0$ with probability one.

Denoting by $NN+1$ the smallest integer $\geqslant K(\rho+1)/\rho$ it follows that $p_{i0}=1$ and $t_i=1$ for $i \geqslant NN+1$. Therefore, Eq. (A1) can be written as

$$\begin{aligned} t_i &= \sum_{i=1}^{NN} p_{ik} t_k + \sum_{i \geqslant NN+1} p_{ik} + 1 \\ &= \sum_{i=1}^{NN} p_{ik} t_k + 2 - \sum_{i=0}^{NN} p_{ik}, \end{aligned} \tag{A5}$$

because P is a stochastic matrix, i.e., $\sum_{k \geqslant 0} p_{ik} = 1$ for all $i \geqslant 0$. Then it is sufficient to solve (A5) for $1 \leqslant i \leqslant NN$, which is numerically straightforward.

If F is given by (1a) or (1b) we show below that Eq. (A1) can be truncated, i.e., a sufficiently large NN can be chosen so that the solution of the finite system

$$t_i = \sum_{k=1}^{NN} p_{ik} t_k + 1, \qquad i = 1, ..., NN, \tag{A6}$$

approximates the solution of (A1) to a preassigned degree. The solution of (A6) is always smaller than the exact solution of (A1), because truncation makes the state 0 equivalent to the states $i \geqslant NN+1$.

Our numerical data on the NS-model are based on solving Eq. (A6) (or (A5)). In order to achieve at least five significant digits it was sufficient to choose $NN \leqslant 3K+40$. In the majority of cases $NN = 2K+20$ was sufficient.

(AIII) Here we prove for the NS-model that the solutions of (A1) can be approximated by the solutions of (A6) if F satisfies (1a) with $\beta \geqslant 1$ or (1b) or (1c) for appropriately chosen NN. The present proof does not apply to case (1a) with $\beta < 1$, although convergence occurs numerically.

Denote by $t = (t_1, t_2, ...)^{\mathrm{T}}$ the column vector of solutions of (A1), by $I^{(n)}$ the $n \times n$ identity matrix, and by $Q^{(n)}$ the matrix consisting of the first n rows and columns of Q. Then Q can be written as the partitioned matrix

$$Q = \begin{pmatrix} Q^{(n)} & A^{(n)} \\ B^{(n)} & C^{(n)} \end{pmatrix} \tag{A7}$$

with $A^{(n)}$, $B^{(n)}$, and $C^{(n)}$ chosen in the obvious way.

If F satisfies one of the above mentioned assumptions then we have seen in AII that $F(N)$ is bounded above, $F(N) \leqslant b$, for all $N \geqslant 1$. Next, the Poisson distribution with parameter λ takes its maximum at the largest integer $\leqslant \lambda$. Denoting by L the integer where $k \mapsto e^{-b} b^k / k!$ takes its maximum, simple computations show that the inequalities

$$p_{ik} = e^{-\lambda_i} \lambda_i^k / k! \leqslant e^{-b} b^k / k! \leqslant e^{-b} b^L / L! \tag{A8}$$

are valid for all $i, k \geqslant 1$. This implies that one can choose n such that the sums over the rows of $A^{(n)}$ and $C^{(n)}$ become arbitrarily small uniformly for all $i \geqslant 1$. This means that for every $\varepsilon > 0$ one can choose n such that

$$\|A^{(n)}\| < \varepsilon \qquad \text{and} \qquad \|C^{(n)}\| < \varepsilon \tag{A9}$$

holds.

Writing the solution t of (A1) as the partitioned vector $t = (t^{(n)}, r^{(n)})^{\mathrm{T}}$ and denoting by $u^{(n)}$ the n-dimensional truncation of u, Eq. (A1) can be written as

$$\begin{aligned} (I^{(n)} - Q^{(n)})\, t^{(n)} - A^{(n)} r^{(n)} &= u^{(n)} \\ -B^{(n)} t^{(n)} + (I - C^{(n)})\, r^{(n)} &= u. \end{aligned} \tag{A10}$$

Substitution for $r^{(n)}$ yields

$$\begin{aligned} &(I^{(n)} - Q^{(n)} - A^{(n)}(I - C^{(n)})^{-1} B^{(n)})\, t^{(n)} \\ &\quad = u^{(n)} + A^{(n)}(I - C^{(n)})^{-1} u. \end{aligned} \tag{A11}$$

It follows from (A9) that $\|A^{(n)}(I - C^{(n)})^{-1} B^{(n)}\| \to 0$ and $\|A^{(n)}(I - C^{(n)})^{-1} u\| \to 0$ as $n \to \infty$. Therefore

$$\|(I^{(n)} - Q^{(n)})\, t^{(n)} - u^{(n)}\| \to 0 \tag{A12}$$

holds.

Denoting the solution of the truncated equation

$$(I^{(n)} - Q^{(n)})\, s^{(n)} = u^{(n)} \tag{A13}$$

by $s^{(n)}$, we obtain together with (A12) that $\|s^{(n)} - t^{(n)}\| \to 0$, as $n \to \infty$, since $\|(I^{(n)} - Q^{(n)})^{-1}\| \leqslant e^{b}$ holds (see AII). This proves the desired numerical convergence.

(AIV) The computational treatment of the SS-model is much more demanding than that of the NS-model since the Markov process is bivariate. However, due to the choice of φ (Eq. (8)) it is biologically and mathematically clear that in this model the probability of reaching very high population size is lower and, therefore, the extinction times are smaller than in the NS-model. In particular, it is again possible to truncate the transition matrix by choosing an appropriate NN and to restrict the state space to $\{(i, j) : 0 \leqslant j \leqslant i \leqslant NN\}$.

Denoting the mean extinction time for the initial value (i, j) by τ_{ij} and

recognizing that $\tau_{00}=0$, $\tau_{i0}=\tau_{ii}=1$ for $i \geqslant 1$ a simple computation shows that it is sufficient to solve

$$\tau_{ij}=\sum_{k=2}^{NN} \sum_{1 \leqslant l \leqslant k-1} p_{ij,kl}\tau_{kl}+2e^{-\lambda_{ij}/2}(1-e^{-\lambda_{ij}/2})+1 \qquad \text{(A14)}$$

for $1 \leqslant j < i \leqslant NN$. This gives $NN(NN-1)/2$ equations to solve. In fact, we have always chosen $NN \leqslant 3K+40$ (usually much smaller), as in the NS-model. Due to limited memory (although 64 MB were available!) calculations for $K > 16$ could not be performed using this method. For these cases Monte Carlo simulation is much more efficient due to the relatively short extinction times.

(AV) The special case FI simplifies SS considerably, since it follows from the transition matrix (Eq. (12)) that $\tau_{i0}=\tau_{ii}=1$ and $\tau_{ij}=\tau_i$ for $1 \leqslant j < i$.

Then some algebra reduces Eq. (A14) to

$$\tau_i=\sum_{k=1}^{NN} e^{-\lambda_i}\frac{\lambda_i^k}{k!}(1-2^{-k+1})\tau_k+2e^{-\lambda_i/2}(1-e^{-\lambda_i/2})+1 \qquad \text{(A15)}$$

for $1 \leqslant i \leqslant NN$. This is computationally much less demanding.

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