

PROBABILITY OF POPULATION EXTINCTION ACCOMPANYING A TEMPORARY DECREASE OF POPULATION SIZE

Yoh IWASA and Hiroshi MOCHIZUKI

Department of Biology Faculty of Science Kyushu University Fukuoka 812, Japan

INTRODUCTION

Extinction of a local population is a key ecological process; its quantitative estimate is very important both in the study of ecological and evolutionary dynamics and in the practice of pest control management and natural resource conservation. However, theoretical studies of population dynamics have concentrated on deterministic models expressed as sets of differential (or difference) equations for continuous variables of population sizes (MAY 1981; ROUGHGARDEN, 1979; HALLAM and LEVIN, 1986; KUNO 1987) which are not tools suitable for analyzing population extinction. This bias may have weakened the applicability of theories and could sometimes make misleading conclusions.

For example, MURDOCH et al. (1984, 1985) reviewed cases of biological control of pest insects performed by releasing parasitoids or predators, and discovered that the extinction of local pest population was observed in most (8 out of 9) successful cases. This result is contrary to the traditional picture of good biological control, derived from the study of host-parasite population dynamics, which recommends a stable coexistence of host and parasitoid at a low level, and regards population extinction as undesirable (HASSELL, 1978; BEDDINGTON et al. 1978; MAY and HASSELL, 1981; KAKEHASHI et al. 1984).

The stochasticity caused by the finiteness of population size is called “demographic stochasticity”, distinguished from “environmental stochasticity” indicating the fluctuation of the average rate of population increase. A deterministic model is a good approximation when the population size is sufficiently large, as guaranteed by the law of large numbers. However, when the population size is small, demographic stochasticity and its consequence of population extinction are important, and then stochastic modelling becomes imperative.

Unfortunately, the difficulty of mathematical analysis and the amount of numerical computation required by full stochastic models are huge. A practical alternative, we here propose, is a “hybrid” approach, in which a deterministic population model is used when the population size is sufficiently large, and the extinction probability accompanying each occasion of temporary reduction of population size is estimated by a formula derived from the study of a stochastic model.

In this paper, we study the probability of population extinction in the case that environmental fluctuation causes a temporary decrease of population size and a recovery following it. We first derive a formula for the probability of population extinction in a simple density independent model by using three techniques: (1) nonstationary branching processes, (2) nonstationary Markov chain, and (3) Monte Carlo simulations. Then we apply the formula to two more realistic population models, confirming its usefulness.

MODEL

We consider a **stochastic population model**, with the following assumptions:

- (a) Generations do not overlap each other.
- (b) Only the number of **females** is considered, assuming that reproductively active **males** are always available, and hence do not limit the rate of population increase. Lineages are traced only through females.
- (c) The initial population is composed of X_0 adult females at **generation** t_0 .
- (d) The number of offspring surviving to maturity produced by a particular female of the t th generation is a **stochastic variable** following a Poisson distribution with the average $\lambda(t)$. If the population size at t is $X(t)$, that in the next generation, $X(t+1)$, is the sum of $X(t)$ independent variables; and therefore follows Poisson distribution with the average $\lambda(t)X(t)$.

$$\text{Prob}[X(t+1)=x|X(t)=y] = \frac{(\lambda(t)y)^x}{x!} \exp[-\lambda(t)y], \quad (1)$$

where $t=t_0, t_0+1, t_0+2, \dots$ with t_0 indicating the initial generation.

The corresponding deterministic population model, having the same average rate of population growth, is

$$X_t^p = X_0 \lambda(t_0) \lambda(t_0+1) \dots \lambda(t-1), \quad (t=t_0, t_0+1, t_0+2, \dots). \quad (2)$$

We consider a particular case in which the deterministic population (2) has a temporary decrease, as expressed by the trajectory:

$$X_t^p = \alpha \exp[2(t-\gamma)^2/\beta^2], \quad (t=t_0, t_0+1, t_0+2, \dots), \quad (3)$$

which is illustrated by a broken curve in Fig. 1. The rate of population increase is:

$$\lambda(t) = \frac{X_{t+1}^p}{X_t^p} = \exp[4(t-\gamma+0.5)/\beta^2], \quad (t=t_0, t_0+1, t_0+2, \dots). \quad (4)$$

The exponential rate of population increase, expressed by the terms between braces of (4), is first negative, linearly increases with time, and turns positive. The population size starts from initial size $X_0 = \alpha \exp(2(t_0-\gamma)^2/\beta^2)$, decreases for a while ($t_0 \leq t < \gamma$) and then increases ($t > \gamma$). Although Eqs. (3) and (4) are used only for integer t , we regard them as functions of a continuous variable t in naming parameters: i.e. α is the minimum population size, and β is the number of risky generations in which the

population size is less than 1.65 times the minimum size α .

We consider the stochastic model corresponding to the deterministic trajectory (3). Thus we have an additional assumption:

(e) The expected per generation growth rate $\lambda(t)$ is given by Eq. (4).

The deterministic model, (3), does not describe a trajectory leading to population extinction. In the stochastic model, however, the population may go extinct because of the stochasticity due to the finite population size. Fig. 1 illustrates ten trajectories generated by computer simulations. For this particular set of parameters, the population went **extinct** in 189 out of 1000 independent replicates of simulation, while in the rest the population survived through the “risky” period and the size went to positive infinity.

Branching processes

The stochastic model (a)–(e) is a particular case of branching processes with time-varying coefficient (HARRIS, 1963; SEVAST'YANOV, 1971). Owing to the basic assumption that the size of a lineage starting from a particular individual is independent of the sizes of other lineages, a **powerful technique of branching processes** is applied in calculating **the extinction probability**. Let $p(t)$ be the probability of ultimate extinction of a lineage starting from a single individual in generation $t(t=t_0, t_0+1, t_0+2, \dots)$. Note that the **extinction of a population starting from X_0 individuals** is equivalent to **the extinction of all the lineages originating from those of the initial population**. We therefore have:

$$P_{ext} = (p(t_0))^{X_0}. \quad (5)$$

Another basic equation is a recurrence equation for $p(t)$, the **probability of ultimate extinction of a lineage starting from an individual in generation t** . We first note the following relation:

$$p(t) = \sum_k \frac{(\lambda(t))^k}{k!} \exp(-\lambda(t)) [p(t+1)]^k, \quad (6)$$

which is derived from the **assumption** that the **number of offspring (indicated by k in (6)) of a single individual at the t th generation is of Poisson distribution with the average $\lambda(t)$** , and that the **probability of ultimate extinction of a lineage starting at the t th generation is equivalent to the extinction of all the lineages starting from their offspring**. Eq. (6) can be rewritten as:

$$p(t) = \exp[\lambda(t)(p(t+1) - 1)], \quad (t=t_0, t_0+1, t_0+2, \dots). \quad (7)$$

Eqs. (5) and (7), together with $p(\infty)=0$ and Eq. (4), give the probability of population extinction.

If $\lambda(t)$ is a constant, we have a standard model of **branching processes**. Then the probability of ultimate extinction of a population can be calculated by iterating Eq. (7), which predicts a positive probability of population extinction even if the average

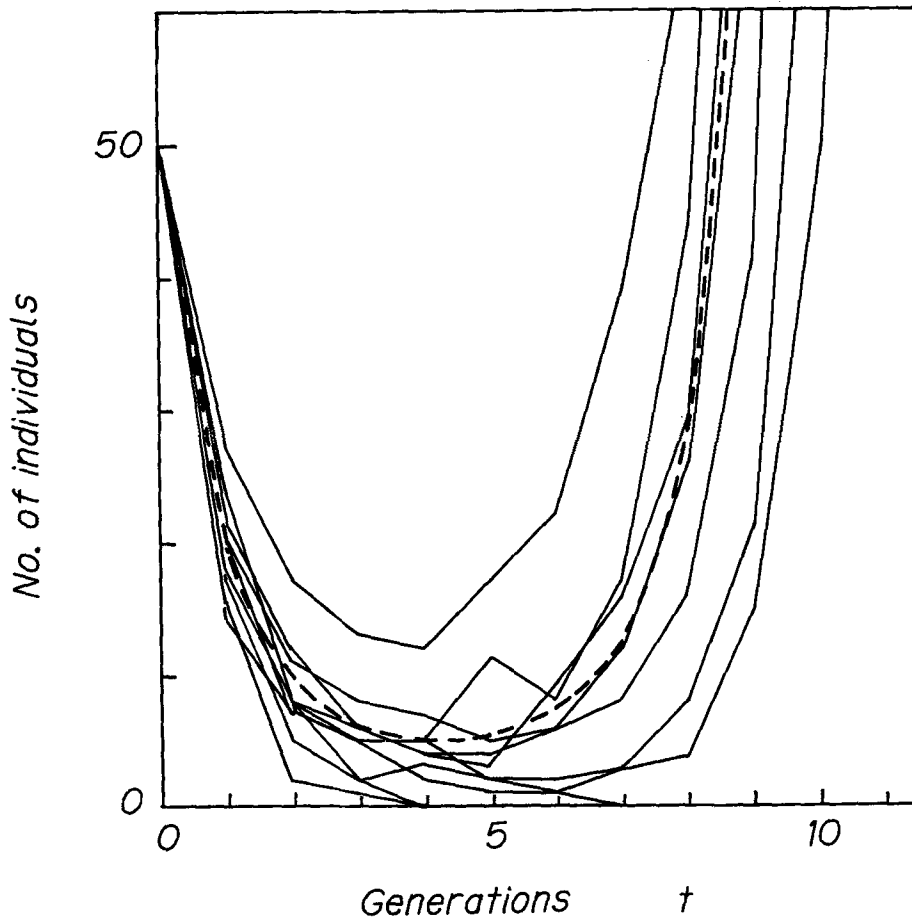


Fig. 1. Trajectories of population size generated by the stochastic model. Parameters are: $X_0 = 50$, $\alpha = 5$, and $\beta = 4$ (hence $\gamma = 4.292$). The trajectory of the corresponding deterministic model is indicated by broken curve. Among ten independent replicates of computer simulation in the figure, the population went extinct in three runs while in others the population recovered through the risky period. Thousand replicates such as these produce 189 extinct and 811 recovered runs; hence $P_{1000} = 0.189$. P_{ext} estimated both by branching processes and by Markov chain is 0.170.

rate of population growth is positive. Here we consider $\lambda(t)$ changing with t , as given by Eq. (4) indicating a temporary drop in population size.

Markov chain

The fraction and the timing of population extinction can also be calculated using Markovian dynamics of probability distribution between discrete states. Let $p(x, t)$ be the probability that the population size is x at the t th generation. Then we have

$$p(x, t+1) = \sum_y T(x; y, t) p(y, t), \quad (t = t_0, t_0 + 1, t_0 + 2, \dots). \quad (8)$$

where $T(x; y, t)$ is the probability of transition from y to x at the t th generation, given by

Eq. (1) with Eq. (4). The initial distribution is:

$$p(x, t_0) = \begin{cases} 1, & x = X_0 \\ 0, & \text{otherwise,} \end{cases} \quad \text{Thomas Speck mentioned this method.} \quad (9)$$

which indicates that the probability is concentrated at X_0 . The repeating application of Eq. (8) starting from Eq. (9) yields the probability distribution. The extinction probability $p(0, t)$ increases with t and converges:

$$P_{ext} = p(0, \infty). \quad (10)$$

After passing through the risky period, if the size of a nonextinct population becomes large (say more than 100), its exponential rate of increase is then significantly positive and the population size increases very rapidly, diverging to positive infinity. Therefore we regard a population as “recovered” if its size exceeds 100. This Markov chain, Eq. (8), then has two absorbing boundaries: one is $X=100$ for “recovered”; and the other, $X=0$ for “extinct”; once the system reaches either of these, it stays there forever. We continue computation until, after 100 or 150 generations, the probability of still remaining between 1 and 99 becomes negligible. In fact most extinctions occurred around γ , the time when population trajectory Eq. (3) is the minimum, and the increase of the population size to infinity is certain for surviving populations in the generation much later than γ .

We use three methods in estimating the probability of population extinction: i) recursive equations for branching processes, Eqs. (5) and (7); ii) Markov chain dynamics of probability distribution, Eq. (8); and iii) computer simulation. The first and the second methods gave exactly the same result for the extinction probability, although the amount of computation was much smaller for the first method. The third method (computer simulation) gives an estimate of extinction probability with some width because of the finite number of replicates, but the result is close to the prediction of the first and the second methods, confirming their validity.

A FORMULA FOR POPULATION EXTINCTION PROBABILITY

In a hybrid approach we propose, the population extinction rate is estimated for the stochastic model starting at the initial population size X_0 at generation t_0 , which is on the trajectory of the deterministic population model (see Fig. 1). For a particular trajectory of the deterministic model given by Eq. (3), the initial population size X_0 should be larger if we start the calculation of the stochastic model earlier. For such a hybrid approach to be useful, the timing of switch from the deterministic to the stochastic models, which is chosen arbitrarily, should not affect the result much.

The shape of a trajectory generated by the deterministic model Eq. (3), apart from horizontal shifting, is described by two parameters: the minimum population size (α) and the length of risky period (β). One more parameter, either $t_0 - \gamma$ or X_0 , specifies

the timing at which the stochastic model starts. We examined the model for different initial size X_0 having the same pair of α and β . The results are summarized in Fig. 2, which shows that the extinction probability P_{ext} is almost independent of the initial size X_0 if α and β are fixed. For example, the extinction probability if the stochastic model starts from $X_0=40$ is very slightly smaller than that starting from $X_0=60$, with the difference less than 1%. However, P_{ext} becomes more sensitive to X_0 if the starting population size X_0 is close to the minimum population size α .

The **robustness** of extinction probability to the change of initial population size X_0 is mathematically proved by analyzing Eqs. (5) and (7) in Appendix A, where it is also shown that the extinction probability is slightly smaller if the stochastic model starts later along the same deterministic trajectory. This result indicates that the extinction probability P_{ext} in the stochastic model can be estimated accurately by two parameters α and β measured for the trajectory of the corresponding deterministic model, Eq. (3), irrespective of the timing at which the stochastic model starts.

Figure 3a shows that the logarithm of the extinction probability (with $X_0=50$) linearly decreases with the minimum population size α , as

$$\log(P_{ext}) = -k(\beta)\alpha. \quad (11)$$

The regression lines pass through the origin, because $P_{ext}=1$ (extinction is certain)

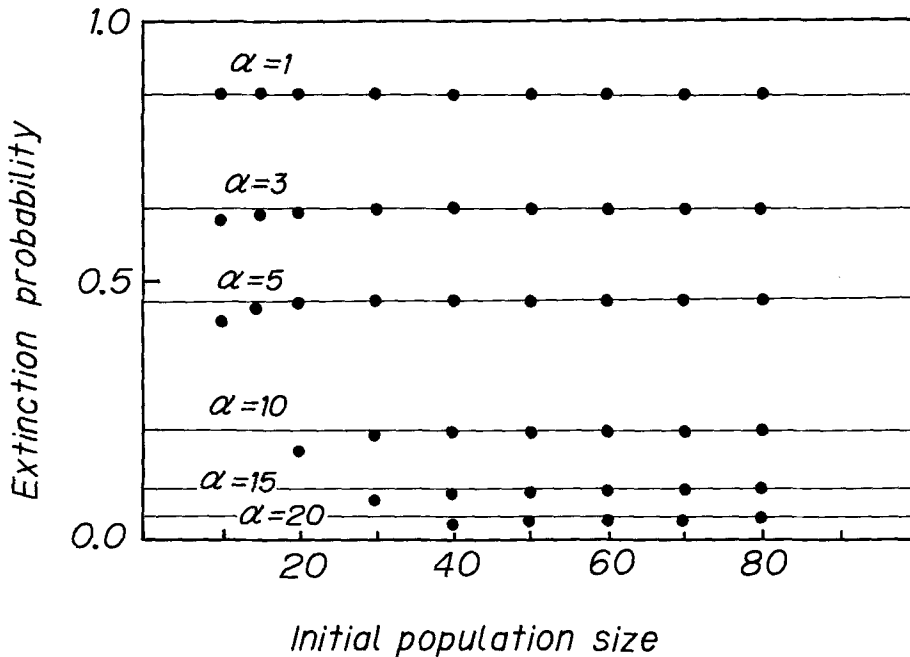


Fig. 2. The relation between the probability of population extinction P_{ext} and the initial population size X_0 for various α . $\beta=10$. P_{ext} is obtained by branching processes Eq. (7) and the Markov chain. The figure indicates that P_{ext} is almost independent of X_0 if X_0 is sufficiently larger than α .

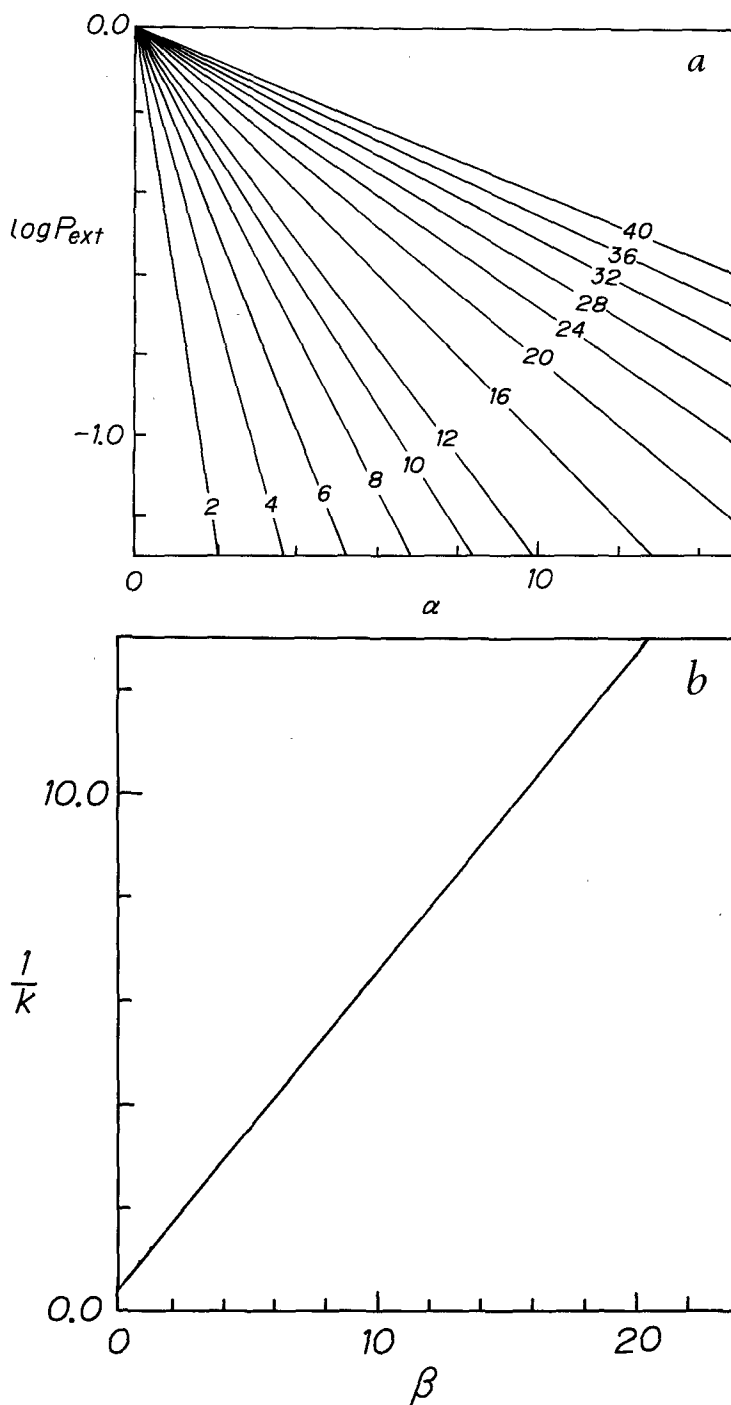


Fig. 3. a) The logarithm of the probability of population extinction P_{ext} (starting with $X_0 = 50$) versus the minimum population size α . Numerals are for β . P_{ext} calculated by branching processes and Markov chains are almost exactly on the straight lines with zero intercept, as predicted by mathematical analysis in Appendix A. We denote the magnitude of the slope by k . b) The relation between the inverse of the coefficient k in Eq. (11) and the parameter β ($0.4 \leq \beta \leq 20$). A line indicates Eq. (12). No deviation is observable on this figure.

when $\alpha=0$. Eq. (11) is proved in Appendix A. The coefficient of proportionality $k(\beta)$ in (11) is given as a function of remaining parameter β . Figure 3b shows that linear relation

$$1/k(\beta)=0.3563+0.6165\beta, \quad (12)$$

is very accurate. Fitting of the data to several functional relations other than (11) and (12) did not give better results. Combining Eq. (11) and (12), we have the following formula of population extinction rate:

$$P_{ext}=\exp [-\alpha/(0.3563+0.6165\beta)]. \quad (13)$$

The error in the values of the extinction rate predicted by formula (13) for all the cases we examined is less than 1%, if the starting population size X_0 is at least five times larger than the minimum size α .

APPLICATION TO PEST CONTROL

Population dynamic models we meet in ecology are not as simple as the one described by Eq. (2). Usually, the rate of population increase $\lambda(t)$ depends on the density of its own and on that of other species (e.g. resources, competitors, predators, or parasites). In this section, we study the probability of population extinction in stochastic models obtained from nonlinear deterministic dynamics by considering demographic stochasticity.

The extinction probability is likely to be controlled by the trajectory around when the population size reaches its minimum in the deterministic model. Therefore we approximate the trajectory of a given deterministic model by a simplified curve Eq. (3), and estimate the extinction probability using Eq. (13). The procedures for determining two parameters α and β are explained in Appendix B.

Example 1—extinction of a pest by pesticide application.

We here consider the following dynamics of pest population $X(t)$:

$$X(t+1)=X(t) \exp [r(1-X(t)/K)-bY(t)], \quad (14)$$

where $Y(t)$ is the concentration of pesticide in the field. In the absence of pesticide, the pest population follows discrete dynamics with density dependence. Pesticide causes density independent mortality. The level of pesticide in a generation is the sum of the effect remaining from the previous generation and the additional amount applied in the generation:

$$Y(t+1)=cY(t)+a(t). \quad (15a)$$

A fraction $1-c$ of the pesticide is decomposed each generation ($0 < c < 1$). The rate of application of pesticide $a(t)$ is:

$$a(t) = \begin{cases} a_0, & 0 \leq t \leq t_c, \\ 0, & t > t_c, \end{cases} \quad (15b)$$

which indicates that the pesticide is used for a fixed period of t_c with an intensity a_0 , then is stopped.

In this deterministic model, the extinction of the pest is impossible—pest population certainly recovers after the pesticide treatment is stopped. However, in the stochastic model with demographic stochasticity considered, population extinction is likely to accompany the temporary drop of population size caused by a sufficiently intense pesticide treatment.

In the stochastic model, we assume that the population size in the next generation $X(t+1)$ follows a Poisson distribution with the average given by the right hand side of Eq. (14).

Table 1. The probability of extinction in pest population by pesticide treatment.

r	b	α	β	P_{1000}	Eq. (13)	diff.	n.b.
1.0	.20	4.49	6.60	.372	.363	.009	
0.8	.20	1.20	7.06	.798	.775	.023	
1.0	.15	17.30	6.36	.008	.018	-.010	
0.5	.19	0.09	6.16	.986	.979	.007	
0.5	.175	0.24	9.90	.959	.964	-.005	
0.5	.15	1.08	8.54	.851	.825	.026	
0.5	.138	2.09	9.22	.709	.708	.001	
0.5	.13	3.13	8.90	.592	.585	.007	
0.5	.125	3.98	8.46	.549	.490	.059	
0.5	.12	5.01	8.70	.444	.416	.028	
0.5	.115	6.25	8.90	.355	.343	.012	
0.5	.11	7.71	9.22	.280	.279	.001	
0.5	.105	9.40	8.78	.195	.196	-.001	
0.5	.10	11.34	8.98	.140	.146	-.006	
0.5	.095	13.56	9.34	.087	.109	-.022	
0.5	.09	16.04	9.58	.044	.077	-.033	
0.5	.085	18.77	8.96	.017	.041	-.024	
0.5	.08	21.87	9.32	.017	.028	-.011	
0.5	.075	25.11	9.70	.002	.019	-.017	
1.0	.20	20.60	4.40	.000	.001	-.001	$c=0.8$
1.0	.15	1.75	6.20	.678	.658	.020	$a_0=1.5$
1.0	.15	0.04	3.14	.990	.983	.007	$a_0=2.0$
1.0	.15	4.83	6.42	.342	.326	.016	$t_c=15$
1.0	.15	0.92	6.16	.874	.801	.073	$t_c=20$
1.0	.15	0.13	5.28	.981	.965	.016	$t_c=25$

Parameters not on the table are $a_0=1.0$, $t_c=10$, $c=0.9$, $K=100$, $X_0=100$, $Y_0=0.0$. In the last six cases, some parameter differs from this standard set, as indicated in the column of n.b. P_{1000} is the fraction of simulation runs in which the population went extinct before $t=50$. The prediction by Eq. (13) is close to P_{1000} , with the error less than 3% in most (24 out of 27) cases.

The branching process calculation, such as Eqs. (5) and (7), is not applicable because of the density dependent nature of the processes. We used computer simulation for analysis of the population extinction probability. The result is summarized in Table 1.

On the other hand, we may use Eq. (13) to predict the extinction probability. To do this, we calculate the deterministic trajectory of Eqs. (14) and (15), and estimate two parameters (the minimum population α and the period β for the population to stay around the minimum) by fitting $\log X(t)$ to a quadratic function of time according to the procedures in Appendix B. Then using formula (13), we estimate the probability that population extinction occurs in the first risky period. The results are also listed on Table 1.

Table 1 indicates that Eq. (13) can predict the probability of population extinction P_{1000} (obtained by direct computer simulation) quite accurately — with the error often less than 3%. This deviation is not statistically significant, because the estimate of a probability by 1000 independent replicates has the standard deviation of $\sqrt{p(1-p)/1000}$ which is 1.56% if $p=1/2$.

Table 1 also shows the cases in which the population extinction is calculated for various values of the intensity of pesticide application and of the period of pesticide treatment. In a case ($r=1.0$, $b=0.15$), doubling the pesticide level (from $a_0=1.0$ to 2.0) increased the probability of pest extinction P_{1000} from 0.8% to 99%. Doubling of the period of pesticide treatment (from $t_c=10$ to 20) also results in a very spectacular increase in P_{1000} (from 0.8% to 87.4%).

Example 2—extinction of a pest by release of its specific parasitoid.

The second example is a system of host and its specific parasitoid. Let $H(t)$ and $P(t)$ be the abundances of host and parasitoid respectively. The host is a pest insect which we aim to extinguish. We start with the following deterministic model:

$$H(t+1)=H(t) \exp [\tau(1-H(t)/K)-aP(t)], \quad (16a)$$

$$P(t+1)=H(t) \exp [\tau(1-H(t)/K)](1-\exp (-aP(t))). \quad (16b)$$

The famous Nicholson and Bailey model (NICHOLSON and BAILEY, 1935) is obtained when the carrying capacity K is infinitely large. Then the equilibrium with both host and parasite coexisting is unstable, and if the system deviates from it only slightly, it would then oscillate with increasingly larger amplitude. In Eq. (16), the host's growth rate is density dependent, as was done by BEDDINGTON et al. (1975). Eq. (16) is different from the system studied by BEDDINGTON et al. (1975) in that we have assumed parasitoids attack after the host population size is regulated by resource competition (also see KAKEHASHI et al. (1984)). The density dependent mechanisms keep the host population size finite even in the absence of the parasitoid, and stabilize the host-parasitoid dynamics.

We can then add a random element to the model, which is caused by finite popula-

tion size. Suppose that the population sizes of host $H(t)$ and parasitoid $P(t)$ are known. Let \tilde{H} be the number of hosts in the next generation but before the stage of parasitoid attack. \tilde{H} is assumed to follow Poisson distribution with the mean $H(t) \exp[\tau(1-H(t)/K)]$. Among these hosts, some are parasitized and the rest remain healthy, the fraction of the latter being $\exp(-abP(t))$. The number of unparasitized hosts $H(t+1)$ is therefore a random number following binomial distribution $B(\tilde{H}, \exp(-abP(t)))$.

The deterministic model Eq. (16) predicts oscillation of host population after the introduction of parasitoid to the system until the system finally converges to the steady state. The first valley is the deepest (see Fig. 4). We are concerned with the fraction of cases in which the populations go extinct on the occasion of the first drop of population size. Let T_a be the time for the local maximum between the first and the second valleys of population size. Monte Carlo computer simulation was carried out and the fraction of cases among 1000 runs in which the population size becomes zero before T_a , denoted by P_{1000} , is listed on Table 2 for various set of parameters.

The density dependence both through resource competition and through the parasitoid's numerical response tends to stabilize the trajectory and makes the extinction probability smaller than that given by formula (13) based on the density independent dynamics. Another factor making the difference is that computer simulation counts only those extinctions realized in a finite time T_a , in contrast to the infinite time horizon assumed in deriving Eq. (13). Both of these processes suggest the

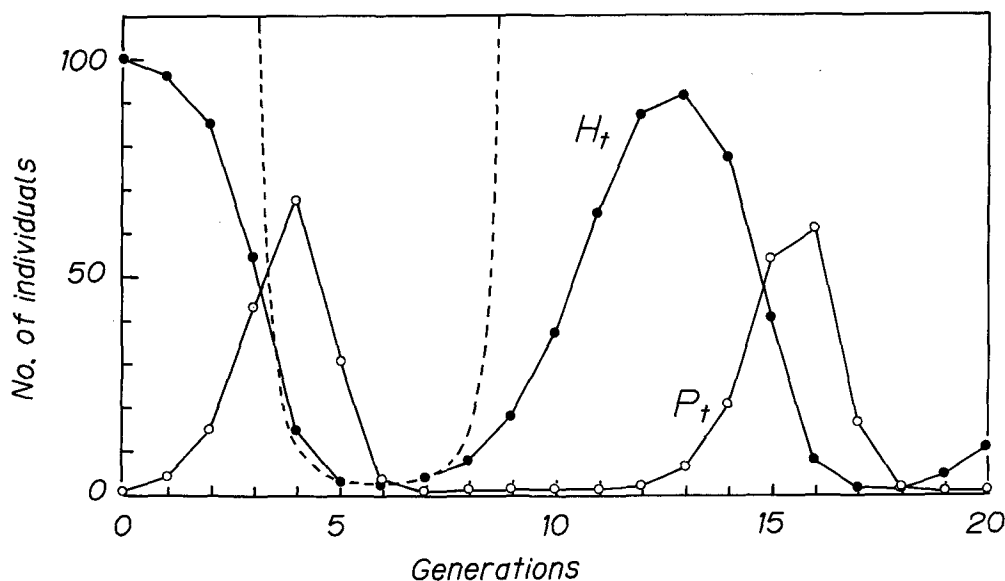


Fig. 4. Illustration of the deterministic trajectory generated by host-parasitoid system Eq. (16) with the parameters: $\tau=0.9$, $a=0.04$, $K=100$, $H_0=100$, and $P_0=1$. The broken curve indicates a log-quadratic function Eq. (3) with parameters: $\alpha=1.56$, $\beta=1.96$ and $\gamma=5.80$ fitted by the method described in Appendix B.

Table 2. The probability of extinction of the host by the release of specific parasitoid.

r	a	α	β	T_a	P_{1000}	Eq. (13)	diff.	n.b.
0.5	.030	7.05	3.10	15	.069	.045	.024	
0.5	.035	3.53	2.16	16	.164	.124	.040	
0.5	.040	2.03	2.48	18	.371	.341	.030	
0.5	.045	0.95	1.50	20	.579	.476	.103	
0.5	.050	0.52	1.48	22	.705	.664	.041	
0.5	.055	0.31	1.58	32	.800	.792	.008	
0.6	.060	0.19	1.74	32	.877	.876	.001	
0.6	.030	6.88	2.92	14	.051	.041	.010	
0.6	.035	3.40	2.04	15	.164	.122	.042	
0.6	.040	1.94	2.34	16	.355	.340	.015	
0.6	.045	0.89	1.44	17	.581	.489	.092	
0.6	.050	0.47	1.42	18	.720	.683	.037	
0.6	.055	0.28	1.50	21	.803	.804	-.001	
0.6	.060	0.18	1.72	27	.878	.881	-.003	
0.7	.030	6.63	2.72	13	.040	.038	.002	
0.7	.035	3.22	1.94	14	.171	.126	.045	
0.7	.040	1.83	2.24	14	.345	.349	-.004	
0.7	.045	0.82	1.38	16	.524	.507	.017	
0.7	.050	0.43	1.36	17	.706	.693	.013	
0.7	.055	0.25	1.44	18	.833	.818	.015	
0.7	.060	0.16	1.62	23	.873	.889	-.016	
0.8	.030	6.30	2.68	12	.040	.043	-.003	
0.8	.035	3.01	1.84	13	.169	.133	.036	
0.8	.040	1.70	2.06	13	.389	.352	.034	
0.8	.045	0.74	1.34	14	.575	.535	.040	
0.8	.050	0.38	1.30	16	.735	.720	.015	
0.8	.055	0.22	1.38	17	.837	.833	.004	
0.8	.060	0.14	1.52	18	.900	.897	.003	
0.8	.065	0.09	1.76	21	.948	.939	.009	
0.9	.030	5.93	2.40	12	.049	.040	.009	
0.9	.035	2.77	1.76	12	.167	.146	.021	
0.9	.040	1.56	1.96	13	.342	.348	-.006	
0.9	.045	0.70	1.24	14	.576	.535	.041	
0.9	.050	0.33	1.24	14	.744	.745	-.001	
0.9	.055	0.19	1.30	15	.857	.849	.008	
0.9	.060	0.12	1.44	17	.921	.908	.013	
0.9	.065	0.07	1.60	18	.917	.949	-.032	
1.0	.030	5.50	2.26	12	.051	.043	.008	
1.0	.035	2.51	1.68	12	.189	.165	.024	
1.0	.040	1.40	1.84	12	.357	.391	-.034	
1.0	.045	0.59	1.26	13	.623	.594	.029	
1.0	.050	0.28	1.20	14	.768	.775	-.007	
1.0	.055	0.15	1.22	14	.865	.873	-.008	
1.0	.060	0.10	1.36	15	.930	.920	.010	
1.0	.065	0.06	1.52	16	.954	.955	-.001	
1.1	.030	5.05	2.14	11	.051	.049	.002	
1.1	.035	2.25	1.60	11	.210	.187	.023	
1.1	.040	1.24	1.74	12	.427	.420	.007	
1.1	.045	0.52	1.24	12	.629	.629	0	
1.1	.050	0.24	1.14	13	.787	.797	-.010	
1.1	.055	0.13	1.20	13	.887	.888	-.001	
1.1	.060	0.08	1.28	14	.932	.933	-.001	
0.7	.035	0.45	1.22	18	.680	.666	.014	$H_o=K=150$
0.5	.035	0.55	1.32	24	.684	.625	.059	$H_o=K=150$
1.0	.035	0.30	1.12	14	.752	.751	.001	$H_o=K=150$
1.0	.02	7.91	2.00	12	.010	.007	.003	$H_o=K=150$
1.0	.045	0.06	1.26	16	.943	.948	-.005	$H_o=K=150$
0.7	.035	3.48	2.66	13	.171	.175	-.004	$P_o=2$
0.7	.035	3.16	1.88	13	.176	.124	.052	$P_o=3$
0.7	.035	3.24	2.04	13	.189	.134	.055	$P_o=4$
0.7	.035	3.33	2.26	12	.166	.149	.017	$P_o=5$
0.7	.035	2.93	1.86	12	.179	.142	.037	$P_o=10$
0.7	.035	2.68	2.62	12	.277	.257	.020	$P_o=20$
0.7	.035	1.86	1.66	12	.344	.260	.084	$P_o=30$
0.7	.035	1.52	1.82	13	.416	.358	.058	$P_o=40$
0.7	.035	1.22	2.06	13	.491	.472	.019	$P_o=50$
0.7	.035	0.17	1.12	20	.850	.850	0	$P_o=100$
0.7	.035	0.06	1.04	22	.944	.942	.002	$P_o=130$
0.7	.035	0.03	1.06	22	.978	.971	.007	$P_o=150$

Parameters not on the table are: $H_o=100$, $K=100$, $P_o=1$. In the last 17 cases, some parameter(s) differs from this standard set, as indicated in the column of n.b. P_{1000} is the fraction of simulation runs in which the population went extinct before T_a , the time for the local maximum between the first and the second valleys of population size. The prediction by Eq. (13) is close to P_{1000} , with the error less than 5% in most (62 among 69) cases.

overestimate of the extinction probability P_{1000} by the formula (13).

The results of simulation in Table 2 show that P_{1000} tends to be smaller than Eq. (13), but the error is very small: less than 1% in more than half of cases, less than 3% 24 of 27, and 8% in the largest.

Table 2 also shows how the probability of extinction varies with the number of parasitoids released. It was amazingly insensitive. A ten fold increase of the initial number of parasitoids (P_0) produced a shift of P_{1000} from 17.1% only to 17.9% in a particular example ($r=0.7$, $a=0.035$). In order to cause 90% extinction, we must release tremendous numbers of parasitoids, more than the number of hosts. On the other hand, an increase in the searching efficiency a is very efficient in enhancing the fraction of population extinction; doubling of a from 0.03 to 0.06 enhanced P_{1000} from 0.4% to 90.0% ($r=0.80$).

DISCUSSION

Stochastic population models dealing with the population extinction have been developed for studying several different phenomena. Models of pure demographic stochasticity under a constant environment have been studied by branching processes or by birth and death processes. MACARTHUR and WILSON (1967) studied the probability of establishment of colonists invading a new habitat, and showed that, even if the average rate of population increase is positive, invaders with small initial population size may go to extinct with a large probability. A high intrinsic rate of increase is effective in raising the colonizing success, which lead to the idea of r -selected species as good colonizers.

Once the population is established, the population size stays around carrying capacity, but occasionally decreases and may happen to become zero because of demographic stochasticity. According to the stochastic calculation, ultimate extinction is certain if the ceiling population size (carrying capacity) is finite. However the expected time until extinction is very large (10^3 generations or longer) if the carrying capacity is larger than 20 (MACARTHUR and WILSON, 1967; RICHTER-DYN and GOEL, 1972; GOEL and RICHTER-DYN, 1974). A more likely course of extinction in natural population is the combination of environmental fluctuation and the demographic stochasticity—a fluctuation of environment causes temporary reduction of the population size and then extinction occurs by way of the demographic stochasticity.

The effect of environmental stochasticity is intensively studied in community ecology, especially concerning the problem of whether and how the environmental fluctuation reduces the number of species coexisting in the same habitat (MAY 1974; TURELLI, 1977, 1979; also see Mangel and Ludwig, 1977). A species is regarded as going extinct if the population size on average approaches zero in the limit, expressed by that the expectation of $\log X_{t+1} - \log X_t$ is negative (TURELLI, 1977, 1979).

These formulations, however, do not allow us to estimate the timing of extinction,

because it takes an infinitely long time for the population size reaches zero. A usual trick is to assume a positive threshold population level, so that population extinction occurs when the population size reaches the threshold for the first time (STREBEL, 1985). LEIGH (1981) for example applied such a calculation to answer a controversy related to the design of biological preserve, whether a single large or many small areas are to be preserved (WILCOX and MURPHY, 1985). QUINN and HASTINGS (1987) reviewed theories on this topic and concluded that the optimal policy is to split a given total area into subareas having the carrying capacity similar to the square root of the total population. A difficulty of the formulation of threshold population size is that the arbitrary choice of extinction threshold often affects the result of extinction probability.

In this paper we study extinction caused by the combination of demographic stochasticity and environmental fluctuation temporarily reducing the population size and which cause the population extinction. A hybrid approach is proposed, in which the population trajectory of the deterministic model is calculated and then, for each drop of population size, the probability of population extinction is calculated by using formula (13) derived for a simple density-independent population. Two illustrating models for pest control show that such an approach is amazingly accurate in predicting the probability of population extinction calculated by computer simulation of the full stochastic model.

It also gives ecologically interesting results: the increase in the intensity and the period of pesticide treatment could considerably enhance the probability of population extinction. In contrast, an increase in the number of release of specific parasitoid does not improve the extinction probability of the pest much, but the increases in searching efficiency does. Choice of parasitoid species to release is therefore very important, but is unfortunately more difficult to manipulate than the amount and the period of pesticide treatment. This suggests that the release of a specific parasitoid may be less effective than pesticide as an agent to cause the extinction of pest population. However, we should be cautious that our models neglect many important processes, such as the evolution of pesticide resistance, alternative hosts for the parasitoid, environmental disturbance caused by pesticide application, immigration of pest from neighboring local populations.

The model includes many simplifying assumptions placed for the sake of mathematical simplicity. Some of these may be removed. First, even if the number of daughters surviving until maturity is not of a Poisson distribution, the calculation of branching processes can still be used under the assumption of the independence between lineages, i.e. density independence of dynamics. According to the analysis in Appendix C, it is concluded that the increase of the variance of offsprings with the same mean expressed by an "aggregated" distribution, such as a negative binomial distribution, should enhance the probability of population extinction.

Second, age structure and overlapping generation may also be included by considering branching processes with multiple states (HARRIS, 1963; SEVAST'YANOV, 1971;

IWASA and TERAMOTO, 1977, 1984).

Density regulating mechanisms of population dynamics such as resource competition and the parasitoid's numerical response would cause the population extinction rate to be smaller than that predicted by Eq. (13). On the contrary, positive feedback, such as the Allee effect, would make extinction more likely to occur. In such density dependent models, techniques of branching processes are not applicable, but Markov chain models or computer simulations may be used to derive a formula of extinction probability. Two examples of pest control models, however, suggest that the deviation due to density dependence may not be very large.

The most important simplification is the neglect of spatial structure. How frequent is the invasion of propagules from other local populations might qualitatively change the conclusion. The study of the extinction of an isolated population, as done in this paper, will serve as a starting point of a more general study.

One of the reasons for the lack of theoretical study of the extinction probability on the occasion of temporary decrease in the population size is the untractability of the full stochastic model. We hope that the hybrid approach we propose here may stimulate the theoretical study of population extinction, in view of tremendous importance of estimating population extinction rate in understanding many ecological processes.

SUMMARY

Local population extinction is the key to understanding many ecological processes, and also to wildlife management and to pest control. We here investigate theoretically the probability of population extinction in an occasion of temporarily unfavorable environment. Because of the stochasticity caused by the finite population size (demographic stochasticity), the population may go extinct even if the corresponding deterministic dynamic model does not predict it.

For the case that the population size of the next generation follows a Poisson distribution, the extinction probability is calculated by using three techniques: (1) branching processes, (2) Markov chain dynamics of probability distribution, and (3) computer simulation. The results are summarized as the following formula for the probability of population extinction:

$$P_{ext} = \exp [-\alpha / (0.3563 + 0.6165\beta)],$$

where two parameters are calculated by the trajectory of the corresponding deterministic model: namely, α is the minimum population size and β is the length of period in danger (the effective number of generations in which the population size stays less than 1.65α). This formula predicts the probability of extinction very accurately (with the error less than 1%) if the initial population size is sufficiently (more than 5 times) larger than the minimum size.

For general population dynamic models, a hybrid approach is proposed, in which

the trajectory of population dynamics is first calculated by the deterministic model and, for each drop of population size, the extinction probability is estimated by above formula. This approach should be practically very important, considering heavy computational load of full stochastic models.

The method is applied to two population models for pest control: (1) extinction of a pest population by applying pesticide for a fixed period. (2) extinction of a pest by releasing a specific parasitoid. In spite of the density dependence of population growth in both models, the probability of extinction of pest population calculated by computer simulation was accurately predicted by the above formula using the trajectory of the corresponding deterministic models.

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個体数の一時的減少にともなう個体群絶滅の確率

巖 佐 庸・望 月 博

局所個体群の絶滅は、生態的諸過程を理解する上にも野生生物の保護や害虫の駆除にも極めて重要である。本論では、一時的に環境が不適になった際に生じる絶滅の確率を理論的に研究した。対応する決定論的モデルでは個体群が絶滅しないと予測される場合でも、個体数が有限であるために生じる確率性（人口学的確率性）のために個体群が減びうる。次世代の個体数がポワソン分布をする場合についての絶滅率を、(1) 分岐過程、(2) マルコフ過程、(3) モンテカルロシミュレーション、の3つの手法によって計算し、絶滅率について次の公式を導いた。

$$P_{ext} = \exp [-\alpha / (0.3563 + 1.239\beta)]$$

ここで2つのパラメーターは対応する決定論モデルの軌跡から計算され、 α は最小個体数、 β は危険世代数（個体数が 1.65α 以下にとどまる期間）である。初期個体数が最小個体数より十分に大きいならば、この公式は絶滅率を極めて正確に予測する（誤差1%以内）。

より一般的な個体群動態モデルについては、まず決定論的モデルでの軌跡を求め、次に個体数が減少するそれぞれの機会ごとに個体群の絶滅率を上記の公式で計算するという混成的方法を提案した。確率モデルの膨大な計算量を考慮すれば、この近似法は実用上重要である。

この方法を、(1) 農薬をある期間にわたって散布するときの害虫の絶滅、および(2) 寄生者を放飼したときの寄主個体群の絶滅、に関する2つの害虫駆除モデルに適用した。両モデルとも密度依存的過程が含まれているにもかかわらず、計算機シミュレーションによって求めた個体群の絶滅確率は、決定論モデルの軌跡にあてはめて決めたパラメータを用いれば上記の公式によって正確に予測された。

APPENDIX A

We consider the stochastic model which starts at the initial population size X_o at generation t_o which lies on the deterministic trajectory Eq. (3). The probability of population extinction P_{ext} should be a function of three parameters: two parameters specifying the shape of the curve (α and β) and a third one for the timing of starting the stochastic model. We here choose X_o as the third parameter.

We first prove the weak dependence of P_{ext} on X_o , demonstrated by Fig. 3. Taking the logarithms of Eq. (5) and (7) leads to

$$\begin{aligned}\log(P_{ext}) &= X_o^D \log(p(t_o)) \\ &= X_o^D \lambda(t_o) [\exp(\log(p(t_o+1))) - 1].\end{aligned}\quad (A1)$$

Eq. (4) gives $X_o^D \lambda(t_o) = X_{o+1}^D$. Using the Taylor expansion of an exponential function, Eq. (A1) is rewritten as

$$\begin{aligned}&= X_{o+1}^D [\log(p(t_o+1)) + (1/2)(\log(p(t_o+1)))^2 \\ &\quad + (1/3!)(\log(p(t_o+1)))^3 + \dots].\end{aligned}\quad (A2)$$

If we start calculating the stochastic model sufficiently before the minimum population, the probability of extinction starting from a single individual is almost certain, and $p(t_o+1)$ is close to unity, hence $\log(p(t_o+1))$ is very small. Then we can neglect higher order terms of (A2) producing:

$$\doteq X_{o+1}^D \log[p(t_o+1)], \quad (A3)$$

which, according to Eq. (5), equals the logarithm of the extinction probability for the population starting from generation t_o+1 with initial size $X_{t_o+1} = X_{t_o} \lambda(t_o)$. Hence the probability of population extinction starting t_o is very close to that start one generation later t_o+1 , but with a smaller initial condition $X_{t_o+1}^D$ having the same the deterministic trajectory.

Higher order terms in Eq. (A2) are always positive, because $\exp(x) - 1 - x$ is positive, and therefore (A3) is smaller than (A1), i.e. the extinction probability tends to decrease as the initial population size X_o approaches to minimum size α , as demonstrated by Fig. 3.

Equation (5) together with Eq. (3) becomes

$$\log P_{ext} = \alpha \exp[2(t_o - \gamma)^2 / \beta^2] \log(p(t_o)). \quad (A4)$$

Now we note that $\lambda(t)$ given by Eq. (4) is a function of $t_o - \gamma$ and β only. Hence $p(t_o)$, as determined by Eq. (7) and $p(\infty) = 0$, is a function of $t_o - \gamma$ and β , and independent of α . Thus we conclude from Eq. (A4) that $\log(P_{ext})$ is proportional to α and of the form:

$$\log P_{ext} = \alpha g(t_o - \gamma, \beta), \quad (A5)$$

where $g(t_o - \gamma, \beta)$ is a function of two variables $t_o - \gamma$ and β . The initial population size

X_o is related to other parameters by $X_o = \alpha \exp(2(t_o - \gamma)^2 / \beta^2)$ and the replacement of $t_o - \gamma$ in (A5) by this relation gives an expression of P_{ext} as a function of α , β and X_o .

Considering this relation with the very weak dependence of P_{ext} on X_o , derived in the above, we conclude that the dependence of $g(t_o - \gamma, \beta)$ in Eq. (4) on the first variable $t_o - \gamma$ is very weak; and hence we have Eq. (11) in text.

APPENDIX B

In Eq. (3), the logarithm of the population size $\log X^p$ is expressed as a quadratic function of time. If the population sizes in three successive generations are known, we can determine the parameters α and β from their logarithm $y_1 = \log X_t$, $y_2 = \log X_{t+1}$, and $y_3 = \log X_{t+2}$, by the following equations:

$$\alpha = \exp [y_2 - (y_3 - y_1)^2 / 8(y_1 - 2y_2 + y_3)], \quad (\text{B1a})$$

$$\beta = 2 \sqrt{(y_1 - 2y_2 + y_3)}^{-1} \quad (\text{B1b})$$

Note that the fitting to Eq. (3) should be done around the local minimum of the population size. Therefore the procedures of application of the formula Eq. (13) is as follows: First, we calculate the deterministic population dynamics and pick up three successive generations such that $X_t > X_{t+1} < X_{t+2}$. Then calculate α and β using Eqs. (B1). Finally, apply the Eq. (13) in text to calculate the probability of population extinction.

The third parameter γ of the deterministic trajectory is given by

$$\gamma = t + 1 - (y_3 - y_1) / 2(y_1 - 2y_2 + y_3), \quad (\text{B2})$$

which, however, is not necessary to estimate the extinction probability.

APPENDIX C

If the number of female offspring surviving until maturity follows a distribution other than Poisson, we use a similar argument for Eq. (7) and we have

$$p(t) = \sum_k q_k(t) [p(t+1)]^k, \quad (\text{C1})$$

where $q_k(t)$ is the probability of the number of female offsprings surviving until maturity exactly equals k . The right hand side of (C1) is $G(p(t+1))$ using the generating function $G(s)$ of the distribution $\{q_k(t)\}_k$. In particular, for the negative binomial distribution (PIELOU, 1969),

$$q_k(t) = \binom{m+k-1}{k} \frac{Q^k}{(1+Q)^{m+k}}, \quad (\text{C2})$$

where $1/m$ indicates the degree of aggregation of the distribution. Eq. (C2) converges to Poisson if m becomes infinitely large (hence $1/m$ becomes zero). Eq. (C1) is

$$p(t) = [1 + (\lambda/m)(1 - p(t+1))]^{-m}, \quad (\text{C3})$$

where $\lambda(t) = Qm$, the average of the number of surviving offspring. Suppose that the distribution of the number of surviving offspring follows the negative binomial distribution with a constant degree of aggregation $1/m$ but with the temporally varying average given by deterministic trajectory (4). Then we use Eq. (C3) instead of Eq. (7). Since Eq. (C3) increases with $p(t+1)$ and decreases with m , we conclude that greater degree of aggregation ($1/m$), i.s. small m , produces a larger $p(t_0)$ and hence a larger extinction probability P_{ext} .

In general, the extinction probability tends to increase if the variance of the distribution increases with the same average.