Unusual dynamics of extinction in a simple ecological model

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ABSTRACT   Studies on natural populations and harvesting biological resources have led to the view, commonly held, that (i) populations exhibiting chaotic oscillations run a high risk of extinction; and (ii) a decrease in emigration/exploitation may reduce the risk of extinction. Here we describe a simple ecological model with emigration/depletion that shows behavior in contrast to this. This model displays unusual dynamics of extinction and survival, where populations growing beyond a critical rate can persist within a band of high depletion rates, whereas extinction occurs for lower depletion rates. Though prior to extinction at lower depletion rates the population exhibits chaotic dynamics with large amplitudes of variation and very low minima, at higher depletion rates the population persists at chaos but with reduced variation and increased minima. For still higher values, within the band of persistence, the dynamics show period reversal leading to stability. These results illustrate that chaos does not necessarily lead to population extinction. In addition, the persistence of populations at high depletion rates has important implications in the considerations of strategies for the management of biological resources.

The spatiotemporal organization of a single-species population can show many different dynamics that can change because of migration. Though unstable dynamics such as chaos has been exhibited by both discrete theoretical models of population growth and experimental data (1–6), populations undergoing chaotic oscillations are assumed to run a high risk of extinction due to large variations and low-minimum population size. This and insect field data (7, 8) has led to the view that chaotic oscillations are unrealistic and hence are likely to be selected against during evolution. It has been shown that common ecological processes, such as immigration, tend to stabilize chaotic oscillations or reestablish the population (5, 9–12), thereby suppressing unstable growth dynamics.

It is also intuitively apparent and generally borne out by data that emigration or increased depletion and harvesting from a population can cause population extinction, especially if the population size is small (9, 13–15). Models of population growth have been used for predicting optimal use of natural biological resources and deciding on harvesting strategies for the maximum sustainable yield from resources such as fisheries (15, 16). However, both natural and laboratory data have always had cases where populations continue to persist in small numbers without going extinct and where some species of large population size go rapidly extinct (7, 17–20; the data in ref. 17 on the small populations of five species of birds that never went extinct irrespective of body sizes needs to be noted.). Therefore, the nonlinear interaction of growth rates, population size, and rates of migration (i.e., addition and depletion to populations) is important for an understanding of population behavior, especially the "fourth regime"—i.e., extinction (4).

In this study with a common discrete population growth model, which is widely used for modeling population growth and harvesting strategies, we show that (i) populations under-

going constant emigration/depletion can persist in chaos with low variation in amplitude, thereby reducing the risk of extinction; and (ii) populations can persist under a high rate of emigration or harvesting even when a lower rate of depletion leads to extinction and the risk of extinction is growth rate dependent. These results shed new light on the properties of the population growth models demonstrating that populations can respond in unexpected ways to changes in emigration/depletion and have important implications in policies of resource management.

We consider the simple, discrete, exponential logistic population growth model (21) for organisms with nonoverlapping generations given by

$$X_{i+1} = f(X_i) = X_i \exp[R(1 - X_i)], \qquad [1]$$

where X_i is the population density in the ith generation and R is the intrinsic growth rate. When such a population undergoes a constant (L) amount of emigration, depletion, or harvesting regularly at every generation, the growth equation (Eq. 1) takes the form,

$$X_{i+1} = F(X_i) = f(X_i) - L = X_i \exp[R(1 - X_i)] - L. \quad [2]$$

Eq. 1 has been studied extensively (3) and is considered to be a simple model for illustrating the occurrence of chaotic oscillations in one-dimensional maps, where increasing R induces period-doubling bifurcations leading to chaos. Eq. 1 possesses one equilibrium point, and the stability of the fixed point and the consequent dynamics exhibited by the system are dependent on R alone. Inclusion of a constant immigration term in this model has been shown (11) to reduce the occurrence of chaos at higher growth rates. When considering populations undergoing a constant emigration at every generation (i.e., for $L > 0$ in Eq. 2), there exist two equilibrium points (x_1 and x_2) of which the first (i.e., x_1) is always unstable, and the dynamics of growth depends on both R and L. In this case, there will be some population sizes (both low and high)—dependent on the first unstable fixed point, x_1—where extinction is inevitable. The maximum population size attained by populations growing according to Eqs. 1 and 2 are different, but both occur at $X = 1/R$.

In what follows we have stated the results of our study of the behavior of populations growing according to Eq. 2 for different emigration rates to understand their survival and extinction dynamics.

Survival and Extinction Under Emigration

The bifurcation diagrams in Fig. 1 a and b show that emigration does not affect the qualitative dynamics of Eq. 2 with small L, and the population takes a period-doubling route to chaos with increasing growth rates. However, the bifurcations from the simple limit cycle to period 4 oscillations and successive period doublings occur at lower values of R (Fig. 1b). Fig. 1b also shows that populations go extinct at higher growth rates after

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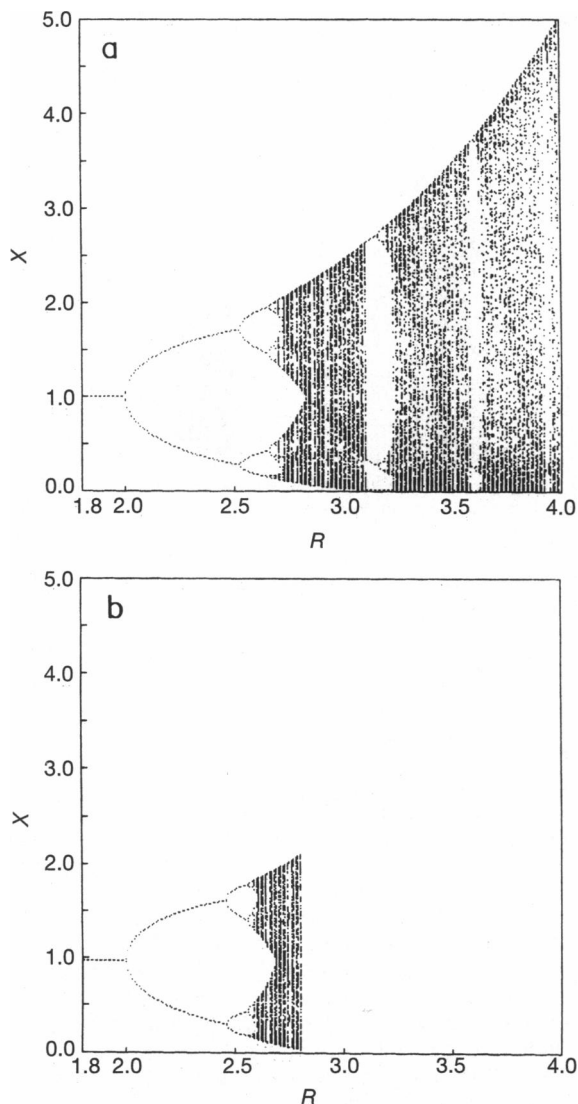
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FIG. 2. Regions of survival and extinction in the R–L parameter space. For $R < R_c$ (see text), the space is divided into two regions—persistence and extinction. For $R > R_c$, there are two bands of persistence separated by an extinction region. These are described by the following three shaded regions. (*i*) Blank region: survival. The population was considered persistent when $X_i > 0$ for $i > 1000$ generations for any given R and L. For $R > R_c$, the persistence band for higher L values is bounded by the dotted line, below and above which populations go extinct. (*ii*) Crossed region: eventual extinction. Here populations go extinct after few generations. This region is bounded by the lower bound (dashed line), at which the population goes extinct for the first time after a few generations, and by the upper bound (continuous line), at which the population goes extinct at the next generation [i.e., when $f(X_0) \leq L$]. (*iii*) Dotted region: immediate extinction. Here populations go extinct immediately at the next generation.

FIG. 1. Bifurcation diagrams for $L = 0$ (*a*) and $L = 0.06$ (*b*) from Eqs. **1** and **2**. Between 1.8 and 4.0, 110 values of R were taken, and for each value of R, the equations were iterated 1000 times, and the last 200 points were plotted. The population was considered extinct when $X_i \leq 0$ within 1000 generations for given values of R and L, which happened for $R = 2.899$ in *b*. Unless otherwise specified, the initial population is chosen as $X_0 = 0.3$ for all calculations. We have checked that the results hold good even for 5000 generations of the population in this and subsequent figures.

showing irregular oscillations for some generations. A population growing at a specific rate can balance regular depletion only up to a certain extent by surviving at a lower density. Beyond a certain rate of depletion, extinction would occur, and the population would survive fewer and fewer generations before going extinct. Thus, a band of L values can describe the lower and upper bounds of gradual extinction, below which the population persists and above which it goes extinct in the first generation. Fig. 2 shows the survival and extinction behavior of a population over a range of growth rates for various depletion rates.

Two major features are to be noted in Fig. 2. First, the lower bound for extinction increases with increasing growth rates until $R = 2.552$, beyond which it drops from $L = 1.5$ to a low value of $L = 0.57$ with a discontinuity and continues to decrease to smaller values close to zero for higher growth rates. The upper bound of L for extinction shows a continuous increase with increasing growth rates. This sudden decrease in
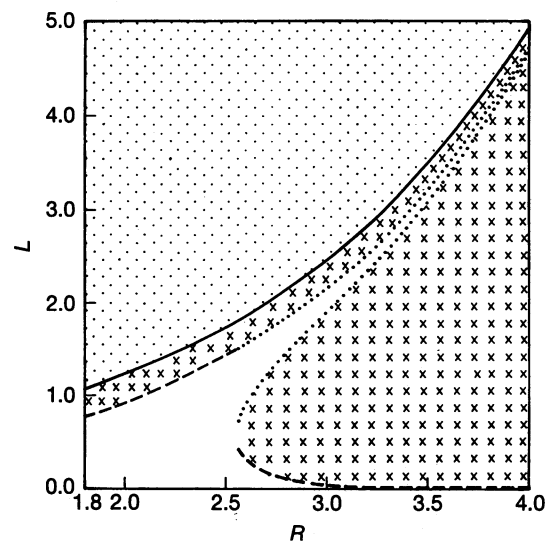
the ability of a population to sustain emigration/depletion beyond a certain "critical growth rate" (R_c) is independent of the starting population sizes. This "critical growth rate" falls in the region after the first bifurcation of the stable limit cycle (i.e., at period 4 oscillations). This implies that the risk of extinction can increase sharply for populations growing at rates in the nonchaotic regime also, and slower growing populations can survive under a continuous range of depletion rates at which a faster growing population might go extinct. This dependence of the survival of populations undergoing depletion on their growth rates needs to be recognized while considering management of wildlife populations or immunization against pathogenic organisms, since populations with different growth rates cannot be considered at par. There have been reports (17, 18) where species in abundant number go extinct in isolated forest patches in a short span of time, whereas other species survive for a long time in small numbers.

The second feature of interest in Fig. 2 is as follows: for $R > R_c$, the populations do not go extinct for all intermediate values of L between the lower and upper bound. There exists a wedge-shaped band in which the population persists under a high rate of depletion. For example, a population growing with a fixed rate, say $R = 2.56$, can exist below $L = 0.46$ and then go extinct at various generations with increasing depletion rates, but it again survives for a band of high L values, $0.71 < L < 1.50$, beyond which it goes extinct quickly. The width of the band reduces for higher growth rates, but the upper limit of the band does not coincide with the upper bound of L. Thus, for populations with any $R > R_c$, the survival-extinction dynamics with increasing depletion shows an unusual structure with alternating regions of survival and extinction, so that populations growing with the same rate can persist under very low and fairly high removal rate, though they are not able to survive at intermediate rates of depletion.

The boundaries of survival and extinction in the R–L plot described in Fig. 2 can also be obtained from Eq. 2 with the following analytical reasonings:

(*i*) The curve for the upper bound of L for extinction is obtained in Fig. 2 for $f(X_0) = L$. The limiting curve, which is independent of population size (X_0), can be obtained from Eq. 2 by setting $f(1/R) = L$ (i.e., when the emigration factor is equal to the maximum size of the population). The $f(X_0) = L$ curve always falls below the limiting curve; therefore, populations may go extinct immediately, depending on the initial size, at a lower value of L.

(*ii*) The curve that forms the lower bound for extinction for $R < R_c$ and continues as the upper bound for the high-L persistence band for $R > R_c$ is the condition for all populations to go extinct eventually, after various numbers of generations. This condition is satisfied when a saddle-node bifurcation takes place for a combination of R and L, and both the equilibrium points (x_1 and x_2) disappear (22).

(*iii*) The bands of high and low L values at which the populations survive for $R > R_c$ occurs whenever the population minimum is above the "threshold level" given by the first unstable equilibrium point [i.e., $F^2(1/R) - x_1 > 0$]. For intermediate values of L, $F^2(1/R) - x_1 < 0$, and populations of all sizes go extinct eventually. Thus, the two curves separating the survival–extinction–survival boundaries in the R–L parameter space for $R > R_c$ in Fig. 2 can be obtained by considering values of R and L that satisfy the expression

$$F^2(1/R) - x_1 = 0. \qquad [3]$$

For $R < R_c$ this expression is never satisfied, whereas for $R > R_c$ it is satisfied for two values of L.

(*iv*) In the "survival" region in Fig. 2, not all initial population sizes (X_0) survive due to the existence of the first equilibrium point. The range of initial population sizes that can continue to exist in the "survival" region indicated in Fig. 2 is bounded by $x(\text{min}) = x_1$ and $x(\text{max})$ which can be obtained from the expression $F[x(\text{max})] - x_1 = 0$.

Earlier theoretical studies have shown (5, 9–11) that additive factors, such as immigration and recolonization, contribute to persistence of a population even at chaos. This is probably natural and expected. Our results show that persistence is possible in a fast-growing population even while that population is undergoing high emigration or depletion. Since this model is commonly used for modeling growth and harvesting strategies of natural resources, this unusual result would seem to imply that a resource may be harvested at a higher rate without leading to extinction even when lower rates of harvesting would lead to extinction. However, we would urge caution before any blind attempt is made to translate this result into practice, since natural populations are regulated by a large number of biological and environmental factors, some of which are stochastic (23–26) and may mask the small zone of persistence at higher depletion rates. Nevertheless our results indicate that changes in depletion rates can have unexpected consequences for the persistence of a population and that these consequences may be different from what conventional wisdom would indicate.

Temporal Dynamics Under Emigration

There are two ranges of L values at which the population growing with $R > R_c$ persists. The population dynamics with increasing L in these two regions of persistence is shown in Fig. 3 for $R = 2.6$. For $0 < L < 0.31$, the population exhibits a transition from period-4 oscillations to chaos, with a continuous decrease in the minimum value of the amplitudes of oscillations. Further increase in the depletion rate ($0.31 < L < 0.9$) results in population extinction after a few generations of irregular cycles. For higher depletion rates ($L > 0.91$), the
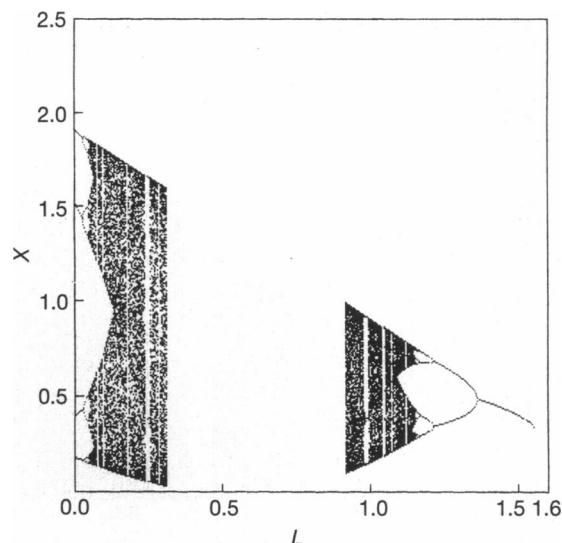

Fig. 3. Bifurcation diagram for a population at growth rate $R = 2.6$ with variation of L.

population again continues to survive, exhibiting chaotic oscillations, though with much reduced amplitude and elevated levels of the population minimum. With increasing L, it undergoes period-doubling reversals and reaches a steady state for $L = 1.37$. Further increase of $L > 1.55$ results in the extinction of the population.

The survival dynamics at high emigration rates (Fig. 3) show two interesting features: (*i*) reduced variation in a population with increased minima of oscillations. The maximum variation of the population density just before the first extinction is 1.7, whereas it is 1.0 when the population persists again. The minimum sizes of the populations while exhibiting chaotic oscillations is increased from 0.033 to 0.158 before and after the first extinction. (*ii*) Period-doubling reversals take place at higher emigration rates, and the population size remains stable at 0.36 before it finally goes extinct.

These results imply that it is not the chaotic oscillations *per se* that introduces the risk of extinction, but it is the large variability in numbers coupled with a low minimum that is responsible for the high risk of extinction in the face of "population crashes," or in the event of a small increase in emigration. Therefore, populations can persist at chaos with low variation and elevated minimum value without the risk of extinction. That extinction risk is correlated with a small population size has been shown in many natural populations of birds, small mammals, and other animals (17). Field studies with birds (17, 27) have also shown that species with more variable populations are more prone to extinction. Thus, a moderately abundant species with variable numbers may be at greater risk than a rare species with small but steadier numbers. Our results do corroborate the studies on natural populations (7, 17, 27, 28) to show that the risk of extinction increases with high variability coupled to a small minimum but argues against the notion, based on field data (7, 8), that chaotic dynamics is unrealistic. To explain the stable growth dynamics attributed to a large number of insect populations (5, 7, 29), theoretical studies have shown that the chaotic dynamics exhibited by model populations can be suppressed under many different ecological conditions (5, 9–12). Our results also show that populations can exhibit stable dynamics under high emigration condition.

Modes of Extinction

To examine the interaction between the growth rate (R) and the rate of depletion (L) with respect to the resultant survival-
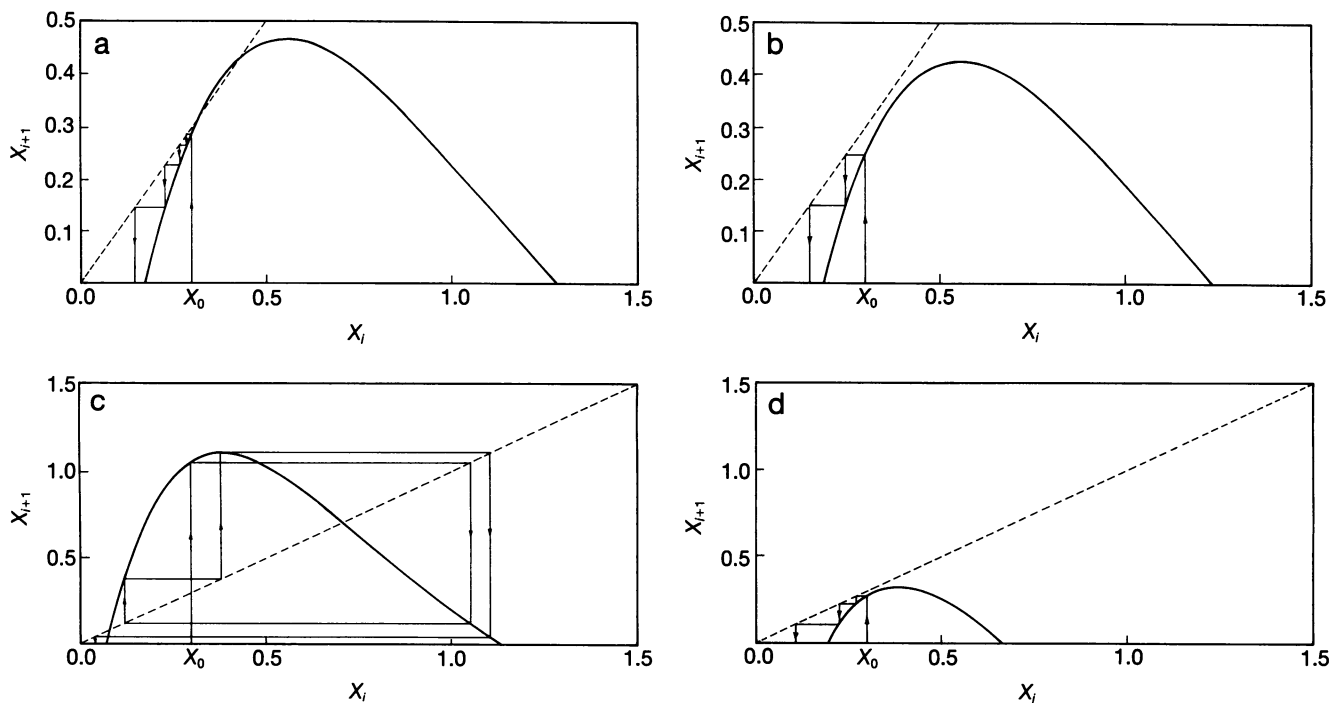
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FIG. 4. Graphical demonstration of the modes of extinction for two representative values of low and high R. (*a*) $R = 1.8, L = 0.77$; (*b*) $R = 1.8, L = 0.81$; (*c*) $R = 2.6, L = 0.8$; and (*d*) $R = 2.6, L = 1.58$.

extinction dynamics of the population, we employ the simple graphical procedure of plotting Eq. **2** as X_{i+1} versus X_i for specific values of R and L as shown in Fig. 4. The effects of increasing R and L are to make the single-hump function steeper and to shift it below the positive x-axis, respectively. The net shape and position of the hump with respect to the $X_{i+1} = X_i$ line decides the stability of the steady states, if any, and the consequent dynamics.

In Fig. 4 we indicate the two modes by which populations with a low ($R = 1.8$, Fig. 4 *a* and *b*) and a high ($R = 2.6$, Fig. 4 *c* and *d*) growth rate go extinct at different rates of emigration. The first mode is through the well-known "Allee effect" (16, 30). In this case the population goes extinct either by decreasing continuously (Fig. 4*a*) or after a few generations of irregular oscillations (Fig. 4*c*) whenever it falls below a "threshold level" given by the first unstable steady state (x_1). The second mode is through the decoupling of the hump and the $X_{i+1} = X_i$ line indicating nonexistence of any fixed point for the system (saddle-node bifurcation). Here populations of all sizes decrease continuously and go extinct after a few generations (Fig. 4 *b* and *d*).

These two modes of extinction are observed for all values of R, but for lower growth rates (i.e., $R < R_c$), medium-size populations can persist because the second steady state (x_2) is stable (Fig. 4*a*) and also because Eq. **3** is never satisfied. However, for higher growth rates ($R > R_c$), populations of all sizes go extinct for medium values of L because Eq. **3** is satisfied, leading to a minimum population size below the "threshold level" x_1 (Fig. 4*c*).

The band of high L values at which the populations survive for $R > R_c$ is achieved when the shape of the hump, due to the interaction of L and R, is such that the population minimum is always above the "threshold" x_1 and the second equilibrium point x_2 is unstable. This leads to continuous chaotic oscillations with reduced amplitude of variation, with the minima being bounded by the value of x_1. For higher values of L in the band, the second steady state (x_2) becomes stable, and period reversals are observed till the decoupling takes place and extinction ensues.

Main Findings of This Study

● Chaotic dynamics does not necessarily lead to species extinction: populations can persist at chaos with low variation and increased minima.

● The dynamics exhibited by faster growing populations undergoing high depletion in the form of emigration or "catches" does not always lead to extinction, even though lower depletion rates can result in extinction of the same population.

● Survival depends on population size.

(*i*) Medium-sized populations may persist both with low growth rates for small and medium depletion rates and with high growth rates for high depletion rates, whereas small and large populations may go extinct rapidly. (*ii*) Faster growing populations of all sizes go extinct at moderate rates of emigration.

These theoretical findings have an important bearing when considering strategies for the management of biological resources such as fisheries and in immunization programs and, more generally, when considering the behavior of natural populations in a range of ecological situations where emigration is taking place.

We wish to point out here that the survival–extinction behavior observed for this commonly used exponential model (Eq. **1**) for population studies is not seen in the case of the quadratic logistic growth model (3, 31–33). However, this behavior is shown by the model used to fit natural insect data (5, 7, 29). Also, it should be noted that this behavior is not observed when emigration is density dependent [i.e., $L \cdot f(X_i)$]. Thus, one needs to look into the specifics of the models and the details of the ecological processes before using these models for interpreting natural population data or deciding on their applicability to resource management policies.

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