

NOTES AND COMMENTS

CHAOTIC MODELS AS REPRESENTATIONS OF ECOLOGICAL SYSTEMS

Interest has been shown in the dynamics of simple models whose predictions can be "chaotic," that is, not tending toward an equilibrium point or limit cycle. Chaotic behavior has been reported in difference equations (e.g., May 1976), differential equations (e.g., Mackey and Glass 1977; Gilpin 1979), and linear differential equations with nonlinear feedback (Sparrow 1980). The most thoroughly studied models are single difference equations describing density-dependent population growth (e.g., Oster 1974; May 1974; Li and Yorke 1975). Speculations about the ecological importance of chaotic behavior include: (1) Populations may vary in an unpredictable manner so that long-term predictions may be impossible (May 1976). (2) Small changes in initial populations or growth rates can yield divergent predictions (Bunow and Weiss 1979). If these speculations are true, they have far-reaching consequences for ecological research and modeling.

Evaluation of these results requires that model formulation, parameter values, and method of simulation be ecologically sound. The following observations seem relevant. (1) Values for the growth rate, r , must be biologically reasonable. (2) Parameter values of ecological models always contain uncertainty (Gardner et al. 1980). (3) Extinction is an ecological reality when predicted values are close to zero.

In addition to studies of the models, attempts have also been made to find populations exhibiting chaotic oscillations (Hassell et al. 1976), to assess the ecological relevance of chaotic models (Poole 1977; Smith and Mead 1980), and to formulate evolutionary explanations for the apparent failure to observe chaos in natural populations (Thomas et al. 1980). Many of these studies have analyzed the equation $N_{t+1} = N_t \exp[r(1 - N_t/K)]$ where N_t is the population size at time t , r is the intrinsic growth rate, and K is the carrying capacity. This model has been widely applied in the ecological literature (Moran 1950; Ricker 1954) and its behavior is typical of a large class of population models (May and Oster 1976).

In this study, we scale the population by its equilibrium value (i.e., $X_t = N_t/K$) to obtain the normalized equation $X_{t+1} = X_t \exp[r(1 - X_t)]$. Dynamic behavior of this equation is determined by the value of r . If $r > 2.69$, model behavior is chaotic and the solution may oscillate aperiodically. We included ecological constraints by selecting r at each time interval from a uniform distribution with expected value r_m and upper and lower limits of $r_m \cdot (1 \pm r\%)$. Extinction was assumed to occur

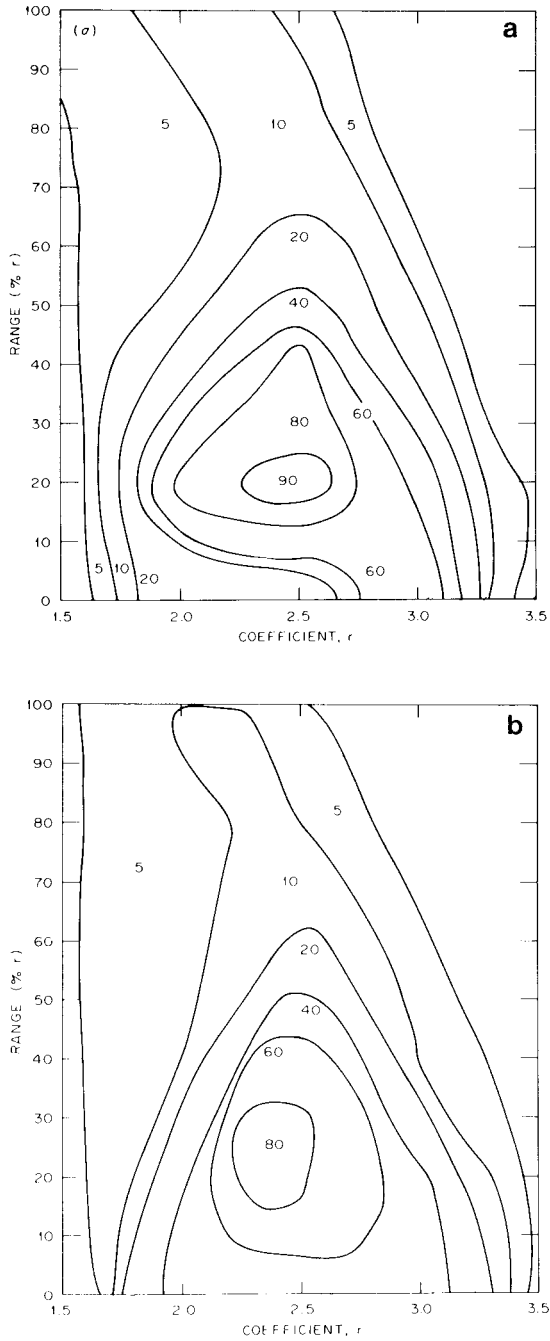


FIG. 1.—Isopleths of c , the index of unpredictability, for values of r and $r\%$ (r is the coefficient of the discrete logistic model and was uniformly varied over the interval $r \pm r\%$). *a*, Constant initial conditions of 0.01 and extinction of $X_t < 0.001$. *b*, Initial conditions varied uniformly from 0.0 to 5.0 and extinction if $X_t < 0.001$.

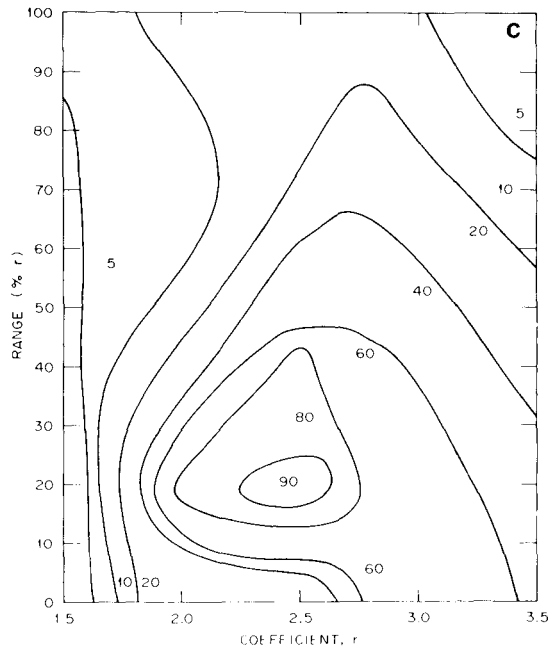


FIG. 1. (Continued)—c, Initial conditions varied uniformly from 0.0 to 5.0 and extinction criterion was removed.

whenever X_t was less than 0.001. For each r_m and $r\%$, 1,000 time series of 100 generations were produced.

To analyze results we adapted the frequency distribution approach of Hoppensteadt and Hyman (1977). The solution for each time, t , was placed in one of 100 frequency intervals from 0.0 to the maximum observed value. The 10 intervals containing the highest counts were eliminated. The total counts in the remaining 90 intervals were divided by the expected value. This measure, c , approaches 0 if the time series approaches an equilibrium or cycles with period 10 or less. As the time series approaches "white noise," c approaches 100.

Figure 1a shows isopleths of c for values of r_m (abscissa) and $r\%$ (ordinate), using an initial condition of 0.01 for all simulations. At $r_m = 1.5$, the system is periodic even at $r\% = 100$. At $r_m = 3.5$, the system appears regular because of the high probability of extinction. At intermediate values of r_m , the situation is more complex. Consider a value of r_m near 2.5. As the range, $r\%$, increases to 20, unpredictability increases dramatically. This is because the randomly chosen r 's cover a wide range of behavior including stable cycles of various periods and chaotic behavior. However, as $r\%$ increases beyond 20, more of the randomly chosen r values lie in the stable region ($r < 2.0$), and more in the region of likely extinction ($r > 3.5$). For example, at $r\% = 100$, 30% of the randomly chosen values will be above 3.5 and 40% will be below 2.0. For this reason the greatest irregularity of the system exists around values of 2.3 to 2.5 for r_m and 20 for $r\%$. It is obvious that the uncertainty in r (i.e., $r\%$) is as important in determining the regularity of

the system as the mean value and that model solutions are never completely unpredictable.

Figure 1*b* illustrates the effect of varying the initial condition, X_0 , from a uniform random distribution between 0.0 to 5.0. Comparison of figures 1*a* and 1*b* indicates that the results are relatively insensitive to initial conditions, contrary to the theoretical expectation.

Figure 1*c* illustrates the effect of removing the extinction criterion. The peak still dominates the graph at r_m of 2.3 to 2.5, but the slope at higher r 's is more gradual. Although this system is less predictable at higher r_m , it is never totally unpredictable (i.e., c is never 100).

It is clear that inferences drawn from purely theoretical studies may be misleading. In this case, the theoretical studies were based on deterministic models. However, it is unlikely that any ecological system could exist for more than a few generations without being disturbed by stochastic effects. Smith and Mead (1980) analyzed a stochastic birth-death process and also concluded that the mathematical details of deterministic dynamics are biologically irrelevant. Only those behaviors of the deterministic model which reflect the behavior of the ecological system can be relevant.

The results point out behaviors of the model which are ecologically relevant. (1) The predictions are always bounded when r remains within biologically reasonable limits. (2) The mean population remains predictable for all values of r . (3) Even when the time sequence seems erratic, the frequency distribution of observed population values is not. (4) If r is allowed to vary the system may, under some situations, become more predictable. These results are robust under different criteria of extinction and variability of the initial conditions.

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