SIMULATING THE DYNAMICS OF NATURAL POPULATIONS USING THE SYSTEM DYNAMICS APPROACH

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ABSTRACT

Based on the knowledge of population ecology and principles of System Dynamics, a general model of natural population dynamics was developed. Population dynamics are assumed to be regulated through non-linear density-dependent mechanisms. The density-dependent mechanisms used in the model are different and more general than those in the traditional models. First, it is assumed that the death rate would become greater than the birth rate not only above a certain "maximum crowding level", but also below a certain "minimum crowding level". Thus, the population would go to extinction if its size is smaller than a threshold value. Secondly, a regulatory delay is incorporated so that crowding effect reaches the death and birth rates after a time delay. The model is thus capable of generating oscillatory behaviors. The model can generate the four major modes of population behavior observed in nature: exponential growth, logistic growth, oscillations, and exponential decay. In addition, the model can be used to suggest factors that are crucial in determining different types of population behavior.

INTRODUCTION

The study of the dynamics and regulatory mechanisms of populations has been fundamental in ecology. Two extreme views, density dependence and density independence, have long existed in population ecological theories. However, the focal point of the debate is over the extent to which self-regulating mechanisms come into play, or in other words, the relative importance of density-dependence and density-independence in nature (Pielou, 1974; Pianka, 1974). The density-dependent regulation paradigm suggests that density-dependent self-regulation operates most of the time in most if not all natural populations. Consequently, populations grow mostly at or close to current carrying capacity and experience competition most of the time (Watt, 1973; Pielou, 1974). This viewpoint emphasizes important roles of density-dependent factors, such as competition, predation and diseases in population growth and regulation.

In contrast, the density-independent theory asserts that density-dependent regulation takes place only rarely and, therefore, populations grow at a density well below saturation level most of the time and experience competition only occasionally. This view stresses influences of density-independent factors, such as climatic conditions, on population dynamics.

"No one population increases indefinitely to blanket the world, and decline to extinction is relatively rare on an ecological time-scale" (May, 1986a). In a recent review, May (1986b) commented: "the dynamical behavior of natural populations will be the outcome of some mixture of density-dependent factors (tending to produce stasis, or stable cycles, or chaos) and density-independent factors (tending to produce unpredictable fluctuations)."   When and how would the density-dependent mechanisms be called into play? How can we quantitatively determine the relative importance of density-dependence and density-independence in population dynamics and regulation? There doesn't seem to be any universal answer. As Horn (1968) pointed out, the relative importance of these two perspectives may vary from population to population, and even within the same population from time to time. Systems theory and methods may help resolve the "puzzle" (e.g., Wiegert, 1975; Berryman, 1981).

Modelling the dynamics of natural populations "presents a greater challenge than finding good representations of molecular behavior" (Roberts, 1978). Geometric, exponential, or Malthusian growth and Verhulst-Pearl logistic growth equations of different versions have long been extensively used (Pielou, 1977; Hutchinson, 1978). Exponential growth models often take the form:

$$dN/dt \; = \; r\,N \tag{1}$$

yielding the solution

$$N_t \; = \; N_0\,e^{rt} \tag{2}$$

where N is the population size and r is the instantaneous per capita growth rate (or the intrinsic rate of increase of the population), which is assumed to be constant. When the effective per capita growth rate of a population is considered to be a linear function of the population size, $r(1 - N/K)$, it brings about the general logistic equation:

$$dN/dt \; = \; r\,N \; (1 - N/K) \tag{3}$$

with an analytical solution of

$$N = \frac{K}{1 \; + \; (K/N_0 \; - \; 1)\,\exp(-rt)} \tag{4}$$

where K is the carrying capacity of the environment or the equilibrium density of the population.

When the time delay (T) for regulatory responses is considered (e.g., May, 1981), the above equation can be modified as

$$dN/dt \; = \; r\,N \; [1 - N(t - T)\,/\,K]. \tag{5}$$

Numerous variations and applications of logistic models for natural populations have been discussed, among many others, by Pielou (1969, 1977), Hutchinson (1978), and Tuckwell and Koziol (1987).   However, such analytical models are seriously limited in their use for exploring real populations in dynamic environments because of their requirements for simplicity and, frequently, linearity in model formulation.

Most dynamic behavior of complex systems, e.g., population systems, can be more realistically represented only by simulation models while their analytical solutions are usually impossible (Forrester, 1968). In addition, by using advanced simulation languages (e.g., DYNAMO, CSMP, STELLA, etc.), ecologists can focus their attention and efforts effectively on the phenomena under study, rather than coding and solution procedures (de Wit and Goudriaan, 1974).

This study examines basic behavioral patterns of population dynamics such as overshooting, undershooting, collapsing and stabilizing using the System Dynamics (SD) approach. The objective is to construct a generalized model which is able to produce the four major types of population behavior observed in nature: exponential growth, logistic growth, exponential decay, and oscillations, and to improve our understanding of regulatory mechanisms of populations through simulation experimentation.

DYNAMICS AND REGULATORY HYPOTHESES OF NATURAL POPULATION SYSTEMS

Empirical and experimental evidence suggests that most existing populations are subject to some forms of density-dependent controls buffering them from extinction (e.g., Wilson and Bossert, 1971; Boughey, 1973). Kormondy (1969) concluded that most species exhibit logistic behavior and are self-regulating through automatic feedback mechanisms. All populations are, at least, potentially food-limited or space-limited (Murray, 1979). Watt (1973) asserted that density-dependent control regulates population size by operating on the reproductive rate, the survival rate, the growth rate, and the dispersal rate. However, the overall dynamic behavior of populations may be simultaneously governed by several to a number of factors both density-dependent and density-independent.

The ubiquitous existence of density-dependent factors does not necessarily mean that they are operating all the time. On the other hand, populations with self-regulating processes do not necessarily maintain a constant, stable size (Pielou, 1974). In fact, observations show that most populations exhibit fluctuating behavior. There are a variety of hypotheses about the population fluctuations. Watt (1973) asserted that the degree of regularity in population fluctuations was related to the number of generations of prior population history. Wilson and Bossert (1971) attributed population cycles to four factors: predation, mass emigration, physiological stress, and genetic changes in the populations. Pianka (1974) listed four hypotheses of population cycles: (1) stress phenomena hypothesis; (2) predator-prey oscillation hypothesis; (3) nutrient recovery hypothesis; and (4) genetic control hypothesis.

Pielou (1974) hypothesized three mechanisms of population fluctuations and affirmed the cause-effect chain relationship of population cycles. As she wrote, "The basic cycle at any place results from plant-herbivore interaction. The herbivore cycles cause the carnivore cycles. And the latter cause the grouse and ptarmigan cycles. The durations of the cycles are presumably linked to the longevities of the most important species." Berryman (1981) asserted that the cycles may be strongly influenced by environment and the erratic fluctuations may be induced by extremely variable environments. However, Murray (1979) argued that in species-rich communities, if the predator has more than one prey species or can shift prey in time, the population cycles are less likely to take place, or at least, less violent in behavior, while the "optimal foraging theory" seems to suggest the possibility of such cycles.

Natural population systems may exhibit a great many distinctive dynamic patterns because of both differences in individual attributes of species and variations in qualitative and quantitative properties of abiotic and biotic environment. However, "generalizations are not

intended to describe nature in its infinite variety", instead, to "bring order to an otherwise disorderly world" (cf., Murray, 1979). With this in mind, we may categorize the dynamic behavior of natural populations into three basic modes: (1) unchecked behavior (exponential growth or delay); (2) equilibrium-seeking behavior (logistic growth and steady-state fluctuation); (3) erratic behavior (unpredictable fluctuations). The equilibrium-seeking behavior is often exhibited by most natural populations. However, the sigmoid growth (logistic growth) is rare in nature. Instead, frequently observed are three types of population oscillations around equilibrium: (1) neutrally stable oscillations with a constant amplitude, (2) unstable oscillations with increasing amplitude, and (3) damped stable oscillations with decreasing amplitude. Although population systems are complex in many respects, it is possible to use simple models to study their basic behaviors by taking a systems approach (Roberts, 1978; Berryman, 1981).

A GENERAL SYSTEMS VIEW OF POPULATION DYNAMICS

Forrester (1968) indicated that a structure (or theory) is essential in comprehending observations in nature because without an organizing structure, information seems a jumble, and "knowledge" may be only a collection of conflicting impressions. Principles of systems can serve as the structure of knowledge about complex systems (Forrester, 1968, 1971; Goodman, 1974). In a similar vein, it is difficult to understand and depict the whole picture of dynamics and regulatory mechanisms of a system based only on empirical observations , because such understanding may require an enormous amount of time and effort and because there is no guarantee for all behavioral patterns to be observed. Berryman (1981) advocated an alternative approach, i.e., deducing and constructing internal structure and processes of the system from systems theory with much less information than. Convinced that the diverse dynamic behavior of populations is a consequence of the system structure governed by simple rules, Berryman (1981) put up the following procedures for systems analysis in population dynamics:

(1) Observing the behavior of the system under an array of environmental conditions;
(2) Deducing the structure of the system, particularly the feedback loops;
(3) Constructing a model of the system from the deductions;
(4) Evaluating whether the model behaves in a manner similar to the real system; and
(5) Returning to (1) if the model is unsatisfactory.

Population growth and regulation can be examined in light of feedback dynamics of population systems in most cases. Feedback loops are the basic elements of the internal structure of the systems. The rather complex behavior of population systems is generated and controlled by their interacting feedback loops. Exponential growth of populations can be generated by positive feedback, a self-enhancing process which induces a "snowball effect." The asymptotic or steady-state growth requires negative feedback, a self-controlling process which tends to keep the population system at equilibrium. The logistic growth and the like necessitate negative feedback following positive one through a nonlinear relationship. Coupling of the feedback loops in different ways can create a variety of distinctive dynamic patterns of populations.

Basically, regulatory mechanisms of population systems involve both negative and positive feedbacks. The degree of stability of these systems depends largely on the dominance of negative feedback. However, delays, inter-dependencies between different populations and

speed at which they approach or return back to the equilibrium may cause various oscillations and even instability. With delays inherent in age structures and population-environment interactions, the resultant "population inertia" may cause the system to overshoot or undershoot the equilibrium, or even collapse. This effect can be surprisingly large especially while the population growth rate is high (Meadows et al., 1972, 1974).

A GENERALIZED SYSTEM DYNAMICS MODEL

In a single-species population system, there are only four basic processes in which population size can change: birth, death, immigration, and emigration. Environmental and genetic properties affect the population dynamics through influencing natality, mortality, immigration and emigration. Environment can significantly alter the carrying capacity and modify the function of density-dependent relation and may also bring stability into population systems. However, in this model, a balance between immigration and emigration and a stable average genetic property of populations are assumed. In addition, the unpredictable changes in physical environment are not taken into account in the present model.
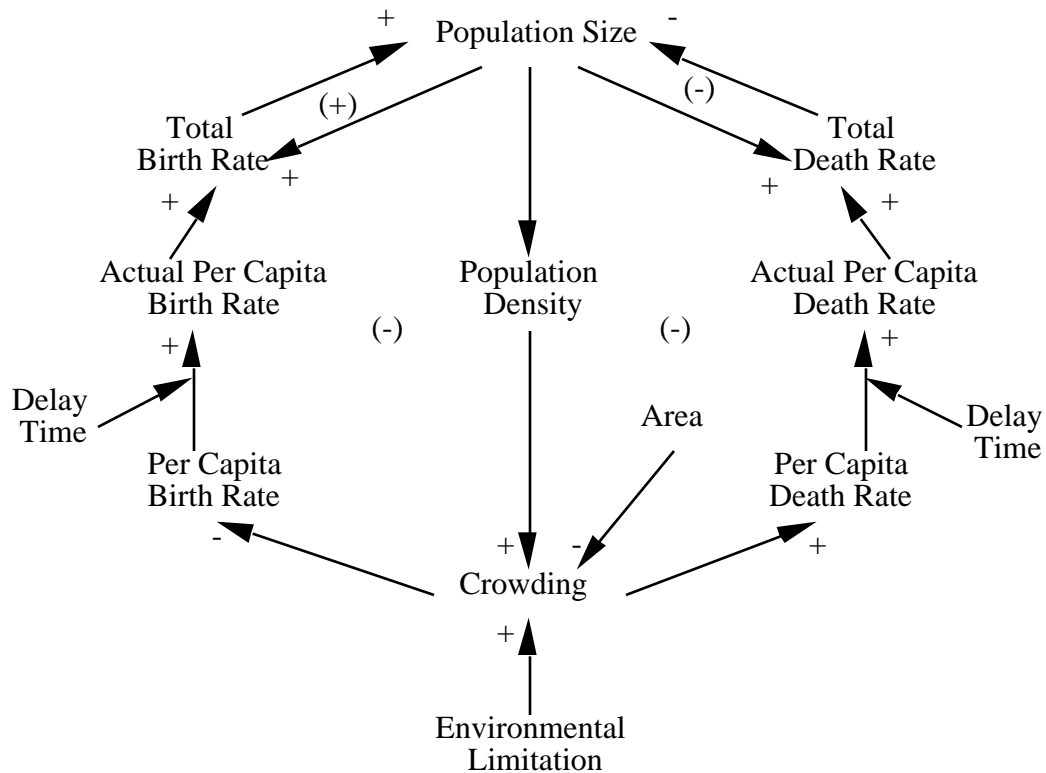

Fig. 1. Causal-loop diagram of a generalized model of population dynamics, showing the basic feedback loops in natural population systems.

There are four major feedback loops in the model (Figs. 1 and 2). Populations are believed to be regulated through a non-linear density-dependent mechanism. The crowding effect, rather than population density or population size itself, directly affects the regulating

processes because crowding can occur at different densities (Murray, 1979). A time delay exists between crowding population and responses in birth and death rates (e.g., May, 1981). Crowding is determined by both current population density and environmental limitation (e.g., food supply, living space, etc.).
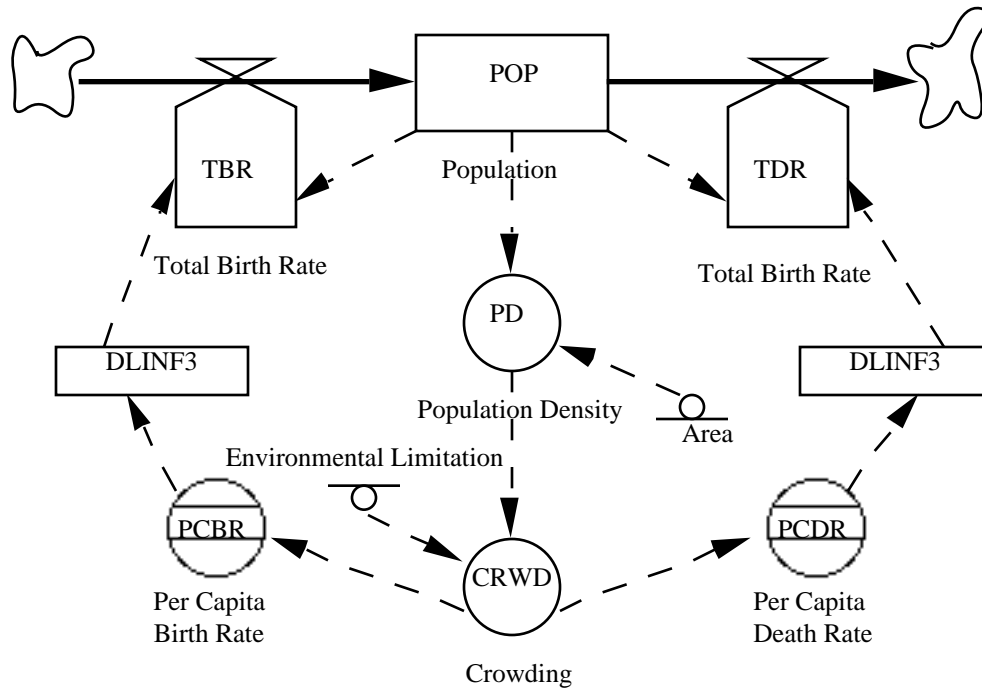

Fig. 2. Flow diagram of the generalized System Dynamics population model.

The response curves of instantaneous per capita birth, death, and growth rates to population density are assumed different from those in exponential or logistic models (Fig. 3a and b). Both effects of undercrowding, i.e., lacking cooperation (e.g., less chance of mating and reproducing unsuccessfully) and crowding (e.g., intraspecific competition) are taken into account (e.g., Berryman, 1981). Accordingly, a minimum carrying capacity (Kmin) and maximum carrying capacity (Kmax) are identified. By referring to Murray (1979), a lower critical density (LCD) is defined as a density below which birth rate declines and an upper critical density (UCD) is defined as a density beyond which birth rate declines and death rate increases (Fig. 3a). Below UCD, death rate keeps constant (minimum death rate), and between LCD and UCD, neither birth rate nor death rate is affected by the crowding population density. Therefore, the assumption also reflects density-independent effect on the regulation of population growth even though it is principally density-dependent.

According to the above verbal model, a flow diagram is designed to give a visual description of the system dynamics model (Fig. 2). A computer simulation model in DYNAMO (Table 1) is developed corresponding to the above flow diagram (Pugh, III, 1973; Richardson and Pugh, 1981).

Table 1. A DYNAMO program listing of the generalized

systems model of population dynamics and regulation

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*        A  SYSTEM  DYNAMICS  POPULATION  MODEL

NOTE AREA   --- AREA         (UNDER STUDY)
NOTE CRWD   --- CROWDING
NOTE ACPCBR --- ACTUAL PER CAPITA BIRTH RATE
NOTE ACPCDR --- ACTUAL PER CAPITA DEATH RATE
NOTE ENVLIM --- CURRENT ENVIRONMENTAL LIMIT
NOTE PCBR   --- PER CAPITA BIRTH RATE
NOTE PCDR   --- PER CAPITA DEATH RATE
NOTE PCGR   --- PER CAPITA GRROWTH RATE
NOTE PD     --- POPULATION DENSITY
NOTE TBR    --- TOTAL (POPULATION) BIRTH RATE
NOTE TDR    --- TOTAL (POPULATION) DEATH RATE
NOTE TGR    --- TOTAL (POPULATION) GROWTH RATE

L   POP.K=POP.J+DT*(TBR.JK-TDR.JK)
N     POP=POPN
C     POPN=150
R   TBR.KL=ACPCBR.K*POP.K
R   TDR.KL=ACPCDR.K*POP.K
A   ACPCBR.K=DLINF3(PCBR.K,CRWDDL)
A   ACPCDR.K=DLINF3(PCDR.K,CRWDDL)
C     CRWDDL=1
A   PCBR.K=TABHL(PCBRT,CRWD.K,0,72,4)
A   PCDR.K=TABHL(PCDRT,CRWD.K,0,72,4)
T    PCBRT=.00/.04/.10/.20/.40/.54/.68/.68/.68/.65/.64/
X     .62/.58/.54/.50/.40/.32/.14/.00
T    PCDRT=.12/.12/.12/.12/.12/.12/.12/.12/.12/.13/.14/
X     .16/.17/.21/.28/.40/.52/.68/.92
A   CRWD.K=PD.K*ENVLIM
C     ENVLIM=1
A   PD.K=POP.K/AREA
C     AREA=10
A   PCGR.K=PCBR.K-PCDR.K
A   TGR.K=TBR.JK-TDR.JK
PRINT POP,PCBR,PCDR,PCGR,TGR
PLOT POP=P,(0,1200)/TGR=G
PLOT PCBR=b,PCDR=d,PCGR=g,(-1,1)
SPEC DT=.01/LENGTH=25/PRTPER=.25/PLTPER=.1
RUN BASE
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MODEL BEHAVIOR

The model was simulated using DYNAMO with a constant time interval (DT=0.01) for all scenarios. The base run (or standard run) is based on "normal" values of parameters (i.e., reaction delay = 1 unit of time, starting population = 150, and environmental limiting factor =

1). However, by changing the values of the parameters, the model can generate a number of behavioral patterns. The base run shows a neutrally stable oscillation of population size in time (Fig. 4a), which is generated by changing per capita birth, death, and growth rates (Fig. 4b).

The delay time plays a critical role in determining the dynamic behavior. When the delay time is shortened to one tenth of the standard value, oscillations disappear and a typical logistic curve is obtained (Fig. 5a). A exponential growth occurs when the delay time is made extremely large (99,999 times larger than that of the base run, Fig. 5a). If delay time is three times larger, the amplitude of the oscillation increases obviously (Fig. 5c). One half of the standard delay time causes the population to reach the equilibrium level with a damped oscillation (Fig. 5c). The effect of different starting populations on the dynamics is shown in Figure 5b. When the population starts with a size larger than that in the base run, it yields a neutrally stable fluctuation, given other parameters constant. However, it goes extinct when the starting population is 50 (Fig. 5b). The change in environmental limitation also affects the dynamic behavior. As an example, if other conditions remain constant, a five-fold increase in environmental limiting factor allows the population to sustain at a lower equilibrium level (Fig. 5d).

CONCLUSIONS

The general System Dynamics model of population dynamics is able to reproduce a series of basic patterns of population dynamics, namely: exponential growth, logistic growth, exponential decay, and different types of oscillations. The simulation experimentation suggests that regulatory time delay and environmental limitation can be very important in regulating the dynamics of population systems. The model shows that with differences in regulating delay times and environmental factors, populations may exhibit a variety of dynamical behavior. The simulation also demonstrates the significance of our generalized density-dependence assumption. Populations go to extinction if they start below the minimum critical density shown in figure 3.

The model can further be used to examine effects of magnitude of growth rate and different regulatory hypotheses on population dynamics by changing the density-per capita rate curve of Figure 3a. With more information, this model may incorporate physiological characteristics of the population and stochastic properties of environment. It can also be extended to be a multi-specific population model with a more complicated feedback structure.

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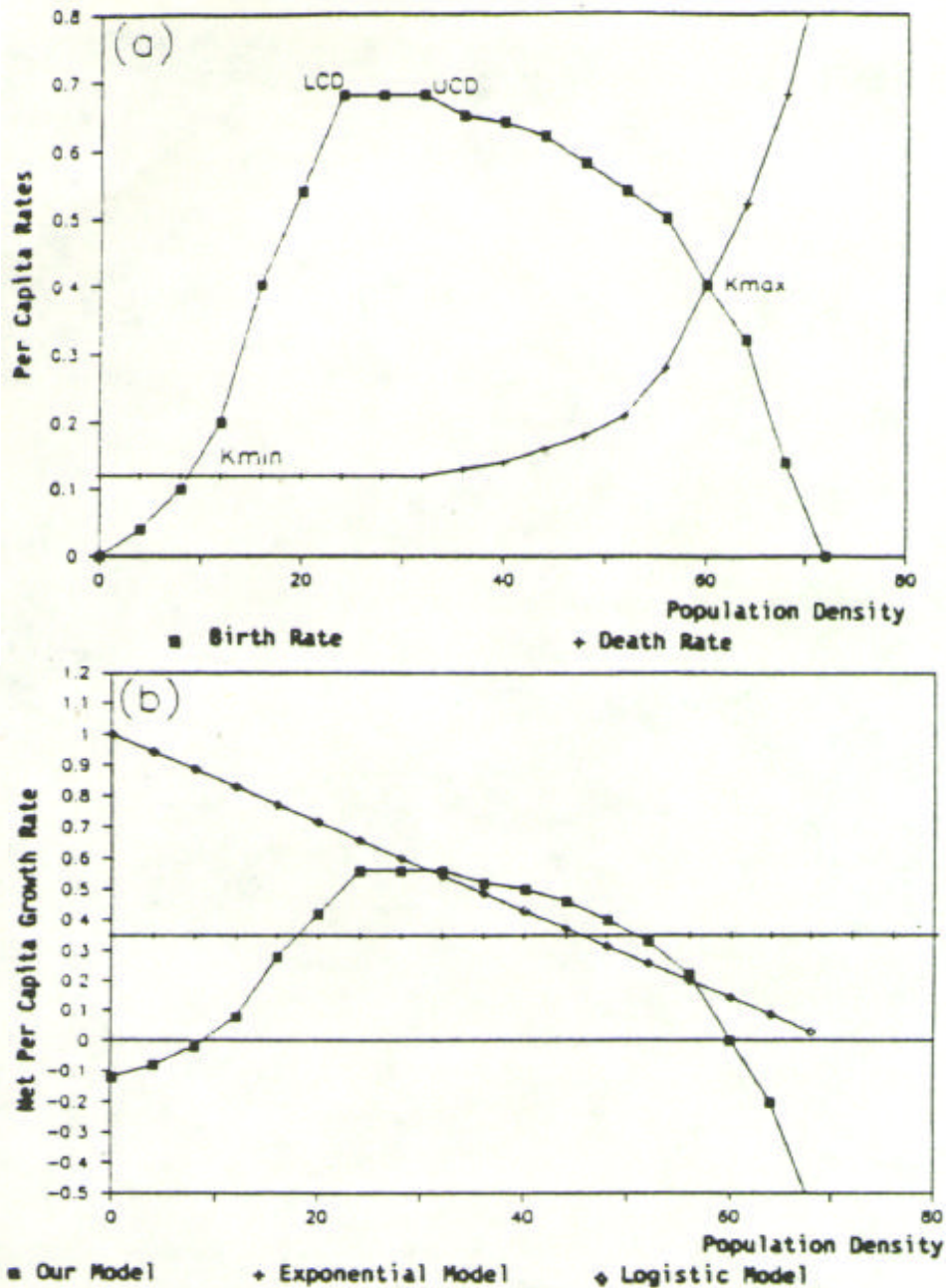
Figure 3. (a) Population density-per capita rate
relationship used in the model, where LCD
and UCD are the lower and upper critical
densities, Kmin and Kmax are the minimum
and maximum carrying capacities.
b) Comparison of the net growth rate curve
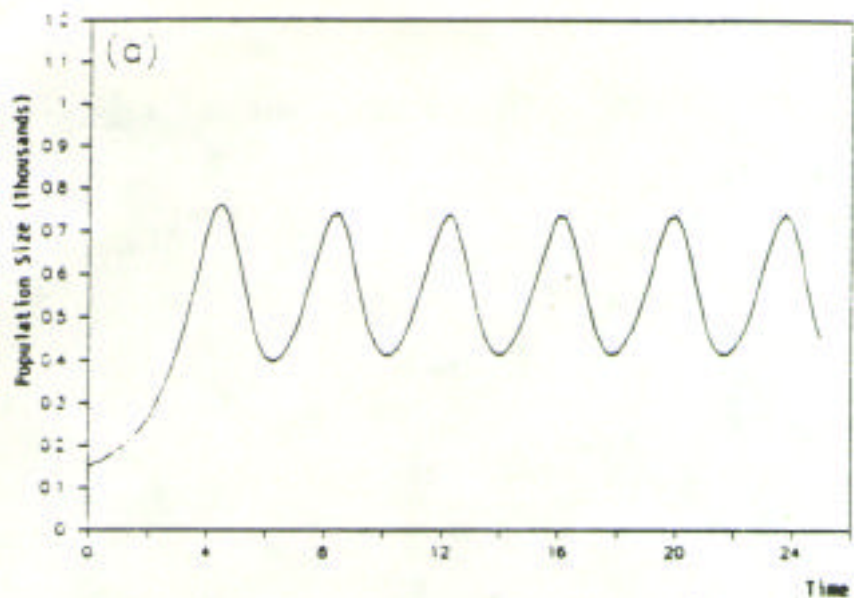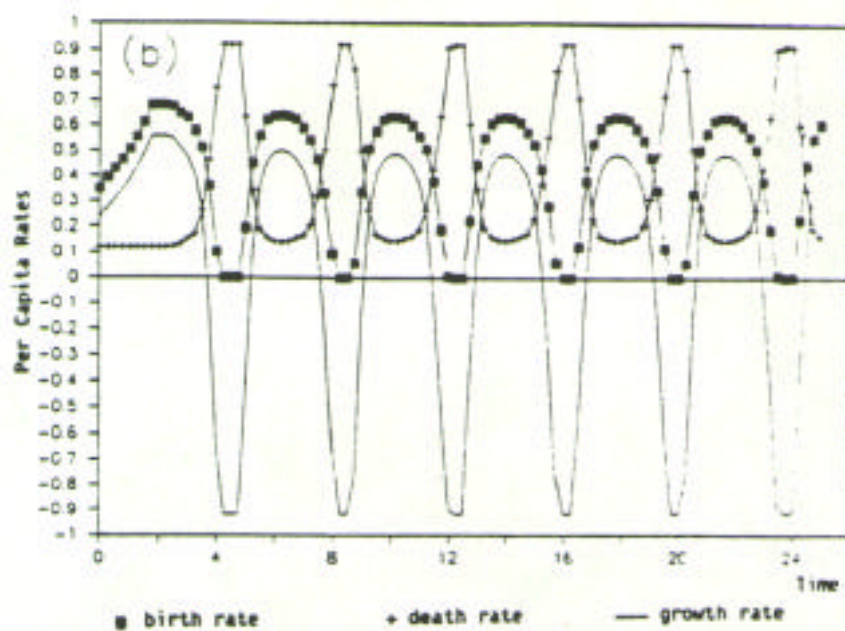used in this model with those in
exponential and logistic models.

Figure 4. (a) A base run of the model, presenting
neutral stable oscillation.

■ birth rate   + death rate   — growth rate

(b) Changes in birth rate, death rate, and
growth rate with the base run. (Fig. 4a-5d
were all plotted using Lotus and Freelance
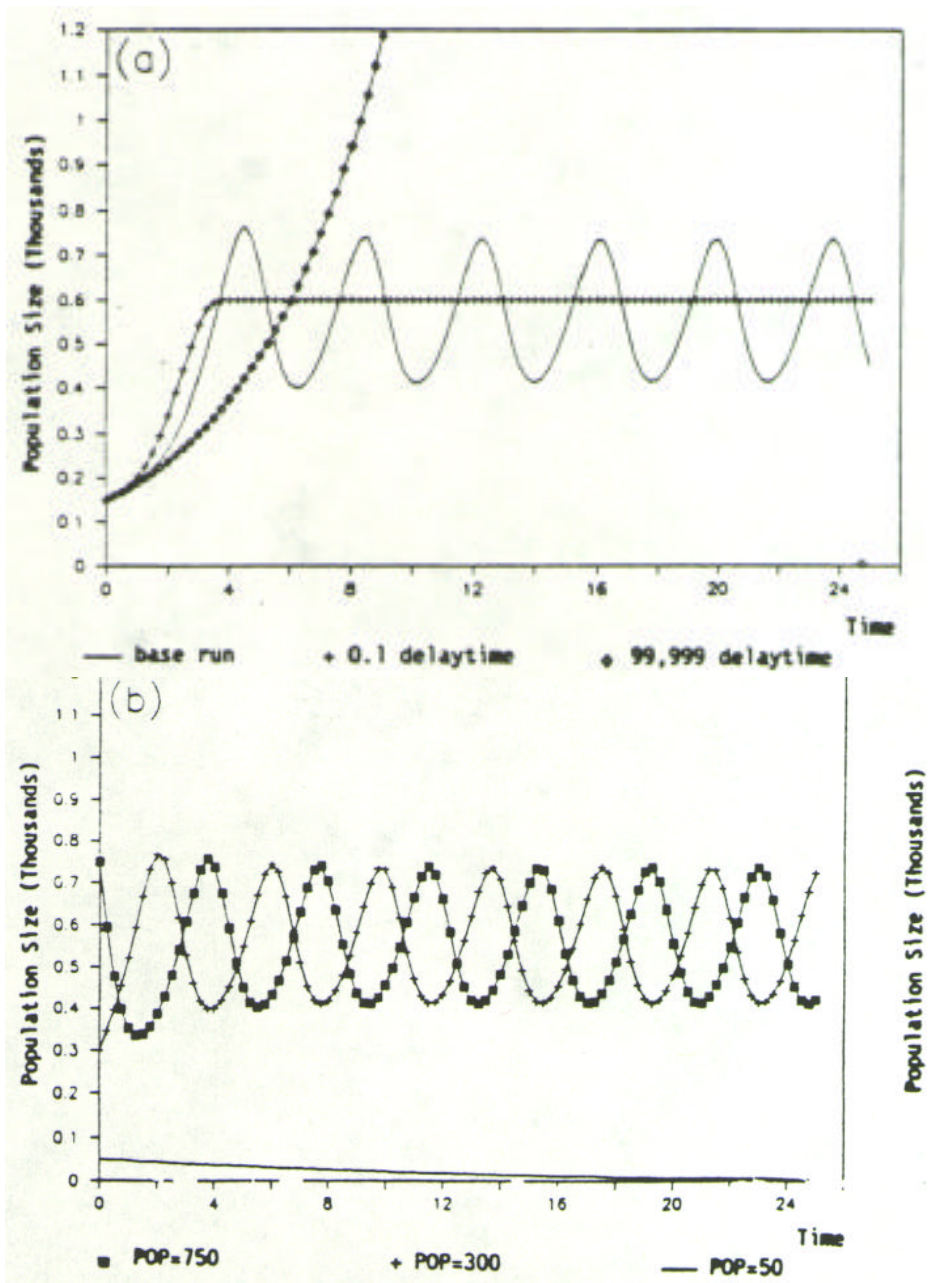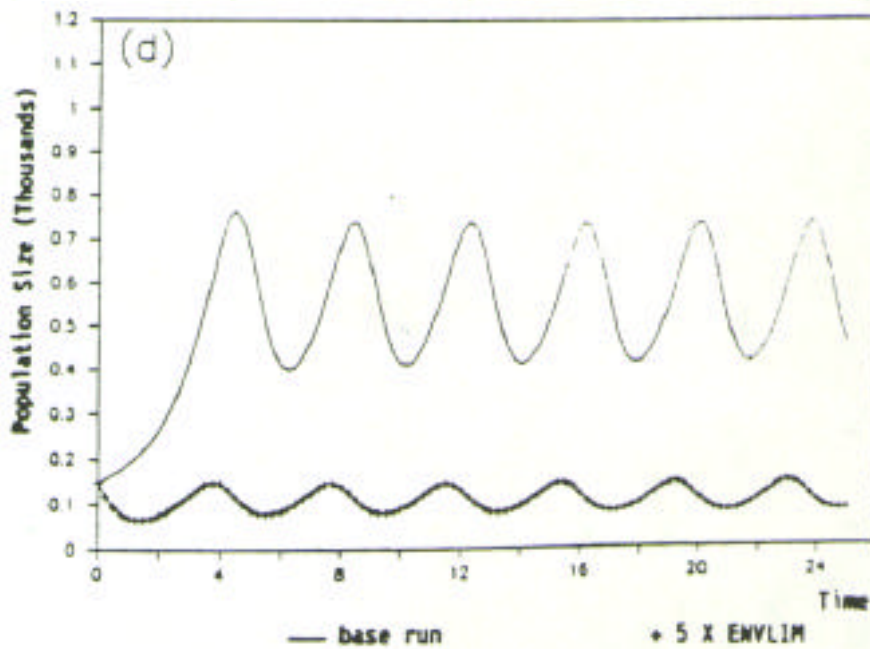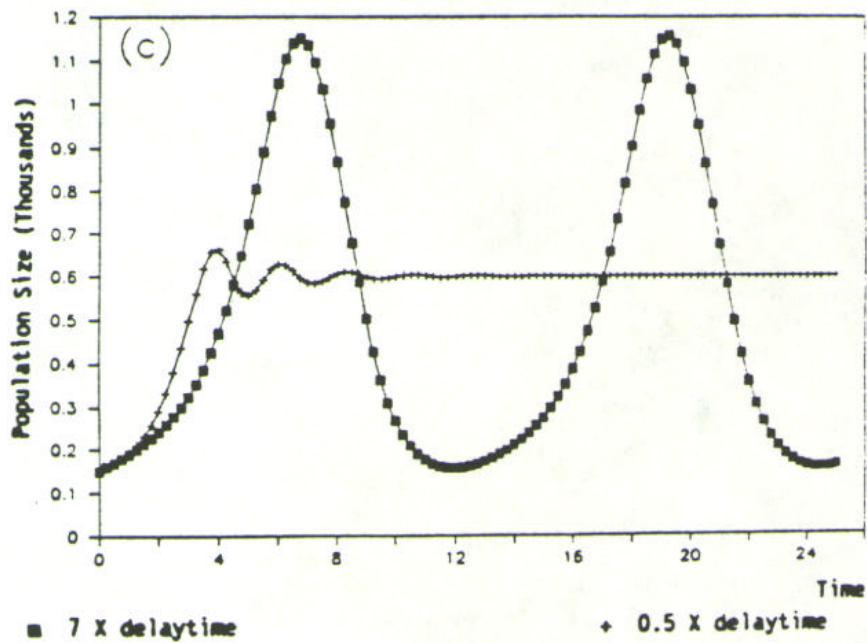Plus with output data from DYNAMO.)

Figure 5. Some dynamic behaviors generated by the
model.
(a) exponential (very large delaytime),
logistic (1/10 of the original delaytime),
and oscillating growth (in the base run).
(b) Oscillation and extinction caused by
changing initial population sizes.

(c) Damped oscillation (1/2 of the
original delaytime) and amplified
oscillation (7-fold delaytime).
(d) Neutral oscillation with a lower
equilibrium value (5-fold environmental
limiting effect).