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## **Density-dependent birth rate, birth pulses and their population dynamic consequences**

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**Abstract.** In most models of population dynamics, increases in population due to birth are assumed to be time-independent, but many species reproduce only during a single period of the year. We propose a single-species model with stage structure for the dynamics in a wild animal population for which births occur in a single pulse once per time period. Using the discrete dynamical system determined by the stroboscopic map, we obtain an exact periodic solution of systems which are with Ricker functions or Beverton-Holt functions, and obtain the threshold conditions for their stability. Above this threshold, there is a characteristic sequence of bifurcations, leading to chaotic dynamics, which implies that the dynamical behaviors of the single species model with birth pulses are very complex, including small-amplitude annual oscillations, large-amplitude multi-annual cycles, and chaos. This suggests that birth pulse, in effect, provides a natural period or cyclicity that allows for a period-doubling route to chaos.

### **1. Introduction**

Plant, insect and animal life histories exhibit enormous diversity. Individuals may live for hours or for centuries; they may lavish parental care on a single offspring or abandon millions of larvae to the vagaries of life in the seas. Metamorphosis may carry the same individual through several totally different niches during a lifetime. Specialized stages may exist for dispersal or for dormancy. The vital rates (rates of survival, development, and reproduction) almost always depend on age, size, or development stage. Stage structure models have received much attention in recent years (Aiello & Freedman, 1990; Aiello et al., 1990; Hastings, 1983, 1984). This is not only because they are much more simple than the models governed by partial differential equations but also they can exhibit phenomena similar to those of partial differential models (see Bence & Nisbet, 1989), and many important physiological parameters can be incorporated.

The key to the formulation of tractable structured population models is the recognition that individuals of many species have life-histories composed of a

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sequence of stages within which their characteristics are broadly similar to those of other individuals in the same stage and markedly different from those of individuals in other stages. In insects such stages are particularly easy to recognize, being separated by short, clearly identifiable, events such as moults or pupation, but most species show discernible morphological, behavioural or biochemical changes which define similar natural stage boundaries, perhaps the most universal being the onset of reproductive activity. Thus, in the first part of this paper, we consider a single species model with stage structure and assume only the mature species can reproduce in which the birth rate of mature population depends on the population density. It is shown that under suitable hypotheses the system has a globally asymptotically stable positive equilibrium (From a biological point of view, we are talking about the asymptotic properties of solutions in the positive orthant), i.e., if the intrinsic net reproductive rate (later defined as  $R_0$ ) is greater than unity, then the positive equilibrium is globally asymptotically stable.

These models have invariably assumed that the mature population reproduce throughout the year, whereas it is often the case that births are seasonal or occur in regular pulses. The continuous reproduction of mature population is then removed from the model, and replaced with an annual birth pulse. These models are subject to short-term perturbations which are often assumed to be in the form of impulses in the modeling process. Consequently, impulsive differential equations provide a natural description of such systems (Bainov & Simeonov, 1989; Lakshmikantham et al., 1989). Equations of this kind are found in almost every domain of applied sciences. Numerous examples are given in Bainov's and his collaborators' books (Bainov & Simeonov, 1989). They generally describe phenomena which are subject to steep and/or instantaneous changes. Some impulsive equations have been recently introduced in population dynamics in relation to: vaccination (Agur, 1993; Shulgin et al., 1988), and chemotherapeutic treatment of disease (Panetta, 1996; Lakmeche and Arino, 2000). In terms of the mathematical treatment, the presence of impulses gives the system a mixed nature, both continuous and discrete. The qualitative properties of the system are embodied in those of the discrete system which determines the state after a pulse in terms of the state after the previous pulse. Thus, in section 4, we deduce the stroboscopic map, where the map determines the number of immature population and mature population, immediately after each pulse birth at the discrete times  $m$  ( $m$  is a positive integer). When the birth rates of mature population are influenced by the population density, the discrete dynamical system determined by the stroboscopic map becomes nonlinear. The population in the pulsed birth time is characterized not by an exponential growth rate, but by the existence and stability of equilibria, by the bifurcations that occur when stability is lost, and by the patterns of dynamics (cycles, chaos) that follow the bifurcations.

In section 5, we focus our attention on the relationships between the differential dynamical system with birth pulses and the discrete dynamical system determined by the corresponding stroboscopic map. It is shown that dynamical behaviors of models with birth pulses are very complex, and include small-amplitude annual oscillations, large amplitude multi annual cycles, and chaos. That is, birth pulse, in effect, provides a natural period or cyclicity that allows for a period-doubling route to chaos. The population fluctuations associated with stage structure

effects have been found by many authors(Nicholson, 1954; Gurney et al., 1983). For Nicholson’s Blowflies, the period of the cycles is 2-3 times the maturation time, and for the Lawton’s Plodia, the irregular fluctuations have a dominant period close to the generation time.

**2. Population model formulation**

In the absence of stage-structure, we assume that the population size changes according to a population growth equation

$$\dot{N} = B(N)N - dN, \tag{2.1}$$

where  $d > 0$  is the death rate constant, and  $B(N)N$  is a birth rate function with  $B(N)$  satisfying the following basic assumptions for  $N \in (0, \infty)$ :

- (A<sub>1</sub>)  $B(N) > 0$ ;
- (A<sub>2</sub>)  $B(N)$  is continuously differentiable with  $B'(N) < 0$ ;
- (A<sub>3</sub>)  $B(0^+) > d > B(\infty)$ .

Note that (A<sub>2</sub>) and (A<sub>3</sub>) imply that  $B^{-}(N)$  exists for  $N \in (B(\infty), B(0^+))$  (where  $B^{-}$  denotes the inverse function of  $B$ ), and (A<sub>3</sub>) gives the existence of a carrying capacity  $K$  such that  $B(N) > d$  for  $N < K$ , and  $B(N) < d$  for  $N > K$ . Under these assumptions, nontrivial solutions of system (2.1) approach the unique positive equilibrium  $N^* = K = B^{-}(d)$  as  $t \rightarrow \infty$ . Examples of birth functions  $B(N)$  found in the biological literature that satisfy (A<sub>1</sub>) – (A<sub>3</sub>) are:

- (B<sub>1</sub>)  $B_1(N) = be^{-N}$ , with  $b > d$ ;
- (B<sub>2</sub>)  $B_2(N) = \frac{p}{q+N^n}$ , with  $p, q, n > 0$  and  $\frac{p}{q} > d$ .

Functions  $B_1$ , and  $B_2$  with  $n = 1$  are used in fisheries, and are known as the Ricker function and Beverton-Holt function, respectively.

**3. Single-species population models with stage structure**

We assume now that the single species population in model (2.1) has stage structure, and that the population  $N$  is divided into immature and mature classes, with the size of each class given by  $x(t)$  and  $y(t)$ , respectively, so that  $N(t) = x(t) + y(t)$ , and only the mature population can reproduce. This leads to the model

$$\begin{cases} \dot{x}(t) = B(N(t))y(t) - dx(t) - \delta x(t), \\ \dot{y}(t) = \delta x(t) - dy(t). \end{cases} \tag{3.1}$$

The maturity rate is  $\delta(\delta > 0)$ , which determines the mean length of the juvenile period.

*3.1. Equilibria and their local stability*

Clearly system (3.1) has the trivial equilibrium  $E_0(0, 0)$ . There exists a unique positive equilibrium  $E^*(x^*, y^*) = (\frac{d}{\delta+d}B^{-}(\frac{d(d+\delta)}{\delta}), \frac{\delta}{\delta+d}B^{-}(\frac{d(d+\delta)}{\delta}))$  if

$$B^{-}(\frac{d(d+\delta)}{\delta}) > 0. \tag{3.2}$$

For the local stability of the equilibria  $E_0$  and  $E^*$ , we have the following results.

**Theorem 3.1.** *Assume  $(A_1)$  and  $(A_2)$  hold. Then  $E_0$  is locally asymptotically stable if (3.2) is reversed, and unstable if (3.2) holds;  $E^*$  is locally asymptotically stable if (3.2) holds.*

3.2. *Boundedness and global stability of equilibria of system (3.1)*

Standard and simple arguments show that solutions of system (3.1) always exist and stay positive.

If  $B(\infty) < d$ , then it is easy to see that system (3.1) is dissipative, that is, there exists a positive constant  $M > 0$  such that the following set

$$\Omega = \{(x, y) | 0 \leq x \leq M, 0 \leq y \leq M\}$$

is positively invariant with respect to system (3.1). Using the Poincaré-Bendixson theory, we can obtain the following global stability results on the equilibria.

**Theorem 3.2.** *Assume  $(A_1)$ ,  $(A_2)$  and  $B(\infty) < d$  hold. Then the set  $\Omega$  is an asymptotic stability region for  $E_0$  if inequality (3.2) is reversed; the set  $\Omega$  is an asymptotic stability region for  $E^*$  if inequality (3.2) holds.*

*Proof.* If  $B^-(\frac{d(d+\delta)}{\delta}) < 0$ , there cannot be any periodic solutions in  $\Omega$  since a periodic solution must contain at least one equilibrium. By the Poincaré-Bendixson theory, paths in  $\Omega$  must approach an equilibrium. Thus, the set  $\Omega$  is an asymptotic region for  $E_0$  if  $B^-(\frac{d(d+\delta)}{\delta}) < 0$ .

If  $B^-(\frac{d(d+\delta)}{\delta}) > 0$ , then  $E^*$  exists, and is locally asymptotically stable. Using Dulac's test with  $P$  and  $Q$  as the right sides of (3.1), we obtain

$$\frac{\partial P}{\partial x} + \frac{\partial Q}{\partial y} = B'(N)y - (2d + \delta) < 0$$

in the interior of  $\Omega$ , which implies that there are no limit cycles or cycle graphs in  $\Omega$ . By the Poincaré-Bendixson theory, all paths in  $\Omega$  must approach the equilibrium  $E^*$ .

Note that inequality (3.2) can be rewritten as  $R_0 > 1$  for the special case of  $B(N)$ , where  $R_0$  represents the intrinsic net reproductive number (sometimes called the net reproductive value or rate). For example, if  $B(N) = be^{-N}$ , inequality (3.2) is equivalent to  $R_0 = \frac{b\delta}{d(d+\delta)} > 1$ . This quantity is defined to be the expected number of offspring per individual per lifetime (Cushing, 1998). Thus, if  $R_0 > 1$  then the equilibrium  $E^*$  is globally asymptotically stable, that is, if on average, individuals do replace themselves before they die, then the population is doomed. The equilibria and stability conditions are listed in Table 1 for each of the models with Ricker function and Beverton-Holt function, respectively.

**4. Single-species population models with stage-structure and birth pulses**

Model (3.1) has invariably assumed that the mature populations are born throughout the year, whereas it is often the case that births are seasonal or occur in regular pulses. An assumption that led to system (3.1) is that births are evenly distributed

**Table 1.** Nontrivial equilibria of the two models with Ricker function and Beverton-Holt function, respectively.

Function	Equilibrium	$B^{-}(\frac{d(d+\delta)}{\delta})$	$R_0$
Ricker	$x^* = -\frac{d}{d+\delta} \ln \frac{1}{R_0}$ $y^* = -\frac{\delta}{d+\delta} \ln \frac{1}{R_0}$	$-\ln \frac{1}{R_0}$	$\frac{b\delta}{d(d+\delta)}$
Beverton-Holt	$x^* = \frac{d}{\delta+d} \sqrt[n]{q(R_0 - 1)}$ $y^* = \frac{\delta}{\delta+d} \sqrt[n]{q(R_0 - 1)}$	$\sqrt[n]{q(R_0 - 1)}$	$\frac{\delta p}{qd(d+\delta)}$

throughout the year. To model a single annual birth pulse  $B(N)$  is set to zero, and the immature population density  $x(t)$  is increased by an amount  $B(N)y$  whenever  $t$  has an integer value. The equations for the dynamics of the single-species population, and the proportion of immature and mature are now:

$$\begin{cases} \dot{x}(t) = -dx(t) - \delta x(t), \\ \dot{y}(t) = \delta x(t) - dy(t), \\ x(m^+) = x(m^-) + B(N(m^-))y(m^-), \end{cases} \tag{4.1}$$

whenever  $m$  is an integer.

In a manner analogous to our analysis of the long-term dynamics of solutions of system (3.1), we now analyze the dynamics of system (4.1). Instead of steady states we investigate period-one solutions, period-doubling bifurcations and chaos of this system. For this purpose, we consider the special cases of  $B(N)$ , i.e., we consider that  $B(N)$  has the form of a Ricker function or a Beverton-Holt function and deduce the stroboscopic map in the following subsection.

*4.1. Stroboscopic map of system (4.1) with Ricker or Beverton-Holt function*

First we analyze system (4.1) with the Ricker function, i.e.,  $B(N) = be^{-(x+y)}$ , and system (4.1) becomes

$$\begin{cases} \dot{x}(t) = -dx(t) - \delta x(t), \\ \dot{y}(t) = \delta x(t) - dy(t), \\ x(m^+) = x(m^-) + be^{-x(m^-)+y(m^-)}y(m^-). \end{cases} \tag{4.2}$$

We integrate and solve for the immature population in system (4.2) between pulses,

$$x(t) = x_m e^{-(\delta+d)(t-m)}, \quad m < t < m + 1, \tag{4.3}$$

with  $x_m$  the initial population of immatures at time  $m$ . Adding the first two equations of system (4.2), yields

$$\dot{x} + \dot{y} = -d(x + y). \tag{4.4}$$

We integrate and solve for the total population between pulses,

$$x(t) + y(t) = (x_m + y_m)e^{-d(t-m)}, \quad m < t < m + 1, \tag{4.5}$$

with  $x_m$  and  $y_m$  the initial population of immatures and matures at time  $m$ . From (4.3) and (4.5) we have

$$\begin{cases} x(t) = x_m e^{-(\delta+d)(t-m)}, \\ y(t) = e^{-d(t-m)} [y_m + x_m (1 - e^{-\delta(t-m)})]. \end{cases} \quad (4.6)$$

Equation (4.6) holds between pulses. At each successive pulse, more of the immature population is added, yielding

$$\begin{cases} x_{m+1} = x_m e^{-(\delta+d)} + b[y_m + x_m (1 - e^{-\delta})] e^{-[d+e^{-d(x_m+y_m)}]}, \\ y_{m+1} = e^{-d} (1 - e^{-\delta}) x_m + e^{-d} y_m. \end{cases} \quad (4.7)$$

If  $B(N) = \frac{p}{q+N^n}$ , then system (4.1) becomes

$$\begin{cases} \dot{x}(t) = -dx(t) - \delta x(t), \\ \dot{y}(t) = \delta x(t) - dy(t), \\ x(m^+) = x(m^-) + \frac{p}{q+(x(m^-)+y(m^-))^n} y(m^-). \end{cases} \quad (4.8)$$

Similarly to system (4.2), we can deduce the following stroboscopic map of system (4.8)

$$\begin{cases} x_{m+1} = x_m e^{-(\delta+d)} + \frac{p e^{-d} [y_m + x_m (1 - e^{-\delta})]}{q + e^{-nd} (x_m + y_m)^n}, \\ y_{m+1} = e^{-d} (1 - e^{-\delta}) x_m + e^{-d} y_m. \end{cases} \quad (4.9)$$

Equations (4.7) and (4.9) are difference equations. They describe the numbers of immature population and mature population at a pulse in terms of values at the previous pulse. We are, in other words, stroboscopically sampling at its pulsing period. The dynamical behavior of system (4.7), coupled with (4.6), determines the dynamical behaviors of system (4.2); similarly the dynamical behavior of system (4.9), coupled with (4.6), determines the dynamical behaviors of system (4.8). Thus, in the following section, we will focus our attention on systems (4.7) and (4.9), and investigate the various dynamical behaviors.

The dynamics of these nonlinear models can be studied as a function of any of the parameters. We will focus here on  $b$  for the Ricker function and  $p$  for the Beverton-Holt function, and document the changes in the qualitative dynamics of the model (4.7)(4.9) as  $b(p)$  varies. First, the trivial equilibrium  $\bar{E}_0(0, 0)$  is always a solution to equation(4.7)(or equation(4.9)). When  $b(p)$  is small enough, this solution is locally stable, and the species cannot increase when rare or invade a habitat from which it is absent. Our first concern will be with the conditions under which  $\bar{E}_0(0, 0)$  becomes unstable, permitting colonization of the population. Second, the destabilization of  $\bar{E}_0$  with increasing  $b(p)$  is always accompanied by the appearance of a stable positive equilibrium  $\bar{E}^*$ . As  $b(p)$  is increased further, this equilibrium in turn becomes unstable. A flip bifurcation occurs and the equilibrium loses stability to a stable two-cycle. Finally, as  $b(p)$  is increased still further, there is a characteristic sequence of bifurcations, leading, in most cases, to chaotic dynamics.

4.2. Bifurcations of  $(x, y) = (0, 0)$

In the neighborhood of  $(x, y) = (0, 0)$ , the dynamics of equations (4.7) and (4.9) are controlled by the linearization

$$X_{m+1} = AX_m, \tag{4.10}$$

with  $A$  as in the linear counterpart of (4.7) or (4.9) and  $X = (x, y)$ .  $X = 0$  is stable when the eigenvalues of  $A$  are less than one in magnitude. This is true only when  $A$  satisfies the three Jury conditions(Jury, 1974):

$$1 - tr A + det A > 0, \tag{4.11a}$$

$$1 + tr A + det A > 0, \tag{4.11b}$$

$$1 - det A > 0. \tag{4.11c}$$

These three conditions correspond to the three ways that an eigenvalue may exit the unit circle in the complex plane. If inequality (4.11a) is violated, then one of the eigenvalues of  $A$  is larger than 1. If inequality (4.11b) is violated, then one of the eigenvalues of  $A$  is less than  $-1$ . Finally, If inequality (4.11c) is violated, then  $A$  has a complex-conjugate pair of eigenvalues lying outside the unit circle.

With  $A$  defined in model 4.7 ((4.9)), it can be shown that inequalities (4.11b) and (4.11c) are always satisfied, and that as  $b(p)$  increases, inequality (4.11a) is violated at a critical point  $b_0(p_0)$ . In terms of the model parameters, and after a bit of rearranging, for equation (4.7) inequality (4.11a) reads

$$b < \frac{(1 - e^{-d})(1 - e^{-(\delta+d)})}{e^{-d}(1 - e^{-\delta})} \equiv b_0, \tag{4.12}$$

and for equation (4.9) inequality (4.11a) reads

$$p < \frac{q(1 - e^{-d})(1 - e^{-(\delta+d)})}{e^{-d}(1 - e^{-\delta})} \equiv p_0. \tag{4.13}$$

Thus  $b(p)$  must be larger than  $b_0(p_0)$  in order for a small population to increase from  $X = 0$ .

For the difference equations (4.7) and (4.9) we can also define the intrinsic net reproductive number  $\bar{R}_0$ (the average number of offspring that an individual produces over the course of its lifetime). For equation (4.7)  $\bar{R}_0$  is given by

$$\bar{R}_0 \doteq R_0^R = \frac{be^{-d}(1 - e^{-\delta})}{(1 - e^{-d})(1 - e^{-(\delta+d)})}.$$

For equation (4.9)  $\bar{R}_0$  is given by

$$\bar{R}_0 \doteq R_0^B = \frac{pe^{-d}(1 - e^{-\delta})}{q(1 - e^{-d})(1 - e^{-(\delta+d)})}.$$

Inequality (4.12) ((4.13)) can be rewritten as  $\bar{R}_0^R < 1$  ( $\bar{R}_0^B < 1$ ). That is, if on average, individuals do not replace themselves before they die then the population is doomed.

#### 4.3. Bifurcations of the positive equilibrium $\bar{E}^*(\bar{x}^*, \bar{y}^*)$

There is a second, non-zero, equilibrium solution to equation (4.7) ((4.9)) which satisfies

$$\begin{cases} \bar{x}^* = e^{-(\delta+d)}\bar{x}^* + b[\bar{y}^* + \bar{x}^*(1 - e^{-\delta})]e^{-[d+e^{-d}(\bar{x}^*+\bar{y}^*)]}, \\ \bar{y}^* = e^{-d}(1 - e^{-\delta})\bar{x}^* + e^{-d}\bar{y}^*. \end{cases} \quad (4.14)$$

or

$$\begin{cases} \bar{x}^* = e^{-(\delta+d)}\bar{x}^* + \frac{pe^{-d}[\bar{y}^* + \bar{x}^*(1 - e^{-\delta})]}{q + e^{-nd}(\bar{x}^* + \bar{y}^*)^n}, \\ \bar{y}^* = e^{-d}(1 - e^{-\delta})\bar{x}^* + e^{-d}\bar{y}^*. \end{cases} \quad (4.15)$$

If  $\bar{R}_0 > 1$ , then there exists a unique positive equilibrium  $\bar{E}^*$ . This equilibrium is listed in Table 2 for each of the models with birth pulses.

Note that when  $b = b_0(p = p_0)$ ,  $\bar{R}_0 = 1$ , and then  $\bar{E}^* = (0, 0)$ . Thus as  $b(p)$  increases through  $b_0(p_0)$ ,  $\bar{E}^*$  passes through the equilibrium at  $(0, 0)$  and exchanges stability with it in a transcritical bifurcation.

As  $b(p)$  increases further,  $\bar{E}^*$  remains stable until  $b(p)$  reaches another critical point at  $b = b_c(p = p_c)$ . Expressions for  $b_c$ ,  $p_c$  are given in Table 3.

The stability of  $\bar{E}^*$  is lost in only one way as  $b(p)$  is increased. In the density-dependence reproduction models (4.7) or (4.9), condition (4.11b) is violated for  $b > b_c(p > p_c)$ . A flip bifurcation results and the equilibrium loses stability to a stable two-cycle (Fig.1).

#### 4.4. Beyond $b_c(p_c)$

Our focus so far has been on the equilibria of the system (4.1) with Ricker function or Beverton-Holt function, and in particular, on the stability of those equilibria. But

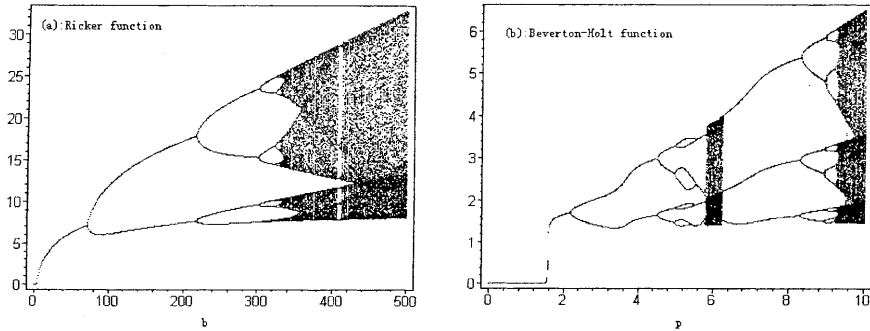
**Table 2.** Nontrivial equilibria of the two models with birth pulses.

Function	Equilibrium	$\bar{R}_0 \doteq R_0^R$ (or $R_0^B$ )
Ricker	$\bar{x}^* = \frac{(1-e^{-d})}{e^{-d}(1-e^{-(\delta+d)})} \ln R_0^R$ $\bar{y}^* = \frac{(1-e^{-\delta})}{(1-e^{-(\delta+d)})} \ln R_0^R$	$R_0^R = \frac{be^{-d}(1-e^{-\delta})}{(1-e^{-d})(1-e^{-(\delta+d)})}$
Beverton-Holt	$\bar{x}^* = \frac{(1-e^{-d})}{e^{-d}(1-e^{-(\delta+d)})} \sqrt[n]{q(R_0^B - 1)}$ $\bar{y}^* = \frac{(1-e^{-\delta})}{(1-e^{-(\delta+d)})} \sqrt[n]{q(R_0^B - 1)}$	$R_0^B = \frac{pe^{-d}(1-e^{-\delta})}{q(1-e^{-d})(1-e^{-(\delta+d)})}$

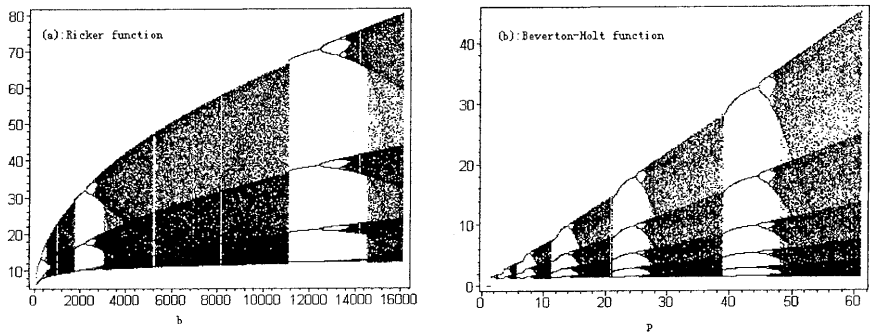
**Table 3.** Critical value  $b_c(p_c)$  of the parameter  $b(p)$  for each of the two types of density dependence.  $b(p)$  must be less than  $b_c(p_c)$  for stability.

Function	Stability condition	Type of bifurcation
Ricker	$b < b_c \equiv b_0 e^{[(1-e^{-d})(1+e^{-d}) + \frac{(1-e^{-d})^3(1-e^{-(\delta+d)})}{(1-e^{-\delta})(1+e^{-\delta+d})}]}$	Flip bifurcation
Beverton-Holt	$p < p_c \equiv p_0 \frac{n(1-e^{-d})(1+e^{-(\delta+d)})}{n(1-e^{-d})(1+e^{-(\delta+d)}) - 2(1+e^{-(\delta+2d)})}$	Flip bifurcation





**Fig. 1.** Bifurcation diagrams of two equations (4.7) and (4.9) for total population. Showing the bifurcation of  $\bar{E}_0(0, 0)$  and  $\bar{E}(\bar{x}^*, \bar{y}^*)$ . Other parameters are  $\delta = 0.4, d = 0.6, n = 14, q = 1$ .



**Fig. 2.** Bifurcation diagrams of two equations (4.7) and (4.9) for total population. Showing the period-adding phenomenon. Other parameters are  $\delta = 0.4, d = 0.6, n = 18, q = 1$ .

beyond  $b_c(p_c)$ , the equations (4.7) and (4.9) exhibit a wide variety of dynamical behaviors.

As  $b(p)$  increases beyond  $b_c(p_c)$ , it passes through a series of bifurcations that eventually lead to chaotic dynamics. In Fig.2, we have displayed bifurcation diagrams for equations (4.7) and (4.9). After the first flip bifurcation, the two models undergo a series of period-doubling bifurcations wherein a cycle of period  $2^k$  loses stability and a stable cycle of period  $2^{k+1}$  is born as  $b$ (or  $p$ ) increases. Successively higher periods are stable for smaller ranges of  $b(p)$ . Eventually, chaotic dynamics set in. This period-doubling route to chaos is the hallmark of logistic and Ricker maps(May, 1974; May and Oster, 1976) and has been studied extensively by mathematicians(Collet and Eckmann, 1980; Eckmann, 1983). As  $b(p)$  increases further, the population locks into cycles of various periods, which in turn proceeds through their own period-doubling sequences.

The bifurcation diagrams of both models reveal another interesting phenomenon. As pointed out above, all of the diagrams are characterized by an alteration of apparently chaotic dynamics and low-period cycles as  $b(p)$  increases. Notice that if the cycles to the left of a given chaotic window are of period  $k$ , then the cycles

to the right are of period  $k + 1$ . These so-called "period-adding" sequences have been observed in chemical reactions (Epstein, 1983; Hauser et al., 1997) and electrical circuits (Hung et al., 1995), and have been studied in one-dimensional difference equations (Kaneko, 1982, 1983; Kawczynski and Misiurewicz, 1990). Period-adding is also present in a delay-difference equation population model with density-dependent reproduction (Botsford, 1992), and in the density-dependent age-structured model studied by Guckenheimer et al. (1977).

## 5. The relationships between system (4.2) and equation (4.7)

In section 4, we presented the dynamics of system (4.2) using the stroboscopic map. This is a special case of the Poincaré map for periodically forced system or periodically pulsed system; the system trajectory is not recorded continuously in time but once every period of the forcing term or pulsing term (for example, the annual birth pulse period). Long-term solutions of system (4.2) will then appear as follows.

(i): Fixed points of the stroboscopic map (corresponding to periodic solutions having the same period as the pulsing term).

(ii): Periodic points of the stroboscopic map, of period  $k$  (corresponding to entrained periodic solutions having exactly  $k$  times the period of the pulsing, often called subharmonic periodic solutions or subharmonic period  $k$ 's).

(iii): Invariant circles (corresponding to quasi-periodic solutions, tori  $T^2$  for the original system of impulsive differential equations).

(iv): Possibly chaotic (strange) attractors.

In the following, we show that the solutions of system (4.2) behave like the above three case (i), (ii), (iv).

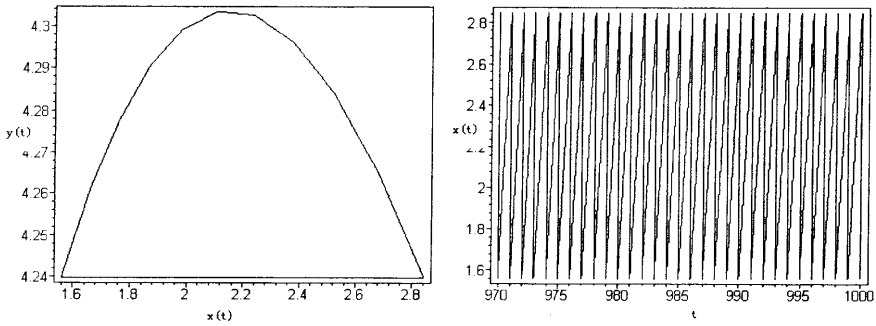
For  $b < b_0$ , equilibrium  $\bar{E}_0(0, 0)$  is stable. For this range of  $b$ , trajectories of model (4.3) approach the origin.

For  $b_0 < b < b_c$ , the equilibrium  $\bar{E}^*$  is stable. For this range of  $b$ , trajectories of model (4.3) approach the periodic solution  $(x_e(t), y_e(t))$  with period 1,

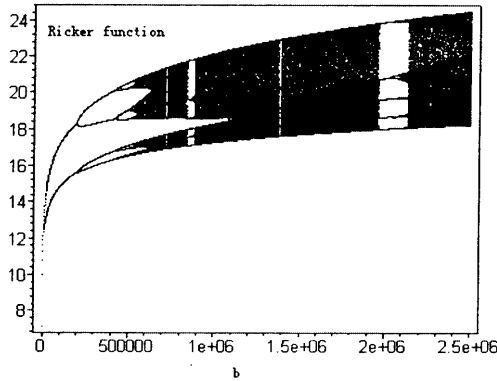
$$\begin{cases} x_e(t) = \bar{x}^* e^{-(\delta+d)(t-m)}, \\ y_e(t) = e^{-d(t-m)} [\bar{y}^* + \bar{x}^*(1 - e^{-\delta(t-m)})], \end{cases} \quad (5.1)$$

where  $m < t \leq m + 1$ . That is, periodic solution (5.1) of system (4.2) is locally asymptotically stable. Right at  $b = b_0$ , there is a transcritical bifurcation of periodic solutions as  $(0, 0)$  and  $(x_e(t), y_e(t))$  pass through each other and exchange stability. We note in passing that  $x_e(t)$  is discontinuous for  $t$  a multiple of  $m$  (see Fig.3).

The influence of  $b$  may be documented by stroboscopically sampling one of the variables over a range of  $b$  values. We numerically integrated system (4.2) for 500 pulsing cycles at each of 1001 values of  $b$ . For each  $b$ , we plotted the last 101 stroboscopic measurements of the total populations. Since we sampled at the forcing period, periodic solutions of period 1 appear as fixed point, periodic solutions of period 2 appear as two-cycles, and so forth. The resulting bifurcation diagram, Fig.4, clearly shows: (1) the first period-doubling at  $b = 7216.5$ , (2) a cascade of



**Fig. 3.** Periodic coexistence of the immature and the mature population with  $b = 100$ ,  $d = 0.2$ ,  $\delta = 0.4$ . (a) Period 1 solution; (b) time series for period 1 solution of the immature population.

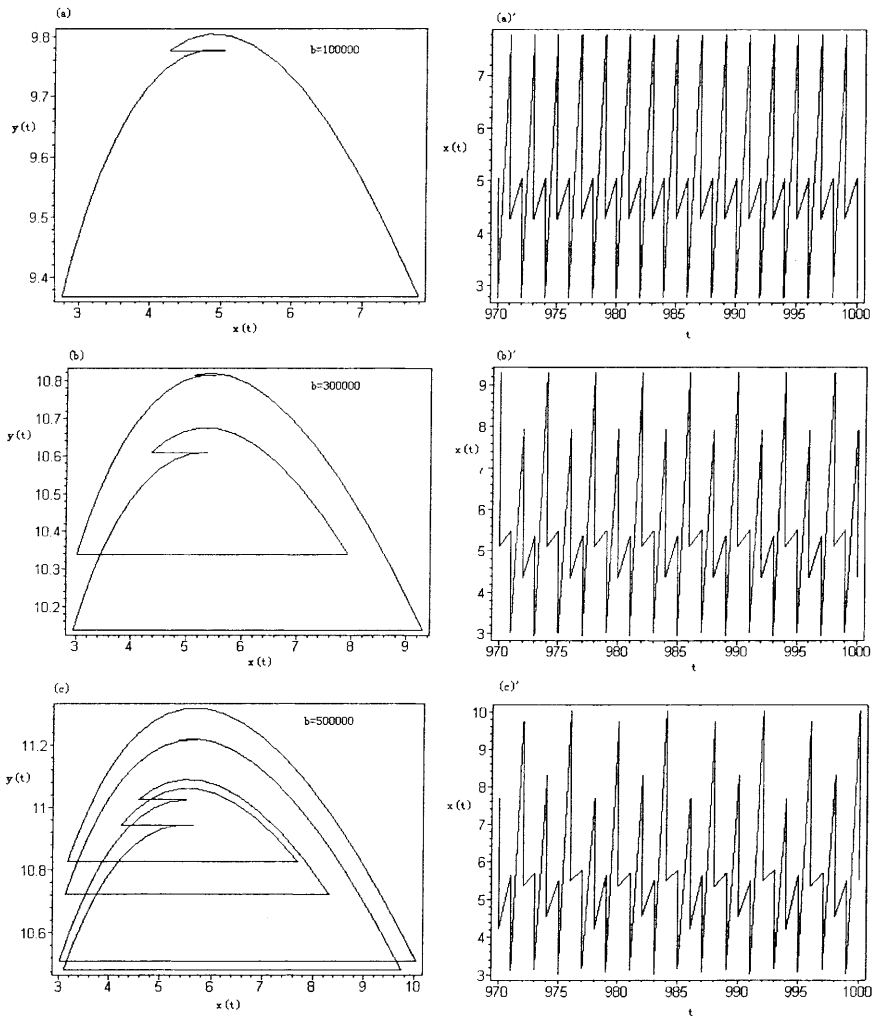


**Fig. 4.** Bifurcation diagrams of equation (4.7). For each of 1001 values of  $b$  between 100 and  $2.5 \times 10^6$ , we allowed 500 convergence iterations and plotted total population size for the next 101 iterations. Other parameters are  $\delta = 0.4$ ,  $d = 0.2$ .

period doublings, (3) chaotic solutions, and (4) periodic windows within the chaotic regime (e.g., the three-cycle at  $b = 2 \times 10^6$ ).

Corresponding to the bifurcation diagrams in Fig.4, Fig.5 illustrates the relationships between model (4.2) and model (4.7) and shows that birth pulse provides a natural period or cyclicity that allows for a period-doubling route to chaos. Fig.3 illustrates a simple cycle of period 1. Increasing  $b$  leads to a cascade of period-doubling bifurcations (Figs.5(a)-(c), (a), a 2-period cycle; (b), a 4-period cycle; (c), a 8-period cycle) and finally to the appearance of chaotic strange attractors. Fig5.(d) captures one such strange attractor, that is, increasing  $b$  is destabilizing: annual oscillations yield to multi-annual cycles of increasing period and amplitude as this parameter is increased (Figs.3 and 5).

By the same method, we can see that the dynamical behavior of system (4.8) is determined by equation (4.9), coupled with (4.6).



**Fig. 5.** Period-doubling cascade to chaos. (a) A 2-periodic solution, (a)' time series for a 2-periodic solution of immature population; (b) a 4-periodic solution, (b)' time series for a 4-periodic solution of immature population; (c) a 8-periodic solution, (c)' time series for a 8-periodic solution of immature population; (d) a strange attractor, (d)' time series for a strange attractor of immature population. Other parameters are  $\delta = 0.4$ ,  $d = 0.2$ .

## 6. Discussion

We have analyzed what can be considered to be the simplest realistic single species continuous ecosystem models with stage structure subject to periodic birth pulses. Firstly, we have considered when the birth rate of the mature population depends on the population density, and shown that the system exhibits a globally asymptotically stable positive equilibrium. Secondly, when the continuous birth of the

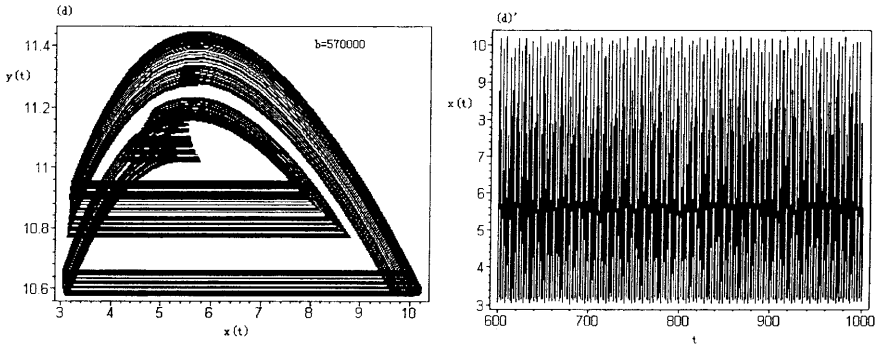


Fig. 5. (continued).

mature population is replaced with an annual birth pulse, we have shown the small amplitude periodic solutions arising from the periodically pulsed models form a sequence of period-doubling bifurcations. By using the stroboscopic map, we have obtained the complete expression for the periodic solution with period 1. As the parameter increases, the solution may pass from a period 1 (annual) cycle to a period 2 to a period 4 (multi-annual cycle), etc., tending to a Feigenbaum transition to chaotic behavior.

Comparing system (3.1) with system (4.1), we can conclude that system (3.1) is, as we have seen, dominated by its equilibria. It possesses two equilibria, corresponding to washout of population and coexistence. These equilibria are the only feasible attractors. System (4.1), in contrast, is dominated by periodic and by chaotic dynamics. The periodic birth pulsing of the mature population (a) destroys equilibria, (b) introduces subharmonic synchronization, and (c) initiates chaos. Pulsing, in effect, provides a natural period of cyclicity that allows for a period-doubling route to chaos.

Many authors have made experiments in order to investigate how stage structure influences the population fluctuations. Laboratory insect cultures in which the critical controlling factor is the supply of larval food (Nicholson, 1954, 1957) often display large quasi-cyclic population fluctuations which the period of the cycles is 2-3 times the maturation time. The experiments by Lawton on populations of Indian meal moth *Plodia interpunctella* (Gurney et al., 1983) have reemphasised that cycles with periods close to the generation time are also possible. Our theoretical results in this paper show that periodic birth pulses make single species model with stage structure occur with various kinds of periodic fluctuations, such as annual cycles and multi-annual cycles, which are in accord with the above experiments. This suggests that it is more in line with reality from a biological point of view when we consider the mature population with an annual birth pulse.

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