

# Discrete-time, discrete stage-structured predator–prey models

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Dedicated to Professor Jim Cushing on the occasion of his 62nd Birthday

Two discrete-time, discrete stage-structured predator–prey models are presented and analyzed. For these models it is shown that both populations go to extinction when the intrinsic growth rate of the prey is less than one. The prey population dynamics exhibits synchronizing phenomenon in the absence of its predator if the prey population is stage-structured with juvenile and adult classes. A unique interior steady state exists for both models when boundary equilibria lose their stability if Beverton–Holt type functional is adopted. This conclusion is not valid if Ricker type functional is used. The results demonstrated that Ricker type equation has more complicated dynamics than that of Beverton–Holt type equation for the stage-structured predator–prey models studied.

**Keywords:** Discrete-time predator–prey model; Discrete stage-structured predator–prey model; Ricker type; Beverton–Holt type

## 1. Introduction

The population dynamics of the predator and its prey reveal a variety of patterns that have appeared in the nature. There are cases where predation has a profoundly detrimental effect on the prey. On the other hand, there are situations where predation has no apparent effect on their prey's dynamics. There are also cases in which a predator retains a fairly constant density in spite of fluctuations in the abundance of its prey.

Mathematical models have been developed and analyzed in an attempt to understand and explain predator–prey interactions. The simple continuous-time Lotka–Volterra predator–prey model leads to coupled oscillations between the predator and the prey populations [1,3]. Nicholson and Bailey [1,3] on the other hand use difference equation models to capture host–parasitoid interaction with discrete generations. It is found that the interaction also possesses cycling behavior.

In these models, individuals within a single population are assumed to have the same biological vital rates despite variations in their size, age or stage. That is, there is no physiological differences among individuals in the same population. However, it is known that the interaction of an individual organism with others and with the physical environment are likely to depend on its developmental stages. Discrete-time, discrete structured population models have proven to be successful in studying population dynamics.

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See Caswell [4], Cushing [6] and Cushing *et al.* [7] for more detailed discussion about matrix population models and their applications.

Although single species matrix population models have received considerable attention, this is not the case for models of multiple populations interaction. This is probably in large part due to the fact that these models are mathematical intractable. Barclay [2] proposed an age-structured host-parasitoid matrix model and examined optimal control strategy for eliminating the parasite. The model was extended and analyzed by Crowe and Cushing [5] to include stage structure. Discrete-time, discrete size-structured chemostat competition models of two populations and multiple populations were studied by Smith [11] and Smith and Zhao [13], respectively. Based on the models given in [11,13], Jang investigated a chemostat model consisting of two populations with an external inhibitor [9]. She also studied competition between plasmid-bearing and plasmid-free organisms in a chemostat [10].

The purpose of this work is to use discrete stage-structured, discrete-time models to investigate the interaction between a predator and its prey. In the first model proposed, individuals in the predator population are assumed to be the same while the prey population is structured into juvenile and adult stages. Furthermore, it is assumed that only adult prey individuals are capable of reproducing and the adult individuals cannot live more than one unit of time. There is no immigration from other prey populations so that adult individuals only mature from juvenile of its own population through transition. The survival probability is assumed to be density dependent on the total prey population size in such a way that it decreases with increasing population density. The predator population only consumes the juvenile prey individuals with a Poisson distribution as an encounter rate.

The second model, on the other hand, ignores individual differences in the prey population while the predator population is classified into juvenile and adult classes. It is assumed that only the adult predator can consume its prey and this consumption return is via reproduction. The adult predators are allowed to live more than one time unit. For simplicity, the survival and transition probabilities for the predator population are assumed to be time and density independent.

Although population growth rate and density-dependent survival probability in this study are modeled using general functionals, specific functional forms of Beverton–Holt and Ricker types are discussed. In the following section a predator–prey model with stage structure in the prey is studied. Section 3 examines a predator–prey model with stage structure in the predator. Some concluding remarks are given in Section 4.

## 2. A predator–prey model with stage structure in the prey

In this section the prey population is classified into two classes, juveniles and adults. Let  $x_1(t)$  and  $x_2(t)$  be the juvenile and adult prey populations at time  $t$ , respectively. The predator population at time  $t$  is denoted by  $p(t)$ . It is assumed that the predator only preys on the juvenile prey population. This simple assumption is motivated by the frequent observation that in many populations adult have high capability of escaping predation. The number of encounters between juvenile prey and predator populations at any time  $t \geq 0$  follows that of simple mass action,  $ax_1(t)p(t)$ , where the searching efficiency  $a$  is a constant. We assume that the number of encounters are distributed randomly with a Poisson distribution. Consequently, the probability that an individual juvenile prey will escape from the predator

when the predator population is of size  $p$  is  $e^{-ap}$ . Therefore, the interaction between the prey and the predator populations is governed by the following system of difference equations:

$$\begin{cases} x_1(t+1) = f_2 x_2(t) \\ x_2(t+1) = s_1(x_1(t) + x_2(t)) x_1(t) e^{-ap(t)} \\ p(t+1) = r x_1(t) (1 - e^{-ap(t)}) \\ x_1(0), \quad x_2(0), \quad p(0) \geq 0, \end{cases} \quad (2.1)$$

where  $f_2 > 0$  is the density-independent fertility of an adult prey individual, the parameter  $r > 0$  is the average number of predators produced for each individual (juvenile) prey consumed, and the per-capita survival probability  $s_1$  of the juvenile prey population is assumed to be density-dependent on the total prey population size  $x_1 + x_2$  with  $s_1$  satisfying

$$(H1) \quad s_1 \in C^1[0, \infty), s_1(0) = \alpha_1, 0 < \alpha_1 < 1, s_1'(x) < 0 \quad \text{for } x \geq 0, \quad \text{and}$$

$$\lim_{x \rightarrow \infty} s_1(x) = 0.$$

Therefore the density dependence in this model has a negative effect on the population growth rate. Specifically, we will focus on the cases when  $s_1(x)x$  is either of Beverton–Holt type or of Ricker type functionals.

Clearly solutions of equation (2.1) exist and remain nonnegative for all  $t \geq 0$ , and system of equation (2.1) always has a trivial steady state  $E_0 = (0, 0, 0)$ . The parameter  $\alpha_1 f_2$  is the inherent net reproductive number or the intrinsic growth rate of the prey population. It is the average number of offspring that an individual prey population can reproduce during its lifetime when the prey population level is very small. Therefore if  $\alpha_1 f_2 < 1$ , then on average each individual in the prey population cannot replace itself during its life span. Thus, the prey population will eventually go to extinction. Since the predator feeds on the juvenile prey population for survival, the predator population will also go to extinction if  $\alpha_1 f_2 < 1$ .

**THEOREM 2.1** *If  $\alpha_1 f_2 < 1$ , then  $\lim_{t \rightarrow \infty} (x_1(t), x_2(t), p(t)) = (0, 0, 0)$  for all solutions of equation (2.1).*

*Proof* From equation (2.1) it is clear that  $x_1(t+1) = f_2 x_2(t)$  and  $x_2(t+1) \leq \alpha_1 x_1(t)$  for  $t \geq 0$ . Therefore, consider the linear system

$$\begin{cases} n_1(t+1) = f_2 n_2(t) \\ n_2(t+1) = \alpha_1 n_1(t) \end{cases} \quad (2.2)$$

with  $n_1(0) = x_1(0)$  and  $n_2(0) = x_2(0)$ . Since  $\alpha_1 f_2 < 1$ , we have  $\lim_{t \rightarrow \infty} n_1(t) = \lim_{t \rightarrow \infty} n_2(t) = 0$ . Thus  $\lim_{t \rightarrow \infty} x_1(t) = \lim_{t \rightarrow \infty} x_2(t) = 0$  and the result follows.  $\square$

Notice that if  $p(0) = 0$  then  $p(t) = 0$  for  $t \geq 0$ , i.e., the nonnegative  $x_1x_2$ -coordinate plane is positively invariant. It is useful to study the  $x_1x_2$ -subsystem of equation (2.1),

$$\begin{cases} x_1(t+1) = f_2x_2(t) \\ x_2(t+1) = s_1(x_1(t) + x_2(t))x_1(t) \\ x_1(0), x_2(0) \geq 0. \end{cases} \quad (2.3)$$

The dynamics of equation (2.3) will enable us to understand the structured prey population in the absence of the predator. A positive steady state  $(x_1x_2)$  of equation (2.3) must satisfy

$$1 = s_1((1 + f_2)x_2)f_2.$$

Hypothesis (H1) implies that the above equation has a positive solution  $\bar{x}_2$  if and only if  $\alpha_1f_2 > 1$ . Therefore, we conclude that a unique steady state  $E_1 = (\bar{x}_1, \bar{x}_2, 0)$  of system (2.1) exists if and only if  $\alpha_1f_2 > 1$ , where  $\bar{x}_1 = f_2\bar{x}_2$ . The local asymptotic stability of the steady state  $\hat{E}_1 = (\bar{x}_1, \bar{x}_2)$  for system (2.3) can be determined by the following Jacobian matrix  $\hat{J}$  evaluated at  $\hat{E}_1$ :

$$\hat{J} = \begin{pmatrix} 0 & f_2 \\ s_1(x_1 + x_2) + s'_1(x_1 + x_2)x_1 & s'_1(x_1 + x_2)x_1 \end{pmatrix},$$

by applying the well-known Jury condition [1]. The condition states that  $\hat{E}_1$  is locally asymptotically stable if  $|\text{tr}\hat{J}| < 1 + \det\hat{J} < 2$ . Since  $s'_1 < 0$  and  $f_2 > 1$ ,  $|\text{tr}\hat{J}| < 1 + \det\hat{J}$  holds for all parameter values with  $\alpha_1f_2 > 1$ . Consequently,  $\hat{E}_1$  is locally asymptotically stable if

$$-s'_1(\bar{x}_1 + \bar{x}_2)\bar{x}_1f_2 < 2. \quad (2.4)$$

We remark that if  $s_1(x)x$  is of Beverton–Holt type,

$$s_1(x)x = \frac{\alpha_1x}{1 + mx},$$

where  $m > 0$  is a constant, then a straightforward computation shows that condition (2.4) is trivially true when  $\alpha_1f_2 > 1$ . Therefore the steady state  $\hat{E}_1$  is always locally asymptotically stable for system (2.3) when it exists if  $s_1(x)x$  is of Beverton–Holt type. On the other hand if  $s_1(x)x$  is of Ricker type,

$$s_1(x)x = \alpha_1e^{-mx}x,$$

then equation (2.4) in general does not hold for all parameter values with  $\alpha_1f_2 > 1$ , i.e.,  $\hat{E}_1$  may be unstable for system (2.3) when it exists.

The linearization of system (2.3) at the trivial steady state  $\hat{E}_0 = (0, 0)$  can be viewed as given by the linear system (2.2). Since the eigenvalues of the coefficient matrix of equation (2.2) are 1 and  $-1$  when  $\alpha_1f_2 = 1$ , it is strongly suspected that both transcritical and period-doubling bifurcations will occur when  $\alpha_1f_2 = 1$ . The transcritical bifurcation is obvious as system (2.3) has a unique positive steady state  $\hat{E}_1$ , which is locally asymptotically stable if equation (2.4) holds when the steady state  $\hat{E}_0$  loses its stability. To understand whether a period-doubling bifurcation does indeed occur when  $\alpha_1f_2 = 1$ , we examine the existence of 2-cycles for equation (2.3).

Assuming  $\alpha_1 f_2 > 1$ , the second iteration of system (2.3) yields the following system

$$\begin{cases} x_1(t+2) = f_2 s_1(x_1(t) + x_2(t))x_1(t) \\ x_2(t+2) = s_1(f_2 x_2(t) + s_1(x_1(t) + x_2(t))x_1(t))f_2 x_2(t). \end{cases} \quad (2.5)$$

Fixed points  $(\hat{x}_1, \hat{x}_2)$  of the above system with  $(\hat{x}_1, \hat{x}_2) \neq \hat{E}_i$ ,  $i = 0, 1$ , correspond to nontrivial 2-cycles of equation (2.3). Notice that the  $x_1$ -component of an interior steady state  $(\hat{x}_1, \hat{x}_2)$  of system (2.5) must satisfy

$$1 = s_1 \left( f_2 s_1^{-1} \left( \frac{1}{f_2} \right) + \left( \frac{1}{f_2} - f_2 \right) x \right) f_2. \quad (2.6)$$

Let  $g(x)$  denote the right hand side of equation (2.6). Since  $\alpha_1 f_2 > 1$ , there exists  $x_0 > 0$  such that  $g(x_0) > 1$ . On the other hand  $g'(x) > 0$  for  $0 \leq x \leq x_0$ . Thus equation (2.6) has a solution  $\hat{x}_1 > 0$  if and only if  $g(0) < 1$ , i.e., if and only if  $f_2 s_1^{-1}(1/f_2) > s_1^{-1}(1/f_2)$ . This inequality is trivially true as  $f_2 > 1$ . Consequently, a positive steady state  $(\hat{x}_1, \hat{x}_2)$  of system (2.5) exists if and only if

$$\hat{x}_2 = s_1^{-1} \left( \frac{1}{f_2} \right) - \hat{x}_1 > 0.$$

A direct computation shows that this last inequality is equivalent to  $s_1^{-1}(1/f_2) > (1/f_2)s_1^{-1}(1/f_2)$ , which is also clearly true as  $f_2 > 1$ . Therefore, we conclude that system (2.5) always has an interior steady state if  $\alpha_1 f_2 > 1$  and this steady state is unique. However, interior steady states of system (2.3) are also fixed points of equation (2.5). Since the fixed point we just derived is unique it can be seen that this positive steady state  $(\hat{x}_1, \hat{x}_2)$  of system (2.5) is the interior steady state  $\hat{E}_1 = (\bar{x}_1, \bar{x}_2)$  of system (2.3). Indeed, since  $\bar{x}_1 + \bar{x}_2 = s_1^{-1}(1/f_2)$  and  $\bar{x}_1 = f_2 \bar{x}_2$ , we have  $s_1(f_2 s_1^{-1}(1/f_2) + (1/f_2 - f_2)\bar{x}_1)f_2 = 1$ . Hence  $\bar{x}_1 = \hat{x}_1$ ,  $\bar{x}_2 = \hat{x}_2$ , and system (2.3) has no interior 2-cycles.

Notice that the coordinate axes are forward invariant for system (2.3). We shall examine the existence of 2-cycles of equation (2.3) on the boundary of  $\mathbb{R}_+^2$ . Letting  $x_1 = 0$ , the boundary steady state  $(0, \hat{x}_2)$  of equation (2.5) must satisfy

$$s_1(f_2 x_2)f_2 = 1.$$

This shows that boundary steady state  $(0, \hat{x}_2)$  always exists for system (2.5) if  $\alpha_1 f_2 > 1$ , where

$$\hat{x}_2 = \frac{1}{f_2} s_1^{-1} \left( \frac{1}{f_2} \right).$$

Similarly, there exists another boundary steady state  $(\hat{x}_1, 0)$  for system (2.5), where

$$\hat{x}_1 = s_1^{-1} \left( \frac{1}{f_2} \right).$$

Therefore when  $\alpha_1 f_2 > 1$ , system (2.5) has three boundary steady states  $(0, 0)$ ,  $(\hat{x}_1, 0)$  and  $(0, \hat{x}_2)$ , where  $\{(\hat{x}_1, 0), (0, \hat{x}_2)\}$  constitutes the unique 2-cycle of system (2.3) and we conclude that a period-doubling bifurcation occurs when  $\alpha_1 f_2 = 1$ .

In what follows we will show that system (2.3) restricted to the boundary has  $\omega$ -limit set  $\{(\hat{x}_1, 0), (0, \hat{x}_2)\}$  when  $s_1(x)x$  is of Beverton–Holt type and  $\alpha_1 f_2 > 1$ . To this end, we rewrite

system (2.5) as

$$\begin{cases} y_1(t+1) = f_2 s_1(y_1(t) + y_2(t)) y_1(t) \\ y_2(t+1) = s_1(f_2 y_2(t) + s_1(y_1(t) + y_2(t)) y_1(t)) f_2 y_2(t). \end{cases} \quad (2.7)$$

Observe that if  $y_1(0) = 0$  and  $y_2(0) > 0$ , then  $y_1(t) = 0$  for  $t \geq 0$  and  $y_2(t)$  corresponds to the solution of system (2.3) with  $y_2(t) = x_2(2t)$ , i.e.,  $\{y_2(t)\}$  is the orbit of  $\{(x_1(t), x_2(t))\}$  restricted to the  $x_2$ -axis when  $x_1(0) = 0$  and  $x_2(0) = y_2(0) > 0$ . Thus letting  $y_1(0) = 0$ , system (2.7) reduces to

$$\begin{cases} y_2(t+1) = s_1(f_2 y_2(t)) f_2 y_2(t) \\ y_2(0) = x_2(0) > 0. \end{cases} \quad (2.8)$$

Equation (2.8) has two steady states 0 and  $\hat{x}_2$ . As  $\alpha_1 f_2 > 1$ , the steady state 0 is unstable. It is then easy to show that  $\lim_{t \rightarrow \infty} y_2(t) = \hat{x}_2$  by the monotonicity property of  $s_1(x)x$ . Indeed, let

$$G(y_2) = s_1(f_2 y_2) f_2 y_2.$$

Then

$$(y_2 - \hat{x}_2)[G(y_2) - y_2] = (y_2 - \hat{x}_2)[s_1(f_2 y_2) f_2 - 1] y_2 < 0$$

for  $0 < y_2 \neq \hat{x}_2$ . If  $0 < y_2(0) < \hat{x}_2$  is given, then  $y_2(1) = G(y_2(0)) > y_2(0)$  by the above inequality and  $y_2(1) = G(y_2(0)) < G(\hat{x}_2) = \hat{x}_2$  as  $G$  is strictly increasing, i.e.,  $y_2(0) < y_2(1) < \hat{x}_2$ . Continuing in this manner, we see that  $\{y_2(t)\}_{t=0}^{\infty}$  is an increasing sequence of real numbers, which is bounded above by  $\hat{x}_2$ . Thus  $\lim_{t \rightarrow \infty} y_2(t)$  exists, and equals to  $\hat{x}_2$  by the continuity of  $G$ . The same argument can be applied to the case when  $y_2(0) > \hat{x}_2$ . We then conclude that  $\lim_{t \rightarrow \infty} y_2(t) = \hat{x}_2$ , i.e.,  $\lim_{t \rightarrow \infty} x_2(2t) = \hat{x}_2$  if  $x_1(0) = 0$  and  $x_2(0) > 0$  when  $\alpha_1 f_2 > 1$  and  $s_1(x)x$  is of Beverton–Holt type.

Clearly  $x_1(2t) = x_2(2t+1) = 0$  for  $t \geq 0$  if  $x_1(0) = 0$ . What happens to  $x_1(2t+1)$ ? This is just the same orbit of system (2.7) with  $y_2(0) = 0$  and  $y_1(0) = x_1(1) > 0$ . Letting  $y_2(0) = 0$  in system (2.7), we have the following first order scalar difference equation:

$$\begin{cases} y_1(t+1) = f_2 s_1(y_1(t)) y_1(t) \\ y_1(0) = x_1(1) > 0. \end{cases} \quad (2.9)$$

Applying the same analysis as above it can be shown that  $\lim_{t \rightarrow \infty} y_1(t) = \hat{x}_1$ , i.e.,  $\lim_{t \rightarrow \infty} x_1(2t+1) = \hat{x}_1$ . Therefore if  $s_1(x)x$  is of Beverton–Holt type, then the 2-cycle  $\{(\hat{x}_1, 0), (0, \hat{x}_2)\}$  is the  $\omega$ -limit set of system (2.3) restricted to the boundary of  $\mathbb{R}_+^2$  when  $\alpha_1 f_2 > 1$ .

Will solutions of equation (2.3) with positive initial conditions have this unique 2-cycle as the  $\omega$ -limit set? The question can be easily answered by looking at the Jacobian matrix associated with system (2.7). Indeed, the Jacobian matrix of equation (2.7) evaluated at  $(\hat{x}_1, 0)$  is given by

$$J_1 = \begin{pmatrix} 1 + f_2 s'_1(\hat{x}_1) \hat{x}_1 & f_2 s'_1(\hat{x}_1) \hat{x}_1 \\ 0 & f_2 s_1(s_1(\hat{x}_1) \hat{x}_1) \end{pmatrix}.$$

A simple calculation for the case when  $s_1(x)x$  is of Beverton–Holt type shows that  $0 < 1 + f_2 s'_1(\hat{x}_1) \hat{x}_1 < 1$  and  $f_2 s_1(s_1(\hat{x}_1) \hat{x}_1) = f_2 s_1(\hat{x}_1/f_2) > 1$ . This illustrates that the stable

manifold of  $(\hat{x}_1, 0)$  as a fixed point of equation (2.7) lies on the  $y_1$ -axis. Moreover, the local unstable manifold of  $(\hat{x}_1, 0)$  can be shown to be pointed towards the interior of  $\mathbb{R}_+^2$ . Indeed, let  $\lambda = f_2 s_1(s_1(\hat{x}_1)\hat{x}_1)$  and  $(a, b)^T$  be the eigenvector of  $J_1$  with respect to  $\lambda$ . By choosing  $b = 1$ , we have  $a = (-f_2 s'(\hat{x}_1)\hat{x}_1)/(1 + f_2 s'_1(\hat{x}_1)\hat{x}_1 - \lambda) < 0$  since  $\lambda > 1$ . Therefore no solution of equation (2.3) with positive initial condition can have the 2-cycle as its  $\omega$ -limit set. However, this linear analysis does not hold for the Ricker type functional for all parameter values with  $\alpha_1 f_2 > 1$ .

As discussed earlier that the interior steady state of equation (2.3) is always locally asymptotically stable for the Beverton–Holt type functional, one would then expect that the steady state is globally asymptotically stable for equation (2.3) in the interior of  $\mathbb{R}_+^2$ . On the other hand, it can be easily seen that the  $x_1 x_2$ -subsystem of equation (2.3) is cooperative when  $s_1(x)x$  is of Beverton–Holt type. This is accomplished by looking at the Jacobian matrix  $\hat{J}$  presented earlier and notice that  $s_1(x_1 + x_2) + s'_1(x_1 + x_2)x_1 > 0$  for all  $x_1, x_2 \geq 0$ . For a functional of Ricker type the corresponding subsystem is not cooperative for all  $x_1, x_2 \geq 0$ . Restriction to the state space is necessary for the system to be cooperative.

Solutions of equation (2.3) are clearly bounded when  $s_1(x)x$  is of Beverton–Holt type, i.e., system (2.3) is point dissipative. The dynamics of point dissipative, cooperative 2-D maps are well-understood. Solutions to such maps either converge to a fixed point or have a 2-cycle of the map as the  $\omega$ -limit set [12]. Since solutions with positive initial conditions cannot have the 2-cycle as the corresponding  $\omega$ -limit set, we have the following result.

**THEOREM 2.2** *Let  $s_1(x)x$  be of Beverton–Holt type with  $s_1(0)f_2 > 1$ . Then solutions of equation (2.1) with  $p(0) = 0$  and either  $x_1(0) = 0$  or  $x_2(0) = 0$  (but  $(x_1(0), x_2(0)) \neq (0, 0)$ ) have the  $\omega$ -limit set equals to the unique 2-cycle  $\{(\hat{x}_1, 0, 0), (0, \hat{x}_2, 0)\}$  on the  $x_1 x_2$ -plane. Solutions of equation (2.1) with  $p(0) = 0$  and  $x_1(0) > 0$ ,  $x_2(0) > 0$  converge to the steady state  $E_1 = (\bar{x}_1, \bar{x}_2, 0)$ .*

When  $s_1(x)x$  is of Ricker type, the dynamics of system (2.3) restricted to the coordinate axes is much more complicated than that of Beverton–Holt type. The 2-cycle  $\{(\hat{x}_1, 0), (0, \hat{x}_2)\}$  may not always be globally asymptotically stable on the boundary when we vary the parameters. It is very likely that period-doubling bifurcations will continuously occur on the boundary and eventually the boundary dynamics will exhibit chaos just like the scalar Ricker equation does [1]. Moreover, the interior steady state may not be always locally asymptotically stable.

Consider now the full system (2.1) with its corresponding Jacobian matrix  $J$  given by

$$J = \begin{pmatrix} 0 & f_2 & 0 \\ s_1(x)e^{-ap} + s'_1(x)x_1e^{-ap} & s'_1(x)x_1e^{-ap} & -as_1(x)x_1e^{-ap} \\ r(1 - e^{-ap}) & 0 & arx_1e^{-ap} \end{pmatrix},$$

where  $x = x_1 + x_2$ . In particular

$$J(E_0) = \begin{pmatrix} 0 & f_2 & 0 \\ \alpha_1 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix},$$

and thus system (2.1) undergoes both transcritical and period-doubling bifurcations when  $\alpha_1 f_2 = 1$ . When  $\alpha_1 f_2 > 1$ , steady state  $E_1 = (\bar{x}_1, \bar{x}_2, 0)$  exists, and

$$J(E_1) = \begin{pmatrix} 0 & f_2 & 0 \\ s_1(x) + s'_1(x)\bar{x}_1 & s'_1(x)\bar{x}_1 & -as_1(x)\bar{x}_1 \\ 0 & 0 & ar\bar{x}_1 \end{pmatrix},$$

where  $x = \bar{x}_1 + \bar{x}_2$ . Therefore  $E_0$  is unstable with stable manifold lying on the  $p$ -axis, and  $E_1$  is locally asymptotically stable if equation (2.4) holds and

$$ar\bar{x}_1 < 1.$$

We next examine the existence of an interior steady state  $(x_1^*, x_2^*, p^*)$  for equation (2.1). It follows from the equilibrium equations

$$e^{ap} = s_1((1 + f_2)x_2)f_2, \quad x_1 = f_2x_2 \quad \text{and} \quad p = rx_1(1 - e^{-ap})$$

that  $p^*$  must satisfy

$$\frac{p}{1 - e^{-ap}} = rf_2F(p), \quad (2.10)$$

where

$$F(p) = \frac{1}{1 + f_2} s_1^{-1} \left( \frac{e^{ap}}{f_2} \right).$$

We immediately conclude that a necessary condition for the existence of an interior steady state is  $\alpha_1 f_2 > 1$ . Notice that  $F'(p) < 0$  for  $p \geq 0$  and  $F(0) = (1/(1 + f_2))s_1^{-1}(1/f_2) > 0$ . Let  $H(p)$  denote the left hand side of equation (2.10). Then  $\lim_{p \rightarrow \infty} H(p) = \infty$ ,  $\lim_{p \rightarrow 0^+} H(p) = 1/a$ , and  $H'(p) > 0$  for  $p > 0$ . Since there exists  $p_0 > 0$  such that  $F(p_0) = 0$ , it follows that equation (2.10) has a solution  $p^* > 0$  if and only if  $H(0) < rf_2F(0)$ , i.e., if and only if

$$\frac{1 + f_2}{arf_2} < s_1^{-1} \left( \frac{1}{f_2} \right). \quad (2.11)$$

Consequently a unique interior steady state  $E_2 = (x_1^*, x_2^*, p^*)$  exists if equation (2.11) holds, where  $p^*$  solves equation (2.10),  $x_2^* = F(p^*)$  and  $x_1^* = f_2x_2^*$ .

We shall express inequality of equation (2.11) in terms of the local stability of the steady state  $E_1 = (\bar{x}_1, \bar{x}_2, 0)$ . Recall that  $\bar{x}_2 = (1/(1 + f_2))s_1^{-1}(1/f_2)$  and  $\bar{x}_1 = f_2\bar{x}_2$ . Therefore equation (2.11) is equivalent to  $r\bar{x}_1 > 1/a$ , i.e., if and only if  $ar\bar{x}_1 > 1$ . When  $s_1(x)x$  is of Beverton–Holt type, since the steady state  $\hat{E}_1$  is always locally asymptotically stable for system (2.3), we see that the interior steady state  $E_2$  exists for equation (2.1) if  $E_1$  is unstable. When  $s_1(x)x$  is of Ricker type, it is possible that  $ar\bar{x}_1 < 1$  but condition (2.4) fails to be true. Therefore it is possible that  $E_2$  does not exist even when  $E_1$  is unstable. This observation supports the common belief that Ricker type nonlinearity generates more complex dynamical behavior than that of Beverton–Holt type.

Furthermore when  $\alpha_1 f_2 > 1$ , since  $x_2^*$  satisfies  $1 = s_1((1 + f_2)x_2)e^{-ap^*}f_2$  and  $\bar{x}_2$  solves  $1 = s_1((1 + f_2)x_2)f_2$ , we see that

$$x_2^* < \bar{x}_2 \quad \text{and} \quad x_1^* < \bar{x}_1$$

if  $E_2 = (x_1^*, x_2^*, p^*)$  exists. Recall also that  $\hat{x}_2$  satisfies  $1 = s_1(f_2x_2)f_2$ . Therefore we conclude that when  $\alpha_1 f_2 > 1$  and the interior steady state  $E_2$  exists, the magnitudes of the steady states



and the 2-cycle can be summarized by the following inequalities

$$x_2^* < \bar{x}_2 < \hat{x}_2 \quad \text{and} \quad x_1^* < \bar{x}_1 < \hat{x}_1.$$

Since  $s_1(x)x$  is either of Beverton–Holt or Ricker type functional, we may assume there exists a constant  $M > 0$  such that

$$s_1(x)x \leq M \quad \text{for all } x \geq 0.$$

Thus

$$x_2(t+1) \leq s_1(x_1(t))x_1(t) \leq M,$$

$$x_1(t+2) \leq f_2M \quad \text{and} \quad p(t+3) \leq rx_1(t+2) \leq rf_2M$$

for  $t \geq 0$ . Consequently solutions of system (2.1) are bounded and the system is point dissipative. On the other hand since  $1 - e^{-ap} \leq ap$  for  $p \geq 0$ , we have

$$p(t+3) \leq arx_1(t+2)p(t+2) \leq arf_2Mp(t+2)$$

for  $t \geq 0$ . Therefore if  $arf_2M < 1$ , then  $\lim_{t \rightarrow \infty} p(t) = 0$ , i.e., the predator population will become extinct. Here  $M$  depends on  $\alpha_1$ .

Observe that if  $p(t_0) = 0$  for some  $t_0 \geq 0$  then  $p(t) = 0$  for  $t \geq t_0$ . It follows that system (2.1) has no 3-cycles of the form:  $\{(x_1, 0, 0), (0, x_2, 0), (0, 0, p)\}$  or  $\{(x_1, x_2, 0), (0, x_2, p), (x_1, 0, p)\}$  with  $x_1, x_2, p > 0$ . Moreover, letting  $x_1(0) = 0$ ,  $x_2(0) > 0$  and  $p(0) > 0$ , we have  $x_1(1) > 0$  and  $x_2(1) = p(1) = 0$ . Consequently, such a solution remains on the  $x_1, x_2$ -axes. Similarly, setting  $x_1(0) > 0$ ,  $x_2(0) = 0$  and  $p(0) > 0$ , then  $x_1(2) > 0$  and  $x_2(2) = p(2) = 0$  and the solution also remains on the  $x_1, x_2$ -axes. We can conclude that such a solution has the 2-cycle  $\{(\hat{x}_1, 0, 0), (0, \hat{x}_2, 0)\}$  as its  $\omega$ -limit set if  $s_1(x)x$  is of Beverton–Holt type, i.e., the nonnegative  $x_1p$  and  $x_2p$ -planes with the  $p$ -axis deleted are in the stable manifold of the 2-cycle.

On the other hand will system (2.1) has 2-cycles on the interior of  $x_1p$  or  $x_2p$ -coordinate planes? The answer seems obvious by the argument just given. To see this analytically we can consider the composite map induced by system (2.1).

$$\begin{cases} x_1(t+2) = f_2s_1(x_1(t) + x_2(t))x_1(t)e^{-ap(t)} \\ x_2(t+2) = s_1(f_2x_2(t) + s_1(x_1(t) + x_2(t))x_1(t)e^{-ap(t)})f_2x_2(t)e^{-arx_1(t)(1-e^{-ap(t)})} \\ p(t+2) = rf_2x_2(t)[1 - e^{-arx_1(t)(1-e^{-ap(t)})}] \\ x_1(0), x_2(0), p(0) \geq 0. \end{cases} \quad (2.12)$$

A simple calculation shows that the only nontrivial fixed points of system (2.12) on the coordinate planes are the 2-cycles  $\{(\hat{x}_1, 0, 0), (0, \hat{x}_2, 0)\}$  derived earlier. The corresponding Jacobian matrix associated with equation (2.12) at the fixed point  $(\hat{x}_1, 0, 0)$  has the following form

$$\begin{pmatrix} f_2s_1(\hat{x}_1) + f_2s_1'(\hat{x}_1)\hat{x}_1 & f_2s_1'(\hat{x}_1)\hat{x}_1 & -af_2s_1(\hat{x}_1)\hat{x}_1 \\ 0 & f_2s_1(s_1(\hat{x}_1)\hat{x}_1) & 0 \\ 0 & 0 & 0 \end{pmatrix},$$

which shows that the stable manifold of the unique 2-cycle  $\{(\hat{x}_1, 0, 0), (0, \hat{x}_2, 0)\}$  of system (2.1) is 2-D and lies on the nonnegative  $x_1p$  and  $x_2p$ -planes with  $p$ -axis removed if  $s_1(x)x$  is of

Beverton–Holt type and  $\alpha_1 f_2 > 1$ . If  $s(x)x$  is of Ricker type, then some restrictions on the parameters are necessary in order for us to reach the same conclusion.

### 3. A predator–prey model with stage structure in the predator

In this section the prey population is unstructured while the predator population is classified into two stages, juveniles and adults. Let  $x(t)$  denote the prey population at time  $t$ , and  $p_1(t)$ ,  $p_2(t)$  be the juvenile and adult predator populations at time  $t$ , respectively. It is assumed that only the adult predator can prey on the prey population and its consumption return is through reproduction. Specifically, our model is given by the following system of nonlinear difference equations.

$$\begin{cases} x(t+1) = g(x(t))x(t)e^{-cp_2(t)} \\ p_1(t+1) = bx(t)(1 - e^{-cp_2(t)}) \\ p_2(t+1) = sp_1(t) + \alpha p_2(t) \\ x(0), p_1(0), p_2(0) \geq 0, \end{cases} \quad (3.1)$$

where  $g(x)$  is the density-dependent growth rate of the prey, which is assumed to satisfy the following hypotheses:

$$(H2) \quad g \in C^1[0, \infty), \quad g(0) = \beta, \quad g'(x) < 0 \text{ for } x \geq 0, \quad \text{and} \quad \lim_{x \rightarrow \infty} g(x) = 0.$$

Therefore the prey population's growth rate decreases as its population density increases. This assumption is the same as that of  $s_1$  given in the previous section.

The parameter  $c > 0$  is the constant searching efficiency of the predator. The encounter rate between the prey and an adult predator also follows simple mass action with a Poisson distribution. The constant  $b > 0$  represents the average number of predator offspring reproduced by each prey consumption. The per-capita survival probability  $s$  of the juvenile predator,  $0 < s < 1$ , is assumed to be density independent. It is also assumed that the predator may live longer than one unit of time so that parameter  $\alpha$  satisfies  $0 < \alpha < 1$ .

As in the previous section we are particularly interested in the case when  $g(x)x$  is either of Beverton–Holt or Ricker type functionals. Therefore we may assume that there exists  $D > 0$  such that  $g(x)x \leq D$  for all  $x \geq 0$ . Consequently,

$$x(t+1) \leq D, \quad p_1(t+2) \leq bx(t+1) \leq bD$$

and

$$p_2(t+3) \leq sbD + \alpha p_2(t+2) \quad \text{for } t \geq 0.$$

Consider

$$q(t+1) = sbD + \alpha q(t)$$

for  $t \geq 0$  with  $q(0) = p_2(2)$ . Since  $\lim_{t \rightarrow \infty} q(t) = sbD/(1 - \alpha)$ , it follows that  $\limsup_{t \rightarrow \infty} p_2(t) \leq sbD/(1 - \alpha)$ . Therefore solutions of equation (3.1) remain nonnegative and are bounded for all forward time.

If  $\beta < 1$ , then it is easy to see that solutions of equation (3.1) all converge to the trivial steady state  $E_0 = (0, 0, 0)$ . Indeed, since  $x(t+1) \leq g(x(t))x(t) \leq \beta x(t)$  for  $t \geq 0$  and  $\beta < 1$

we clearly see that  $\lim_{t \rightarrow \infty} x(t) = 0$ . Consequently  $\lim_{t \rightarrow \infty} p_1(t) = \lim_{t \rightarrow \infty} p_2(t) = 0$  and the steady state  $E_0 = (0, 0, 0)$  is globally asymptotically stable when  $\beta < 1$ .

**THEOREM 3.1** *If  $\beta = g(0) < 1$ , then solutions of system (3.1) all converge to the trivial steady state  $E_0 = (0, 0, 0)$ .*

The conclusion of Theorem 3.1 remains true for any function  $g$  that satisfies (H2). The parameter  $\beta$  is the intrinsic growth rate of the prey population. Two interacting populations go to extinction when  $\beta < 1$ . Suppose  $\beta > 1$  for the remaining discussion. Clearly if  $x(0) = 0$ , then  $x(t) = 0$  and  $p_1(t) = 0$  for  $t \geq 0$ , and  $p_2(t+1) = \alpha p_2(t)$  implies  $\lim_{t \rightarrow \infty} p_2(t) = 0$  as  $0 < \alpha < 1$ . Therefore the  $p_1 p_2$ -coordinate plane belongs to the stable manifold of  $E_0$ . Furthermore, since  $\beta > 1$  there exists another steady state  $E_1 = (\bar{x}, 0, 0)$  on the  $x$ -axis for system (3.1), where  $\bar{x}$  satisfies

$$g(\bar{x}) = 1.$$

The Jacobian matrix associated with the system is

$$J = \begin{pmatrix} g(x)e^{-cp_2} + g'(x)xe^{-cp_2} & 0 & -cg(x)xe^{-cp_2} \\ b(1 - e^{-cp_2}) & 0 & bcxe^{-cp_2} \\ 0 & s & \alpha \end{pmatrix}.$$

In particular,

$$J(E_0) = J(0, 0, 0) = \begin{pmatrix} \beta & 0 & 0 \\ 0 & 0 & 0 \\ 0 & s & \alpha \end{pmatrix},$$

and

$$J(E_1) = J(\bar{x}, 0, 0) = \begin{pmatrix} 1 + g'(\bar{x})\bar{x} & 0 & -c\bar{x} \\ 0 & 0 & bc\bar{x} \\ 0 & s & \alpha \end{pmatrix}.$$

Therefore unlike the model given in the previous section, only transcritical bifurcation occurs when  $\beta = 1$  as seen by the Jacobian matrix  $J(E_0)$  given above. Moreover, it follows from the Jacobian matrix at  $E_1$  that  $E_1$  is locally asymptotically stable if

$$g'(\bar{x})\bar{x} > -2 \quad \text{and} \quad sbc\bar{x} < 1 - \alpha.$$

Notice that the inequality  $g'(\bar{x})\bar{x} > -2$  is equivalent to the local asymptotic stability of  $\bar{x}$  for the scalar difference equation  $x(t+1) = g(x(t))x(t)$ . Therefore if  $g(x)x$  is of Beverton–Holt type, then  $g'(\bar{x})\bar{x} > -2$  is trivially true and moreover  $\bar{x}$  is globally asymptotically stable for the scalar Beverton–Holt equation as  $\beta > 1$  [1].

Suppose  $sbc\bar{x} < 1 - \alpha$  and  $g(x)x$  is of Beverton–Holt type. The monotonicity of  $g(x)x$  makes the dynamics of equation (3.1) completely understood as seen below. Since  $x(t+1) \leq g(x(t))x(t)$  for  $t \geq 0$ , we have  $\limsup_{t \rightarrow \infty} x(t) \leq \bar{x}$  for any solution  $(x(t), p_1(t), p_2(t))$  of equation (3.1). Therefore for any  $\epsilon > 0$  there exists  $t_0 > 0$  such that  $x(t) \leq \bar{x} + \epsilon$  for  $t \geq t_0$ . Since  $sbc\bar{x} < 1 - \alpha$ , we can choose  $\epsilon > 0$  such that  $sbc(\bar{x} + \epsilon) < 1 - \alpha$ . Consequently as

$1 - e^{-cp} \leq cp$  for  $p \geq 0$  we have

$$p_1(t+1) \leq bx(t)cp_2(t) \leq bc(\bar{x} + \epsilon)p_2(t)$$

and

$$p_2(t+2) \leq sbc(\bar{x} + \epsilon)p_2(t) + \alpha p_2(t+1)$$

for  $t \geq t_0$ . Consider the following second order scalar difference equation

$$q(t+2) = sbc(\bar{x} + \epsilon)q(t) + \alpha q(t+1)$$

with  $q(t_0) = p_2(t_0)$ . The characteristic equation associated with this difference equation is  $\lambda^2 - \alpha\lambda - sbc(\bar{x} + \epsilon) = 0$ . Since  $sbc(\bar{x} + \epsilon) < 1 - \alpha$ , the eigenvalues  $\lambda_i$  satisfy  $|\lambda_i| < 1$  for  $i = 1, 2$ . Therefore  $\lim_{t \rightarrow \infty} q(t) = 0$  and we may conclude that  $\lim_{t \rightarrow \infty} p_2(t) = 0$ . As a result  $\lim_{t \rightarrow \infty} p_1(t) = 0$ , and for any  $\epsilon > 0$  there exists  $t_1 > 0$  such that  $p_2(t) < \epsilon$  for  $t \geq t_1$ . Choosing  $\epsilon > 0$  such that  $\beta(1 - c\epsilon) > 1$ , we get

$$x(t+1) \geq g(x(t))x(t)[1 - cp_2(t)] \geq g(x(t))x(t)(1 - c\epsilon)$$

for  $t \geq t_1$ . Now consider the difference equation

$$y(t+1) = g(y(t))y(t)(1 - c\epsilon) \quad (3.2)$$

with  $y(t_1) = x(t_1)$ . Since  $\beta(1 - c\epsilon) > 1$ , this scalar equation has a unique positive steady state  $\bar{x}(\epsilon)$  and its nontrivial solutions all converge to the steady state, where  $\bar{x}(\epsilon) \rightarrow \bar{x}$  as  $\epsilon \rightarrow 0^+$ . This shows that  $\liminf_{t \rightarrow \infty} x(t) \geq \bar{x}(\epsilon)$  for any solution of equation (3.1) with  $x(0) > 0$ . Letting  $\epsilon \rightarrow 0^+$ , we have  $\liminf_{t \rightarrow \infty} x(t) \geq \bar{x}$ . Hence steady the state  $E_1$  is globally asymptotically stable for system (3.1) if  $\beta > 1$ ,  $sbc\bar{x} < 1 - \alpha$  and  $g(x)x$  is of Beverton–Holt type. We summarize our discussion into the following.

**THEOREM 3.2** *Let  $g(x)x$  be of Beverton–Holt type with  $g(0) = \beta > 1$ . Then the system (3.1) has two steady states  $E_0 = (0, 0, 0)$  and  $E_1 = (\bar{x}, 0, 0)$ . If in addition  $sbc\bar{x} < 1 - \alpha$ , then every solution of equation (3.1) with  $x(0) > 0$  converges to  $E_1$ .*

In the proof of Theorem 3.2 we used the fact that  $g(x)x$  is of Beverton–Holt type to deduce global asymptotic dynamics of equation (3.2). However, under some restrictions on the parameter values, equation (3.2) has only equilibrium dynamics even when  $g(x)x$  is of Ricker type [1]. Therefore, Theorem 3.2 remains valid for the Ricker type functional with smaller parameter space than that of Beverton–Holt type.

Notice that system (3.1) has no other steady states on the coordinate planes. We next examine the existence of interior steady states. It follows from the equilibrium equations

$$\begin{aligned} g(x) &= e^{cp_2} \\ x &= \frac{p_1}{b(1 - e^{-cp_2})} \end{aligned}$$

and

$$p_2 = \frac{sp_1}{1 - \alpha}$$

that the  $p_1$ -component of a positive steady state  $(x^*, p_1^*, p_2^*)$  must satisfy

$$g(h(p_1)) = e^{cp_1/(1-\alpha)}, \quad (3.3)$$

where

$$h(p_1) = \frac{p_1}{b(1 - e^{-csp_1/(1-\alpha)})}.$$

Note  $\lim_{p_1 \rightarrow 0^+} g(h(p_1)) = g(1 - \alpha/sbc)$ . A direct computation shows  $h'(p_1) > 0$  for  $p_1 > 0$  and thus  $g'(h(p_1))h'(p_1) < 0$  for  $p_1 > 0$ . Therefore equation (3.3) has a solution  $p_1^* > 0$  if and only if

$$g\left(\frac{1-\alpha}{bsc}\right) > 1. \quad (3.4)$$

We conclude that a unique interior steady state  $E_2 = (x^*, p_1^*, p_2^*)$  exists if inequality (3.4) holds, where  $x^* = h(p_1^*)$  and  $p_2^* = sp_1^*/1 - \alpha$ .

Similar to the previous section, we can express equation (3.4) in terms of the local stability of  $E_1$ . Recall that  $E_1 = (\bar{x}, 0, 0)$  is locally asymptotically stable if  $g'(\bar{x})\bar{x} > -2$  and  $sbc\bar{x} < 1 - \alpha$ . Since  $g(\bar{x}) = 1$  and  $g'(x) < 0$  for  $x \geq 0$ , equation (3.4) is equivalent to  $sbc\bar{x} > 1 - \alpha$ . Therefore  $E_2$  exists if and only if

$$sbc\bar{x} > 1 - \alpha.$$

Consequently if  $g(x)x$  is of Beverton–Holt type, then  $E_2$  exists if and only if  $E_1$  is unstable. However, if  $g(x)x$  is of Ricker type, it is possible that  $g'(\bar{x})\bar{x} < -2$  and  $sbc\bar{x} < 1 - \alpha$ , i.e., steady state  $E_2$  does not exist even when  $E_1$  is unstable. This finding is similar to that obtained in section 2.

Clearly  $x^* < \bar{x}$  if an interior steady state  $(x^*, p_1^*, p_2^*)$  for system (3.1) exists. We remark that if either  $s$  or  $\alpha$  or both parameters are density dependent in such a way that they decrease with increasing population density, then Theorems 3.1 and 3.2 remain true. However, the existence of an interior equilibrium will be much harder if not impossible to derive.

We now consider two numerical examples with the following parameter values. We choose  $\beta = 8.49$ ,  $\alpha = 0.3$ ,  $s = 0.05$ ,  $c = 3.5$  and  $b = 3$ . If  $g(x) = \beta e^{-2x}$ , then  $g'(\bar{x})\bar{x} < -2$  and  $sbc\bar{x} < 1 - \alpha$  so that the boundary state  $E_1 = (\bar{x}, 0, 0)$  is unstable but the interior steady state also fails to exist. It can be seen in these simulations that both juvenile and adult predator populations exhibit period 2 solutions as shown in figure 1(a). The simulations are recorded for the last 200 iterations after the original 3000 iterations have been removed to eliminate initial fluctuations. If we change  $\beta$  to 12.65 and keep other parameter values fixed, then the model has period four solutions as demonstrated in figure 1(b). Although the  $x$ -component of the solutions for both examples are not shown here, the corresponding  $x$ -component also exhibits period two and period four phenomenon, respectively.

#### 4. Concluding remarks

Unlike competition and mutualism, population dynamics of predator–prey interactions are prone to cycling phenomena in both discrete- and continuous-time models. In this manuscript we proposed two discrete-time, discrete stage-structured predator–prey models to study predator–prey interactions.

In the first model, system (2.1), the prey population is classified into juvenile and adult individuals such that the predator only preys on the juvenile prey population. Since we assume the adult prey individuals can only survive at most one time unit, the prey population

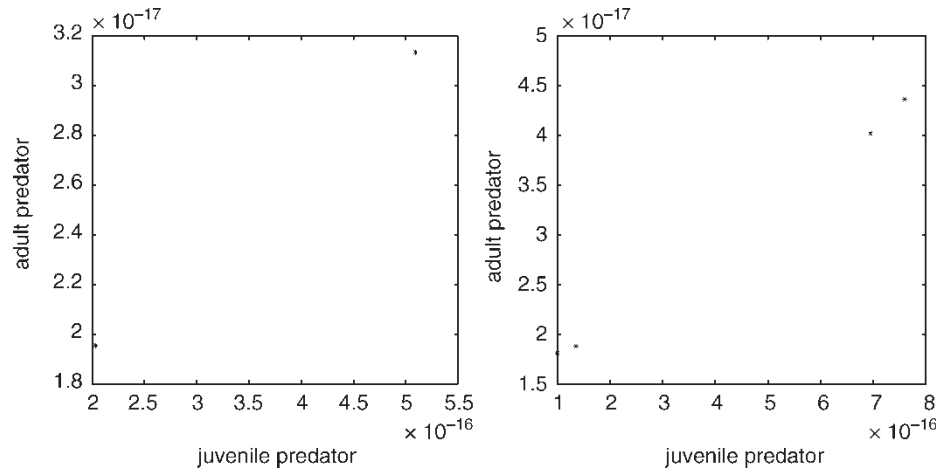


Figure 1. We use parameters  $\alpha = 0.3$ ,  $s = 0.05$ ,  $c = 2.5$  and  $b = 3$  for both graphs, and parameter  $\beta = 8.49$  and  $12.65$  for (a) and (b), respectively. Solutions of system (3.1) with Ricker type functional exhibit periodic solutions with period equals 2 for (a) and 4 for (b).

may exhibit synchronizing phenomenon. In particular, if prey population consists of only juvenile or adult to start with, then the prey population will be synchronizing and eventually drive the predator population into extinction. Synchronizing behavior is also observed in the single species LPA model [8].

For the second model, system (3.1), individuals in the prey population are assumed to have a uniform biological vital rates while individuals in the predator population are classified as either juveniles or adults. We assume that only the adult predator is capable of predation with reproduction as its consumption return. Since the life expectancy of adult predator may be longer than one time unit, there is no synchronizing phenomenon observed in the model.

For both of these models, sufficient conditions for the extinction of both populations are derived. These conditions depend on the intrinsic growth rate of the prey population. When Beverton–Holt type equations are used, a unique interior steady state (which represents coexistence of both populations) exists when the boundary steady states are unstable. This conclusion is not true when Ricker type functional is used. In particular, interior equilibria may not exist even when boundary steady state are unstable. In this case it is expected that the coexisting attractors are much more complicated.

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