Self-limitation in a discrete predator–prey model ☆

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Abstract

We study the ecological and mathematical significance of a nonlinear discrete predator–prey model that includes several types of self-limitation on the prey. The model is derived for the dynamics of two interacting populations where predators feed only on prey of a certain age. We show how the introduction of different limitation factors can account for several important phenomena that affect the dynamic output of the models. We show why some of these factors contribute to a viable interaction between the two populations and some other factors originate unstable behavior with unbounded oscillations.
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1. Introduction

Continuous predator–prey and host–parasitoid models have a well-known tendency to oscillate. If the effect of structured ages is included in the dynamics of the prey–predator along with the effects of predators feeding only on prey of a certain age then the resulting system is unstable, with nonlimited oscillations in the population of both species [1–3].

Unstable situations are originated because a model fails to take into account important saturation interactions. There is also the matter of modeling a discrete system with continuous processes. The goal of this work is to model some biological mechanisms, which are reasonable candidates to stabilize a structure age discrete predator–prey system where predators feed only on young prey. The modifications of the predator–prey model analyzed in this work, such as the introduction of the effects of self-limitation of the prey will have tremendous relevance in the stabilization of the system, thus obtaining a more appropriate description of the ecosystem. Our main interest is in observing the appearance of stable periodical phenomena and their dependence on the factors we have introduced.

This paper is organized as follows: In Section 2, we derive our model, in Section 3, effects of self-limitations on the prey are introduced and analyzed numerically. Three outstanding examples of self-limitation are studied. Finally in Section 4, the main conclusions of the paper are included.

2. The model

The basis of the structure age continuous time model was developed for one and two populations by several authors [4–6]. Here we will derive a structure age discrete model for two interacting populations. If $\rho(m, n)$ is the total number of individuals (preys) of age m at time n, then adding over all ages we get the total prey population.

$$P_1(n) = \sum_{m=0}^{\infty} \rho(m, n). \tag{1}$$

Convergence of the above series is guaranteed by the fact that the total number of individuals is finite. If we consider the variation in the number of individuals of a certain age, m, we obtain

$$\rho(m, n + 1) - \rho(m, n) = -\mu\rho(m, n) + \rho(m, n) - \rho(m + 1, n). \tag{2}$$

Simplifying we obtain the equation of evolution

$$\rho(m, n + 1) + (\mu - 2)\rho(m, n) + \rho(m + 1, n) = 0, \tag{3}$$

similar to the McKendrick–Von Foester equation. The function μ is the rate of mortality for individuals of age m in the time interval $(n, n + 1)$ and it can depend on the age of the total population or on the number of individuals of another population, for example, the predators. In our case we will consider μ to be independent of age. We assume the birth rate of the population is, at time n, given by a law of births of the type:

$$B(n) = \sum_{m=0}^{\infty} \beta(m)\rho(m, n), \tag{4}$$

where $\beta(m) = \beta m e^{-\alpha m}$ with $\beta > 0$ and $\alpha \geq 0$ is the reproductive rate of individuals of age m. We choose this form for β since this rate is expected to be close to zero for newborns and old individuals and to increase to a maximum for the young adults. Now let us find equations for the total prey population, $P_1(n)$ and the population of newborns $B(n)$. In order to do this we add (3) from $m = 0$ to infinity obtaining:

$$P_1(n + 1) = (1 - \mu(P_1))P_1(n) + \rho(0, n). \tag{5}$$

If we multiply (3) by $\beta m e^{-\alpha m}$, and add over m, we get

$$B(n + 1) = -(\mu(P_1) - 2 + e^{\alpha})B(n) + \beta e^{\alpha} \sum_{m=1}^{\infty} e^{-\alpha m}\rho(m, n). \tag{6}$$

To complete our system, we define

$$A(n) = e^{\alpha} \sum_{m=1}^{\infty} e^{-\alpha m}\rho(m, n), \tag{7}$$

which satisfies the equation

$$A(n + 1) = -(\mu(P_1) - 2 + e^{\alpha})A(n) - e^{\alpha}(\rho(0, n + 1) + (\mu - 2)\rho(0, n)). \tag{8}$$

In order to obtain Eq. (8) we multiply (3) by $e^{-\alpha m}$ and then add over m to get $A(n + 1) = -(\mu(P_1) - 2 + e^{\alpha})A(n) + e^{\alpha}\rho(1, n)$. Finally we use (3) to get $\rho(1, n) = -((\mu - 2)\rho(0, n) + \rho(0, n + 1))$.

We will assume that the predator population, P_2, behaves according to a discrete Lotka–Volterra type equation, but feeds only on the newborns. We will add the term $\lambda(1 - \exp(-g P_2))$, which can be thought of as representing the control over the predators, to this last equation. The parameter λ is the rate of control in a time unit. We must find an equation for $\rho(0, n)$ in terms of $B(n)$, the births, following [6] we choose $\rho(0, n) = \frac{cB(n)}{1+kP_2(n)}$ as the proposed model. This hypothesis, combined with previous equations leads us to the following system:

$$P_1(n + 1) = (1 - \mu)P_1(n) + \frac{cB(n)}{1 + kP_2(n)}, \tag{9}$$

$$B(n + 1) = -(\gamma - 2)B(n) + \beta A, \tag{10}$$

$$A(n + 1) = -(\gamma - 2)A(n) - e^{\alpha} \left(\frac{cB(n + 1)}{1 + kP_2(n + 1)} + \frac{(\mu - 2)cB(n)}{1 + kP_2(n)} \right), \tag{11}$$

$$P_2(n + 1) = bP_2(n) + dB(n)P_2(n) - \lambda \left(1 - e^{-gP_2(n)} \right), \tag{12}$$

where b, c, and $\gamma = e^{\alpha} + \mu$ are positive constants. We will only consider $\beta > \gamma^2$; which means the reproduction rate for the prey is at least one.

We first assume the function μ in (3) to be a constant, since the predators do not affect the adult prey. In this case, Eq. (3) has the solution

$$\rho(m, n) = (-1)^m (\mu - 2)^m \sum_{k=0}^{m} \binom{m}{k} (\mu - 2)^{-k} \rho(0, n + k),$$

where $\rho(0, n)$ are known initial conditions and $\mu \neq 2$. In case that $\mu = 2$, we have $\rho(m, n) = (-1)^m \rho(0, n + m)$. Therefore we obtain an implicit solution for B namely,

$$B(n) = \begin{cases} \beta \sum_{m=0}^{\infty} (-1)^m (\mu - 2)^m m e^{-\alpha m} \sum_{k=0}^{m} \binom{m}{k} (\mu - 2)^{-k} \rho(0, n + k) & \text{if } \mu \neq 2, \\ \beta \sum_{m=0}^{\infty} (-1)^m m e^{-\alpha m} \rho(0, n + m) & \text{if } \mu = 2, \end{cases}$$

which shows the oscillatory nature of the newborns. In the next section, we will analyze numerically the proposed model (9)–(12).

3. Analysis of the model

In this section we will analyze numerically our model to find out if the prey population reduces its growing process. To try to control the growth of the predators we will vary the parameter λ. We will fix every parameter except λ, with values $\mu = k = 1.5$, $e^{\alpha} = 1.7$, $d = 5$, $\beta = 0.01$, $b = 0.9$, $\gamma = 3.2$ and $c = g = 1$.

As we vary λ, we discover that there are no periodic solutions and the equilibrium states are unstable. For $\lambda = 0$ there are two possible families of equilibrium states for the system (9)–(12), namely $\left(\frac{(1-\gamma)^2(1+b)}{e^{\alpha}\mu(1-\mu)\beta d}, \frac{1+b}{d}, \frac{(\gamma-1)(1+b)}{\beta d}, D^* \right)$ and $\left(\frac{B^*}{\mu}, B^*, \frac{(\gamma-1)B^*}{\beta}, 0 \right)$ where D^* and B^* are arbitrary numbers. The second family exists only if the condition $(\gamma - 1)^2 = \beta e^{\alpha}(1 - \mu)$ holds, which implies that $\mu > 1$. The prey population, as well as the newborn population shows unbounded oscillations, although not at the same rate, when the control rate increases. The predator population also presents unbounded oscillations but the increment is more dramatic than the other two populations. So at first we can conclude that controlling the predator population does not affect the unbounded oscillations of the prey. In ecological terms, these results were in some sense predictable since we are only controlling, in a limited way, the size of the predator population and there is no control on the newborn population. This is a common result when a predator is introduced in a new environment to control a pest population and the result is that both populations blow up in finite time. In order to rectify our model let us now introduce self-limitation on the prey without control on the predators.

3.1. Self-limitation of the prey population

In order to improve the biological properties of our model we modify the prey growth rate to include intraspecific competition for resources in the lower trophic level. In other words, the prey population is self-limited by the struggle for existence in a finite environment. The effect of such self-limitation is modeled in our system by considering that the mortality function depends on the total prey population, that is,
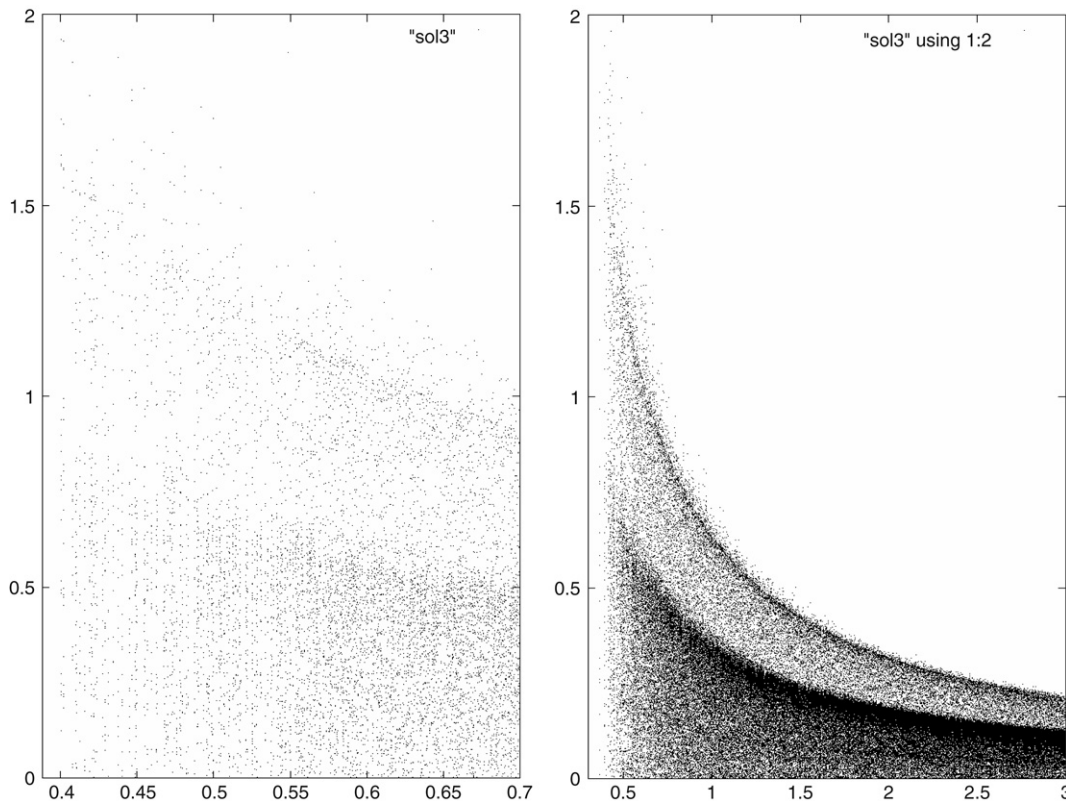
$$\mu = \mu(P_1) = \mu_o + rf(P_1), \tag{13}$$

Fig. 1. The horizontal axis is the parameter r and the vertical axis is the norm of the solution.

with $f(0) = 0$, r and μ_o being positive constants. If we incorporate (13) into the system, the resulting equations are:

$$P_1(n+1) = (1 - \mu_o)P_1(n) - rf(P_1(n))P_1(n) + \frac{c^2 B(n)}{c + (\mu_o + rf(P_1))P_2(n)},$$

$$B(n+1) = -(\gamma - 2)B(n) - rB(n)f(P_1(n)) + \beta A,$$

$$A(n+1) = -(\gamma - 2)A(n) - rA(n)f(P_1(n))$$
$$- e^{\alpha} \left(\frac{c^2 B(n+1)}{c + (\mu_o + rf(P_1))P_2(n+1)} + \frac{(\mu + rf(P_1(n)) - 2)c^2 B(n)}{c + (\mu_o + rf(P_1))P_2(n)} \right),$$

$$P_2(n+1) = -bP_2(n) + dBP_2(n) - \lambda(1 - e^{-gP_2(n)}).$$

Now we will vary the parameter r, which reflects the self-limitation of the prey, to analyze how the structure of the solution depends on this parameter. As before, we will fix the other constants to the same value, except now that we will not incorporate the control over the predators.

We will consider three examples, the first one is a nontrivial example of a function $f(P_1)$ which we choose to be the identical function, that is $f(P_1) = P_1$. This is a typical way of introducing logistic terms into our model. We will use this example to show how the dependence on the parameter r can avoid unbounded behavior. In the second example we choose $f(P_1) = P_1^2$ in order to show some negative consequences of self-limitation. Finally in the final example we choose $f(P_1) = P_1(1 - P_1)$ in order to obtain a viable interaction between both populations.

For $f(P_1) = P_1$, the model exhibits a complicated behavior. For values of r not in the interval $I \approx (0.388, 3.1380)$ there are only unbounded oscillations for both populations. For values of r in the interval I we obtain mixed behavior. For small values of r in the interval I there are bounded and unbounded oscillations of the newborns and the preys. The predator population becomes extinct and also there are other solutions which are not of biological interest. These facts can be seen more clearly in the first bifurcation diagram of Fig. 1 where we plot the parameter r against the asymptotic solution of the prey population. Notice that in this diagram there are some vertical white regions which
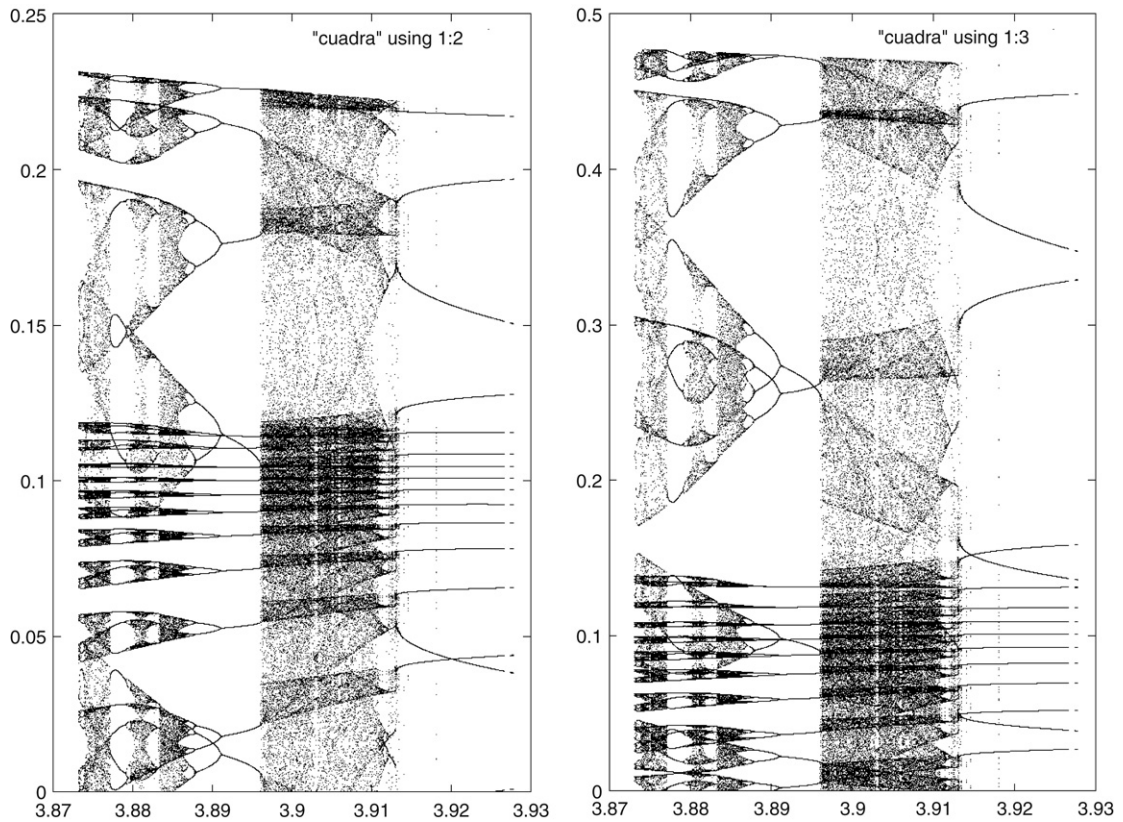
Fig. 2. The horizontal axis is the parameter r and the vertical axis is the norm of the solution.

correspond to values of r where the populations become unbounded. All bounded oscillations are shown in the second diagram where we can observe a distinct exponential decay of the oscillation bound.

For $f(P_1) = P_1^2$, the model exhibits only unbounded oscillations for all populations. The possible explanation is that this type of self-limitation is not strong enough to avoid the growth of the prey population. In mathematical terms, the term P_1^2 is not a dominant term for small values of P_1, that is $P_1 > P_1^2$ for small values of P_1. This fact is equivalent to having a small value of r in the linear case for μ.

In contrast with the previous case, for $f(P_1) = P_1(1 - P_1)$ our model presents different characteristics. For values of r in the complement of the interval $A = (3.873, 3.92776)$ the behavior of the system is the same as the previous case, that is, the model exhibits unbounded oscillations for all populations. For $B = (3.873, 3.877) \cup (3.8795, 3.8829) \cup (3.8835, 3.887) \cup (3.896, 3.913)$ the behavior of the system becomes chaotic in those small subintervals of the rate of self-limitation. Finally for $A - B$ the system is nonchaotic, the model starts with several branches of a single period followed by a double periodicity bifurcation. It is in this region where stable periodicity behavior only appears. these facts are shown in Fig. 2, where we present two bifurcation diagrams. The first one is the bifurcation diagram of the prey population versus the r and the second one is the newborns versus r. So far, with the inclusion of this type of self-limitation of the prey we have obtained stable periodic solutions at least for a small parameter regime, meaning there is a viable coexistence in both populations.

The bifurcation diagram of the prey population versus the newborns consists of a bounded set with fractal structure. The mathematical properties of this set will be the subject of a future investigation. In Fig. 3 we show this bifurcation diagram together with a blowup of its left-upper corner.

4. Conclusions

Our discrete prey–predator system with the effect of structured age without self-limitation, where predators feed only on the young, is unstable with unbounded oscillations on both populations. A viable coexistence of prey and
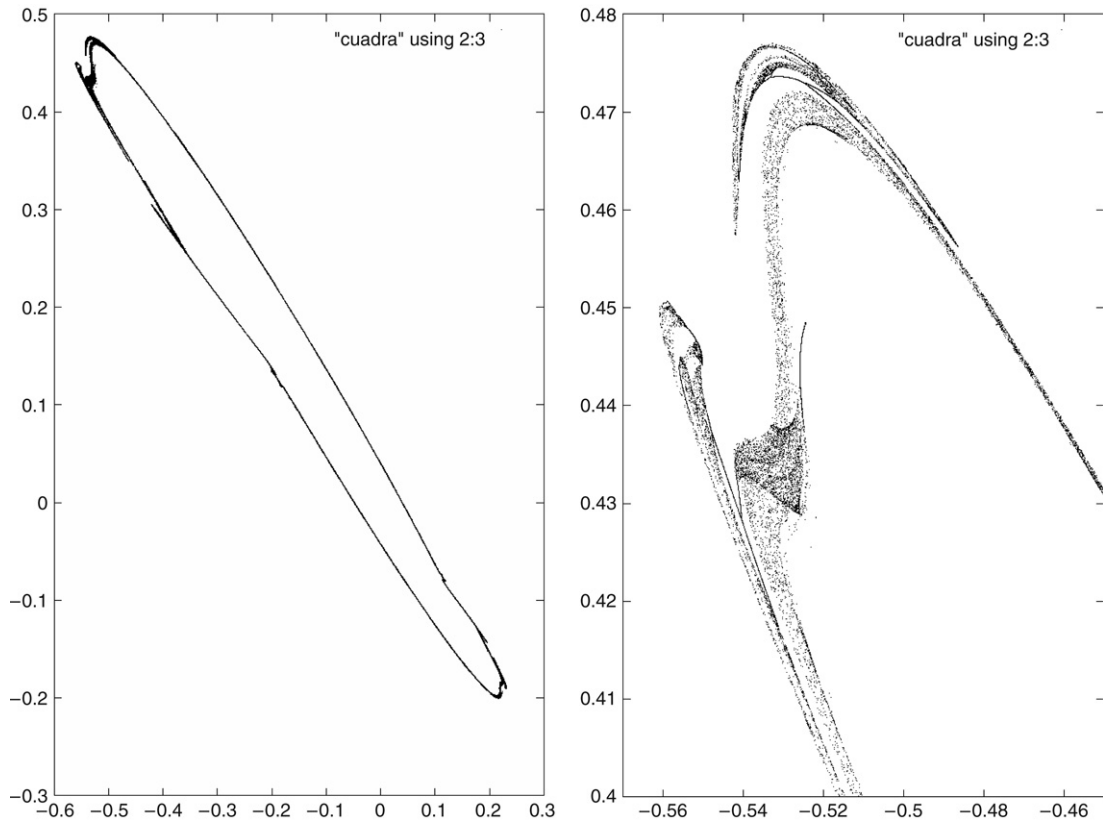
Fig. 3. Bifurcation diagram of the prey population versus the newborns and a blowup of its left-upper corner.

predators can be achieved by introducing some types of self-limitation on the prey. The inclusion of these factors include new complex behavior on the modified system, a topic of future investigation.

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