Advanced Studies in Pure Mathematics 53, 2009
Advances in Discrete Dynamical Systems
pp. 87–94

Cannibalism in a discrete predator-prey model with an age structure in the prey

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Abstract.

A discrete-time predator-prey model with an age structure in the prey population in which both the predator and the adult prey can consume juvenile prey population is proposed. The fecundity of the adult prey population is assumed to be a constant and the juvenile survival probability is density dependent on its own population size. It is shown that both populations go to extinction if the inherent net reproductive number of the prey is less than 1. Both populations can survive if the prey's inherent net reproductive number is larger than one and the predator's reproductive number is greater than 1 when the prey population is stabilized in the steady state fashion.

§1. Model derivation and analysis

Cannibalism has been observed in a variety of species, including some fish species such as adult Atlantic cod which eat large numbers of their young [1]. On the other hand, the adult cod is also preyed upon by some fish species such as killer whales and sharks. It has been demonstrated mathematically that cannibalism can have some effects on population dynamics [2, 3, 5, 11, 12]. Kohlmeier and Ebenhoh [10] illustrated that cannibalism in the prey can increase equilibrium population sizes for a predator-prey system modeled by ordinary differential equations. See also [8, 9] and references cited therein for continuous-time predator-prey models with cannibalism.

In this manuscript we propose a simple discrete-time predator-prey model, where each prey individual is classified as either juvenile or adult, and the adults may prey on its own juveniles. Let $x_1(t), x_2(t)$ and $p(t)$ denote the juvenile prey, adult prey, and predator population sizes at

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Received October 12, 2007.

2000 *Mathematics Subject Classification.* 92D25.

Key words and phrases. Cannibalism, inherent net reproductive number, Liapunov-Schmidt expansion, uniform persistence.

time t, respectively. The probability that a juvenile will escape from being cannibalized is e^{-cx_2} when the adult prey population is of size x_2, where $c > 0$ may be interpreted as the cannibalism rate. It is assumed that only the adult prey population can reproduce with a constant birth rate $b > 0$. The transition probability from juvenile to adult is density dependent on the juvenile prey population and is modeled by a Bervton-Holt type equation.

In addition, the predator also preys on the juvenile prey but not on the adult prey population. Let β be the average number of offspring that a predator can reproduce from a consumed juvenile prey, and the probability that an individual juvenile prey will escape from the predator when the predator population is of size p is e^{-ap}, where the searching efficiency a is a constant. Under the above biological assumptions, our model of predator-prey interaction can be written in terms of the following system of difference equations:

$$\begin{aligned} x_1(t+1) &= bx_2(t)e^{-cx_2(t)} \\ x_2(t+1) &= \frac{\alpha x_1(t)}{1+mx_1(t)}e^{-ap(t)} \\ p(t+1) &= \beta x_1(t)(1-e^{-ap(t)}) \\ x_1(0), x_2(0), &p(0) \geq 0, \end{aligned} \tag{1}$$

where $b, a, c, m, \beta > 0$ and $0 < \alpha < 1$.

The following result shows that the model is biologically sound and there exists a threshold below which populations become extinct. The proof is straightforward and is therefore omitted.

Lemma 1.1. *Solutions of (1) remain nonnegative and are bounded. Moreover, solutions* $(x_1(t), x_2(t), p(t))$ *of (1) satisfy* $\lim_{t\to\infty}(x_1(t), x_2(t), p(t)) = (0,0,0)$ *if* $\alpha b < 1$.

The threshold αb can be interpreted as the inherent net reproductive number of the prey population. It is the average number of offspring that a juvenile prey individual can reproduce during its lifetime when the prey population is very small. Denote $n = \alpha b$. Then both populations go extinct if $n < 1$ by the above lemma.

A simple calculation shows that an x_2-component of a nontrivial steady state $(x_1, x_2, 0)$ with the absence of the predator must satisfy the following equation:

$$\frac{ne^{-cx}}{1+m\frac{n}{\alpha}xe^{-cx}} = 1. \tag{2}$$

Since the left hand side of (2) as a function of x is decreasing with value n at $x = 0$, (2) has a positive solution $\bar{x}_2$ if and only if $n > 1$. In which case the positive solution is unique. Consequently, (1) has a unique biologically feasible steady state $E_1 = (\bar{x}_1, \bar{x}_2, 0)$ if $n > 1$, where $\bar{x}_2$ satisfies (2) and $\bar{x}_1 = b\bar{x}_2 e^{-c\bar{x}_2}$. The linearization of system (1) yields the following Jacobian matrix:

$$J = \begin{pmatrix} 0 & be^{-cx_2} - cbx_2e^{-cx_2} & 0 \\ \dfrac{\alpha}{(1+mx_1)^2} & 0 & \dfrac{-a\alpha x_1}{1+mx_1} \\ 0 & 0 & a\beta x_1 \end{pmatrix}. \tag{3}$$

The local stability of E_1 then depends on the eigenvalues of J evaluated at E_1 [4], $J(E_1)$, which consists of $a\beta\bar{x}_1$ and the eigenvalues of the submatrix

$$\hat{J} = \begin{pmatrix} 0 & be^{-cx_2} - cbx_2e^{-cx_2} \\ \dfrac{\alpha}{(1+mx_1)^2} & 0 \end{pmatrix} \tag{4}$$

evaluated at $(\bar{x}_1, \bar{y}_1)$. Notice $\hat{J}$ is the Jacobian matrix of the x_1x_2-subsystem of (1):

$$\begin{aligned} x_1(t+1) &= bx_2(t)e^{-cx_2(t)} \\ x_2(t+1) &= \frac{\alpha x_1(t)}{1+mx_1(t)} \\ x_1(0), x_2(0) &\geq 0, \end{aligned} \tag{5}$$

where $(\bar{x}_1, \bar{x}_2)$ is the interior steady state of (5). In the following we show that steady state $(\bar{x}_1, \bar{x}_2)$ is locally asymptotically stable for (5) when $n > 1$ but sufficiently close to 1. We shall use the Liapunov-Schmidt expansion method as given in [2]. Let $\epsilon = n - 1$ be positive and every small. Since $(\bar{x}_1, \bar{x}_2) \to (0, 0)$ as $\epsilon \to 0^+$, we have the following expansion

$$\begin{aligned} x_1(\epsilon) &= x_{11}\epsilon + x_{12}\epsilon^2 + O(\epsilon^3) \\ x_2(\epsilon) &= x_{21}\epsilon + x_{22}\epsilon^2 + O(\epsilon^3) \\ n(\epsilon) &= 1 + n_1\epsilon + n_2\epsilon^2 + O(\epsilon^3) \end{aligned}$$

for $\epsilon > 0$ sufficiently small. Substituting these expressions into the equilibrium equations and equating similar terms with respect to ϵ we arrive at

$$x_{11} = \frac{1}{\alpha}x_{21} \text{ and } x_{21} = \alpha x_{11}$$

and hence $x_{11} = 1$ and $x_{21} = \alpha$, up to scalar multiplications. Similarly, equating like terms of ϵ^2, we have

$$x_{12} = (-bx_{21}^2 + x_{22} + x_{21}n_1)/\alpha \text{ and } x_{22} = \alpha x_{12} - mx_{11}x_{21}.$$

Therefore $n_1 = m + c\alpha$ and thus

$$\begin{array}{rcl} x_1(\epsilon) & = & \epsilon + O(\epsilon^2) \\ x_2(\epsilon) & = & \alpha\epsilon + O(\epsilon^2) \\ n(\epsilon) & = & 1 + (m + c\alpha)\epsilon + O(\epsilon^2) \end{array} \tag{6}$$

for $\epsilon > 0$ small. Notice (6) corresponds to the x_1, x_2-components of an interior steady state for system (5) when $\epsilon > 0$ is sufficiently small, i.e., when $n > 1$ is sufficiently close to 1. The Jacobian matrix of system (5) evaluated at $(\bar{x}_1, \bar{x}_2)$ can be rewritten in terms of n and can be expressed as $\hat{J}(\bar{x}_1, \bar{x}_2) = \hat{J}_1 + \hat{J}_2\epsilon + O(\epsilon^2)$. Since

$$\frac{n}{\alpha}e^{-c\bar{x}_2} - \frac{bn}{\alpha}e^{-c\bar{x}_2} = \frac{1}{\alpha} + \frac{m - \alpha c}{\alpha}\epsilon - c(2m + \alpha c)\epsilon^2 + O(\epsilon^3)$$

and

$$\frac{\alpha}{(1 + m\bar{x}_1)^2} = \alpha - 2m\alpha\epsilon + 3m^2\alpha\epsilon^2 + O(\epsilon^3)$$

for $\epsilon > 0$ sufficiently small, we have

$$\hat{J}_1 = \begin{pmatrix} 0 & \frac{1}{\alpha} \\ \alpha & 0 \end{pmatrix} \text{ and } \hat{J}_2 = \begin{pmatrix} 0 & \frac{m - \alpha c}{\alpha} \\ -2m\alpha & 0 \end{pmatrix}. \tag{7}$$

Let $\lambda_i = \lambda_{i1} + \lambda_{i2}\epsilon + O(\epsilon^2)$ and $v_i = v_{i1} + v_{i2}\epsilon + O(\epsilon^2)$ be the corresponding eigenvalue and eigenvector of $\hat{J}_1 + \hat{J}_2\epsilon + O(\epsilon^2)$ respectively, $i = 1, 2$. Then

$$\begin{array}{l} \hat{J}_1 v_{i1} = \lambda_{i1} v_{i1} \\ \hat{J}_1 v_{i2} + \hat{J}_2 v_{i1} = \lambda_{i1} v_{i2} + \lambda_{i2} v_{i1} \end{array} \tag{8}$$

for $i = 1, 2$. It follows that λ_{i1} is an eigenvalue of $\hat{J}_1$ with corresponding eigenvector v_{i1}, $i = 1, 2$. Consequently, we have $\lambda_{11} = 1$ with eigenvector $v_{11} = (1\ \alpha)^T$ and $\lambda_{21} = -1$ with eigenvector $v_{21} = (-1\ \alpha)^T$, where T denotes transpose.

Furthermore, the second equation of (8) can be rewritten as

$$(\hat{J}_1 - \lambda_{i1}I)v_{i2} = (\lambda_{i2}I - \hat{J}_2)v_{i1},$$

$i = 1, 2$. It follows from the Fredholm alternative that the right hand side of the above equation must be orthogonal to the solutions y of the homogeneous equation $(\hat{J}_1^T - \lambda_{i1} I)y = 0$ in order for the above equation to have a solution. This implies $\lambda_{12} = -\dfrac{m+\alpha c}{2}$, and $\lambda_{22} = \dfrac{m+\alpha c}{2}$. Consequently for $\epsilon > 0$ sufficiently small, we have

$$\lambda_1 = 1 - \frac{m+\alpha c}{2}\epsilon + O(\epsilon^2) \text{ and } \lambda_2 = -1 + \frac{m+\alpha c}{2}\epsilon + O(\epsilon^2).$$

Therefore if $\epsilon > 0$ is sufficiently small, i.e., if $n > 1$ is sufficiently close to 1, then the interior steady state $(\bar{x}_1, \bar{x}_2)$ is locally asymptotically stable for system (5). Furthermore, since the left hand side of (2) as a function of n is increasing, $\bar{x}_2$ is an increasing function of n. On the other hand, since $\bar{x}_1 = \frac{n}{\alpha}\bar{x}_2 e^{-c\bar{x}_2}$ and $\lim_{n\to 1^+} \bar{x}_2(n) = 0$, we see that $\bar{x}_1$ is an increasing function of n when $n > 1$ is sufficiently close to 1. Therefore, we can conclude that when $n > 1$ is small enough so that $\beta a \bar{x}_1 < 1$, then $E_1 = (\bar{x}_1, \bar{x}_2, 0)$ is locally asymptotically stable for the original system (1).

Lemma 1.2. *System (5) has a unique interior steady state* $(\bar{x}_1, \bar{x}_2)$ *when* $n > 1$. *The interior steady state is locally asymptotically stable for system (5) when* $n > 1$ *is sufficiently close to* 1. *Similarly, system (1) has a nontrivial boundary steady state* $E_1 = (\bar{x}_1, \bar{x}_2, 0)$ *if* $n > 1$. *The steady state* E_1 *is locally asymptotically stable for (1) if* $n > 1$ *is sufficiently close to* 1.

We next prove that both populations can survive when $n > 1$ and $\beta a \bar{x}_1 > 1$, where $\beta a \bar{x}_1 > 1$ can be interpreted as the reproductive number of the predator when the prey population is stabilized at the steady state. The predator population can survive if this reproductive number is larger than 1.

Theorem 1.3. *System (1) is uniformly persistent if* $n > 1$ *and* $\beta a \bar{x}_1 > 1$, *i.e., there exists* $M > 0$ *such that* $\liminf_{t\to\infty} x_1(t) \geq M$, $\liminf_{t\to\infty} x_2(t) \geq M$, *and* $\liminf_{t\to\infty} p(t) \geq M$ *for all solutions* $(x_1(t), x_2(t), p(t))$ *of (1) with* $x_1(0) > 0, x_2(0) > 0$ *and* $p(0) > 0$.

Proof. The proof of uniform persistence is standard. Indeed, it is clear that system (1) has a global attractor X. Let Y be the union of nonnegative coordinate planes. Then $R_+^3 \backslash Y$ is forward invariant for (1). The only invariant set in Y is $\{E_0, E_1\}$, where $\{E_0\}$ and $\{E_1\}$ are isolated in X. It remains to prove that the stable sets of E_0 and E_1 lie in Y.

Suppose there exists a solution $(x_1(t), x_2(t), p(t))$ of (1) with $x_1(0) > 0, x_2(0) > 0, p(0) > 0$ such that $\lim_{t\to\infty} (x_1(t), x_2(t), p(t)) = E_0$. Then for any $\epsilon > 0$ there exists $t_0 > 0$ such that $x_1(t) < \epsilon, x_2(t) < \epsilon$, and $p(t) < \epsilon$ for $t \geq t_0$. Since $n > 1$, we can choose $\epsilon > 0$ such that $ne^{-c\epsilon}e^{-a\epsilon} > 1$. Note

$$\begin{aligned} x_1(t+1) &> bx_2(t)e^{-c\epsilon} \\ x_2(t+1) &> \frac{\alpha e^{-a\epsilon}x_1(t)}{1+mx_1(t)} \end{aligned} \tag{9}$$

for $t \geq t_0$. Consider the following system of difference equations

$$\begin{aligned} y_1(t+1) &= by_2(t)e^{-c\epsilon} \\ y_2(t+1) &= \frac{\alpha e^{-a\epsilon}y_1(t)}{1+my_1(t)} \\ y_1(0) &= x_1(t_0), y_2(0) = x_2(t_0). \end{aligned} \tag{10}$$

Since $bxe^{-c\epsilon}$ and $\dfrac{\alpha e^{-a\epsilon}x}{1+mx}$ are increasing functions of x, we see that $x_1(t+t_0) \geq y_1(t)$ and $x_2(t+t_0) \geq y_2(t)$ for $t \geq 0$. Furthermore, since $ne^{-c\epsilon}e^{-a\epsilon} > 1$, system (10) has a unique interior steady state $(\bar{y}_1, \bar{y}_2)$ where $\bar{y}_1 > 0$ satisfies

$$1 = \frac{ne^{-a\epsilon}e^{-c\epsilon}}{1+my}. \tag{11}$$

On the other hand, (10) is equivalent to the following second order difference equation

$$y_1(t+2) = \frac{ne^{-c\epsilon}e^{-a\epsilon}y_1(t)}{1+my_1(t)}. \tag{12}$$

Since the map induced by (12) is increasing, using a result of [6, Theorem 1.10], one can show that solutions of (12) with $y_1(0), y_1(1) > 0$ converge to $\bar{y}_1$. As a result, we have $\liminf_{t\to\infty} x_1(t) \geq \bar{y}_1 > 0$. We obtain a contradiction and conclude that the stable set of E_0 lies on Y. Using $\beta a\bar{x}_1 > 1$, a similar argument can be applied to show that the stable set of E_1 lies on Y. Therefore, system (1) is uniformly persistent with respect to Y by [7, Theorem 4.1]. Q.E.D.

Using the same argument as in Theorem 1.3, one can show that system (5), the stage-structured prey population model, is uniformly persistent if $n > 1$. Notice the inherent net reproductive number of the prey, n, does not depend on the cannibalism rate c. However, it follows from equation (2) that $\bar{x}_2$ is a decreasing function of c. Therefore increasing cannibalism of the adult prey population can diminish its own population density at the steady state. In particular, $\lim_{c\to\infty} \bar{x}_2(c) = 0$ and cannibalism can have severe deleterious effect to the prey population at the population level. On the other hand, if $n > 1$ and c is large so that $\beta b\bar{x}_1 < 1$, then the full system may not be uniformly persistent. Consequently, cannibalism of the prey may drive the predator population to extinction.

Finally we use an example to study system (5). We choose $\alpha = 0.7$, $m = 0.5$, $a = 0.6$, $\beta = 20$ and $b = 100$. The bifurcation parameter is the cannibalism rate c, where c ranges from 0.01 to 13. Figure 1 although not shown here plots the bifurcation diagram for the juvenile prey population. From this numerical simulation it seems that the interior steady state is globally asymptotically stable when c is small and period-doubling bifurcations occur when c is large.

We acknowledge that our model is derived under very simple biological assumptions. Different models may reach different biological conclusions than stated here. We shall continue to study systems (1) and (5) in more details and to investigate a parallel model when the predator is stage-structured and the adult predator population can consume its own juveniles.

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