

Asymptotic Behavior of a Predator-Prey Population Model with Stage-Structure

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Abstract: This paper studies the asymptotic behavior of a predator-prey system with stage structure. It is assumed that the transition rate from immature stage to mature stage depends on the density of immature individuals. Conditions for the permanence and extinction of the predator are obtained. It is also found that the model admits an orbitally asymptotically stable periodic orbit.

Key words: Stage structure ; Permanence ; Stability ; Periodic orbit

CLC number: O175.1 **MR number:** 34C25; 92D25

Document code: A **Article ID:** 1001-9626(2007)01-0129-09

0 Introduction

The predator-prey models are important population models ^[1,3-7,10]. G.W.Harrison in paper [3] proposed a general predator-prey model

$$\begin{cases} \frac{dx}{dt} = f(x) - a(x)g(y), \\ \frac{dy}{dt} = ka(x)g(y) - c(y), \end{cases} \quad (1)$$

where

$$\begin{aligned} f(x) &= \rho x \min \left[1, \frac{r-x}{r-\alpha} \right], & \rho > 0, \quad r > 0, \quad \alpha \geq 0; \\ g(y) &= \frac{y}{1+\beta y}, & \beta \geq 0; \\ a(x) &= \frac{bx}{x+\varphi}, & b > 0, \quad \varphi > 0; \\ c(y) &= \gamma y + \delta y^2, & \gamma > 0, \quad \delta \geq 0; \end{aligned}$$

Received date: 2005-04-05

Foundation item: The project are supported by the Foundation of the State Education Commission of China and the National Natural Science Foundation of China (10271096)

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x is the density of the prey, y is the density of the predator. The term $f(x)$ is the intrinsic growth rate of the prey at density x due to all factors except predation, and the term $c(y)$ is the intrinsic rate of increase (or decrease) of the predator. The term $a(x)g(y)$ gives the functional response of the predator, that is, $\frac{a(x)g(y)}{y}$ is the rate of prey consumption per predator at prey density x and predator density y . Many authors simply take $g(y) = y$, but a function $g(y)$ that increases slower than the linearity could be used to model interference among the predators hunting each other, or a function $g(y)$ that increases faster than the linearity could be used to model predator cooperation. The term $ka(x)g(y)$ is the numerical response of the predator. It represents the difference between the predator's actual rate of increase $\frac{dy}{dt}$ and its intrinsic rate of increase $c(y)$ when the prey is at density x . In paper [3], the author assumed that each individual of predators admits the same ability to attack prey.

Harrison [3] proved that the model (1) fits well with the experimental results. Thus, the model (1) is studied by many authors [3, 4, 5].

1 The Model

We set $\delta = 0$, $\beta = 0$, $a(x) = bx$ in model (1) and obtain the following model:

$$\begin{cases} \frac{dx}{dt} = f(x) - bxy, \\ \frac{dy}{dt} = kby - \gamma y, \end{cases} \quad (2)$$

where

$$f(x) = \rho x \min \left[1, \frac{r-x}{r-\alpha} \right] = \begin{cases} \rho x, & 0 \leq x \leq \alpha, \\ \frac{\rho}{r-\alpha} x(r-x), & x \geq \alpha. \end{cases} \quad (3)$$

By constructing the same Lyapunov function as that in paper [3], We can easily obtain the following theorem:

Theorem 1.1 *If $r > \frac{\gamma}{kb}$, then there exists a positive equilibrium (x^*, y^*) of the system (2) which is asymptotically stable.*

Based on the model (2), we introduce the stage-structure on the predator. We classify the individuals of predators as the immature ones and the mature ones and suppose that immature population does not feed on prey. This seems reasonable for a number of mammals, of whom immature predators are raised by their parents, thus the rate they attack at prey and the reproduction rate can be ignored. We assume the transition rate depends on the density of the immature individuals. Stage-structured models have been studied by several papers [10]. We consider the following predator-prey system with stage structure and density dependent transition

rate:

$$\begin{cases} \frac{dx}{dt} = f(x) - bxy_2, \\ \frac{dy_1}{dt} = kbx_2 - \gamma_1 y_1 - m(y_1)y_1, \\ \frac{dy_2}{dt} = m(y_1)y_1 - \gamma_2 y_2, \end{cases} \quad (4)$$

where $x(t)$ is the density of the prey at time t ; $y_1(t)$ is the density of the immature predators at time t ; $y_2(t)$ is the density of the mature predators at time t ; γ_1 is the death rate of immature predators and γ_2 is the death rate of mature predators; constant $k > 0$ denotes the coefficient in converting prey into new immature predators; $m(y_1)$ denotes the rate of immature predators becoming mature predators, which is assumed to be a function of the density of immature predators; $f(x)$ is the same as (3); r is the intrinsic growth rate of the prey.

The purpose of this paper is to study the asymptotic behavior of the predator-prey model (4) with stage-structure. The organization of this paper is as follows. In section 3, we investigate the existence conditions of a unique positive equilibrium which is asymptotically stable. In section 4, we will state and prove the results on the permanence of (4), and give a result on the existence of periodic solutions.

2 Equilibria and Their Stability

In this section, we give the conditions on the existence of a unique equilibrium of (4) which is asymptotically stable. Let us assume:

$$(H1) \quad m(0) > 0, \quad m'(y_1) \leq 0 \text{ for } y_1 \in [0, \infty) \text{ and } \lim_{y_1 \rightarrow \infty} m(y_1) = 0.$$

$$(H2) \quad m(y_1)y_1 \text{ is monotonically increasing, i.e., } (m(y_1)y_1)' \geq 0.$$

If the first one of (3) holds, by setting the right hand of (4) to zero, we obtain

$$y_2 = \frac{\rho}{b}, \quad x = \frac{1}{k\rho} \left(\frac{\rho\gamma_2}{b} + \gamma_1 y_1 \right).$$

According to the third equation of (4), we get

$$m(y_1)y_1 = \frac{\rho\gamma_2}{b}. \quad (5)$$

The conditions $0 < \frac{\rho\gamma_2}{b}$ and (H2) imply that the equation (5) has a unique positive solution \bar{y}_1 .

Thus, the system (4) admits a unique positive equilibrium $E \left(\bar{x}, \bar{y}_1, \frac{\rho}{b} \right)$ if

$$\alpha > \frac{\gamma_2(m(0) + \gamma_1)}{k b m(0)} \quad (6)$$

where

$$\bar{y}_2 = \frac{\rho}{b}, \quad \bar{x} = \frac{1}{k\rho} \left(\frac{\rho\gamma_2}{b} + \gamma_1 \bar{y}_1 \right), \quad \bar{x} \leq \alpha.$$

If the second one of (3) holds, by setting the right hands of (4) to zero, we obtain

$$y_2 = \frac{m(y_1)y_1}{\gamma_2}, \quad x = r - \frac{b(r - \alpha)}{\rho\gamma_2} m(y_1)y_1 = \frac{\gamma_2}{k b} \left(\frac{\gamma_1}{m(y_1)} + 1 \right).$$

Substituting them into the right hand of second equation of (4) and setting it to zero, we have

$$\frac{kb^2(r-\alpha)}{\rho\gamma_2^2}m^2(y_1)y_1 + \left(1 - \frac{kbr}{\gamma_2}\right)m(y_1) + \gamma_1 = 0. \quad (7)$$

Note that (7) is equivalent to

$$G(y_1) \stackrel{\text{def}}{=} \frac{\gamma_1}{m(y_1)} = -\left(1 - \frac{kbr}{\gamma_2}\right) - \frac{kb^2(r-\alpha)}{\rho\gamma_2^2}m(y_1)y_1 \stackrel{\text{def}}{=} F(y_1). \quad (8)$$

We have

$$G(0) = \frac{\gamma_1}{m(0)}, \quad F(0) = -\left(1 - \frac{kbr}{\gamma_2}\right).$$

Assume that

$$\alpha < \frac{\gamma_2(m(0) + \gamma_1)}{kbm(0)} < r, \quad (9)$$

Clearly, $G(0) < F(0)$. Note that (H1) implies that $G(y_1)$ is monotonically increasing and tends to infinity as y_1 tends to infinity and (H2) implies that $F(y_1)$ is monotonically decreasing. Thus, (8) or (7) has a unique positive solution y_1^* . We have

$$y_2^* = \frac{m(y_1^*)y_1^*}{\gamma_2} \quad x^* = \frac{\gamma_2}{kb} \left(\frac{\gamma_1}{m(y_1^*)} + 1 \right) > \frac{\gamma_2(m(0) + \gamma_1)}{kbm(0)} > \alpha.$$

Then the system (4) admits a unique positive equilibrium $E^*(x^*, y_1^*, y_2^*)$, $x^* \geq \alpha$ if (9) holds.

Let us study their stability of E and E^* respectively.

The Jacobian matrix of (4) at E is

$$A = \begin{bmatrix} 0 & 0 & -b\bar{x} \\ k\rho & -\gamma_1 - M & kb\bar{x} \\ 0 & M & -\gamma_2 \end{bmatrix},$$

where $M = (m(\bar{y}_1)\bar{y}_1)' = m'(\bar{y}_1)\bar{y}_1 + m(\bar{y}_1)$.

The characteristic equation of A is

$$\lambda^3 + c_1\lambda^2 + c_2\lambda + c_3 = 0,$$

where

$$c_1 = \gamma_1 + \gamma_2 + M > 0, \quad c_2 = \gamma_1\gamma_2 + M\gamma_2 - kbM\bar{x}, \quad c_3 = kb\rho M\bar{x} > 0.$$

Calculations show that

$$c_1c_2 - c_3 = (\gamma_1 + \gamma_2 + M)(\gamma_1\gamma_2 + M\gamma_2) - kbM(\gamma_1 + \gamma_2 + M + \rho)\bar{x}.$$

By Routh-Hurwitz theory, we can obtain

Theorem 2.1 *Let (H1), (H2) and (9) hold. Then (4) has a unique positive equilibrium E which is asymptotically stable if*

$$bM\gamma_1\bar{y}_1(\gamma_1 + \gamma_2 + M + \rho) < \rho\gamma_2(\gamma_1^2 + \gamma_1\gamma_2 + \gamma_1M - \rho M). \quad (10)$$

The Jacobian matrix of (4) at E^* is

$$A^* = \begin{bmatrix} -\frac{\rho}{r-\alpha}x^* & 0 & -bx^* \\ kby_2^* & -\gamma_1 - M & kb x^* \\ 0 & M & -\gamma_2 \end{bmatrix},$$

where $M = (m(y_1^*)y_1^*)' = m'(y_1^*)y_1^* + m(y_1^*)$.

The characteristic equation of A^* is

$$\lambda^3 + c_1\lambda^2 + c_2\lambda + c_3 = 0,$$

where

$$\begin{aligned} c_1 &= \gamma_1 + \gamma_2 + M + \frac{\rho}{r-\alpha}x^* > 0, \\ c_2 &= (\gamma_1 + M) \left(\gamma_2 + \frac{\rho}{r-\alpha}x^* \right) + \frac{\rho}{r-\alpha}\gamma_2 x^* - kbMx^*, \\ c_3 &= \frac{\rho}{r-\alpha}x^*(kbMr - 2kbMx^* + \gamma_2(\gamma_1 + M)). \end{aligned}$$

Setting

$$\begin{aligned} s &= \gamma_1 + \gamma_2 + M, \\ p_0 &= -k(r-\alpha)M\gamma_1m(y_1^*)y_1^*, \\ p_1 &= ks(r-\alpha)\gamma_1\gamma_2m(y_1^*) - ks(r-\alpha)M\gamma_1\gamma_2 - \rho s\gamma_1m(y_1^*)y_1^* - \\ &\quad k\rho M\gamma_2r m(y_1^*) - \rho s(m(y_1^*))^2 y_1^*, \\ p_2 &= \left(s + \frac{\rho r}{r-\alpha} \right) \rho s\gamma_2 m(y_1^*) + \rho \left(\gamma_2 + \frac{\rho r}{r-\alpha} \right) \gamma_1\gamma_2^2 + \rho\gamma_1^2\gamma_2^2 + \rho M\gamma_2^2 m(y_1^*) + \\ &\quad 2\rho M\gamma_1\gamma_2^2 + \left(s + \frac{\rho r}{r-\alpha} \right) (\gamma_1 + M)\rho\gamma_1\gamma_2, \end{aligned}$$

we have

$$\begin{aligned} c_1c_2 - c_3 &= \frac{1}{kb(r-\alpha)m(y_1^*)}(b^2p_0 + bp_1 + p_2), \\ c_3 &= \frac{x^*}{(1-\alpha)\gamma_1\gamma_2}(-2b^2p_0 - bkM\rho\gamma_1\gamma_2r + \rho\gamma_1\gamma_2^2(\gamma_1 + M)). \end{aligned}$$

By Routh-Hurwitz theory, we obtain

Theorem 2.2 *Let (H1), (H2) and (9) hold. Then (4) has a unique positive equilibrium E^* which is asymptotically stable if*

$$b^2p_0 + bp_1 + p_2 > 0, \quad (11)$$

$$\rho\gamma_1\gamma_2^2(\gamma_1 + M) > 2b^2p_0 + bkM\rho\gamma_1\gamma_2r. \quad (12)$$

3 Permanence of Populations

The first objective of this section is to establish conditions for the permanence and for the extinction of the predator.

We easily obtain the following lemma:

Lemma 3.1 *Each solution $(x(t), y_1(t), y_2(t))$ of system (4) with nonnegative initial values $(x(0), y_1(0), y_2(0))$ is nonnegative on its maximum existence interval.*

We call solutions with nonnegative initial values *positive solutions* and have the following result:

Lemma 3.2 *There is an $N > 0$ such that any positive solution $(x(t), y_1(t), y_2(t))$ of system (4) satisfies $(x(t), y_1(t), y_2(t)) < (N, N, N)$ for all large t .*

Define

$$X = \{(x, y_1, y_2) : x \geq 0, y_i \geq 0, i = 1, 2.\},$$

$$X_0 = \{(x, y_1, y_2) \in X : x > 0, y_i > 0, i = 1, 2.\},$$

$$\partial X_0 = X \setminus X_0.$$

By the form of system (4), it is not difficult to prove that X and X_0 are positively invariant. Clearly, ∂X_0 is relatively closed in X . Let

$$M_\partial = \{(x(0), y_1(0), y_2(0)) : (x(t), y_1(t), y_2(t)) \text{ satisfies (4)} \\ \text{and } (x(t), y_1(t), y_2(t)) \in \partial X_0, \forall t \geq 0\}.$$

Now we show that

$$M_\partial = \{(x, 0, 0) : x \geq 0\}. \quad (13)$$

Clearly, $\{(x, 0, 0) : x \geq 0\} \subseteq M_\partial$. We will prove $M_\partial \subseteq \{(x, 0, 0) : x \geq 0\}$. Suppose $(x(0), y_1(0), y_2(0)) \in M_\partial$. It suffices to show that $y_i(t) = 0, i = 1, 2$, for all $t \geq 0$. If not, then there exists a $t_0 \geq 0$, such that $y_1(t_0) > 0$ or $y_2(t_0) > 0$. Without loss of generality, we assume $y_1(t_0) > 0$. Choose $\eta_1 > 0$ small enough such that $y_1(t) > 0$ for $t_0 \leq t < t_0 + \eta_1$. If we also have $y_2(t_0) > 0$, similarly we can choose $\eta_2 > 0$ small enough such that $y_2(t) > 0$ for $t_0 \leq t < t_0 + \eta_2$. Thus $y_i(t) > 0$ for $t_0 \leq t < t_0 + \min[\eta_1, \eta_2]$, which contradicts the definition of M_∂ . Thus $y_2(t_0) = 0$. The third equation of (4) and (H1) yield

$$y_2'(t_0) = m(y_1(t_0))y_1(t_0) - \gamma_2 y_2(t_0) = m(y_1(t_0))y_1(t_0) > 0.$$

Hence, if we further restrict η , then $y_2(t) > 0$ for $t_0 \leq t < t_0 + \eta$, which leads to a contradiction. Thus $M_\partial = \{(x, 0, 0) : x \geq 0\}$.

Theorem 3.1 *Let (H1) hold. Then (4) is permanent if*

$$r > \frac{\gamma_2(m(0) + \gamma_1)}{k b m(0)}. \quad (14)$$

Proof By Lemma 3.1 and Lemma 3.2, we prove that nonnegative solutions of (4) are point dissipative. According to the definitions above, it then suffices to show that ∂X_0 repels uniformly nonnegative solutions of (4). It is clear that there are two equilibria $E_0(0, 0, 0)$ and $E_1(r, 0, 0)$ in M_∂ . We now show that $W^s(E_0) \cap X_0 = \emptyset$ and $W^s(E_1) \cap X_0 = \emptyset$. We restrict our attention to the

second equation, since the proof of the first one is easy. Assume $W^s(E_1) \cap X_0 \neq \emptyset$. Then there exists a positive solution $(\tilde{x}(t), \tilde{y}_1(t), \tilde{y}_2(t))$ of system (4) such that

$$(\tilde{x}(t), \tilde{y}_1(t), \tilde{y}_2(t)) \rightarrow (r, 0, 0) \text{ as } t \rightarrow \infty. \quad (15)$$

Assume $\tilde{x}(t) > \alpha$, $(\tilde{x}(t), \tilde{y}_1(t), \tilde{y}_2(t))$ is the positive solution of system (4), if the second one of (3) holds. Choose $\xi > 0$ small enough such that

$$r > r - \xi > \frac{\gamma_2(m(0) + \gamma_1)}{kbm(\xi)} > \frac{\gamma_2(m(0) + \gamma_1)}{kbm(0)}. \quad (16)$$

Due to (15), there exists a $t_1 > 0$, such that for $t > t_1$,

$$\begin{aligned} r - \xi &< \tilde{x}(t) < r + \xi, \\ \tilde{y}_i(t) &< \xi, \quad i = 1, 2. \end{aligned}$$

Then for $t > t_1$,

$$\begin{cases} \frac{d\tilde{y}_1(t)}{dt} \geq kb(r - \xi)\tilde{y}_2(t) - (m(0) + \gamma_1)\tilde{y}_1(t), \\ \frac{d\tilde{y}_2(t)}{dt} \geq m(\xi)\tilde{y}_1(t) - \gamma_2\tilde{y}_2(t). \end{cases} \quad (17)$$

Let

$$A_\xi = \begin{pmatrix} -m(0) - \gamma_1 & kb(r - \xi) \\ m(\xi) & -\gamma_2 \end{pmatrix}.$$

Since A_ξ admits positive off-diagonal elements, Perron-Frobenius theorem implies that there is a positive eigenvector v for the maximal eigenvalue λ of A_ξ . Suppose λ_1, λ_2 are the eigenvalues of A_ξ . By (16),

$$\begin{aligned} \lambda_1 + \lambda_2 &= -m(0) - \gamma_1 - \gamma_2 < 0, \\ \lambda_1\lambda_2 &= (m(0) + \gamma_1)\gamma_2 - kb(r - \xi)m(\xi) < 0, \end{aligned}$$

Thus we see that the maximal eigenvalue λ of A_ξ is positive.

Let us consider

$$\begin{cases} \frac{dy_1(t)}{dt} = kb(r - \xi)y_2(t) - (m(0) + \gamma_1)y_1(t), \\ \frac{dy_2(t)}{dt} = m(\xi)y_1(t) - \gamma_2y_2(t). \end{cases} \quad (18)$$

Let $v = (v_1, v_2)$ and let $l > 0$ be small enough such that

$$lv_1 < \tilde{y}_1(t_1), \quad lv_2 < \tilde{y}_2(t_1). \quad (19)$$

If $(y_1(t), y_2(t))$ is a solution of system (18) satisfying $y_i(t_1) = lv_i, i = 1, 2$. Because the semi-flow of (18) is monotone and $A_\xi v > 0$, it follows from paper [8] that $y_i(t)$ is strictly increasing and $y_i(t) \rightarrow +\infty$ as $t \rightarrow +\infty$. Note that (17) and (19) imply that $\tilde{y}_i(t) \geq y_i(t)$ for $t > t_1$. We have $\tilde{y}_i(t) \rightarrow +\infty$ as $t \rightarrow +\infty$. This contradicts the ultimate boundedness of nonnegative solutions of (4). Thus $W^s(E_1) \cap X_0 = \emptyset$.

Note that every orbit except E_0 in M_∂ approaches to E_1 as t approaches to infinity. This result, together with the arguments $W^s(E_i) \cap X_0 = \emptyset$, shows that E_0 and E_1 are isolated invariant sets in X . Clearly E_0 and E_1 are acyclic in M_∂ . By paper [9], ∂X_0 repels uniformly nonnegative solutions of (4). Then it follows that (4) is permanent. \square

In above case, system (4) admits a unique positive equilibrium. If inequality (14) is reversed, it implies that (4) does not have a positive equilibrium and it is not hard to obtain the following theorem:

Theorem 3.2 *Let (H1) hold. Then the predator becomes extinct if*

$$r < \frac{\gamma_2(m(0) + \gamma_1)}{k b m(0)}. \quad (20)$$

We can also obtain some conditions for a stable periodic orbit.

Theorem 3.3 *Let (H1), (H2) and (14) hold. Then (4) has an orbitally asymptotically stable periodic solution if (12) holds and the inequality (11) is reversed.*

Proof A change of variables $z_1 = -x$, $z_2 = y_1$, $z_3 = -y_2$ transforms system (4) into

$$\begin{cases} \frac{dz_1}{dt} = -g(z_1) + b z_1 z_3, \\ \frac{dz_2}{dt} = k b z_1 z_3 - \gamma_1 z_2 - m(z_2) z_2, \\ \frac{dz_3}{dt} = -m(z_2) z_2 - \gamma_2 z_3, \end{cases} \quad (21)$$

where $g(z_1) = f(-z_1)$, which can be expressed as

$$g(z_1) = \begin{cases} -\rho z_1, & -\alpha \leq z_1 \leq 0, \\ -\frac{\rho}{r - \alpha} z_1 (r + z_1), & z_1 \leq -\alpha. \end{cases} \quad (22)$$

Set

$$D = \{(z_1, z_2, z_3) | z_1 < 0, z_2 > 0, z_3 < 0\}.$$

The Jacobian matrix of (21) is

$$J(z) = \begin{bmatrix} -g'(z_1) + b z_3 & 0 & b z_1 \\ k b z_3 & -\gamma_1 - (m'(z_2) z_2 + m(z_2)) & k b z_1 \\ 0 & -(m'(z_2) z_2 + m(z_2)) & -\gamma_2 \end{bmatrix}.$$

Due to (H2), $J(z)$ has nonpositive off-diagonal elements at each point of D . Thus (21) is competitive in D . Let $z_1^* = -\bar{x}$, $z_2^* = \bar{y}_1$, $z_3^* = -\frac{\rho}{b}$. It is obvious that (z_1^*, z_2^*, z_3^*) is the unique equilibrium of system (21) when $-\alpha \leq z_1 \leq 0$. Let $z_1^* = -x^*$, $z_2^* = y_1^*$, $z_3^* = -y_2^*$. It is obvious that (z_1^*, z_2^*, z_3^*) is the unique equilibrium of system (21) when $z_1 \leq -\alpha$. Since the inequality (11) is reversed, the analysis above shows that (z_1^*, z_2^*, z_3^*) is unstable and $\det J(z^*) < 0$. Moreover, since system (4) is permanent, there exists a compact subset B of D such that for each $z_0 \in D$, there exists a $T(z_0) > 0$ such that $z(t, z_0) \in B$ for all $t \geq T(z_0)$. Consequently, by the theorem 1.2 of paper [11], system (21) has an orbitally stable periodic solution.

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一类具阶段结构的捕食者 - 食饵模型的渐进性质

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摘要: 研究了一类具阶段结构的捕食者 - 食饵模型的渐近性质. 文中假设由幼年阶段转化为成年阶段的转化率依赖于幼年个体数量. 建立了捕食种群一致持续生存与绝灭的条件. 证明了稳定的周期解的存在性.

关键词: 阶段结构; 持续生存; 稳定性; 周期轨