

Permanence and Stability of a Stage-Structured Predator–Prey Model

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A predator–prey model with a stage structure for the predator which improves the assumption that each individual predator has the same ability to capture prey is proposed. It is assumed that immature individuals and mature individuals of the predator are divided by a fixed age and that immature predators do not have the ability to attack prey. We obtain conditions that determine the permanence of the populations and the extinction of the populations. Furthermore, we establish necessary and sufficient conditions for the local stability of the positive equilibrium of the model. By exploiting the monotonicity of one equation of the model, we obtain conditions for the global attractivity of the positive equilibrium, which allow for long delay as long as the predator birth rate is large or the death rate of immature predators is small. By constructing Liapunov functionals, we also obtain conditions under which the positive equilibrium is globally stable when the delay is small.

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1. INTRODUCTION

Stage-structured models have received much attention in recent years. This is not only because they are much simpler than the models governed by partial differential equations but also because they can exhibit phenomena similar to those of partial differential models and many important physiological parameters can be incorporated [1]. Mathematical analyses for single species models with stage structure were performed by Aiello and Freedman [2], Freedman and Wu [3, 4], Kuang and So [5], and Brauer and Ma [6]. Recently, Wang and Chen [7] and Magnusson [8] considered predator-prey models with a stage structure for the predator in order to analyse the influences of a stage structure for the predator on the dynamics of predator-prey models. But these models ignore the duration time of immature predators and adopt functional responses of Lotka-Volterra type. The purpose of the present paper is to perform a global analysis of the model by introducing the duration times of immature individual predators into the model and by incorporating the ratio-dependent functional response of Michaelis-Menten type into the model, motivated by recent works of Kuang and Beretta [10] and Beretta and Kuang [11].

Let $x(t)$ denote the density of prey at time t , $y(t)$ the density of immature individual predators at time t , and $z(t)$ the density of mature individual predators at time t . It is assumed that immature individuals and mature individuals are divided by age τ' and that immature individual predators do not feed on prey and do not have the ability to reproduce. This seems reasonable for a number of mammals where immature predators are raised by their parents and their reproduction rate and attacking rate for prey can be neglected. Based upon the above assumptions, we have the model

$$\begin{aligned}\frac{dx}{dt} &= x(t) \left(r - a_1 x(t) - \frac{a_2 z(t)}{mz(t) + x(t)} \right) \\ \frac{dy}{dt} &= \frac{b_1 x(t) z(t)}{mz(t) + x(t)} - b_2 y(t) \\ &\quad - \exp(-b_2 \tau') b_1 \frac{x(t - \tau') z(t - \tau')}{mz(t - \tau') + x(t - \tau')} \\ \frac{dz}{dt} &= \exp(-b_2 \tau') b_1 \frac{x(t - \tau') z(t - \tau')}{mz(t - \tau') + x(t - \tau')} - cz(t),\end{aligned}\tag{1.1}$$

where r is the intrinsic growth rate of the prey, a_1 is the density-dependent coefficient of the prey, a_2 is the capturing rate of mature predators, m is

the half capturing saturation constant, b_1/a_2 is the rate of conversion of nutrients into the reproduction rate of the mature predator, b_2 is the death rate of immature predators and c is the death rate of mature predators. The term

$$\exp(-b_2\tau')b_1\frac{x(t-\tau')z(t-\tau')}{mz(t-\tau')+x(t-\tau')}$$

represents the number of immature predators that were born at time $t - \tau'$ which still survive at time t and are transferred from the immature stage to the mature stage at time t .

Note that the first equation and the third equation of (1.1) can be separated from the whole system. Thus, we only consider the model

$$\begin{aligned}\frac{dx}{dt} &= x(t)\left(r - a_1x(t) - \frac{a_2z(t)}{mz(t) + x(t)}\right) \\ \frac{dz}{dt} &= \exp(-b_2\tau')b_1\frac{x(t-\tau')z(t-\tau')}{mz(t-\tau') + x(t-\tau')} - cz(t)\end{aligned}\quad (1.2)$$

with initial conditions

$$\begin{aligned}x(\theta) &= \varphi_1(\theta), & -\tau' \leq \theta \leq 0 \\ z(\theta) &= \varphi_2(\theta), & -\tau' \leq \theta \leq 0,\end{aligned}\quad (1.3)$$

where φ_i are nonnegative continuous functions on $\theta \in [-\tau', 0]$. Since b_2 is a positive constant and we are only interested in the permanence and stability of (1.1), it is easy to see that (1.1) inherits the permanence and stability of (1.2). Because of this, we will concentrate on (1.2).

What we shall emphasize is that this model is different from the model studied by Beretta and Kuang in [11], where the first term of the second equation is $(b_1z(t)x(t-\tau'))/(mz(t-\tau') + x(t-\tau'))$. The delay in (1.2) represents the duration time of immature individuals predators and has a different biological meaning from the delay in the model of [11]. In [11], they established nice conditions for the global stability of the model when the delay is small. Since the delay in (1.2) is the duration time of immature individual predators which is uncontrollable in a number of cases, we will establish sufficient conditions for the global stability of a positive equilibrium where there is much less restriction of the length of delay. Specifically, our conditions for the global stability of positive equilibrium admit a long delay when the predator birth rate is large or the death rate of juvenile predators is very small. Before proceeding further, let us scale (1.2) by putting

$$X = \alpha x, \quad Z = \beta z, \quad s = \theta_1 t,$$

where $\alpha = a_1/r$, $\beta = a_1m/r$, $\theta_1 = r$. By rewriting X, Z, s as x, z , and t , respectively, we obtain the new dimensionless system

$$\begin{aligned}\frac{dx}{dt} &= x(t) \left(1 - x(t) - \frac{az(t)}{z(t) + x(t)} \right) \\ \frac{dz}{dt} &= \nu \frac{x(t - \tau)z(t - \tau)}{z(t - \tau) + x(t - \tau)} - dz(t)\end{aligned}\tag{1.4}$$

where $a = a_2/(rm)$, $\nu = (b_1/r)\exp(-b_2\tau')$, $\tau = r\tau'$, $d = c/r$.

The organization of this paper is as follows. In the next section we establish the conditions that determine the permanence of the model and the extinction of the predator. Our results show that the duration length of juvenile predators play an important role in determining the permanence of the populations. Section 3 presents necessary and sufficient conditions for the local stability of a positive equilibrium, which show that the stability of the positive equilibrium can be changed due to an increase of the delay. In Section 4, we derive two types of sufficient conditions for the global stability of the positive equilibrium of the model, the first of which allows for long delay, while the second one applies when the delay is small. The paper concludes with a brief discussion about the biological meaning of our results.

2. PERMANENCE AND EXTINCTION

The purpose of this section is to present conditions that determine the permanence of (1.4) and the extinction of the populations. Let us begin by considering the positivity of solutions of (1.4). It is easy to see that the solutions of (1.4) with the initial conditions of the form (1.3) are always nonnegative on their existence intervals. If we further restrict $x(0) > 0$ and $z(0) > 0$, then each component of the solutions will be positive as long as $t > 0$ and the solutions exist. Such solutions will be called positive solutions.

We say that (1.4) is permanent if there exist positive constants M and ϵ such that each positive solution of (1.4) satisfies

$$\begin{aligned}\epsilon &\leq \liminf_{t \rightarrow +\infty} x(t) \leq \limsup_{t \rightarrow +\infty} x(t) \leq M, \\ \epsilon &\leq \liminf_{t \rightarrow +\infty} z(t) \leq \limsup_{t \rightarrow +\infty} z(t) \leq M.\end{aligned}$$

We now show that positive solutions of (1.4) are ultimately bounded. Define

$$V = \nu x(t - \tau) + az(t).$$

Calculating the derivative of V along positive solutions of (1.4), we obtain

$$\dot{V} = -dV(t) + \nu x(t - \tau)(1 + d - x(t - \tau)). \quad (2.1)$$

From the first equation of (1.4), we see that

$$\dot{x} < x(t)(1 - x(t)).$$

It follows that $\limsup_{t \rightarrow +\infty} x(t) \leq 1$. As a consequence, we have from (2.1) that

$$\limsup_{t \rightarrow +\infty} V(t) \leq \nu(1 + d)/d. \quad (2.2)$$

Hence, positive solutions of (1.4) are ultimately bounded.

The next theorem states the condition for the extinction of the predator.

THEOREM 2.1. *Adult predator becomes extinct if $\nu < d$.*

Proof. Let $(x(t), z(t))$ be a positive solution of (1.4). We will show that $\lim_{t \rightarrow \infty} z(t) = 0$. Choose a positive constant $p > 1$ such that $p\nu < d$. Then if $z(t + \theta) < pz(t)$ for $-\tau \leq \theta \leq 0$, by the second equation of (1.4) we have

$$\dot{z} < z(t) \left(\nu p \frac{x(t - \tau)}{x(t - \tau) + pz(t)} - d \right) < z(t)(p\nu - d).$$

It follows from Theorem 4.2, Chapter 5, of Hale and Lunel [12] that $\lim_{t \rightarrow \infty} z(t) = 0$. The proof is complete.

Since $\nu < d$ is equivalent to $c > b_1 \exp(-b_2 \tau')$, Theorem 2.1 shows that high mortality rates for adult and juvenile predators, a low conversion rate of prey biomass into juveniles, and a long delay guarantee the extinction of predators; i.e., the low net productivity of the predator leads to the extinction of predators.

THEOREM 2.2. *System (1.4) is permanent if $\nu > d$ and $a < 1$.*

Proof. By the first equation of (1.4), we have

$$\dot{x} \geq x(1 - x - a).$$

It follows that $\liminf_{t \rightarrow +\infty} x(t) \geq 1 - a$. As a consequence, from the second equation of (1.4) we obtain

$$\dot{z} > -dz(t) + \frac{\nu z(t - \tau)(1 - a - \epsilon)}{1 - a - \epsilon + z(t - \tau)},$$

where $\epsilon > 0$ is sufficiently small, when t is sufficiently large. By the comparison principle, we see that $\liminf_{t \rightarrow +\infty} z(t) \geq (\nu - d)(1 - a - \epsilon)/d$. The proof is complete.

Since $a < 1$ is equivalent to $a_2 < rm$ and the net growth rate of the prey at low prey density is $r - a_2/m$, Theorem 2.2 indicates that the populations will be permanent if the net productivity of the predator is high and the net growth rate of the prey at low prey density is positive.

Let us consider the permanence of (1.4) in the case that $a > 1$. Set $u = z/x$. Then (1.4) is transformed into

$$\begin{aligned}\dot{x} &= x \left(1 - x - \frac{au}{1+u} \right), \\ \dot{u} &= u \left(-1 - d + x + \frac{au}{1+u} \right) + \frac{\nu x(t-\tau)}{x(t)} \frac{u(t-\tau)}{1+u(t-\tau)}.\end{aligned}\quad (2.3)$$

Solving (2.3) on intervals $[0, \tau], [\tau, 2\tau], \dots$ successively, it is easy to see that positive solutions of (2.3) exist on $[0, \infty)$. Furthermore, it is easy to see that the permanence of positive solutions of (2.3) implies that (1.4) is permanent. In order to obtain such conditions, let us consider the ultimate boundedness of positive solutions of (2.3).

LEMMA 2.3. *Suppose $1 < a < 1 + d$. Then positive solutions of (2.3) are ultimately bounded.*

Proof. It is easy to see from the first equation of (2.3) that $x(t) < 1$ when t is sufficiently large. For simplicity of notation, we suppose that $x(t) < 1$ for $t \geq 0$ in what follows. Note that the first equation of (2.3) implies that

$$e^{-(t-s)} \leq \frac{x(t)}{x(s)} \leq e^{a(t-s)} \quad \text{for } t \geq s. \quad (2.4)$$

Since $1 < a < 1 + d$, one can choose $u_0 > 0$ large enough that

$$\begin{aligned}1 - \frac{au_0}{1+u_0} &< \frac{1-a}{2}, \\ \frac{\nu}{u_0} e^{a\tau} &< \frac{a-1-d}{4}.\end{aligned}\quad (2.5)$$

Then select sufficiently large T_1 that

$$(\exp(1-a)T_1/2) < -\frac{a-1-d}{4}. \quad (2.6)$$

Let $(x(t), u(t))$ be a positive solution of (2.3). We claim that it is impossible that $u(t) \geq u_0$ for all large t . Suppose not. Then there is a t^* such that $u(t) \geq u_0$ for $t \geq t^*$. Note that the first equation of (2.3) implies that

$$\dot{x} < x \left(1 - \frac{au_0}{1+u_0} \right) < \frac{(1-a)x}{2} \quad \text{for } t \geq t^*.$$

It implies that

$$x(t) < x(t^*) \exp((1-a)T_1/2) < -\frac{a-1-d}{4} \quad \text{for } t \geq t^* + T_1, \quad (2.7)$$

where the assumption of $x(t) < 1$ is used. By the second equation of (2.3) and (2.4), (2.5), we obtain

$$\begin{aligned} \dot{u} &\leq u(-1-d+a+x) + v \frac{x(t-\tau)}{x(t)} \\ &\leq u(-1-d+a+x) + ve^{a\tau} \\ &\leq u \left(-1-d+a+x - \frac{a-1-d}{4} \right). \end{aligned} \quad (2.8)$$

In view of (2.7), we have

$$\dot{u} < \frac{(a-1-d)u}{2} \quad \text{for } t \geq t^* + T_1,$$

which implies that $u(t) \rightarrow 0$ as $t \rightarrow \infty$. This contradiction proves the claim.

We claim now that $u(t) \leq u_0 \exp(T_1(1+(1+d-a)/4)) \equiv M_1$ when t is sufficiently large. If not, the previous claim shows that one can find an interval $[t_1, t_2]$, where $T_1 < t_1 < t_2$, such that $u(t_1) = u_0$, $u(t_2) = M_1$, $u_0 \leq u(t) \leq M_1$ for $t_1 < t < t_2$ and $\dot{u}(t_2) \geq 0$. Since $-1-d+a < 0$ and $x(t) < 1$, by (2.8) we have

$$\dot{u} < u(1+(1+d-a)/4) \quad \text{for } t_1 \leq t \leq t_2,$$

which yields

$$u(t_2) < u(t_1) \exp(1+(1+d-a)/4)(t_2-t_1)).$$

Thus, we have $t_2 > t_1 + T_1$. By similar arguments to those above, we see that

$$x(t_2) \leq x(t_1) e^{(1-a)T_1/2} < e^{(1-a)T_1/2} < -\frac{a-1-d}{4}.$$

It follows from (2.8) that

$$\dot{u}(t_2) < u(t_2)(-1 - d + a)/2 < 0.$$

This contradicts $\dot{u}(t_2) \geq 0$, and the claim is proved. Since M_1 is independent of the choice of positive solutions, we conclude that positive solutions of (2.3) are ultimately bounded when $1 < a < 1 + d$. The proof is complete.

THEOREM 2.4. *Suppose $\nu > d$, $1 < a < 1 + d$, and $a < \nu/(\nu - d)$. System (2.3) or (1.4) is permanent provided that one of the following conditions holds:*

- (i) $\nu(1 + \tau(1 - a)) > a$.
- (ii) $\nu < ae^{-\tau(a-1)}$.
- (iii) *If $ae^{-\tau(a-1)} < \nu$ and $\nu[1 + \tau(1 - a)] < a$, then $g(\bar{x}) < 0$ where \bar{x} is the unique root of $g'(x)$ in $(1, a)$ and*

$$g(x) = -1 - d + x + \nu(a - x)\exp(\tau(x - 1))/a \quad \text{for } x \in (0, a].$$

Proof. Let $(x(t), u(t))$ be an arbitrary positive solution of (2.3). We will show that there is a positive constant η , independent of the choice of a positive solution, such that $\liminf_{t \rightarrow +\infty} x(t) \geq \eta$ and $\liminf_{t \rightarrow +\infty} u(t) \geq \eta$. Since $a < 1 + d$, Lemma 2.3 implies that positive solutions of (2.3) are ultimately bounded. For simplicity, we suppose that $x(t) < 1$ and $u(t) < K$ for all $t \geq 0$ in what follows, where K is a positive constant.

The function $g(y)$ defined in the statement of theorem plays an important role in what follows. Note that

$$g'(y) = \exp(\tau(y - 1))[-\nu(1 + \tau(y - a)) + a \exp(-\tau(y - 1))]/a \quad (2.9)$$

and note that $\nu(1 + \tau(y - a))$ is strictly increasing on $(0, a]$ and $a \exp(-\tau(y - 1))$ is strictly decreasing on $(0, a]$. It is easy to see that $g'(y)$ satisfies one of the following properties:

- (P1) $g'(y) < 0$ for all $y \in (0, a)$.
- (P2) $g'(y) > 0$ for all $y \in (0, a)$.
- (P3) $g'(y)$ has a unique root \bar{y} in $(0, a)$. $g'(y) > 0$ for all $y \in (0, \bar{y})$ and $g'(y) < 0$ for all $y \in (\bar{y}, a)$.

If (ii) holds, (2.9) implies that $g'(y) > 0$ for all $y \in (0, a)$. If (i) holds, (2.9) implies that $g'(y) < 0$ for all $y \in [1, a)$. If (iii) holds, (2.9) implies

that there is a unique root of $g'(y) = 0$ in $(1, a)$. Since

$$g(1) = -d + \frac{\nu(a-1)}{a} = \frac{\nu-d}{a} \left(a - \frac{\nu}{\nu-d} \right) < 0,$$

$$g(a) = -1 - d + a < 0,$$

it follows that $g(y) < 0$ for $y \in [1, a)$.

Set

$$f(u, \epsilon) = -1 - d + \epsilon + \frac{au}{1+u} + \frac{\nu}{1+u} \exp\left(\tau \left(\frac{au}{1+u} - 1 + \epsilon \right)\right).$$

If we define $y = \frac{au}{1+u}$, the function $f(u, \epsilon)$ can be rewritten as

$$g(y, \epsilon) = -1 - d + \epsilon + y + \frac{\nu(a-y)}{a} \exp(\tau(y-1+\epsilon)).$$

Let us denote by $u^M(\epsilon)$ the maximal nonnegative root of the equation $uf(u, \epsilon) = 0$ and set $y^M(\epsilon) = au^M(\epsilon)/(1+u^M(\epsilon))$. Then $y^M(\epsilon)$ is the maximal root of the equation $g(y, \epsilon) = 0$ in $[0, a)$ and $g(y, \epsilon) < 0$ for $y^M(\epsilon) < y < a$. Since $y^M(0)$ is the maximal root of $g(y) = 0$ in $[0, a)$ and $g(y) < 0$ for $y \in [1, a)$, we must have $y^M(0) < 1$.

Choose $\epsilon > 0$ and $\epsilon_1 > 0$ small enough such that

$$\epsilon + \epsilon_1 < \frac{1 - y^M(0)}{2},$$

$$\frac{a(u^M(\epsilon) + \epsilon)}{1 + u^M(\epsilon) + \epsilon} < y^M(0) + \epsilon_1. \quad (2.10)$$

We claim that it is impossible that $x(t) < \epsilon$ for all large t . Conversely, suppose $x(t) < \epsilon$ for all $t \geq t_0$. Then we have

$$\dot{x} > x \left(1 - \epsilon - \frac{au}{1+u} \right) \quad \text{for } t \geq t_0.$$

It follows that

$$x(t) > x(t - \tau) \exp\left(\int_{t-\tau}^t \left(1 - \epsilon - \frac{au(s)}{1+u(s)} \right) ds\right) \quad \text{for } t \geq t_0 + \tau. \quad (2.11)$$

As a consequence, we have

$$\begin{aligned} \dot{u} &< u \left(-1 - d + \epsilon + \frac{au}{1+u} \right) \\ &+ \frac{\nu u(t-\tau)}{1+u(t-\tau)} \exp \left(\int_{t-\tau}^t \frac{au(s)}{1+u(s)} ds - (1-\epsilon)\tau \right) \end{aligned} \quad (2.12)$$

for $t \geq t_0 + \tau$.

Let us consider

$$\begin{aligned} \dot{u} &= u \left(-1 - d + \epsilon + \frac{au}{1+u} \right) \\ &+ \frac{\nu u(t-\tau)}{1+u(t-\tau)} \exp \left(\int_{t-\tau}^t \frac{au(s)}{1+u(s)} ds - (1-\epsilon)\tau \right). \end{aligned} \quad (2.13)$$

It is easy to see that positive solutions of (2.13) are monotonic with respect to initial values [13]. Furthermore, it is easy to check that $u^M(\epsilon)$ is a maximal nonnegative equilibrium of (2.13) and $f(u, \epsilon) < 0$ if $u > u^M(\epsilon)$. Let us define $\varphi_0(\theta) = nK$ for $\theta \in [-\tau, 0]$ where $n > 1$ is sufficiently large such that $u^M(\epsilon) < nK$, $f(nK, \epsilon) < 0$, and denote by $u(t, t_0, \varphi_0)$ the solution of (2.13) through (t_0, φ_0) . It follows from [18] or [19] that $u(t, t_0, \varphi_0)$ tends to $u^M(\epsilon)$ as t tends to infinity. Consequently, by the comparison principle [13], $u(t) < u^M(\epsilon) + \epsilon$ for sufficiently large t . This, together with (2.10), leads to

$$\dot{x} > x(1 - \epsilon - y^M(0) - \epsilon_1) > x(1 - y^M(0))/2,$$

which implies that $x(t) \rightarrow +\infty$ as $t \rightarrow \infty$. This contradicts $x(t) < \epsilon$ for all large t . Therefore, the claim is proved.

Choose $T_1 > 0$ large enough such that $u(T_1, 0, \varphi_0) < u^M(\epsilon) + \epsilon_1$, where $u(t, 0, \varphi_0)$ is the solution of (2.13) through $(0, \varphi_0)$. We show below that

$$x(t) \geq \epsilon \exp((- \epsilon - a)T_1) \equiv \eta_1 \quad \text{for all large } t. \quad (2.14)$$

Suppose not. Then the previous claim shows that there are $t_1 < t_2$ such that $x(t_1) = \epsilon$, $x(t_2) = \eta_1$, $\eta_1 < x(t) < \epsilon$ for $t_1 < t < t_2$, and $\dot{x}(t_2) \leq 0$. Note that

$$\eta_1 = x(t_2) > x(t_1) \exp((- \epsilon - a)(t_2 - t_1)) = \epsilon \exp((- \epsilon - a)(t_2 - t_1)).$$

We must have $t_2 - t_1 > T_1$. By repeating the arguments in the proof of the claim, we see that $u(t_2) < u^M(\epsilon) + \epsilon$. As a consequence,

$$\dot{x}(t_2) > x(t_2)(1 - \epsilon - y^M(0) - \epsilon_1) > x(t_2)(1 - y^M(0))/2 > 0.$$

which contradicts $\dot{x}(t_2) \leq 0$. This proves that (2.14) is valid. Note that the positive constant η_1 is independent of the choice of the positive solution. We have actually verified that η_1 is an ultimate lower bound of the first argument of positive solutions of (2.3).

We now turn to the existence of the positive ultimate lower bound of the second argument of the positive solutions of (2.3). Choose $1 > \epsilon_2 > 0$ small enough such that

$$\frac{\epsilon_2}{a} < \frac{\nu - d}{2d} < \frac{\nu(1 - \epsilon_2)}{(d + \epsilon_2)(1 + \epsilon_2)} - 1,$$

where the assumption of $\nu > d$ is used. We now claim that it is impossible that

$$u(t) \leq \epsilon_2/(2a) \quad \text{for all large } t. \quad (2.15)$$

Conversely, suppose $u(t) \leq \epsilon_2/(2a)$ for all $t \geq t_3$. Then the first equation of (2.3) implies that

$$x(1 - \epsilon_2/2 - x) < \dot{x} < x(1 - x).$$

It follows that there is a $T_2 > t_3$ such that

$$1 - \epsilon_2 < x(t) < 1 + \epsilon_2 \quad \text{for } t \geq T_2.$$

It follows from the second equation of (2.3) that

$$\dot{u} > u(-d - \epsilon_2) + \frac{\nu(1 - \epsilon_2)}{1 + \epsilon_2} \frac{u(t - \tau)}{1 + u(t - \tau)}.$$

Let us consider

$$\dot{u} = u(-d - \epsilon_2) + \frac{\nu(1 - \epsilon_2)}{1 + \epsilon_2} \frac{u(t - \tau)}{1 + u(t - \tau)}. \quad (2.16)$$

Since positive solutions of this equation are monotonic with respect to initial values, it is easy to check that positive solutions of (2.16) tend to

$$u_l = \frac{\nu(1 - \epsilon_2)}{(d + \epsilon_2)(1 + \epsilon_2)} - 1$$

as t tends to infinity. Since $u_l > \frac{\nu - d}{2d}$, by the comparison principle we have

$$u(t) > \frac{\nu - d}{2d} > \frac{\epsilon_2}{a} \quad \text{when } t \text{ is sufficiently large,}$$

which contradicts $u(t) \leq \epsilon_2/(2a)$ for large t . The claim is thus proved.

Since we have verified that (2.14) is valid, for simplicity of notation we assume that $x(t) \geq \eta_1$ for all $t \geq 0$ in what follows. Let us consider

$$\dot{x} = x(1 - \epsilon_2/2 - x).$$

Suppose $x(t, \eta_1)$ is the solution of this equation through $(0, \eta_1)$. Choose T_3 large enough such that

$$x(t, \eta_1) > 1 - \epsilon_2 \quad \text{for } t \geq T_3. \quad (2.17)$$

Set $\eta_2 = \epsilon_2 \exp((-1 - d)(T_3 + \tau))/(2a)$. We claim that

$$u(t) \geq \eta_2 \quad \text{for all large } t.$$

If it were not valid, by the previous claim there would be $t_4 < t_5 < t_6$ such that $u(t_4) = \epsilon_2/(2a)$, $\epsilon_2/(2a) \geq u(t) \geq \eta_2$ for $t_4 < t < t_5$, $u(t_5) = \eta_2$, and $u(t) < \eta_2$ for $t_5 < t < t_6$. Since the second equation of (2.3) implies that

$$\dot{u} \geq u(-1 - d),$$

we have

$$\begin{aligned} u(t_5) &> u(t_4) \exp(-(1 + d)(t_5 - t_4)) \\ &= \epsilon_2 \exp(-(1 + d)(t_5 - t_4))/(2a). \end{aligned}$$

We must have $t_5 > t_4 + T_3 + \tau$. Since $\dot{x} > x(1 - \epsilon_2/2 - x)$ for $t_4 \leq t < t_6$, it follows from the comparison principle and (2.17) that $x(t) > 1 - \epsilon_2$ for $t_4 + T_3 \leq t < t_6$. Thus, we have

$$\dot{u} \geq u(-d - \epsilon_2) + \frac{\nu(1 - \epsilon_2)}{1 + \epsilon_2} \frac{u(t - \tau)}{1 + u(t - \tau)}, \quad t \in [t_4 + T_3, t_6].$$

On the other hand, let us define $\psi(\theta) = \eta_2$ for $\theta \in [-\tau, 0]$ and denote by $u(t, t_5, \psi)$ the solution of (2.16) through (t_5, ψ) . Since $\eta_2 < u_l$, it is easy to see that $u(t, t_5, \psi)$ is monotonically increasing for $t > t_5$. As a consequence, by the comparison principle we have $u(t) \geq u(t, t_5, \psi) > \eta_2$ for $t_5 < t < t_6$, contradicting $u(t) < \eta_2$ for $t_5 < t < t_6$. This contradiction shows that the claim is valid and therefore the second argument of the positive solutions of (2.3) is bounded from below by η_2 when t is sufficiently large. In view of all the discussions above, we conclude that (2.3) is permanent. The proof of Theorem 2.4 is complete.

By the proof of Theorem 2.4, we see that the conditions of Theorem 2.4 guarantee that the eventual upper bound of $\frac{au(t)}{1 + u(t)}$ is less than 1 at low density of the prey. Since $a = a_2/(rm)$, $u = mz/x$, where x and z are the

densities of the prey and adult predators, respectively, we see that $\frac{au}{1+u} < 1$ is equivalent to $a_2 z/(x + mz) < r$. Since $a_2 z/(x + mz)$ is the probability that one individual of the prey species is captured by adult predators during one unit time. Theorem 2.4 shows that the system is permanent if the intrinsic growth rate of the prey is greater than the probability that one individual of the prey species is captured by adult predators during one unit of time when the prey density is low.

Although conditions of Theorem 2.4 can be checked easily by numerical calculations, we give sufficient conditions for practical purposes.

COROLLARY 2.5. *Suppose $\nu > d$, $1 < a < \nu/(\nu - d)$, and $a < 1 + d$. Then the system (2.3) is permanent provided that*

$$a < 1 + \frac{d}{1 + d\tau}. \quad (2.18)$$

Proof. It suffices to verify that (2.18) ensures that the requirements from (iii) of Theorem 2.4 are satisfied. Suppose $1 < y < a$ such that $g'(y) = 0$. We wish to show that (2.18) ensures $g(y) < 0$. Since (2.9) implies that $g'(x) > 0$ for $0 < x < y$ and $g'(x) < 0$ for $y < x < a$, $g(y) < 0$ will lead to $g(x) < 0$ for all $0 < x < a$. Then the permanence of (2.3) follows from discussions with the same spirit as the proof of Theorem 2.4.

By $g'(y) = 0$, we have

$$\nu \exp(\tau(y - 1)) = a/(1 - \tau(a - y)).$$

This implies that

$$g(y) = -1 - d + y + \frac{a - y}{1 - \tau(a - y)}.$$

Since $1 - \tau(a - y) > 0$, it is easily seen that the sign of $g(y)$ is determined by

$$p(y) \equiv \tau y^2 + (-\tau - d\tau - \tau a)y - 1 + \tau a - d + d\tau a + a.$$

Since (2.18) implies that

$$p(1) = -d\tau - 1 - d + d\tau a + a < 0$$

and $p(a) = a - 1 - d < 0$, it is easy to see that $p(y) < 0$. This proves $g(y) < 0$, and therefore the proof of Corollary 2.5 is complete.

Since $a < 1 + d/(1 + d\tau)$ is equivalent to $a_2 < (r + rc\tau' + c)m/(1 + c\tau')$, this corollary provides a simple upper bound for the capture rate in order to maintain the permanence of the populations.

THEOREM 2.6. Suppose $a > 1$. System (1.4) cannot be permanent provided that one of the following conditions holds:

- (i) $a > 1 + d$;
- (ii) $a > \frac{\nu}{\nu-d}$ where $\nu > d$;
- (iii) if $1 < a < 1 + d$, $a < \frac{\nu}{\nu-d}$, $ae^{-\tau(a-1)} < \nu$, and $\nu[1 + \tau(1 - a)] < a$, then $g(\bar{x}) > 0$ where \bar{x} is the unique root of $g'(y)$ in $(1, a)$.

Proof. By the discussions in the proof of Theorem 2.4, we see that each of the three conditions guarantees that there exists an interval $[y_1, y_2]$ with $y_1 > 1$ and $y_2 < a$ such that $g(y) > 0$ for $y \in [y_1, y_2]$. Set $\bar{u}_1 = y_1/(a - y_1)$ and $\bar{u}_2 = y_2/(a - y_2)$. It implies that $f(u, 0) > 0$ for $u \in [\bar{u}_1, \bar{u}_2]$.

From the first equation of (2.3), we have

$$\dot{x} \leq x \left(1 - \frac{au}{1+u} \right), \quad (2.19)$$

which leads to

$$\frac{x(t-\tau)}{x(t)} \geq \exp \left(\int_{t-\tau}^t \left(-1 + \frac{au(s)}{1+u(s)} \right) ds \right),$$

which yields

$$\dot{u} \geq u \left(-1 - d + \frac{au}{1+u} \right) + \frac{\nu u(t-\tau)}{1+u(t-\tau)} \exp \left(\int_{t-\tau}^t \frac{au(s)}{1+u(s)} ds - \tau \right). \quad (2.20)$$

Let us consider

$$\dot{u} = u \left(-1 - d + \frac{au}{1+u} \right) + \frac{\nu u(t-\tau)}{1+u(t-\tau)} \exp \left(\int_{t-\tau}^t \frac{au(s)}{1+u(s)} ds - \tau \right). \quad (2.21)$$

Set $\varphi_1(\theta) = \alpha$ and $\varphi_2(\theta) = (\bar{u}_1 + \bar{u}_2)/2$ for $\theta \in [-\tau, 0]$ where $0 < \alpha < 1$ is a constant. Let $\bar{u}(t, \varphi_1, \varphi_2)$ be the solution of (2.21) through (φ_1, φ_2) at $t = 0$. Since positive solutions of (2.21) are monotone with respect to initial values and $f((\bar{u}_1 + \bar{u}_2)/2, 0) > 0$, it follows that $\bar{u}(t, \varphi_1, \varphi_2)$ is monotonically increasing as t increases. Let $u(t, \varphi_1, \varphi_2)$ be the solution of (2.3) through (φ_1, φ_2) at $t = 0$. Then by the comparison principle we have

$$u(t, \varphi_1, \varphi_2) > \bar{u}(t, \varphi_1, \varphi_2) \geq (\bar{u}_1 + \bar{u}_2)/2 > \bar{u}_1$$

for $t > 0$. As a consequence,

$$\dot{x} \leq x \left(1 - \frac{a\bar{u}_1}{1 + \bar{u}_1} \right) = x(1 - y_1).$$

Since $y_1 > 1$, it follows that $x(t) \rightarrow 0$ as $t \rightarrow \infty$. In view of the relationship between (1.4) and (2.3), we see that there exists a positive solution in (1.4) which satisfies $x(t) \rightarrow 0$ as $t \rightarrow \infty$. Thus, we conclude that (1.4) is not persistent if any of the conditions of this theorem holds. The proof is complete.

Remark. The biological meaning of Theorem 2.6 can be interpreted in a manner similar to those for Theorem 2.4. From Theorem 2.6, we see that the conditions in Theorem 2.4 are also necessary for the permanence of (1.4) if we ignore equality cases. Furthermore, we see that the length of the life span of juveniles plays an important role in the permanence of populations. We will illustrate this by examples in Section 5.

3. LOCAL STABILITY

The objective of this section is to establish sufficient conditions for local stability of a positive equilibrium of (1.4). Let us begin by stating conditions for the existence of a positive equilibrium of (1.4). By simple computations, we see that there is a unique positive equilibrium (x^*, z^*) in (1.4) if

$$\nu > d, \quad ad + \nu(1 - a) > 0, \quad (3.1)$$

where

$$\begin{aligned} x^* &= ad/\nu + 1 - a, \\ z^* &= (ad/\nu + 1 - a)(\nu/d - 1). \end{aligned} \quad (3.2)$$

In order to study the local stability of the positive equilibrium, let us consider the system

$$\begin{aligned} \frac{dx}{dt} &= \left(a - 1 - \frac{ad^2}{\nu^2} \right) x(t) - \frac{ad^2}{\nu^2} z(t), \\ \frac{dz}{dt} &= d^2(\nu/d - 1)^2 x(t - \tau)/\nu + \frac{d^2}{\nu} z(t - \tau) - dz(t), \end{aligned} \quad (3.3)$$

which is a linearization of (1.4) at (x^*, z^*) . Its characteristic equation takes the form

$$\begin{vmatrix} \lambda + 1 + \frac{ad^2}{\nu^2} - a & \frac{ad^2}{\nu^2} \\ -\frac{d^2}{\nu} \left(\frac{\nu}{d} - 1 \right)^2 e^{(-\lambda\tau)} & -\frac{d^2 e^{(-\lambda\tau)}}{\nu} + d + \lambda \end{vmatrix} = 0$$

which is equivalent to

$$a_0 \lambda^2 + a_1 \lambda + a_2 + (b_0 \lambda + b_1) \exp(-\lambda\tau) = 0, \quad (3.4)$$

where

$$\begin{aligned} a_0 &= \nu^2 \\ a_1 &= \nu^2 d + ad^2 + \nu^2 - \nu^2 a \\ a_2 &= d(\nu^2 - \nu^2 a + ad^2) \\ b_0 &= -\nu d^2 \\ b_1 &= -d^2(\nu - 2a\nu + 2ad). \end{aligned}$$

In order to know the distribution of characteristic roots of this equation, we need the following results from [5] or [14].

LEMMA 3.1. *In (3.4), assume that $a_2 + b_1 \neq 0$, $a_1^2 + b_0^2 + b_1^2 \neq 0$. The number of different positive (negative) imaginary roots of (3.4) can be 0, 1, or 2 only.*

(1) *If $a_2^2 > b_1^2$ and $b_0^2 + 2a_2a_0 - a_1^2 < 2a_0\sqrt{a_2^2 - b_1^2}$, then (3.4) has the same stability or instability as when $\tau = 0$.*

(2) *Suppose $a_2^2 \leq b_1^2$. If (3.4) is unstable when $\tau = 0$, then it remains unstable for $\tau > 0$. If (3.4) is stable when $\tau = 0$, then it remains stable until $\tau = \tau_0$ and becomes unstable afterward, where $\tau_0 = \theta/\omega$, $\theta \in [0, 2\pi]$, $\omega > 0$,*

$$\begin{aligned} (a_0 \omega)^2 &= \frac{1}{2} \left\{ b_0^2 + 2a_2a_0 - a_1^2 + \left[(b_0^2 + 2a_2a_0 - a_1^2)^2 - 4(a_2^2 - b_1^2) \right]^{1/2} \right\}, \\ \cos \theta &= \frac{a_1 b_0 \omega^2 + b_1(a_2 - a_0 \omega^2)}{b_1^2 + b_0^2 \omega^2}. \end{aligned}$$

We now apply Lemma 3.1 to study the stability of (3.4). Substituting $\tau = 0$ in (3.4), we obtain

$$\begin{aligned} \lambda^2 \nu^2 + (-\nu d^2 - \nu^2 a + ad^2 + \nu^2 + \nu^2 d) \lambda \\ + d(\nu - d)(\nu - a(\nu - d)) = 0, \end{aligned} \quad (3.5)$$

from which it is easy to know that the positive equilibrium is stable at $\tau = 0$ if

$$a < \min \left\{ \frac{\nu(-d^2 + \nu + \nu d)}{(\nu - d)(\nu + d)}, \frac{\nu}{\nu - d} \right\} \quad (3.6)$$

and is unstable at $\tau = 0$ if

$$\frac{\nu(-d^2 + \nu + \nu d)}{(\nu - d)(\nu + d)} < a < \nu/(\nu - d). \quad (3.7)$$

By direct calculations, we obtain

$$b_1^2 - a_2^2 = d^2(-\nu + d)(3ad^2 - 2d\nu a - a\nu^2 + d\nu + \nu^2)(\nu + ad - a\nu),$$

which implies that

$$\begin{aligned} b_1^2 &< a_2^2 && \text{if } 0 < a < a^*, \\ b_1^2 &> a_2^2 && \text{if } a^* < a < \nu/(\nu - d), \end{aligned}$$

where

$$a^* = \frac{\nu(d + \nu)}{(\nu - d)(3d + \nu)}.$$

By Lemma 3.1, we have the following stability results for (1.4).

THEOREM 3.2. *Suppose*

$$a^* < a < \min \left\{ \frac{\nu(-d^2 + \nu + \nu d)}{(\nu - d)(\nu + d)}, \frac{\nu}{\nu - d} \right\}.$$

Then there is a positive number τ_0 such that the positive equilibrium of (1.4) is stable if $0 \leq \tau < \tau_0$ and is unstable if $\tau_0 < \tau$. The positive equilibrium is always (i.e., for any $\tau \geq 0$) unstable if

$$\frac{\nu(-d^2 + \nu + \nu d)}{(\nu - d)(\nu + d)} < a < \nu/(\nu - d).$$

Let us consider the case where $0 < a < a^*$. We will show that

$$\left(\frac{b_0}{a_0} \right)^2 + \frac{2a_2}{a_0} - \left(\frac{a_1}{a_0} \right)^2 < 0.$$

It is equivalent to show

$$A \equiv b_0^2 + 2a_2a_0 - a_1^2 < 0.$$

By direct calculations, we obtain

$$A = p_0a^2 + p_1a + p_2,$$

where

$$p_0 = -(d - \nu)^2(d + \nu)^2,$$

$$p_1 = -2\nu^2(d - \nu)(d + \nu),$$

$$p_2 = \nu^2(d^4 - d^2\nu^2 - \nu^2).$$

Since $\nu > d$, $p_0 < 0$ and

$$p_1^2 - 4p_0p_2 = 4d^2\nu^2(d - \nu)^3(d + \nu)^3 < 0,$$

it follows that $A < 0$. Since the positive equilibrium is stable when $\tau = 0$, it follows from Lemma 3.1 that it remains stable as long as $a < a^*$. This is stated as Theorem 3.3.

THEOREM 3.3. *The positive equilibrium is asymptotically stable if $a < a^*$.*

4. GLOBAL STABILITY

The purpose of this section is to derive sufficient conditions for the global stability of the positive equilibrium of (1.4). In what follows, we always suppose

$$(\hat{H}) \quad a < 1 \text{ and } \nu > d.$$

This assumption guarantees the existence of a positive equilibrium of the system (1.4).

THEOREM 4.1. *Let the hypothesis (\hat{H}) hold. Then the positive equilibrium of (1.4) is globally stable provided that*

$$a < \frac{\nu^2}{(\nu - d)(\nu + 2d)}. \quad (4.1)$$

Proof. Note that (4.1) implies

$$a < \frac{\nu(d + \nu)}{(\nu - d)(\nu + 3d)}.$$

It follows from Theorem 3.3 that the positive equilibrium is asymptotically stable. Thus, it is sufficient to show that the equilibrium is globally attractive. Let $(x(t), z(t))$ be an arbitrary positive solution of (1.4). Define

$$\begin{aligned} u_1 &= \liminf_{t \rightarrow +\infty} x(t), & v_1 &= \limsup_{t \rightarrow +\infty} x(t), \\ u_2 &= \liminf_{t \rightarrow +\infty} z(t), & v_2 &= \limsup_{t \rightarrow +\infty} z(t). \end{aligned}$$

We wish to show that $u_1 = v_1 = x^*$ and $u_2 = v_2 = z^*$. We only present the proof of $u_2 = v_2 = z^*$. The proof of $u_1 = v_1 = x^*$ is similar and is omitted. Conversely, suppose that $v_2 > z^*$. Then for sufficiently small $\epsilon > 0$ there is a $T_1 > 0$ such that

$$\dot{x} \geq x \left(1 - x - \frac{a(v_2 + \epsilon)}{x + v_2 + \epsilon} \right) \quad \text{for } t \geq T_1. \quad (4.2)$$

Let us consider

$$\dot{x} = x \left(1 - x - \frac{a(v_2 + \epsilon)}{x + v_2 + \epsilon} \right).$$

This equation has a unique positive equilibrium $x_l(\epsilon)$ defined by

$$x_l(\epsilon) = \frac{1 - v_2 - \epsilon + \sqrt{(1 - v_2 - \epsilon)^2 + 4(1 - a)(v_2 + \epsilon)}}{2}.$$

It is easy to see that this positive equilibrium is globally stable. As a consequence, there is a $T_2 > T_1$ such that

$$x(t) \geq x_l(\epsilon) - \epsilon \quad \text{for } t \geq T_2.$$

We now give further restrictions to ϵ so that $x_l(\epsilon) - \epsilon > 0$. Then this leads to

$$\dot{z} \geq \frac{\nu(x_l(\epsilon) - \epsilon)z(t - \tau)}{x_l(\epsilon) - \epsilon + z(t - \tau)} - dz(t) \quad \text{for } t \geq T_2 + \tau.$$

Let us consider

$$\dot{z} = \frac{\nu(x_l(\epsilon) - \epsilon)z(t - \tau)}{x_l(\epsilon) - \epsilon + z(t - \tau)} - dz(t). \quad (4.3)$$

Note that the positive solutions of this equation are monotonic [13] with respect to the initial data. If we define

$$g(z) = \frac{\nu(x_l(\epsilon) - \epsilon)z}{x_l(\epsilon) - \epsilon + z} - dz,$$

it is easy to see from $\nu > d$ that $d(z) > 0$ if $z < z_l(\epsilon)$, where $z_l(\epsilon)$ is defined by

$$z_l(\epsilon) = (\nu - d)(x_l(\epsilon) - \epsilon)/d$$

and $g(z) < 0$ if $z > z_l$. As a consequence, paper [18] or paper [19] implies that the positive solutions of (4.3) tend to $z_l(\epsilon)$. Thus, there is a $T_3 > T_2$ such that $z(t) \geq z_l(\epsilon) - \epsilon$ for $t \geq T_3$. By similar discussions to those above, we see that there is a $T_4 > T_3$ such that

$$x(t) \geq x^u(\epsilon) + \epsilon \quad \text{for } t \geq T_4,$$

where

$$x^u(\epsilon) = \frac{1 - z_l(\epsilon) + \epsilon + \sqrt{(1 - z_l(\epsilon) + \epsilon)^2 + 4(1 - a)(z_l(\epsilon) - \epsilon)}}{2}.$$

Furthermore, if we set

$$z^u(\epsilon) = (\nu - d)(x^u(\epsilon) + \epsilon)/d$$

there is a $T_5 > T_4$ such that

$$z(t) \leq z^u(\epsilon) + \epsilon \quad \text{for } t \geq T_5.$$

Let us define the function $x = f(z)$ by

$$f(z) = (\nu - d) \frac{1 - z + \sqrt{(1 - z)^2 + 4(1 - a)z}}{2d}.$$

Then,

$$z_l(\epsilon) = f(v_2 + \epsilon) - \epsilon(\nu - d)/d,$$

$$z^u(\epsilon) = f(z_l(\epsilon) - \epsilon) + \epsilon(\nu - d)/d.$$

Taking $\epsilon \rightarrow 0$, we obtain

$$z^u(0) = f(z_l(0)),$$

$$z_l(0) = f(v_2).$$

It follows that $z^u(0) = f(f(v_2))$.

Claim. Under the assumptions of this theorem, we have $f(f(v_2)) < v_2$, provided that $v_2 > z^*$.

The proof of this claim will be postponed to the end of the proof of this theorem. By the claim, we have

$$\limsup_{t \rightarrow +\infty} z(t) \leq z^u(0) = f(f(v_2)) < v_2 = \limsup_{t \rightarrow +\infty} z(t).$$

This contradiction shows that we must have $v_2 \leq z^*$.

Replacing v_2 with z^* and repeating the above arguments, one can obtain

$$\liminf_{t \rightarrow +\infty} z(t) \geq f(z^* + \epsilon) - \epsilon(\nu - d)/d - \epsilon.$$

Taking $\epsilon \rightarrow 0$ in both sides, we reach $\liminf_{t \rightarrow +\infty} z(t) \geq f(z^*)$. By direct calculations, we see that $f(z^*) = z^*$. Hence, we can conclude that $\lim_{t \rightarrow \infty} z(t) = z^*$. Using this and arguing as before we may conclude that $\lim_{t \rightarrow \infty} x(t) = x^*$. At this time, we are left to prove the claim.

Proof of the Claim. By direct calculations, we see that $f(f(z^*)) = z^*$. Note also that $\limsup_{t \rightarrow +\infty} x(t) \leq 1$. It follows that, for $\epsilon > 0$ sufficiently small, there is a $T_6 > 0$ such that

$$\dot{z} \leq \frac{\nu(1 + \epsilon)z(t - \tau)}{1 + \epsilon + z(t - \tau)} - dz(t) \quad \text{for } t > T_6 + \tau.$$

Arguing as before, we have $z(t) < (\nu - d)(1 + \epsilon)/d + \epsilon$ for all large t . Replacing v_2 with $(\nu - d)(1 + \epsilon)/d + \epsilon$ and repeating the discussions above, we see that there are positive constants T_7, T_8, T_9 such that

$$z(t) \geq f((\nu - d)(1 + \epsilon)/d + 2\epsilon) - \epsilon(\nu - d)/d - \epsilon \equiv z_l \quad \text{for } t > T_7,$$

$$z(t) \leq \frac{1 - z_l + \sqrt{(1 - z_l)^2 + 4(1 - a)z_l}}{2} + \epsilon \equiv x^u \quad \text{for } t > T_8,$$

$$z(t) \leq (\nu - d)x^u/d + \epsilon \equiv z^u \text{ for } t > T_9. \quad (4.4)$$

Note that

$$\frac{1 - z_l + \sqrt{(1 - z_l)^2 + 4(1 - a)z_l}}{2} < \frac{1 - z_l + \sqrt{(1 - z_l)^2 + 4z_l}}{2} = 1.$$

We have $x^u < 1$ for sufficiently small $\epsilon > 0$. It follows that $z^u - \epsilon = (\nu - d)x^u/d < \nu - d/d$. If we let $\epsilon \rightarrow 0$, together with (4.4), this leads to

$$f(f((\nu - d)/d)) \leq (\nu - d)/d.$$

We shall show below that

$$f(f(z)) \neq z \quad \text{for } z^* < z. \quad (4.5)$$

This means that we must have $f(f((\nu - d)/d)) < (\nu - d)/d$, since $(\nu - d)/d > z^*$. As a consequence, we have $f(f(v_2)) < v_2$. Otherwise, there exists a \tilde{z} , $v_2 < \tilde{z} < (\nu - d)/d$, such that $f(f(\tilde{z})) = \tilde{z}$, which contradicts

(4.5). At this time, we are now left to show that (4.5) is true. Suppose, on the contrary, that there is a $z^* < z$ such that $f(f(z)) = z$. Then the system

$$\begin{aligned}x &= f(y), \\y &= f(x)\end{aligned}\tag{4.6}$$

would have a positive solution (x, y) with $y > z^*$. If we set $\alpha = d/(\nu - d)$, then the equation $x = f(y)$ can be transformed into

$$\alpha^2 x^2 + \alpha xy + ay - \alpha x - y = 0,\tag{4.7}$$

and the equation $y = f(x)$ can be transformed into

$$\alpha^2 y^2 + \alpha xy + ax - \alpha y - x = 0.\tag{4.8}$$

Subtracting (4.8) from (4.7), we obtain

$$(y - x)(-\alpha^2 x + a + \alpha - 1 - \alpha^2 y) = 0.$$

If $y = x$, it is easy to see from $x = f(y)$ that $y = z^*$. This is not the case we are interested in because we are considering the case where $y > z^*$. Thus, we only consider

$$-\alpha^2(x + y) + a + \alpha - 1 = 0.\tag{4.9}$$

Solving y from it, we obtain

$$y = \frac{-\alpha^2 x + a + \alpha - 1}{\alpha^2}.$$

If $y \leq z^*$, there is nothing to prove. Suppose now $y > z^*$. Then substituting it into equation $x = f(y)$ and simplifying, we obtain

$$F(x) \equiv A_0 x^2 + A_1 x + A_2 = 0,\tag{4.10}$$

where

$$A_0 = \alpha^3(\alpha - 1),$$

$$A_1 = -\alpha(\alpha - 1)(a - \alpha - 1),$$

$$A_2 = (-1 + a)(a + \alpha - 1).$$

Equation (4.10) implies that $\alpha \neq 1$. Let us consider the case where $\alpha > 1$. In this case, $A_0 > 0$, $A_1 < 0$, $A_2 < 0$. We claim that $x = f(y)$ is strictly decreasing. In fact, the sign of $f'(z)$ is determined by

$$\begin{aligned}1 + z - 2a - \sqrt{(1 - z)^2 + 4(1 - a)z} \\= 1 + z - 2a - \sqrt{1 + z^2 + 2z - 4az}.\end{aligned}\tag{4.11}$$

If $1 + z - 2a \leq 0$, there is nothing to prove. If $1 + z - 2a > 0$, we have

$$(1 + z - 2a)^2 - (1 + z^2 + 2z - 4az) = 4a(a - 1) < 0.$$

Hence, the sign of $f'(z)$ is negative and therefore it is strictly decreasing. Because of this and $f(z^*) = z^*$ and because we consider the case where $y > z^*$, all the x solving (4.10) satisfy $0 < x < z^*$. As a consequence of which and $A_0 > 0$, $A_1 < 0$, $A_2 < 0$, we have $F(x) < 0$ if $F(z^*) \leq 0$.

Note that $z^* = (1 - a + ad/\nu)(\nu/d - 1)$, $\alpha = d/(\nu - d)$. By direct calculations, we obtain

$$F(z^*) = \frac{(2ad^2 - ad\nu + \nu^2 - a\nu^2) da}{\nu^2(-\nu + d)}.$$

It is easy to verify that (4.1) implies $F(z^*) < 0$. This shows that (4.10) does not admit a solution when $0 < x < z^*$.

Let us consider the case where $\alpha < 1$. Note that (4.9) implies that $a + \alpha - 1 > 0$ because $x > 0$ and $y > 0$. Then we turn to Eq. (4.10). Note that $A_0 < 0$, $A_1 > 0$, $A_2 < 0$ in this case. If we define

$$\Delta \triangleq A_1^2 - 4A_0A_2,$$

it follows from $\alpha < 1$, $a + \alpha - 1 > 0$ that the sign of Δ is determined by

$$\Delta_1 = (1 - \alpha)(a + \alpha - 1) + 4\alpha(a - 1).$$

Substituting $\alpha = d/(\nu - d)$ into it, we obtain

$$\Delta_1 = - \frac{-a\nu^2 - \nu ad + \nu^2 + 2ad^2}{(-\nu + d)^2}.$$

Clearly, its sign is determined by

$$a\nu^2 + \nu ad - \nu^2 - 2ad^2$$

from which we see that $\Delta < 0$ is equivalent to

$$a < \frac{\nu^2}{(\nu - d)(\nu + 2d)}.$$

This shows that the assumptions of this theorem ensure that Eq. (4.10) does not admit a solution in $(0, z^*)$ in any case. Consequently, the proof of the claim is complete and therefore the proof of Theorem 4.1 is complete.

We are now in a stage to present sufficient conditions for the global stability of the positive equilibrium by constructing Liapunov functionals. Let us begin by making the change of variables of the system (1.4). Set $u = z/x$. Note that

$$\begin{aligned}\dot{u} &= -u\dot{x}/x + \dot{z}/x \\ &= -u\left(1 + d - x - \frac{au}{1+u} - \frac{\nu}{1+u}\right) - \frac{\nu}{x} \int_{t-\tau}^t \left(\frac{x(s)z(s)}{x(s)+z(s)} \right)' ds.\end{aligned}$$

Then the system (1.4) is transformed into

$$\begin{aligned}\dot{x} &= x\left(1 - x - \frac{au}{1+u}\right) \\ \dot{u} &= u\left(-1 - d + x + \frac{au + \nu}{1+u}\right) - \frac{\nu}{x} \\ &\quad \times \int_{t-\tau}^t \frac{1}{(1+u)^2} \left\{ \frac{\nu x(s-\tau)u(s-\tau)}{1+u(s-\tau)} - du(s)x(s) \right. \\ &\quad \left. + u^2(s)x(s)\left(1 - x(s) - \frac{au(s)}{1+u(s)}\right)\right\} ds.\end{aligned}\tag{4.12}$$

If we set $u^* = z^*/x^*$, it is easy to see that (x^*, u^*) is a positive equilibrium of (4.12). Because of this, we can rewrite (4.12) into

$$\begin{aligned}\dot{x} &= x\left[-(x - x^*) - a\left(\frac{u}{1+u} - \frac{u^*}{1+u^*}\right)\right], \\ \dot{u} &= u\left[(x - x^*) + a\left(\frac{u}{1+u} - \frac{u^*}{1+u^*}\right) - \frac{\nu(u - u^*)}{(1+u)(1+u^*)}\right] \\ &\quad - \frac{\nu}{x} \int_{t-\tau}^t \frac{1}{(1+u)^2} \\ &\quad \times \left\{ \frac{\nu u(s-\tau)(1+u^*)(x(s-\tau) - x^*) + \nu x^*(u(s-\tau) - u^*)}{(1+u(s-\tau))(1+u^*)} \right. \\ &\quad \left. - dx(s)(u(s) - u^*) - du^*(x(s) - x^*) + u^2(s)x(s) \right. \\ &\quad \left. \times \left(- (x(s) - x^*) - \frac{a(u(s) - u^*)}{(1+u(s))(1+u^*)}\right)\right\} ds.\end{aligned}\tag{4.13}$$

Let us define

$$V_1 = x - x^* - x^* \ln(x/x^*) + a \int_{u^*}^u \frac{U(s) - U(u^*)}{s} ds$$

where $U(s) = s/(1+s)$. Calculating the derivative of V_1 along the positive solutions of (4.13), we obtain

$$\begin{aligned} \dot{V}_1 &\leq -(x - x^*)^2 - \frac{a(\nu - a)(u - u^*)^2}{(1+u)^2(1+u^*)^2} \\ &\quad - \frac{a\nu(u - u^*)}{x(1+u)(1+u^*)} \int_{t-\tau}^t \frac{1}{(1+u)^2} \\ &\quad \times \left\{ -dx(s)(u(s) - u^*) - du^*(x(s) - x^*) \right. \\ &\quad + \frac{\nu u(s - \tau)(1+u^*)(x(s - \tau) - x^*) + \nu x^*(u(s - \tau) - u^*)}{(1+u(s - \tau))(1+u^*)} \\ &\quad \left. + u^2(s)x(s) \left(-(x(s) - x^*) - \frac{a(u(s) - u^*)}{(1+u(s))(1+u^*)} \right) \right\} ds \\ &\leq -(x - x^*)^2 - \frac{a(\nu - a)(u - u^*)^2}{(1+u)^2(1+u^*)^2} + \frac{\nu a}{x(1+u^*)} \\ &\quad \times \left\{ \frac{3\tau(u - u^*)^2}{(1+u)^2} + \int_{t-\tau}^t \left[\frac{u^4(s)x^2(s)(x(s) - x^*)^2}{2(1+u(s))^4} \right. \right. \\ &\quad + \frac{a^2u^4(s)x^2(s)(u(s) - u^*)^2}{2(1+u(s))^6(1+u^*)^2} + \frac{d^2(u^*)^2(x(s) - x^*)^2}{2(1+u(s))^4} \\ &\quad + \frac{d^2x^2(s)(u(s) - u^*)^2}{2(1+u(s))^4} \\ &\quad + \frac{\nu^2(x^*)^2(u(s - \tau) - u^*)^2}{2(1+u(s - \tau))^2(1+u^*)^2(1+u(s))^4} \\ &\quad \left. \left. + \frac{\nu^2(x(s - \tau) - x^*)^2}{2(1+u(s))^4} \right] ds \right\}. \end{aligned}$$

Set

$$\begin{aligned}
 V_2 = & \frac{\nu a}{x_l(1+u^*)} \\
 & \times \int_{t-\tau}^t \left\{ \int_s^t \left[\frac{u^4(\theta)x^2(\theta)(x(\theta)-x^*)^2}{2(1+u(\theta))^4} \right. \right. \\
 & + \frac{a^2u^4(\theta)x^2(\theta)(u(\theta)-u^*)^2}{2(1+u(\theta))^6(1+u^*)^2} \\
 & + \frac{d^2(u^*)^2(x(\theta)-x^*)^2}{2(1+u(\theta))^4} + \frac{d^2x^2(\theta)(u(\theta)-u^*)^2}{2(1+u(\theta))^4} \\
 & + \frac{\nu^2(x^*)^2(u(\theta-\tau)-u^*)^2}{2(1+u(\theta-\tau))^2(1+u^*)^2(1+u(\theta))^4} \\
 & \left. \left. + \frac{\nu^2(x(\theta-\tau)-x^*)^2}{2(1+u(\theta))^4} \right] d\theta \right\} ds,
 \end{aligned}$$

where $x_l = 1 - a - \epsilon$. If $a < 1$ and $\epsilon > 0$ is sufficiently small, it is easy to see that $1 \geq x(t) \geq x_l$ when t is sufficiently large. As a consequence, we have

$$\begin{aligned}
 (V_1 + V_2)' \leq & -(x - x^*)^2 \left(1 - \frac{\nu a \tau (1 + d^2(u^*)^2)}{2x_l(1+u^*)} \right) \\
 & + \frac{a\nu^3\tau}{2x_l(1+u^*)} (x(t-\tau) - x^*)^2 - \frac{(u - u^*)^2}{(1+u)^2(1+u^*)^2} \\
 & \times \left[a(\nu - a) - \frac{a\nu(1+u^*)\tau}{x_l} \left(\frac{a^2}{2(1+u^*)^2} + \frac{d^2+6}{2} \right) \right] \\
 & + \frac{a\nu^3\tau(x^*)^2}{2x_l(1+u^*)^3} \frac{(u(t-\tau) - u^*)^2}{(1+u(t-\tau))^2}.
 \end{aligned}$$

Set

$$\begin{aligned}
 V_3 = & \frac{\tau a \nu^3}{2x_l(1+u^*)} \\
 & \times \int_{t-\tau}^t \left[(x(\theta) - x^*)^2 + (x^*)^2 \frac{(u(\theta) - u^*)^2}{(1+u^*)^2(1+u(\theta))^2} \right] d\theta.
 \end{aligned}$$

Then we obtain

$$\begin{aligned}
 & (V_1 + V_2 + V_3)' \\
 & \leq -(x - x^*)^2 \left[1 - \frac{\nu a \tau (1 + d^2 (u^*)^2)}{2x_l (1 + u^*)} - \frac{\tau a \nu^3}{2x_l (1 + u^*)} \right] \\
 & \quad - \frac{a(u - u^*)^2}{(1 + u)^2 (1 + u^*)^2} \\
 & \quad \times \left[\nu - a - \frac{\tau \nu^3 (x^*)^2}{2x_l (1 + u^*)} - \frac{\nu \tau (1 + u^*)}{2x_l} \left(\frac{a^2}{(1 + u^*)^2} + d^2 + 6 \right) \right].
 \end{aligned}$$

Note that Theorem 2.2 implies that u is bounded since we assume $a < 1$. We are able to state the following result.

THEOREM 4.2. *Let (\hat{H}) hold. Assume further that*

- (i) $\tau < \frac{2x_l}{ad(1 + (\nu - d)^2 + \nu^2)},$
- (ii) $\tau d[(d^2 + 6)\nu^2/d^2 + \nu^2(x^*)^2 + a^2] < 2(1 - a)(\nu - a).$

Then, the positive equilibrium of (1.4) is globally stable.

This theorem essentially means that $a < 1$, $a < \nu$ with small τ imply that the positive equilibrium is globally stable.

5. DISCUSSIONS

In this paper, we have incorporated the stage structure of a predator into a classical predator-prey model and analyzed its global dynamics. We have obtained thresholds between the permanence and extinction of populations in Theorem 2.4 and Theorem 2.6. Our results indicate that the capture rate a_2 plays an important role in determining the permanence of the populations. This is quite different from its counterpart of the classical predator-prey model with a Holling type-II response functional and without time delay,

$$\begin{aligned}
 x' &= x \left[r - a_1 x - \frac{a_2 z}{1 + mx} \right], \\
 z' &= z \left[\frac{b_1 z}{1 + mx} - c \right].
 \end{aligned}$$

It is well known that this system is permanent if $c < b_1 r / (a_1 + mr)$, which is independent of the capture rate a_2 . It is also found that the duration length of juvenile individuals plays an important role for the permanence. First, this can be seen from Theorem 2.1 and Theorem 2.2. Suppose $a_2 < rm$, $b_1 > c$. Since $a < 1$ is equivalent to $a_2 < rm$, and $\nu > d$ is equivalent to $c < b_1 \exp(-b_2 \tau')$, it follows from Theorem 2.1 and Theorem 2.2 that it remains permanent if the length of duration of a juvenile predator lies in $(0, \ln(b_1/c)/b_2)$ and that an adult predator (thus, a juvenile predator) goes to extinction if it lies in $(\ln(b_1/c)/b_2, \infty)$. Second, the negative effect of the duration length of a juvenile predator for the permanence of the model can be seen from the following example.

EXAMPLE 1. Suppose $r = c = m = 1$, $a_2 = 1.6$, $b_1 = 1.5$, and $b_2 = 0.01$. Then $a = 1.6$, $\tau = \tau'$, $d = 1$, and $\nu = 1.5e^{-0.01\tau}$. Let us check the conditions of Theorem 2.4. It is evident that $1 < a < 1 + d$. Moreover, it is easy to see that $\nu > d$ if $\tau < \ln(1.5)/0.01$, and $a < \frac{\nu}{\nu-d}$ as long as $0 \leq \tau < \ln(1.5)/0.01$. Let us now check conditions (i), (ii), and (iii) in Theorem 2.4. It is easy to see that $\nu[1 + \tau(1 - a)] < a$ for all $\tau \geq 0$ (condition (i) of Theorem 2.4 cannot be satisfied). Furthermore, $a \exp(-\tau(a - 1)) > \nu$ when $0 \leq \tau < 0.109$, which shows that Condition (ii) of Theorem 2.4 is satisfied in this case. Moreover, we have $a \exp(-\tau(a - 1)) < \nu$ when $\tau > 0.109$. When $\tau > 0.109$, by numerical calculations we see that $g(\bar{x}) < 0$ for $0.109 < \tau < 2.975$, where \bar{x} is the unique root of $g'(x)$ in $(1, a)$, which shows that Condition (iii) in Theorem 2.4 is satisfied. Further, we have $g(\bar{x}) > 0$ for $2.975 < \tau < \ln(1.5)/0.01$, which shows that Condition (iii) in Theorem 2.6 is satisfied. Consequently, Theorem 2.4 and Theorem 2.6 imply that the populations remain permanent if $0 \leq \tau < 0.109$ and $0.109 < \tau < 2.975$, and the prey (therefore, the predator) goes to extinction for some initial values when $2.975 < \tau < \ln(1.5)/0.01$. Finally, if $\tau > \ln(1.5)/0.01$, we have $\nu < d$. Then Theorem 2.1 shows that the adult predator goes to extinction.

From local stability analysis, we see that the delay is also a destabilizing factor. Theorem 3.2 shows that the local stability of the positive equilibrium can be changed due to an increase of the delay.

Since

$$a^* = b_1 \exp(-b_2 \tau')(c + b_1 \exp(-b_2 \tau')) / \\ [(-c + b_1 \exp(-b_2 \tau'))(3c + b_1 \exp(-b_2 \tau'))]$$

and $a = a_2/(rm)$, Theorem 3.3 states that the positive equilibrium is stable if

$$a_2 < rmb_1 \exp(-b_2 \tau')(c + b_1 \exp(-b_2 \tau')) / \\ [(-c + b_1 \exp(-b_2 \tau'))(3c + b_1 \exp(-b_2 \tau'))].$$

Note that

$$\begin{aligned} & \nu(d\nu + \nu - d^2)/((\nu - d)(d + \nu)) \\ &= b_1 \exp(-b_2 \tau') (cb_1 \exp(-b_2 \tau') + b_1 \exp(-b_2 \tau') r - c^2) / \\ & \quad [r(-c + b_1 \exp(-b_2 \tau'))(c + b_1 \exp(-b_2 \tau'))] \end{aligned}$$

and $\nu/(\nu - d) = b_1 \exp(-b_2 \tau') / (b_1 \exp(-b_2 \tau') - c)$. Theorem 3.2 indicates that the positive equilibrium is stable if

$$\begin{aligned} & a_2 < rmb_1 \exp(-b_2 \tau') / (b_1 \exp(-b_2 \tau') - c), \\ & a_2 < rmb_1 \exp(-b_2 \tau') (cb_1 \exp(-b_2 \tau') + b_1 \exp(-b_2 \tau') r - c^2) / \\ & \quad [r(-c + b_1 \exp(-b_2 \tau'))(c + b_1 \exp(-b_2 \tau'))] \end{aligned}$$

and the length of delay is small. From these results, we see that the capture rate a_2 is limited from above to maintain the local stability of the positive equilibrium.

Global stability is an interesting topic for population ecology (see the papers [15–17, 20, 21]). We have obtained two types of sufficient conditions for the global stability of (1.4). Theorem 4.2 is one of these obtained by controlling the length of the delay directly. Since (4.1) is equivalent to

$$a_2 < rmb_1^2 \exp(-2b_2 \tau') / [(-c + b_1 \exp(-b_2 \tau'))(b_1 \exp(-b_2 \tau') + 2c)],$$

conditions in Theorem 4.1 have much less restriction to their length of delay. It can be long as long as the birth rate of adults is large or the death rate of juvenile predators is small. Theorem 3.3 is a counterpart of Theorem 4.1 in the local stability case. By comparison, we see that the parameter region for global stability of the positive equilibrium is near to its local stability region if the death rate c of adult predators is small.

An interesting observation is that the stability conditions and permanence conditions for (1.1) are independent of the density-dependent coefficient a_1 . This indicates that the coefficient does not influence the qualitative behavior of the model. This behavior is quite different from that in the classical predator-prey model.

In this paper we have assumed that an immature predator does not have the ability to attack prey. We will consider the case where immature predators can feed on prey in future work.

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REFERENCES

1. J. R. Bence and R. M. Nisbet, Space-limited recruitment in open systems: The importance of time delays, *Ecology* **70** (1989), 1434–1441.
2. W. G. Aiello and H. I. Freedman, A time-delay model of single-species growth with stage-structure, *Math. Biosci.* **101** (1990), 139–153.
3. H. I. Freedman and J. H. Wu, Persistence and global asymptotic stability of single species dispersal models with stage structure, *Quart. Appl. Math.* **49** (1991), 351–371.
4. W. G. Aiello, H. I. Freedman, and J. H. Wu, Analysis of a model representing stage-structured population growth with stage-dependent time delay, *SIAM J. Appl. Math.* **52** (1992), 855–869.
5. Y. Kuang and J. W. H. So, Analysis of a delayed two-stage population with space-limited recruitment, *SIAM J. Appl. Math.* **55** (1995), 1675–1695.
6. F. Brauer and Ma Zhien, Stability of stage-structured population models, *J. Math. Anal. Appl.* **126** (1987), 301–315.
7. W. Wang and Chen Lansun, A predator–prey system with stage-structure for predator, *Comput. Math. Appl.* **33** (1997), 83–91.
8. K. G. Magnusson, Destabilizing effect of cannibalism on a structured predator–prey system, *Math. Biosci.* **155** (1999), 61–75; Dimensional population models, *Math. Biosci.* **102** (1990), 121–124.
9. F. Salemi, V. Salone, and W. Wang, Stability of a competition model with two-stage structure, *Appl. Math. Comput.* **99** (1999), 221–231.
10. Y. Kuang and E. Beretta, Global qualitative analysis of a ratio-dependent predator–prey systems, *J. Math. Biol.* **36** (1998), 389–406.
11. E. Beretta and Y. Kuang, Global analysis in some delayed ratio-dependent predator–prey system, *Nonlinear Anal.* **32** (1998), 381–408.
12. J. K. Hale and S. M. V. Lunel, “Introduction to Functional Differential Equations,” Springer-Verlag, New York/Berlin, 1993.
13. H. L. Smith, Monotone semiflows generated by functional differential equations, *J. Differential Equations* **66** (1987), 420–442.
14. Y. Kuang, “Delay Differential Equations with Applications in Population Dynamics,” Academic Press, Boston, 1993; Systems governed by difference equations of Lotka–Volterra type, *J. Math. Biol.* **25** (1987), 553–570.
15. W. Wang and Ma Zhien, Asymptotic behavior of a predator–prey system with diffusion and delays, *J. Math. Anal. Appl.* **206** (1997), 191–204.
16. W. Wang, P. Fergola, and C. Tenneriello, Global attractivity of periodic solutions of population models, *J. Math. Anal. Appl.* **211** (1997), 498–511.
17. W. Wang, Chen Lansun, and Lu Zhengyi, Global stability of a competition model with periodic coefficients and time delays, *Canad. Appl. Math. Quart.* **3** (1995), 365–378.
18. R. D. Holt, Population dynamics in two patch environment: Some anomalous consequences of optional habitat selection, *Theoret. Popul. Biol.* **28** (1985), 181–208.
19. H. L. Smith, “Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems,” Math. Surveys Monographs, Vol. 41, American Mathematical Society, Providence, RI, 1995.
20. Ruan Shigui and He Xuezhong, Global stability in chemostat-type competition models with nutrient recycling, *SIAM J. Appl. Math.* **58** (1998), 170–192.
21. He Xuezhong and Ruan Shigui, Global stability in chemostat-type equations with distributed delays, *SIAM J. Math. Anal.* **29** (1998), 681–696.