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GLOBAL DYNAMICS OF A PREDATOR-PREY MODEL WITH STAGE STRUCTURE FOR THE PREDATOR*

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Abstract. The global properties of a predator-prey model with nonlinear functional response and stage structure for the predator are studied using Lyapunov functions and LaSalle's invariance principle. It is found that, under hypotheses which ensure the uniform persistence of the system and the existence of a unique positive steady state, a feasible a priori lower bound condition on the abundance of the prey population ensures the global asymptotic stability of the positive steady state. A condition which leads to the extinction of the predators is indicated. We also obtain results on the existence and stability of periodic solutions. In particular, when (4.2) fails to hold and the unique positive steady state E^* becomes unstable, the coexistence of prey and predator populations is ensured for initial populations not on the one-dimensional stable manifold of E^*, albeit with fluctuating population sizes.

Key words. predator-prey model, stage structure, global stability, uniform persistence, Lyapunov function

AMS subject classifications. 92D25, 92D30, 34D20, 34D23, 93D20

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1. Introduction.

In classical models of Lotka–Volterra type it is assumed that all individuals of a single species have largely similar capabilities to hunt or reproduce. However, the life cycle of most, if not all, animals and insects consists of at least two stages, immature and mature, and the individuals in the first stage often can neither hunt nor reproduce, being raised by their mature parents. Furthermore, immediately recognizable morphological and behavioral differences may exist between these stages and other adaptive stages, such as dormancy stages for immediate survival purposes.

To study this situation theoretically, stage-structured models have attracted much attention in recent decades. Fundamental work towards a systematic approach to stage-structured model formulation has been made by Gurney, Nisbet, and Blythe [7], Nisbet and Gurney [27], and Nisbet, Gurney, and Metz [28]. Further progress has been made by Aiello and Freedman, who proposed and studied in their often quoted work [1] a single species model with stage structure and discrete delay, predicting the global attractivity of the positive steady state and thereby suggesting that the stage structure does not generate sustained oscillations, at least for a single species model. General consistency criteria to be satisfied by models which describe stage-structured ecological interactions have been laid out in Kuang [18] or Arditi and Michalski [2]. See also Liu, Chen, and Agarwal [24] for a recent survey on the dynamics of stage-structured population models with an emphasis on modeling issues.

Predator-prey models with stage structure for the predator have received considerable attention in recent years. See Wang [35] and Xiao and Chen [38] for global

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stability and persistence analysis of a stage-structured predator-prey model without delay terms. See also Wang and Chen [36], Wang et al. [37], and Gourley and Kuang [9] for stability analyses of staged predator-prey models with time delays due to gestation of the predator and crowding of the prey.

Apart from analyzing the stability of their delayed model, Gourley and Kuang [9] also discussed its oscillatory dynamics for a linear functional response of the mature predator and observed that sustained oscillations took place only for a limited interval of maturation delays. This happens since, for small delays, their model inherits the properties of the nondelayed (of Lotka–Volterra type) system. However, if the maturation delay is too long, then the highest possible recruitment rate to adulthood drops below the adult death rate and the predator population dies out.

As far as the asymptotic behavior of predator-prey systems is concerned, it is known from Poincaré–Bendixson theory that two-dimensional continuous time models can approach either an equilibrium state or a limit cycle with any type of chaotic behavior being excluded, while three- and higher-dimensional models can exhibit more complex behavior. In this regard, staged models may provide in some situations a richer dynamics which leads to a better understanding of the interactions within the biological system under consideration. Such models may also incorporate meaningful biological parameters, such as different death rates for mature and immature predators and various delay effects.

In [36], [35], [38] the following predator-prey model with stage structure for the predator has been considered:

$$
\begin{cases}
x'(t) = x(t)\left(r - ax(t)\right) - \dfrac{bx(t)}{1+mx(t)} y_2(t), \\
y_1'(t) = k\dfrac{bx(t)}{1+mx(t)} y_2(t) - (D+d_1)y_1(t), \\
y_2'(t) = Dy_1(t) - d_2 y_2(t).
\end{cases}
\tag{1.1}
$$

Here $x(t)$, $y_1(t)$, $y_2(t)$ are the densities of prey, respectively of immature and mature predators at time t. It is assumed that in the absence of the predators the prey grows according to a logistic law with intrinsic growth rate r and carrying capacity r/a, while predators feed on prey only and do not count towards the carrying capacity. It is also assumed that the immature predators are either raised by their parents or consume a resource which is available in abundance and for which they do not have to compete. As a consequence, neither crowding nor intraspecies competition terms are added into the equation which models the growth of the immature predator class. The function $x \mapsto bx/(1+mx)$ represents the Holling type 2 functional (behavioral) response of the mature predator, which describes how the consumption rate of the predator depends on prey density, b being the search rate and m being the search rate multiplied by the handling time; while the function $x \mapsto kbx/(1+mx)$ is the associated numerical (reproductive) response of the mature predator which quantifies the relation between the numerical growth of the predator class and the prey consumption, with k representing the conversion coefficient under the assumption that the reproduction rate of the mature predators is directly proportional to the amount of prey consumed. The constants d_1 and d_2 represent the death rates of immature and mature predators, and D denotes the rate at which immature predators become mature predators.

It was proved in Wang [35] that if the condition

$$
d_2(D+d_1) < \frac{kbrD}{a+mr}
\tag{1.2}
$$

holds, then the system (1.1) is uniformly persistent and a unique positive steady state $E^* = (x^*, y_1^*, y_2^*)$ exists. Moreover, it is shown that if, in addition to (1.2), conditions

$$x^*(D+d_1+d_2)(a+2max^*-mr)\left(D+d_1+d_2+\frac{x^*(a+2max^*-mr)}{1+mx^*}\right) > \frac{by_2^* d_2(D+d_1)}{1+mx^*}, \tag{1.3}$$

$$a > b + \frac{bmy_2^*}{1+mx^*}, \quad D+d_1 > \frac{kbr}{a+mr} + \frac{kby_2^*}{1+mx^*}, \quad d_2 > D, \tag{1.4}$$

are also satisfied, then the positive steady state $E^* = (x^*, y_1^*, y_2^*)$ is globally asymptotically stable. The proof uses the theory of competitive systems as developed in Smith [33], with condition (1.3) being used to establish the local stability of E^*.

More recently, Xiao and Chen [38] noted that condition (1.4) contradicts condition (1.2), and showed that the positive steady state E^* is globally asymptotically stable if (1.2) and (1.3) hold, in addition to one of the following two conditions:

$$\text{(H1) } D+d_1 > r \text{ and } \underline{x} > \frac{r}{2a}; \qquad \text{(H2) } D+d_1 < r \text{ and } \underline{x} > \frac{r+D+d_1}{2a}.$$

Here $\underline{x} > 0$ is the persistency constant for x, which satisfies $\underline{x} \leq \liminf_{t\to\infty} x(t)$. The proof is again based on the theory of competitive systems and uses a result given by Li and Muldowney in [23], which amounts to the fact that for competitive and permanent systems which are defined on convex and bounded sets and have the property of stability of periodic orbits, the local asymptotic stability of a unique positive steady state implies its global asymptotic stability. Essentially, the proof in [38] amounts to showing that the system (1.1) has the property of the stability of periodic orbits under either (H1) or (H2), a fact which is established using a criterion of Muldowney [26] and the theory of additive compound matrices.

Consider the conditions (1.3), (H1), and (H2). It is clear that if the inequality $\underline{x} > (r+D+d_1)/(2a)$, which is required in (H2), can be weakened to $\underline{x} > r/(2a)$ and either (H1) or (H2) can be modified to cover the case $D+d_1 = r$, then (H1) and (H2) can be combined into a single condition $\underline{x} > r/(2a)$, where $r/(2a)$ is the prey population size at the inflection point of the logistic curve in a prey-only system. Moreover, condition (1.3), which a priori ensures the local stability of the positive steady state, was motivated by specifics of the method used for the proof, which roughly inputs local asymptotic stability and outputs global asymptotic stability under certain assumptions.

However, it is clear that once the global asymptotic stability of the positive steady state is proved, then its local asymptotic stability is superseded anyway. Moreover, we shall indicate in section 4 that in fact (1.3) is satisfied if $x^* > r/(2a)$ (and consequently if $\underline{x} > r/(2a)$), and so there is no need to assume (1.3) separately.

In this article, we will study the global dynamics of (1.1) by constructing a suitable Lyapunov function and using LaSalle's invariance principle rather than by using the theory of competitive systems, as has been done in [35] and [38]. This will enable us to obtain the global asymptotic stability of the positive steady state under weaker hypotheses than those used in Xiao and Chen [38] and by a simpler method. In our setting, the persistence condition $\underline{x} > r/(2a)$ used in [38] will appear in a natural way as a monotonicity condition. We will also discuss in section 4 the existence of periodic solutions, together with their stability. Finally, we will discuss the biological significance of our results and indicate possible extensions to the study of more comprehensive models in section 5.

2. The model and its well-posedness. In this section we analyze the global existence of the solutions of (1.1) and their positivity properties.

Let us define $n : [0, \infty) \to \mathbb{R}$ and $f : [0, \infty) \to [0, \infty)$ by $n(x) = x(r - ax)$ and $f(x) = bx/(1 + mx)$ for all $x \in [0, \infty)$. Using the newly defined functions n and f we can rewrite (1.1) as

$$\begin{cases} x' = n(x) - f(x)y_2, \\ y_1' = kf(x)y_2 - (D + d_1)y_1, \\ y_2' = Dy_1 - d_2y_2. \end{cases} \tag{2.1}$$

Note that n is strictly decreasing on $[r/(2a), +\infty)$, while f is strictly increasing on $[0, \infty)$.

First, it is easy to see that if $x(0)$, $y_1(0)$, $y_2(0) \geq 0$, then $x(t), y_1(t), y_2(t) \geq 0$ on their respective intervals of existence. For this purpose, we observe that the vector (R_1, R_2, R_3) points inside the closed set $Q_1 = [0, \infty)^3$ at all points of ∂Q_1, where R_1, R_2, R_3 are the right-hand sides appearing in (1.1), and so Nagumo's tangency conditions are satisfied and Q_1 is a positively invariant set for (1.1). See Pavel [29] for further reference on flow invariance problems for ODEs and abstract ODEs.

To prove that $Q_2 = (0, \infty)^3$ is also a positively invariant set for (1.1), suppose that $x(0), y_1(0), y_2(0) > 0$ and note first that $\frac{d}{dt}(y_2 e^{d_2 t}) = Dy_1 e^{d_2 t} \geq 0$, and so $t \mapsto y_2(t)e^{d_2 t}$ is increasing. It follows that $y_2(t) \geq y_2(0)e^{-d_2 t}$ for all t for which $y_2(t)$ is well defined, and hence y_2 remains strictly positive. Also, $\frac{d}{dt}(y_1 e^{(D+d_1)t}) \geq 0$, consequently, $y_1(t) \geq y_1(0)e^{-(D+d_1)t}$ and y_1 remains strictly positive. To prove that x also remains strictly positive, suppose that $x(t_0) = 0$ for some $t_0 > 0$. Then one may find $\tilde{y_1}(0)$ and $\tilde{y_2}(0) > 0$ such that the solution which starts at $t = 0$ from $(0, \tilde{y_1}(0), \tilde{y_2}(0))$ also reaches $(0, y_1(t_0), y_2(t_0))$ at $t = t_0$. By the uniqueness property of (1.1), this solution should coincide with the solution which starts at $t = 0$ from $(x(0), y_1(0), y_2(0))$, which is an obvious contradiction.

We shall now show that x, y_1, y_2 are bounded on their intervals of existence, which in turn will imply by a standard continuability argument that they are defined on $[0, \infty)$. Denote $M_1 = \max(r/a, x(0))$ and $d = \min(d_1, d_2)$. Since $x' \leq x(r - ax)$, it follows that $x(t) \leq M_1$ for all t. That is, x is bounded and consequently defined on $[0, \infty)$. Let us consider the Lyapunov function

$$U(x, y_1, y_2) = x + (1/k)y_1 + (1/k)y_2.$$

We now compute the time derivative of U along the solutions of (1.1). One then has

$$\dot{U} = n(x) - \frac{d_1}{k}y_1 - \frac{d_2}{k}y_2,$$

which implies

$$\dot{U} + dU \leq (r + d)x.$$

Consequently,

$$U(x(t), y_1(t), y_2(t)) \leq U(x(0), y(0), z(0))e^{-dt} + \frac{M_1(r + d)}{d}\left(1 - e^{-dt}\right) \quad \text{for all } t.$$

This implies that y_1, y_2 are also bounded and consequently defined on $[0, \infty)$. Finally, we analyze the behavior of solutions which start with initial data (x_i, y_{1i}, y_{2i}) on the boundary of $(0, \infty)^3$.

If $x_i = 0$, then $(x(t), y_1(t), y_2(t)) \to (0, 0, 0)$ irrespective of the initial values $y_{1i}, y_{2i} \geq 0$. If $x_i > 0$, then $(x(t), y_1(t), y_2(t)) \to (r/a, 0, 0)$ for $y_{1i} = y_{2i} = 0$, while $(x(t), y_1(t), y_2(t))$ enters $(0, \infty)^3$ (and stays there) otherwise.

3. Global dynamics of the model. In this section we perform a global stability analysis for the system (1.1) regarding both the stability of the boundary equilibrium $(r/a, 0, 0)$ (i.e., the case in which the predator classes tend to extinction) and of the positive steady state (x^*, y_1^*, y_2^*) (i.e., the case in which the coexistence of both species is assured for all future time). As a result, we find sufficient conditions for the stability of the equilibria and establish the existence of a threshold parameter.

Let us denote $T = d_2(D + d_1)/D$ and $x_0 = r/a$. First, we give a condition for the extinction of the predators.

Theorem 3.1. *Suppose that* $T \geq kf(x_0)$. *Then* $(x_0, 0, 0)$ *is globally asymptotically stable on* $(0, \infty)^3$.

Proof. Let us consider the Lyapunov function

$$U_1(x, y_1, y_2) = \int_{x_0}^{x} \frac{f(\tau) - f(x_0)}{f(\tau)} d\tau + \frac{1}{k} y_1 + \frac{1}{k} \frac{D + d_1}{D} y_2.$$

We now compute the time derivative of U_1 along the solutions of (1.1). One then has

$$\begin{aligned} \dot{U}_1 &= \frac{f(x) - f(x_0)}{f(x)} \left(n(x) - f(x) y_2\right) + \frac{1}{k} \left(kf(x) y_2 - (D + d_1) y_1\right) \\ &\quad + \frac{1}{k} \frac{D + d_1}{D} \left(D y_1 - d_2 y_2\right) \\ &= \frac{f(x) - f(x_0)}{f(x)} n(x) + \frac{1}{k} \left(kf(x_0) - \frac{(D + d_1) d_2}{D} \right) y_2. \end{aligned}$$

Since c is strictly increasing on $[0, \infty)$ and $\operatorname{sgn} n(x) = \operatorname{sgn}(x_0 - x)$ for $x \in (0, \infty)$, it is seen that $\dot{U}_1 \leq 0$, with equality if and only if $x = x_0$ and either $y_2 = 0$ or $T = kf(x_0)$. In both cases, the only invariant subset $\tilde{M}$ within the set $M = \{(x, y_1, y_2); x = x_0\}$ is $\tilde{M} = \{(x_0, 0, 0)\}$.

Since $\dot{U}_1 \leq 0$ on $(0, \infty)^3$ and the only possible ω-limit sets of $(x(t), y_1(t), y_2(t))$ on the boundary of $(0, \infty)^3$ are $\{(x_0, 0, 0)\}$ and $\{(0, 0, 0)\}$, our conclusion follows from LaSalle's invariance principle (see [22]). □

We now attempt to analyze the existence of the positive steady state E^* and the uniform persistence of the system (1.1). We recall that the system (1.1) is said to be *uniformly persistent* if there is $\varepsilon_0 > 0$ such that any solution of (1.1) which starts with $x(0), y_1(0), y_2(0) > 0$ satisfies

$$\liminf_{t \to \infty} x(t) \geq \varepsilon_0, \quad \liminf_{t \to \infty} y_1(t) \geq \varepsilon_0, \quad \liminf_{t \to \infty} y_2(t) \geq \varepsilon_0.$$

For other (weaker) types of persistence and criteria to establish the persistence of a given system, see Butler, Freedman, and Waltman [4], Freedman, Ruan, and Tang [6], and Hofbauer and So [11].

Theorem 3.2. *Suppose that* $T < kf(x_0)$. *Then the positive steady state* E^* *exists, is unique, and the system* (1.1) *is uniformly persistent.*

Proof. Let us consider the Lyapunov function

$$U_2(x, y_1, y_2) = \frac{1}{k} y_1 + \frac{1}{k} \frac{D + d_1}{D} y_2.$$

We now compute the time derivative of U_2 along the solutions of (1.1). One then has

$$\begin{aligned}\dot{U_2} &= \frac{1}{k}(kf(x)y_2 - (D+d_1)y_1) + \frac{1}{k}\frac{D+d_1}{D}(Dy_1 - d_2y_2)\\ &= \left(f(x) - \frac{(D+d_1)d_2}{kD}\right)y_2.\end{aligned}$$

If $T < kf(x_0)$, then $\dot{U_2}$ is positive in all strictly positive points of a vicinity of $(x_0, 0, 0)$, and so $(x_0, 0, 0)$ is unstable. Since the only invariant subsets on the boundary of $(0,\infty)^3$ are $\{(x_0, 0, 0)\}$ and $\{(0, 0, 0)\}$ and their stable manifolds are also contained in the boundary of $(0,\infty)^3$, it follows from a result of Hofbauer and So [11] that the system (1.1) is uniformly persistent. Also see Margheri and Rebelo [25] for a slightly different approach towards showing the persistence of dynamical systems based on a result of Fonda [5], which establishes necessary and sufficient conditions for a given compact set S to be a uniform repeller.

To show the existence of E^*, we need to find positive solutions for the system

$$\begin{cases} x^*(r - ax^*) - \dfrac{bx^*}{1+mx^*}y_2^* = 0,\\ k\dfrac{bx^*}{1+mx^*}y_2^* - (D+d_1)y_1^* = 0,\\ Dy_1^* - d_2y_2^* = 0. \end{cases} \tag{3.1}$$

After some algebraic manipulations, one obtains

$$x^* = \frac{(D+d_1)d_2}{bkD - m(D+d_1)d_2}, \quad y_1^* = \frac{x^*(r-ax^*)k}{(D+d_1)}, \quad y_2^* = \frac{x^*(r-ax^*)kD}{(D+d_1)d_2}. \tag{3.2}$$

Since $d_2(D+d_1)/D < kbr/(a+mr)$, it follows that $bkD/((D+d_1)d_2) > (a+mr)/r$, and so $x^* < r/a$. From the above, it also follows that $bkD/((D+d_1)d_2) > m$, and hence $x^* > 0$. Consequently, x^*, y_1^*, y_2^* are all well defined and positive. We also remark that since the system (1.1) is uniformly persistent, it follows that there is an $\underline{x} > 0$ such that $\liminf_{t\to\infty} x(t) \geq \underline{x}$. ☐

From Theorems 3.1 and 3.2, combined with the remark about the behavior of the solutions starting on the boundary of $[0,\infty)^3$ which was made at the end of section 2, it also follows that $(0, 0, 0)$ is an unstable equilibrium and its stable manifold consists of the positive quadrant $\{(0, y_{1i}, y_{2i}); y_{1i}, y_{2i} \geq 0\}$. That is, our model predicts that the predator and the prey cannot simultaneously face extinction, with the sole exception of the case in which the size of the initial prey populations equals zero, justified by the fact that the predators feed on prey only and do not consume other resource, and therefore in the absence of prey they are condemned to extinction.

Having established the existence and uniqueness of the positive steady state E^*, we now turn our attention to its stability. For this purpose, we employ a condition on the persistence constant $\underline{x}$, which ensures that the size of the prey population remains ultimately higher than a certain value.

THEOREM 3.3. *Suppose that* $T < kf(x_0)$ *and* $\underline{x} > r/(2a)$. *Then the positive steady state* E^* *is globally asymptotically stable on* $(0,\infty)^3$.

Proof. Since $\underline{x} > r/(2a)$, it is seen that there is $t_0 \geq 0$ such that $x(t) > r/(2a)$ for all $t \geq t_0$ and also that $x^* > r/(2a)$. Let us consider the Lyapunov function

$$U_3(x, y_1, y_2) = \int_{x^*}^{x} \frac{f(\tau) - f(x^*)}{f(\tau)}d\tau + \frac{1}{k}\int_{y_1^*}^{y_1} \frac{\tau - y_1^*}{\tau}d\tau + \frac{1}{k}\frac{D+d_1}{D}\int_{y_2^*}^{y_2} \frac{\tau - y_2^*}{\tau}d\tau.$$

It is easily seen that $U_3(x, y_1, y_2) \geq 0$ and $U_3(x, y_1, y_2) = 0$ if and only if $x = x^*$, $y_1 = y_1^*$, $y_2 = y_2^*$. We now compute the time derivative of U_3 along the solutions of (1.1). One obtains that

$$\begin{aligned}
\dot{U_3} &= \frac{f(x) - f(x^*)}{f(x)}\left(n(x) - f(x)y_2\right) + \frac{1}{k}\frac{y_1 - y_1^*}{y_1}\left(kf(x)y_2 - (D + d_1)y_1\right) \\
&\quad + \frac{1}{k}\frac{D + d_1}{D}\frac{y_2 - y_2^*}{y_2}\left(Dy_1 - d_2y_2\right) \\
&= n(x)\frac{f(x) - f(x^*)}{f(x)} + f(x^*)y_2 - \frac{D + d_1}{k}y_1^*\left(\frac{f(x)}{f(x^*)}\frac{y_2}{y_2^*}\frac{y_1^*}{y_1} + \frac{y_2^*}{y_2}\frac{y_1}{y_1^*} + \frac{f(x^*)}{f(x)} - 3\right) \\
&\quad + \frac{D + d_1}{k}y_1^*\frac{f(x^*)}{f(x)} - \frac{D + d_1}{k}y_1^* - \frac{D + d_1}{kD}d_2y_2.
\end{aligned}$$

Since $f(x^*) = (D + d_1)d_2/(kD)$, this yields

$$\begin{aligned}
\dot{U_3} &= n(x)\frac{f(x) - f(x^*)}{f(x)} - \frac{D + d_1}{k}y_1^*\left(\frac{f(x)}{f(x^*)}\frac{y_2}{y_2^*}\frac{y_1^*}{y_1} + \frac{y_2^*}{y_2}\frac{y_1}{y_1^*} + \frac{f(x^*)}{f(x)} - 3\right) \\
&\quad + \frac{D + d_1}{k}y_1^*\left(\frac{f(x^*)}{f(x)} - 1\right) \\
&= \frac{1}{f(x)}(n(x) - n(x^*))(f(x) - f(x^*)) \\
&\quad - \frac{D + d_1}{k}y_1^*\left(\frac{f(x)}{f(x^*)}\frac{y_2}{y_2^*}\frac{y_1^*}{y_1} + \frac{y_2^*}{y_2}\frac{y_1}{y_1^*} + \frac{f(x^*)}{f(x)} - 3\right).
\end{aligned}$$

From the *AM-GM* inequality, it is clear that

$$\frac{f(x)}{f(x^*)}\frac{y_2}{y_2^*}\frac{y_1^*}{y_1} + \frac{y_2^*}{y_2}\frac{y_1}{y_1^*} + \frac{f(x^*)}{f(x)} \geq 3,$$

with equality if and only if

$$\frac{f(x)}{f(x^*)}\frac{y_2}{y_2^*}\frac{y_1^*}{y_1} = \frac{y_2^*}{y_2}\frac{y_1}{y_1^*} = \frac{f(x^*)}{f(x)} = 1,$$

that is, $x = x^*$ and $y_1/y_1^* = y_2/y_2^*$.

If $x(t) > r/(2a)$ for $t \geq t_0$, then since n is strictly decreasing on $[r/(2a), \infty)$ and f is strictly increasing on $[0, \infty)$, it follows that

$$\frac{1}{f(x)}(n(x) - n(x^*))(f(x) - f(x^*)) \leq 0,$$

with equality if and only if $x = x^*$. This implies that $\dot{U_3} \leq 0$, with equality if and only if $x = x^*$ and $y_1/y_1^* = y_2/y_2^*$. We now find the invariant subsets $\tilde{M}$ within the set

$$M = \left\{(x, y_1, y_2); x = x^*, \frac{y_1}{y_1^*} = \frac{y_2}{y_2^*}\right\}.$$

Since $x = x^*$ on $\tilde{M}$ and consequently $x' = n(x^*) - f(x^*)y_2$, it follows that $x' = f(x^*)(y_2 - y_2^*)$, and so $y_2 = y_2^*$. This implies $y_1 = y_1^*$, and consequently the only invariant set in M is $\tilde{M} = \{(x, y_1^*, y_2^*)\}$. From LaSalle's invariance principle one then obtains the desired conclusion. $\square$

4. The local stability of the positive steady state and the existence of the periodic solutions. Suppose now that $T < kf(x_0)$ and consequently that the system (1.1) is persistent and the positive steady state E^* exists and is unique. As seen in Wang [35] and Xiao and Chen [38], it is possible to study the local stability of the positive steady state and the existence of the periodic solutions together with their orbital stability by using a result on the behavior of three-dimensional competitive systems established by Zhu and Smith in [39].

It is easy to see that the Jacobian of the system (1.1) at (x, y_1, y_2) is given by

$$J_{(1.1)}(x, y_1, y_2) = \begin{pmatrix} r - 2ax - \frac{b}{(1+mx)^2} y_2 & 0 & -\frac{bx}{1+mx} \\ k\frac{b}{(1+mx)^2} y_2 & -(D+d_1) & \frac{kbx}{1+mx} \\ 0 & D & -d_2 \end{pmatrix}.$$

Using the equilibrium relations (3.1), one finds that the characteristic equation of the system (1.1) at E^* is given by

$$\begin{aligned} \lambda^3 + &\left[D + d_1 + d_2 + x^*\left(2a - \frac{rm+a}{1+mx^*}\right)\right]\lambda^2 \\ &+ x^*\left(2a - \frac{rm+a}{1+mx^*}\right)(D + d_1 + d_2)\lambda + \frac{r - ax^*}{1+mx^*} d_2(D+d_1) = 0. \end{aligned} \tag{4.1}$$

Consequently, by the classical Routh–Hurwitz theorem, all roots of (4.1) have negative real parts if

$$\begin{aligned} &\left[D + d_1 + d_2 + x^*\left(2a - \frac{rm+a}{1+mx^*}\right)\right] x^*\left(2a - \frac{rm+a}{1+mx^*}\right)(D + d_1 + d_2) \\ &\quad > \frac{r - ax^*}{1+mx^*} d_2(D+d_1), \end{aligned} \tag{4.2}$$

and if the reverse of the above inequality is satisfied, then two of the characteristic roots have positive real parts. Note that since $(r - ax^*)/(1 + mx^*)d_2(D + d_1) > 0$, there is always a negative real root of (4.1). It is also important to note that (4.2) is satisfied if $x^* > r/(2a)$. Toward this goal, we remark that if $x^* > r/(2a)$, one has

$$x^*(2a(1 + mx^*) - (rm + a)) = x^*\left(2am\left(x^* - \frac{r}{2a}\right) + a\right) \geq ax^* \geq r - ax^*$$

and

$$\left[D + d_1 + d_2 + x^*\left(2a - \frac{rm+a}{1+mx^*}\right)\right](D + d_1 + d_2) > 4d_2(D + d_1),$$

from which (4.2) results immediately. It then follows that all equilibria E^* with $x^* > r/(2a)$ are locally asymptotically stable. Moreover, a quick inspection of our argument shows that E^* is also stable for some $x^* < r/(2a)$, provided that $x^* > r/(2a) - \tilde{c}/(2m)$, where

$$\tilde{c} = \left(1 + \frac{a}{mr} - \sqrt{1 - \left(1 - \frac{a}{mr}\right)^2 + 4\frac{a}{mr}\frac{d_2(D+d_1)}{(D+d_1+d_2)^2}}\right)\frac{mr}{2a}. \tag{4.3}$$

In particular, this shows that the inequality (4.2), which has been a priori assumed in Xiao and Chen [38] (stated under the equivalent form (1.3)), does actually follow if either (H1) or (H2) are assumed, since $\underline{x} > r/(2a)$ implies $x^* > r/(2a)$, and so there is no need to assume (4.2) separately. Also, it is perhaps interesting to remark that while the inequality $\underline{x} > r/(2a)$ ensures the global stability of E^*, a somewhat similar but weaker estimate $x^* > r/(2a)$ ensures its local stability. We do not know, however, whether or not the inequality $\underline{x} > r/(2a)$ is sharp, that is, if $r/(2a)$ is the smallest constant C with the property that $\underline{x} > C$ ensures the converge of the respective solution of (1.1) to E^*, under the condition $kf(r/a) > T$.

Consider now

$$C = \begin{pmatrix} 1 & 0 & 0 \\ 0 & -1 & 0 \\ 0 & 0 & 1 \end{pmatrix}, \quad S = [0, \infty) \times (-\infty, 0] \times [0, \infty).$$

One then has

$$CJ_{(1.1)}(x, y_1, y_2)C = \begin{pmatrix} r - 2ax - \frac{b}{(1+mx)^2} y_2 & 0 & -\frac{bx}{1+mx} \\ -k\frac{b}{(1+mx)^2} y_2 & -(D + d_1) & -\frac{kbx}{1+mx} \\ 0 & -D & -d_2 \end{pmatrix}.$$

It is then seen that the matrix $CJ_{(1.1)}(x, y_1, y_2)C$ has negative off-diagonal entries for $(x, y_1, y_2) \in S$, and so the system (1.1) is competitive on S. By the previously established persistence and boundedness results, it follows that (1.1) is point dissipative. It is also easy to see that (1.1) is irreducible in S.

Since (1.1) has a unique equilibrium point $E^* = (x^*, y_1^*, y_2^*)$ and

$$\det J_{(1.1)}(x^*, y_1^*, y_2^*) = -\frac{r - ax^*}{1 + mx^*} d_2(D + d_1) < 0,$$

it follows from Theorem 1.2 in Zhu and Smith [39] that either E^* is stable, or, if it is unstable, there is at least one but no more than finitely many periodic orbits and at least one of these is orbitally asymptotically stable. Also, if E^* is stable but not globally stable, then since (1.1) is a three-dimensional competitive system, it follows from Theorem 4.1 in Smith [34, Chapter 3] that (1.1) has a periodic orbit which is necessarily orbitally unstable. Moreover, if E^* is hyperbolic and unstable with a two-dimensional unstable manifold, it follows from Theorem 4.2 in Smith [34, Chapter 3] that the ω-limit of any orbit of (1.1) which does not start on the stable manifold of E^* is a nontrivial periodic orbit. Summarizing the above discussion, one obtains the following result.

THEOREM 4.1. *Suppose that $T < kf(x_0)$ and that E^* is not globally asymptotically stable.*

1. *If either (4.2) or its reverse is satisfied, then E^* is hyperbolic and there is at least a nontrivial periodic orbit. The ω-limit of any orbit with positive initial data is either E^* or a nontrivial periodic orbit.*
2. *If (4.2) is satisfied (which happens in particular when $x^* > r/(2a)$), then the positive equilibrium E^* is locally asymptotically stable and there is at least a periodic orbit which is necessarily orbitally unstable.*
3. *If the reverse of (4.2) is satisfied, then the positive equilibrium E^* is unstable with a two-dimensional unstable manifold and there is at least one but no more than finitely many periodic orbits and at least one of these is orbitally asymptotically stable. Any solution which does not start on the one-dimensional stable manifold of E^* converges to a nontrivial periodic orbit.*

Unfortunately, we are not able to study analytically whether or not the periodic solutions mentioned in parts 2 and 3 above are unique.

5. Concluding remarks. First, we discuss the biological significance of our results. From the above results, we know that $T = d_2(D + d_1)/D$ is a threshold parameter for the stability of the system and that the numerical response of the mature predator plays a major role in the long-term behavior of the system (1.1). More precisely, Theorem 3.1 indicates that if the numerical response of the mature predator for the prey at carrying capacity is lower than the threshold value T, i.e., if few mature predators introduced in a predator-free ambient with prey at carrying capacity cannot reproduce fast enough, the predator classes tend to extinction. Moreover, we can define the basic reproduction number of the system by $R_0 = kf(x_0)\frac{D}{D+d_1}\frac{1}{d_2}$, and then the condition $T \geq kf(x_0)$ is equivalent to $R_0 \leq 1$. This basic reproduction number has a clear biological interpretation: the first term in R_0, $kf(x_0)$, gives the mean number of newborn predators per mature predator; the second term, $\frac{D}{D+d_1}$, gives the probability that an immature predator will survive to adulthood; and the third term, $\frac{1}{d_2}$, is simply the average lifespan of a mature predator. Subsequently, the product of these three terms yields the mean number of offspring by every predator, which is precisely the biological meaning of a basic reproduction number. A similar threshold condition for the coexistence of a predator-prey system had previously been formulated and explained by Pielou [30], among others, but had not been termed a "basic reproduction number" to the best of our knowledge.

Furthermore, if the numerical response of the mature predator for the prey at carrying capacity is higher than the threshold value T and also the prey population ultimately remains higher than another value $\underline{x} > r/(2a)$, that is, if the prey is always abundant enough, it is seen from Theorem 3.3 that the system tends to a positive steady state. We also note that if the death rate d_1 of the immature predator is negligible compared to the rate D at which the immature predators become mature predators, then the inequality $T < kf(x_0)$ becomes a very simple comparison between the death rate of the mature predators and their reproductive rate. Moreover, the stage structure affects the capability of the predator species to survive and become persistent, since it is now $(D + d_1)/D$ times easier for the predator species to become extinct, as can be seen from Theorem 3.1. This means that if it takes too much for the immature predators to mature, or the through-stage death rate of the immature predator is high (that is, D is small compared to d_1), then the total number of offspring produced during the adult stage will not be enough to compensate the total loss of immature predators and the predator classes will tend to extinction.

However, the situation where $R_0 > 1$ (or $T < kf(x_0)$) but $\underline{x} \leq r/(2a)$ is more complicated. When $x^* > r/(2a)$, we know that E^* is locally asymptotically stable, but we do not know of its global properties. This is similar for the case $x^* \leq r/(2a)$, and (4.2) holds (see Theorem 4.1). Moreover, the precise conditions for the existence and uniqueness of the periodic orbits, namely when E^* is not globally stable, are unknown under part 3 of Theorem 4.1. Therefore, we proceed to investigate further by using numerical simulations.

We use the following parameter values for all numerical simulations below: $k = 1$, $b = 1$, $m = 1$, $D = 1$, $d_1 = 0.1$, and $d_2 = 0.2$. For case 1 (see Figure 5.1), we let $r = 1$ and $a = 2$, and subsequently $x_0 = \frac{r}{a} = 0.5$, $R_0 = \frac{kbx_0}{1+mx_0}\frac{D}{d_2(D+d_1)} = 1.515 > 1$, and $x^* > \frac{r}{2a}$. Since $x^* > r/(2a)$, the positive steady state E^* is locally asymptotically stable. Numerical simulations of trajectories starting at various initial populations seem to indicate that the stability is also global for the parameter values we used. Note that, in all the figures below, the black dot located on the x-axis is E_0^*, while the other black dot is E^*. For case 2 (see Figure 5.2), we let $r = 1$ and $a = 1$ so

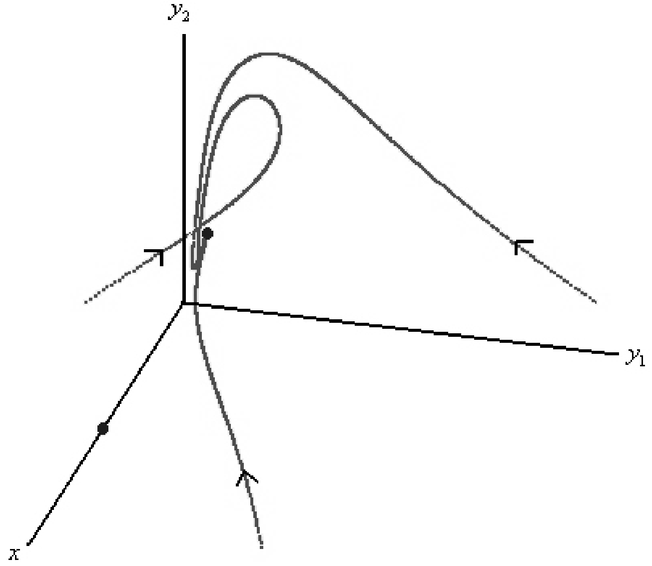

FIG. 5.1. *Simulation for case* 1 *with* $R_0 = 1.515 > 1$ *and* $x^* > \frac{r}{2a}$. *All trajectories approach* E^*.

that $x_0 = \frac{r}{a} = 1$, $R_0 = 2.273 > 1$, $x^* < \frac{r}{2a}$, and (4.2) holds. Since (4.2) holds, we know that the positive equilibrium E^* is locally asymptotically stable. Numerical simulations indicate that its stability is global. It is interesting to note that we are unable to find parameter values under which E^* satisfies (4.2), and hence it is locally asymptotically stable but not globally stable.

We also consider case 3 (see Figure 5.3), where $r = 3$ and $a = 2$, and subsequently $x_0 = \frac{r}{a} = 1.5$, $R_0 = 2.727 > 1$, and $x^* < \frac{r}{2a}$, but (4.2) does not hold. From part 3 of Theorem 4.1, we know the positive equilibrium E^* is unstable and there exists an orbitally asymptotically stable periodic orbit. Our simulation shows that this orbitally stable periodic orbit is unique and its orbital stability appears to be global. We summarize our stability results in Table 5.1. The three cases described by the last three rows of the table are illustrated with Figures 5.1–5.3, respectively. We note that, biologically, when (4.2) fails to hold and E^* becomes unstable, the coexistence of prey and predator populations is still ensured for initial populations not on the one-dimensional stable manifold of E^*, albeit with fluctuating population sizes.

We now continue with a few comments regarding the a priori estimate $\underline{x} > r/(2a)$, which was used to establish the global asymptotic stability of the positive steady state.

Let $0 < l < r/a$. It is seen that

$$x^* > l \Leftrightarrow bkDl < (1 + ml)(D + d_1)d_2,$$

from which it is easy to infer that

$$x^* > l \Leftrightarrow kf(l) < T.$$

Since $\underline{x} > l$ necessarily implies that $x^* > l$ (though this condition is only necessary and is not sufficient), it is seen that in order to have the inequality $\underline{x} > l$ satisfied, it

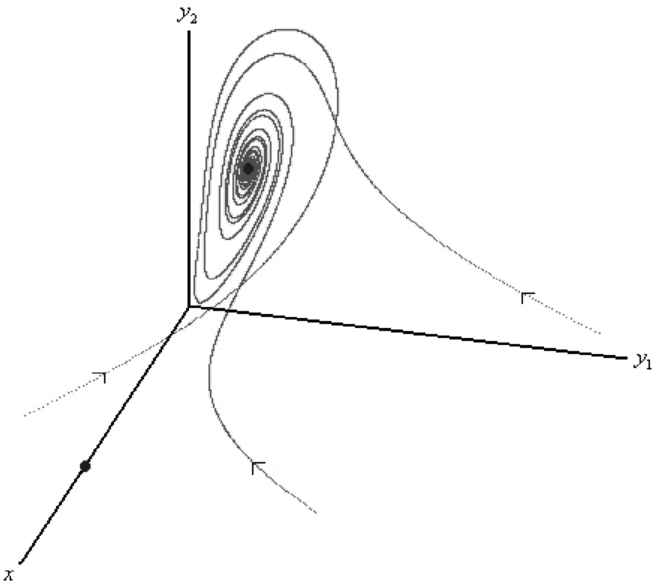

FIG. 5.2. *Simulation for case* 2 *where* $R_0 = 2.273 > 1$, $x^* < \frac{r}{2a}$, *and* (4.2) *holds. All trajectories approach* E^*.

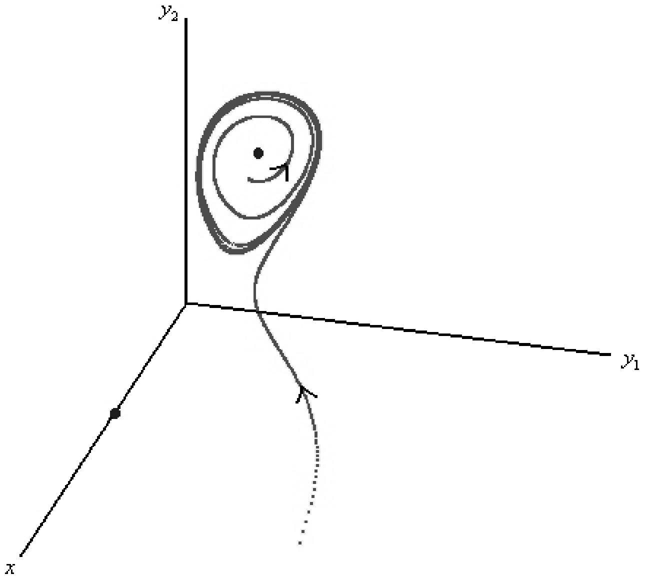

FIG. 5.3. *Simulation for case* 3 *where* $R_0 = 2.727 > 1$ *and* $x^* < \frac{r}{2a}$, *but* (4.2) *does not hold.* E^* *is unstable, and all trajectories approach an orbitally stable periodic orbit.*

TABLE 5.1

Asymptotic states of the system. “NE” denotes nonexistent, “NA” denotes not applicable, “NI” denotes no influence, “OASLC” denotes orbitally asymptotically stable limit cycle, “GAS” and “LAS” denote globally and locally asymptotically stable, respectively, and “$^{(1)}$” denotes the conclusion from the simulation result.

R_0	E_0	x^*	$\underline{x}$	(4.2)	E^*	$(x, y_1, y_2) \to$
≤ 1	GAS	NE	NI	NA	NE	E_0
> 1	unstable	$> \frac{r}{2a}$	$> \frac{r}{2a}$	YES	GAS	E^*
		$> \frac{r}{2a}$	$\le \frac{r}{2a}$	YES	LAS	$E^{*(1)}$
		$\le \frac{r}{2a}$	$\le \frac{r}{2a}$	YES	LAS	$E^{*(1)}$
		$\le \frac{r}{2a}$	$\le \frac{r}{2a}$	NO	unstable	OASLC$^{(1)}$

is necessary that $kf(l) < T$. Note that this inequality alone does not suffice to establish that $\underline{x} > l$. Again, this inequality has a certain biological interpretation. In order to have the prey population ultimately staying above a certain level l, one needs as a prerequisite that the numerical response of the predator for prey at density l be lesser than the threshold value T. Particularizing $l = r/(2a)$, it is seen that in order to obtain that $\underline{x} > r/(2a)$, one needs the inequality $kf(r/(2a)) < T$ satisfied.

Also, it is perhaps fitting to give sufficient conditions here which ensure the validity of our boundedness estimate $\underline{x} > r/(2a)$. From the first equation in (1.1), one obtains

$$(1 + mx)x'(t) = x(t)\left[(r - ax(t))(1 + mx(t)) - by_2(t)\right],$$

which implies

$$(1 + mx)x' \ge x\left[(r - b(\bar{M} + \varepsilon)) + x(rm - a) - amx^2\right]$$

for t large enough, where $\bar{M}$ is an ultimate upper bound for y_2 and $\varepsilon > 0$ is an arbitrary constant. If $r - b(\bar{M} + \varepsilon) > 0$, it follows that $\liminf_{t\to\infty} x(t) \ge x_2$, where x_2 is the positive root of

$$(r - b(\bar{M} + \varepsilon)) + x(rm - a) - amx^2 = 0.$$

From the above relations, one may deduce that $\underline{x} > r/(2a)$ whenever the following conditions are satisfied:

$$r - b(\bar{M} + \varepsilon) > 0, \quad a + \sqrt{(a - rm)^2 + 4(r - b(\bar{M} + \varepsilon))am} > 2mr.$$

Since $\varepsilon > 0$ was arbitrary, a set of conditions which ensures that $\underline{x} > r/(2a)$ is therefore

$$r > b\bar{M}, \quad a + \sqrt{(a - rm)^2 + 4(r - b\bar{M})am} > 2mr. \tag{5.1}$$

However, it is difficult to give a clear biological interpretation of the inequalities (5.1), and we would like to point out that our a priori estimate $\underline{x} > r/(2a)$ is easier to interpret and represents a theoretical device readily adaptable for the study of other systems of a certain structure, in connection with monotonicity properties. For explicit estimations of type (5.1), this sort of adjustment may not be transparent. Note that, from the discussions in section 2 on the boundedness of the solutions of system (1.1), an ultimate upper bound for y_2 is $\bar{M} = k \max(r/a, x(0))(r+d)/d$, where $d = \min(d_1, d_2)$. See also [38] for a numerical example regarding the feasibility of the condition $\underline{x} > r/(2a)$.

Since the mature predator functional response f depends only on the size of the prey population x, our model (1.1) may be called, following the terminology given in Huisman and DeBoer [13], prey-dependent. By the same terminology, a system in which the mature predator functional response f is a function of the prey-to-predator ratio x/y is called ratio-dependent (or, more generally, predator-dependent). It is also easy to see that our model can be thought as a stage-structured version of the classical predator-prey model given below:

$$\begin{cases} x' = rx\left(1 - \dfrac{x}{K}\right) - \dfrac{bx}{1+mx}y, \\ y' = k\dfrac{bx}{1+mx}y - dy. \end{cases} \tag{5.2}$$

It is therefore not surprising that, as is easily seen from (3.2), our model inherits the structure which generates the so-called paradox of enrichment, formulated by Hairston, Smith, and Slobodkin [10] and by Rosenzweig [32], which states that increasing the carrying capacity of the environment will cause an increase in the sizes of the predator classes at equilibrium but not in that of prey. Also, since the left-hand side of (4.2) is a decreasing function of the carrying capacity r/a while the right-hand side of (4.2) is an increasing function of the same variable, it is seen that an increase in the carrying capacity may destabilize an otherwise stable positive equilibrium.

It has already been noted that all prey equilibria x^* for which $x^* > r/(2a)$ are locally asymptotically stable; that is, high prey equilibrium densities are stable. Moreover, it can also be observed that low prey equilibrium densities are unstable, since the limit of the left-hand side of (4.2) as x^* tends to 0 is also 0, while the same limit of the right-hand side of (4.2) is positive.

Note that, by the Rosenzweig–MacArthur graphical stability criterion, any equilibrium of (5.2) with $x^* > r/(2a) - 1/(2m)$ is stable, while any equilibrium of (5.2) with $x^* < r/(2a) - 1/(2m)$ is unstable. Furthermore, by Theorem 3.2 in Kuang [20], one may prove that if $\underline{x} > r/(2a)$, then (x^*, y^*) is globally asymptotically stable. One may then expect a stability threshold for (1.1) which is sharper than $r/(2a)$. Unfortunately, this result does not carry out nicely for our system (1.1) (see (4.3)). Note also that the equilibria of (1.1) with x^* close to $r/(2a) - 1/(2m)$ are unstable, as the left-hand side of (4.2) becomes arbitrarily small, while the right-hand side remains above a strictly positive lower bound.

It has also been observed in this study that, for the most part of the parameter space, the dynamical outcome does not depend on the initial population sizes and the prey and predator species cannot face extinction simultaneously. These are hallmarks of prey-dependent models, as opposed to ratio-dependent models; as seen, for instance, in Jost, Arino, and Arditi [14] or in Beretta and Kuang [3], mutual extinction may occur for ratio-dependent models, together with other rich dynamics, and the behavior of the system may depend on the initial population sizes (see also Kuang [19]). In this regard, it is believed that prey-dependent predator-prey models are more appropriate for situations in which predation involves a random or no search process, while ratio-dependent predator-prey models are more appropriate for situations in which predation involves a thorough search process. See, for instance, Kuang and Beretta [21].

Our considerations may be easily extended to systems of the form

$$\begin{cases} x' = n(x) - f(x)g(y_2), \\ y_1' = kf(x)g(y_2) - c_1 h(y_1), \\ y_2' = c_2 h(y_1) - c_3 r(y_2), \end{cases} \tag{5.3}$$

to encompass different types of functional responses from the mature predator and possible nonlinearities in the behavior of species, including nonlinearity in the predation process, under appropriate monotonicity assumptions on the functions f, g, h, r. Some examples of f and n which fit into our framework are $f(x) = mx^c$, $0 < c \leq 1$, $f(x) = m(1 - e^{-cx})$, $m, c > 0$, $f(x) = bx^p/(1 + mx^p)$, $0 < p \leq 1$ and $n(x) = x(r - ax)/(1 + \varepsilon x)$, $\varepsilon > 0$, $n(x) = rx(1 - (x/(r/a))^c)$, $0 < c \leq 1$, provided that the threshold value T and the minimal value $r/(2a)$ for $\underline{x}$ are modified accordingly. Another simple extension is to a model in which predators pass through $p > 2$ life stages, as long as the consumption of prey occurs only in the last stage. Note that the last form of $n(x)$ given above is the Richards model, a generalized logistic-type model (which simplifies to the logistic model when $c = 1$) often used to model growth of biological populations [31] or severity of disease outbreak [12].

The function n need not be monotone on its whole domain but only on $[\underline{\tilde{x}}, +\infty)$, $\underline{\tilde{x}}$ being the persistency constant of the prey for the system under consideration. In this situation, condition $\liminf_{t\to\infty} x(t) \geq \underline{\tilde{x}}$ is used to restrict n to its monotonicity domain. See Georgescu and Hsieh [8] for a related argument concerning the global stability of the endemic equilibrium for the propagation of a virus in vivo, with the remark that in [8] there is no need to impose any a priori lower bound condition, since the function which corresponds to n is monotone on the whole feasibility domain. Finally, regarding our construction of a Lyapunov function, we mention that functions of type $V(x_1, x_2, x_3, x_4) = \sum_{i=1}^{4} a_i(x_i - x_i^* \ln x_i)$, to which our function U_3 relates, have also been found useful for the study of SEIR epidemiological models. See Korobeinikov [15] and Korobeinikov and Maini [16] for details. In this regard, global stability results for models which incorporate nonlinear incidence rates of a very general form have recently been obtained by Korobeinikov and Maini in [17].

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REFERENCES

[1] W. G. Aiello and H. I. Freedman, *A time-delay model of single species growth with stage structure*, Math. Biosci., 101 (1990), pp. 139–153.

[2] R. Arditi and J. Michalski, *Nonlinear food web models and their response to increased basal productivity*, in Food Webs: Integration of Patterns and Dynamics, G. A. Polis and K. O. Winemiller, eds., Chapman and Hall, New York, 1996, pp. 122–133.

[3] E. Beretta and Y. Kuang, *Global analysis in some ratio-dependent predator-prey systems*, Nonlinear Anal., 32 (1998), pp. 381–408.

[4] G. Butler, H. I. Freedman, and P. Waltman, *Uniformly persistent systems*, Proc. Amer. Math. Soc., 96 (1986), pp. 425–430.

[5] A. Fonda, *Uniformly persistent dynamical systems*, Proc. Amer. Math. Soc., 104 (1988), pp. 111–116.

[6] H. I. Freedman, S. Ruan, and M. Tang, *Uniform persistence near a closed positively invariant set*, J. Dynam. Differential Equations, 6 (1994), pp. 583–600.

[7] S. C. Gurney, R. M. Nisbet, and S. P. Blythe, *The systematic formulation of models of stage-structured populations*, in The Dynamics of Physiologically Structured Populations, Lecture Notes in Biomath. 68, Springer, Berlin, 1986, pp. 474–494.

[8] P. Georgescu and Y.-H. Hsieh, *Global stability for a virus dynamics model with nonlinear incidence of infection and removal*, SIAM J. Appl. Math., 67 (2006), pp. 337–353.

[9] S. A. Gourley and Y. Kuang, *A stage structured predator-prey model and its dependence on maturation delay and death rate*, J. Math. Biol., 49 (2004), pp. 188–200.

[10] N. G. Hairston, F. E. Smith, and L. B. Slobodkin, *Community structure, population control, and competition*, Am. Naturalist, 94 (1960), pp. 421–425.

[11] J. Hofbauer and J. W. H. So, *Uniform persistence and repellors for maps*, Proc. Amer. Math. Soc., 107 (1989), pp. 1137–1142.

[12] Y.-H. Hsieh, J. Y. Lee, and H. L. Chang, *SARS epidemiology modeling*, Emerg. Infect. Dis., 10 (2004), pp. 1165–1167.

[13] C. Huisman and R. J. DeBoer, *A formal derivation of the Beddington functional response*, J. Theoret. Biol., 185 (1997), pp. 389–400.

[14] C. Jost, O. Arino, and R. Arditi, *About deterministic extinction in ratio-dependent predator-prey models*, Bull. Math. Biol., 61 (1999), pp. 19–32.

[15] A. Korobeinikov, *Global properties of basic virus dynamics models*, Bull. Math. Biol., 66 (2004), pp. 879–883.

[16] A. Korobeinikov and P. K. Maini, *A Lyapunov function and global properties for SIR and SEIR epidemiological models with nonlinear incidence*, Math. Biosci. Eng., 1 (2004), pp. 57–60.

[17] A. Korobeinikov and P. K. Maini, *Non-linear incidence and stability of infectious disease models*, Math. Med. Biol., 22 (2005), pp. 113–128.

[18] Y. Kuang, *Basic properties of mathematical population models*, J. Biomath., 17 (2002), pp. 129–142.

[19] Y. Kuang, *Rich dynamics of Gause-type ratio-dependent predator-prey system*, Fields Inst. Commun., 21 (1999), pp. 325–337.

[20] Y. Kuang, *Global stability of Gause-type predator-prey systems*, J. Math. Biol., 28 (1990), pp. 463–474.

[21] Y. Kuang and E. Beretta, *Global qualitative analysis of a ratio-dependent predator-prey system*, J. Math. Biol., 36 (1998), pp. 389–406.

[22] J. P. LaSalle, *The Stability of Dynamical Systems*, CBMS-NSF Regional Conf. Ser. in Appl. Math. 25, SIAM, Philadelphia, 1976.

[23] M. Y. Li and J. S. Muldowney, *Global stability for the SEIR model in epidemiology*, Math. Biosci., 125 (2005), pp. 155–164.

[24] S. Liu, L. Chen, and R. Agarwal, *Recent progress on stage-structured population dynamics*, Math. Comput. Modelling, 36 (2002), pp. 1319–1360.

[25] A. Margheri and C. Rebelo, *Some examples of persistence in epidemiological models*, J. Math. Biol., 46 (2003), pp. 564–570.

[26] J. S. Muldowney, *Compound matrices and ordinary differential equations*, Rocky Mountain J. Math., 20 (1990), pp. 857–872.

[27] R. M. Nisbet and W. S. C. Gurney, *"Stage-structure" models of uniform larval competition*, in Mathematical Ecology, Lecture Notes in Biomath. 54, Springer, Berlin, 1984, pp. 97–113.

[28] R. M. Nisbet, W. S. C. Gurney, and J. A. J. Metz, *Stage structure models applied in evolutionary ecology*, in Applied Mathematical Ecology, S. A. Levin, T. G. Hallam, and L. J. Gross, eds., Springer, Berlin, 1989, pp. 428–449.

[29] N. H. Pavel, *Differential Equations, Flow Invariance, and Applications*, Res. Notes in Math. 113, Pitman, London, 1984.

[30] E. C. Pielou, *Introduction to Mathematical Ecology*, Wiley-Interscience, New York, 1969.

[31] F. J. Richards, *A flexible growth function for empirical use*, J. Exp. Bot., 10 (1959), pp. 290–300.

[32] M. R. Rosenzweig, *Paradox of enrichment: Destabilization of exploitation systems in ecological time*, Science, 171 (1969), pp. 385–387.

[33] H. L. Smith, *A classification theorem for three dimensional competitive systems*, J. Differential Equations, 70 (1987), pp. 325–332.

[34] H. L. Smith, *Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems*, Math. Surveys Monogr. 41, AMS, Providence, RI, 1995.

[35] W. Wang, *Global dynamics of a population model with stage structure for predator*, in Advanced Topics in Biomathematics, L. Chen, S. Ruan, and J. Zhu, eds., World Scientific, River Edge, NJ, 1997, pp. 253–257.

[36] W. Wang and L. Chen, *A predator-prey system with stage structure for predator*, Comput. Math. Appl., 33 (1997), pp. 83–91.

[37] W. Wang, G. Mulone, F. Salemi, and V. Salone, *Permanence and stability of a stage-structured predator-prey model*, J. Math. Anal. Appl., 262 (2001), pp. 499–528.

[38] Y. N. Xiao and L. Chen, *Global stability of a predator-prey system with stage structure for the predator*, Acta Math. Sin. (Engl. Ser.), 20 (2004), pp. 63–70.

[39] H.-R. Zhu and H. L. Smith, *Stable periodic orbits for a class of three-dimensional competitive systems*, J. Differential Equations, 110 (1994), pp. 143–156.