

GLOBAL STABILITY FOR A CLASS OF PREDATOR-PREY SYSTEMS*

SZE-BI HSU[†] AND TZY-WEI HUANG[‡]

Abstract. This paper deals with the question of global stability of the positive locally asymptotically stable equilibrium in a class of predator-prey systems. The Dulac's criterion is applied and Liapunov functions are constructed to establish the global stability.

Key words. global stability, Holling's type 1, Holling's type 2, Holling's type 3, functional response, Holling-Tanner model, predator-prey system, Dulac criterion, Liapunov function, limit cycle

AMS subject classifications. 34C35, 92A17

1. Introduction. The question of global stability in predator-prey systems is an interesting mathematical problem. When the system has a unique positive equilibrium, it is often conjectured that local and global asymptotic stability of the equilibrium are equivalent.

Several well-known methods have been used to prove global stability of the unique positive equilibrium of a predator-prey system. In [G] and [HSU], the authors construct a Liapunov function for the predator-prey system and establish the global stability by LaSalle's invariance principle [H]. The second method is to employ the Dulac criterion to eliminate the existence of periodic orbits and prove the global stability by the Poincaré-Bendixson theorem. Interested readers may consult [HHW1] and [K]. The third method is the method of comparison. In [CHL], Cheng, Hsu, and Lin provided some important and effective criteria for the global stability of the positive equilibrium by the comparison method. The method is basically geometric. The authors compare the trajectories of the system with that of an auxiliary system which is obtained by "mirror" reflection. The method was generalized by Liou and Cheng in [LC] and by Kuang in [K] for a Gause-type predator-prey system. The fourth method is the method of limit cycle stability analysis. Cheng, Hsu, and Lin [CHL] were the first to prove global stability by this method. The idea of this method is to prove the nonexistence of periodic solutions by contradiction. Suppose there exist periodic orbits, and we are able to show that all periodic orbits is orbitally asymptotically stable. Then the uniqueness of the limit cycle follows. If the positive equilibrium is locally asymptotically stable, we obtain the contradiction that it is in the interior of a stable limit cycle. Interested readers may consult [CHL], [BHW], and [K].

In this paper we study the global stability property of the following predator-prey system:

$$(1.1) \quad \begin{aligned} \frac{dx}{dt} &= rx \left(1 - \frac{x}{K}\right) - yp(x), \\ \frac{dy}{dt} &= y \left[s \left(1 - \frac{hy}{x}\right) \right], \\ x(0) &> 0, \quad y(0) > 0, \quad r, s, K, h > 0, \end{aligned}$$

* Received by the editors August 4, 1993; accepted for publication (in revised form) March 11, 1994. This work was supported by the National Science Council of the Republic of China.

[†] Institute of Applied Mathematics, National Tsing Hua University, Hsinchu, Taiwan, Republic of China (sbhsu@am.nthu.edu.tw).

[‡] Department of Mathematics, Kaohsiung Normal University, Kaohsiung, Taiwan, Republic of China.

where x is the population of the prey and y is the population of the predator. In (1.1) we assume the prey grows logistically with carrying capacity K and intrinsic growth rate r in the absence of predation. The predator consumes the prey according to the functional response $p(x)$ and grows logistically with intrinsic growth rate s and carrying capacity proportional to the population size of prey. The parameter h is the number of prey required to support one predator at equilibrium when y equals x/h . In [HO], the functional response $p(x)$ is classified into three types. When the functional response $p(x)$ is of type 1, i.e., $p(x) = mx$, then we have the following Leslie-Gower model [LG]:

$$(1.2) \quad \begin{aligned} \frac{dx}{dt} &= rx \left(1 - \frac{x}{K}\right) - mxy, \\ \frac{dy}{dt} &= y \left[s \left(1 - \frac{hy}{x}\right) \right], \\ x(0) &> 0, \quad y(0) > 0. \end{aligned}$$

When the functional response $p(x)$ is of type 2, in particular, $p(x) = \frac{mx}{A+x}$, then we have the following Holling-Tanner models [M], [MAY], [R], [T]:

$$(1.3) \quad \begin{aligned} \frac{dx}{dt} &= rx \left(1 - \frac{x}{K}\right) - \frac{mx}{A+x}y, \\ \frac{dy}{dt} &= y \left[s \left(1 - \frac{hy}{x}\right) \right], \\ x(0) &> 0, \quad y(0) > 0. \end{aligned}$$

The saturating predator functional response $\frac{mx}{A+x}$ used in (1.3) is of Michaelis-Menten type in enzyme-substrate kinetics. The parameter m is the maximum specific rate of product formation, x is the substrate concentration, and A (the half-saturation constant) is the substrate concentration at which the rate of product formation is half maximal. The functional response $\frac{mx}{A+x}$ was proposed by Holling [HO] for "non-learning" predators. The label nonlearning is a bit misleading because even predators capable of learning should exhibit this type of response when given only one type of prey for which to search. According to Holling's derivation [HO], [HHW2], [R], $m = 1/t_h$ and $A = \frac{1}{ct_h}$, where t_h is the handling time per prey item and c is the encounter rate per unit prey density.

When the functional response $p(x)$ is of type 3, in particular, $p(x) = \frac{mx^2}{(A+x)(B+x)}$ (see [S]), then we have

$$(1.4) \quad \begin{aligned} \frac{dx}{dt} &= rx \left(1 - \frac{x}{K}\right) - \frac{mx^2}{(A+x)(B+x)}y, \\ \frac{dy}{dt} &= y \left[s \left(1 - \frac{hy}{x}\right) \right], \\ x(0) &> 0, \quad y(0) > 0. \end{aligned}$$

The function $\frac{mx^2}{(A+x)(B+x)}$ is an S-shaped curve. The sigmoidal-type curves are indicative of predators which show some form of learning behavior in which, below a certain level of threshold density, the predator will not utilize the prey for food at any great intensity. However, above that density level, the predators increase their feeding rates

until some saturation level is reached. Holling reasoned that these animals tend both to learn slowly and to forget the value of a food unless they encounter it fairly often. Holling gave some field evidence that an S-shaped functional response is typical for vertebrate predators with alternative prey available.

We shall show in §2 that the positive equilibrium of (1.2) is a global attractor in the positive cone. However, for some parameters in the Holling-Tanner model (1.3), the positive equilibrium is unstable, and the model produces the interesting phenomenon of stable limit cycle (see Theorem 3.2 (iv)). A study of several pairs of interacting species, ranging from house sparrows and European sparrow hawk to mule deer and mountain lion [T], shows that the theoretical predictions of (1.3) based on estimated parameter values are broadly in line with practical reality. The local stability analysis of the positive equilibrium of the model (1.3) was done in [MAY] and [M]. In [FM] the authors showed that the system (1.3) is persistent. In [L] the author analyzed the following predator-prey model which is a generalization of (1.3):

$$(1.5) \quad \begin{aligned} \frac{dx}{dt} &= xg(x) - yp(x) - zf(x), \\ \frac{dy}{dt} &= yI(y/x), \end{aligned}$$

where the constant z is the generalist predator density. The model (1.5) describes the interaction of the small rodents and their predator, Tengmalm's owl, in Fennoscandia. It attempts to explain the multiannual microtine rodent cycle observed in boreal Fennoscandia.

In §2 we derive the criterion for the local stability of the positive equilibrium of (1.1). The models (1.2), (1.3), and (1.4) are written in nondimensional forms. Some global results are also given for (1.2), (1.3), and (1.4).

In §3 we analyze the model (1.3). The global stability property of (1.3) is established by the application of the Dulac criterion and the construction of the Liapunov function. The application of the Dulac criterion to the system (1.3) is rather complicated. We use the technique of separation of variables to construct an auxiliary function $H(x, y)$ for the Dulac criterion in the form of $\ell(x)r(y)$. Unfortunately, the application of Dulac criterion does not work for all parameter ranges. For the unsolved part, we first convert (1.3) into a Gause-type predator-prey system. Then a Liapunov function is constructed to obtain a partial result.

In §4 we analyze the model (1.4) by the methods similar to those in §3. The analysis of (1.4) also does not cover all parameter ranges.

Section 5 is the discussion section, where the biological interpretations are given for the results in §§3 and 4.

2. The models. We write the models (1.2), (1.3), and (1.4) in nondimensional forms. Let

$$(2.1) \quad \begin{aligned} \tilde{t} = rt, \quad \tilde{x}(\tilde{t}) &= \frac{x(t)}{K}, \quad \tilde{y}(\tilde{t}) = \frac{my(t)}{rK}, \\ \delta &= \frac{s}{r}, \quad \beta = \frac{sh}{m}, \quad a = \frac{A}{K}, \quad b = \frac{B}{K}. \end{aligned}$$

Then (1.2), (1.3), and (1.4) take the forms

$$(2.2) \quad \begin{aligned} \frac{dx}{dt} &= x(1-x) - xy, \\ \frac{dy}{dt} &= y \left(\delta - \beta \frac{y}{x} \right), \\ x(0) &> 0, \quad y(0) > 0, \end{aligned}$$

$$(2.3) \quad \begin{aligned} \frac{dx}{dt} &= x(1-x) - \frac{x}{a+x}y, \\ \frac{dy}{dt} &= y \left(\delta - \beta \frac{y}{x} \right), \\ x(0) &> 0, \quad y(0) > 0, \end{aligned}$$

and

$$(2.4) \quad \begin{aligned} \frac{dx}{dt} &= x(1-x) - \frac{x^2}{(a+x)(b+x)}y, \\ \frac{dy}{dt} &= y \left(\delta - \beta \frac{y}{x} \right), \\ x(0) &> 0, \quad y(0) > 0, \end{aligned}$$

respectively.

For simplicity, we consider the following general model of (2.2), (2.3), and (2.4):

$$(2.5) \quad \begin{aligned} \frac{dx}{dt} &= xg(x) - p(x)y, \\ \frac{dy}{dt} &= y \left(\delta - \beta \frac{y}{x} \right), \\ x(0) &> 0, \quad y(0) > 0, \end{aligned}$$

where $g(x)$ and $p(x)$ satisfy

(H1) $g(1) = 0$ and $g'(x) < 0$ for $x > 0$,

(H2) $p(0) = 0$, $p'(x) > 0$ for all $x > 0$.

The following lemma states that the system (2.5) under the hypotheses (H1) and (H2) is as "well behaved" as one intuitively from the biological problem. The proof is easy and we omit it.

LEMMA 2.1. *Let (H1) and (H2) hold. The solutions of (2.5) are positive and bounded, and furthermore, there exists $T \geq 0$ such that $x(t) < 1$, $y(t) < \delta/\beta$ for $t \geq T$.*

Obviously $E_1 = (1, 0)$ is an equilibrium of (2.5). Hypotheses (H1) and (H2) immediately imply that the graph of $g(x)$ and $p(x)\delta/\beta$ has a unique intersection x^* satisfying $0 < x^* < 1$. Thus system (2.5) possesses a unique positive equilibrium $E^* = (x^*, y^*)$, where $y^* > 0$ satisfies

$$(2.6) \quad y^* = \frac{x^*g(x^*)}{p(x^*)} = \frac{\delta}{\beta}x^*.$$

The variational matrix of (2.5) takes the form

$$J = \begin{bmatrix} j_{11} & j_{12} \\ j_{21} & j_{22} \end{bmatrix},$$

where

$$\begin{aligned} j_{11} &= \frac{d}{dx}(xg(x)) - p'(x)y, \\ j_{12} &= -p(x), \\ j_{21} &= \beta \left(\frac{y}{x}\right)^2, \\ j_{22} &= \delta - \frac{2\beta y}{x}. \end{aligned}$$

At E_1 ,

$$J(E_1) = \begin{pmatrix} \frac{d}{dx}(xg(x))|_{x=1} & -p(1) \\ 0 & \delta \end{pmatrix}.$$

From (H1), $\frac{d}{dx}(xg(x))|_{x=1} < 0$. The equilibrium E_1 is a saddle point with the positive x -axis as its stable manifold.

At E^* ,

$$J(E^*) = \begin{pmatrix} \frac{d}{dx}(xg(x))|_{x=x^*} - p'(x^*)y^* & -p(x^*) \\ \beta\left(\frac{y^*}{x^*}\right)^2 & \delta - 2\beta\frac{y^*}{x^*} \end{pmatrix}.$$

From (2.6), we rewrite

$$\frac{d}{dx}(xg(x))|_{x=x^*} - p'(x^*)y^* = p(x^*)h'(x^*),$$

where $h(x) = \frac{xg(x)}{p(x)}$ is the prey isocline of (2.5). Then

$$J(E^*) = \begin{pmatrix} p(x^*)h'(x^*) & -p(x^*) \\ \frac{\delta^2}{\beta} & -\delta \end{pmatrix}.$$

The eigenvalue λ of $J(E^*)$ satisfies

$$\lambda^2 + \lambda(\delta - p(x^*)h'(x^*)) + \delta p(x^*)\left(\frac{\delta}{\beta} - h'(x^*)\right) = 0.$$

Hence E^* is locally asymptotically stable provided

$$(2.7) \quad \delta - p(x^*)h'(x^*) > 0$$

and

$$(2.8) \quad \frac{\delta}{\beta} - h'(x^*) > 0.$$

In particular, from (2.7) and (2.8), E^* is locally asymptotically stable if $h'(x^*) \leq 0$, i.e., the prey isocline $y = h(x)$ is nonincreasing at $x = x^*$.

In the following we present a sufficient condition for the global stability of E^* for the system (2.5). The condition says that if the horizontal line $y = y^*$ divides the prey isocline $y = h(x)$ into two disjoint parts, then E^* is globally asymptotically stable in

the positive cone. In particular, if the prey isocline is nonincreasing on $0 \leq x \leq 1$, E^* is globally asymptotically stable.

THEOREM 2.2. *Let (H1) and (H2) hold. If*

$$(x - x^*) \left(\frac{xg(x)}{p(x)} - y^* \right) < 0 \text{ for } 0 < x < 1, x \neq x^*,$$

then the solutions of (2.5) satisfy

$$(2.9) \quad \lim_{t \rightarrow \infty} x(t) = x^* \text{ and } \lim_{t \rightarrow \infty} y(t) = y^*.$$

Proof. Construct the following Liapunov function:

$$V(x, y) = \int_{x^*}^x \frac{\xi - x^*}{\xi p(\xi)} d\xi + c \int_{y^*}^y \frac{\eta - y^*}{\eta} d\eta,$$

where $c > 0$ is to be determined. Then the time derivative of V computed along the solutions of (2.5) is

$$\begin{aligned} \dot{V} &= \frac{(x - x^*)}{x} \left(\frac{xg(x)}{p(x)} - y^* \right) - \frac{(x - x^*)(y - y^*)}{x} \\ &\quad + c\beta(y - y^*) \frac{y^*(x - x^*) - x^*(y - y^*)}{xx^*}. \end{aligned}$$

Let $c = \frac{x^*}{\beta y^*}$. Then

$$\dot{V} = \frac{(x - x^*)}{x} \left(\frac{xg(x)}{p(x)} - y^* \right) - c\beta \frac{(y - y^*)^2}{x} \leq 0$$

for $x, y > 0$. Then (2.9) follows directly from Lemma 2.1 and LaSalle's invariance principle [H].

Remark 2.3. For the system (2.2), the prey isocline is $y = 1 - x$, which is monotone decreasing. For the system (2.3), the prey isocline is $y = (1 - x)(x + a)$, which is monotone decreasing provided $a \geq 1$. Hence, for either case, the positive equilibrium $E^* = (x^*, y^*)$ is globally asymptotically stable.

Remark 2.4. For the system (2.4), the prey isocline is $y = h(x) = \frac{(1-x)(a+x)(b+x)}{x}$. An easy computation yields

$$h'(x) = \frac{Q(x)}{x^2},$$

where

$$Q(x) = -2x^3 + x^2(1 - (a + b)) - ab.$$

If $a + b \geq 1$ then $h'(x) < 0$ for all $x > 0$.

Let $a + b < 1$. Since

$$Q'(x) = 2x(1 - (a + b)) - 3x,$$

$$Q(0) = -ab \text{ and } Q(1) = -(a + b) - ab - 1 < 0,$$

then $h(x)$ is monotone decreasing if and only if

$$Q\left(\frac{1-(a+b)}{3}\right) \leq 0$$

or

$$(1-(a+b))^3 \leq 27ab.$$

If

$$(2.10) \quad (1-(a+b))^3 > 27ab,$$

then the prey isocline $y = h(x)$ has one local minimum and one local maximum in the interval $[0,1]$. From Theorem 2.2, if

(i) $a + b \geq 1$ or

(ii) $a + b < 1$ and $(1-(a+b))^3 \leq 27ab$,

then $E^* = (x^*, y^*)$ is globally asymptotically stable.

3. Holling-Tanner model. In this section we restrict our attentions to the global stability of the system (2.3),

$$(3.1) \quad \begin{aligned} \frac{dx}{dt} &= x(1-x) - \frac{x}{a+x}y = f(x,y), \\ \frac{dy}{dt} &= y\left(\delta - \beta\frac{y}{x}\right) = g(x,y), \\ x(0) &> 0, \quad y(0) > 0. \end{aligned}$$

For the local asymptotic stability of $E^* = (x^*, y^*)$, it suffices to check (2.7) and (2.8) with $h(x) = (1-x)(a+x)$. Then (2.8) becomes

$$\frac{y^*}{x^*} - ((1-a) - 2x^*) > 0$$

or

$$\frac{1}{x^*} [(1-x^*)(a+x^*) - ((1-a) - 2x^*)x^*] > 0,$$

which is automatically satisfied. (2.7) can be rewritten as the following:

$$(3.2) \quad P(x^*) > 0,$$

where

$$(3.3) \quad P(x) = 2x^2 + (a + \delta - 1)x + a\delta.$$

LEMMA 3.1. *The equilibrium $E^* = (x^*, y^*)$ of (3.1) is locally asymptotically stable if (3.2) holds, and E^* is an unstable focus or node if $P(x^*) < 0$.*

Our basic hypothesis is (3.2), which implies that the positive equilibrium $E^* = (x^*, y^*)$ is locally asymptotically stable. We divide the condition (3.2) into two cases.

Case 1. $P(x) \geq 0$ for all $x > 0$.

We note that from (3.3), $P(x) \geq 0$ for all $x > 0$ if and only if

$$(3.4) \quad a + \delta \geq 1$$

or

$$(3.5) \quad a + \delta < 1 \quad \text{and} \quad (1 - a - \delta)^2 - 8a\delta \leq 0.$$

Case 2.

$$(3.6) \quad a + \delta < 1 \quad \text{and} \quad (1 - a - \delta)^2 - 8a\delta > 0.$$

Then $P(x) = 2(x - \alpha_1)(x - \alpha_2)$, where

$$\alpha_1 = \frac{1}{4} \left[1 - a - \delta - \sqrt{(1 - a - \delta)^2 - 8a\delta} \right],$$

$$\alpha_2 = \frac{1}{4} \left[1 - a - \delta + \sqrt{(1 - a - \delta)^2 - 8a\delta} \right],$$

$$0 < \alpha_1 < \alpha_2 < 1.$$

The condition (3.2) for local asymptotic stability can be reformulated as

$$(3.7) \quad \alpha_2 < x^* < 1$$

or

$$(3.8) \quad 0 < x^* < \alpha_1.$$

The instability condition for the equilibrium E^* is

$$(3.9) \quad \alpha_1 < x^* < \alpha_2.$$

For fixed $\delta > 0$ satisfying (3.6), the conditions (3.7), (3.8), and (3.9) can be expressed explicitly in terms of the parameter β in the following:

$$(3.7)' \quad \beta > \beta_2,$$

$$(3.8)' \quad 0 < \beta < \beta_1,$$

$$(3.9)' \quad \beta_1 < \beta < \beta_2,$$

where

$$\beta_i = \frac{\delta\alpha_i}{(1 - \alpha_i)(a + \alpha_i)}, \quad i = 1, 2.$$

We now state and prove our main results in this section.

THEOREM 3.2.

- (i) Let (3.4) or (3.5) hold. Then the equilibrium $E^* = (x^*, y^*)$ is globally asymptotically stable in the interior of the first quadrant.
- (ii) Let (3.6) and (3.7) hold. Then the conclusion of (i) holds.
- (iii) Let (3.6) hold. For $\beta > 0$ sufficiently small, $x^* = x^*(\beta)$ is sufficiently close to zero and (3.8) holds. Furthermore, the conclusion of (i) holds for $\beta > 0$ sufficiently small.
- (iv) Let (3.9) hold. Then there exists a limit cycle for (3.1).

Proof. From Lemma 2.1 the solution $(x(t), y(t))$ of (3.1) is positive and bounded. If (3.9) holds, then the equilibrium E^* is an unstable focus, and part (iv) follows directly from the Poincaré-Bendixson theorem. From the assumptions in (i) and (ii), the equilibrium E^* is locally asymptotically stable; by the Poincaré-Bendixson theorem it suffices to show the global stability of E^* , provided we are able to eliminate the existence of periodic solutions. We prove (i) and (ii) by the Dulac criterion. For (i), we construct

$$H(x, y) = \left(\frac{x}{a+x}\right)^{-1} y^{-2}, \quad x > 0, \quad y > 0.$$

Then from (3.1) and the hypothesis in (i), an easy computation yields

$$\frac{\partial(fH)}{\partial x} + \frac{\partial(gH)}{\partial y} = \frac{H(x, y)}{a+x} (-P(x)) \leq 0, \quad x > 0, \quad y > 0.$$

Hence there are no nontrivial periodic solutions, and we complete the proof of (i). For part (ii), we let

$$H(x, y) = \ell(x)r(y),$$

where $\ell(x)$ and $r(y)$ will be determined. Then

$$\begin{aligned} \Delta &= \frac{\partial(fH)}{\partial x} + \frac{\partial(gH)}{\partial y} \\ &= H(x, y) \left[\frac{\partial f}{\partial x} + \frac{\partial g}{\partial y} + f \frac{\ell'(x)}{\ell(x)} + g \frac{r'(y)}{r(y)} \right] \\ &= H(x, y) \left[1 + \delta - 2x + \frac{\ell'(x)}{\ell(x)} x(1-x) - \frac{y}{(a+x)^2} \left(a + \frac{\ell'(x)}{\ell(x)} x(a+x) \right) \right. \\ &\quad \left. + \frac{r'(y)}{r(y)} y\delta - \frac{\beta y}{x} \left(2 + \frac{r'(y)}{r(y)} y \right) \right]. \end{aligned}$$

Let $r(y) = y^{R-2}$, where R will be determined. Then

$$\frac{r'(y)}{r(y)} y = R - 2$$

and

$$(3.10) \quad \Delta = H(x, y) \left\{ 1 - \delta + R\delta - 2x + \frac{\ell'(x)}{\ell(x)} x(1-x) - y \left[\frac{\beta R}{x} + \frac{1}{(a+x)^2} \left(a + \frac{\ell'(x)}{\ell(x)} x(a+x) \right) \right] \right\}.$$

In (3.10), we choose $\ell(x) = \frac{x+a}{x^{1+\beta R}} e^{\frac{\beta R a}{x}}$. Then $\ell(x)$ satisfies

$$\frac{\beta R}{x} + \frac{1}{(a+x)^2} \left(a + \frac{\ell'(x)}{\ell(x)} x(a+x) \right) = 0$$

or

$$(3.11) \quad \frac{\ell'(x)}{\ell(x)} = -\frac{a+x}{x} \left[\frac{\beta R}{x} + \frac{a}{(a+x)^2} \right].$$

From (3.10) and (3.11), it follows that

$$(3.12) \quad \begin{aligned} \Delta &= H(x, y) \left(1 - \delta + R\delta - 2x - \beta R \frac{(1-x)(a+x)}{x} - \frac{a(1-x)}{a+x} \right) \\ &= H(x, y) I(x). \end{aligned}$$

We rewrite $I(x)$ in (3.12) in the following form:

$$\begin{aligned} I(x) &= \left[R\delta - \beta R \frac{(1-x)(a+x)}{x} \right] - \frac{1}{a+x} \left[a - ax + (a+x)(2x + \delta - 1) \right] \\ &= R\beta \left[\frac{y^*}{x^*} - \frac{(1-x)(a+x)}{x} \right] - \frac{1}{a+x} P(x) \\ &= R\beta \left[\frac{(1-x^*)(a+x^*)}{x^*} - \frac{(1-x)(a+x)}{x} \right] - \frac{1}{a+x} P(x) \\ &= R\beta \frac{(x-x^*)(x+\frac{a}{x^*})}{x} - \frac{2}{a+x} (x-\alpha_1)(x-\alpha_2). \end{aligned}$$

To make $I(x) < 0$ for $0 < x < 1$, we shall determine $R > 0$ satisfying

$$(3.13) \quad \frac{\beta R}{2} (x+a) \left(x + \frac{a}{x^*} \right) (x-x^*) \leq x(x-\alpha_1)(x-\alpha_2) \quad \text{for } 0 < x < 1.$$

Let

$$W(x) = \frac{x(x-\alpha_1)(x-\alpha_2)}{(x+a)(x+\frac{a}{x^*})(x-x^*)}$$

and

$$Q(x) = \frac{x(x-\alpha_1)}{(x+a)(x+\frac{a}{x^*})}.$$

Then

$$(3.14) \quad W(x) = Q(x) + (x^* - \alpha_2) \frac{x(x-\alpha_1)}{(x+a)(x+\frac{a}{x^*})(x-x^*)}.$$

For $x \in (0, \alpha_1) \cup (\alpha_2, x^*)$, (3.13) holds for any $R > 0$. From (3.14), the hypothesis $x^* > \alpha_2$, and the fact that $Q(x)$ is increasing on $(\alpha_1, 1)$, it follows that

$$(3.15) \quad W(x) < Q(x) \leq Q(\alpha_2) \quad \text{for } \alpha_1 < x < \alpha_2.$$

Choose $R > 0$ such that $\frac{\beta R}{2} = Q(\alpha_2)$. Then for $x^* \leq x \leq 1$, we have

$$(3.16) \quad W(x) > Q(x) > Q(\alpha_2) = \frac{\beta R}{2}.$$

From (3.16) and (3.15), it follows that (3.13) holds. Thus we complete the proof for part (ii).

To prove part (iii), we first reduce the system (3.1) to a Gause-type predator-prey system by the following change of variable. Let

$$(3.17) \quad u = y\ell(x),$$

where $\ell(x)$ is to be determined. From (3.1) and (3.17), it follows that

$$(3.18) \quad \frac{du}{dt} = u \left\{ \left(x(1-x) \frac{\ell'(x)}{\ell(x)} + \delta \right) - y \left(\frac{\ell'(x)}{\ell(x)} \frac{x}{a+x} + \frac{\beta}{x} \right) \right\}.$$

Choose $\ell(x)$ satisfying

$$(3.19) \quad x(1-x) \frac{\ell'(x)}{\ell(x)} + \delta = 0,$$

i.e.,

$$\ell(x) = \left(\frac{1-x}{x} \right)^\delta.$$

Then from (3.18) and (3.19), we have

$$\frac{\ell'(x)}{\ell(x)} \frac{x}{a+x} + \frac{\beta}{x} = \frac{\beta}{x} - \frac{\delta}{(1-x)(a+x)}$$

and

$$\begin{aligned} \frac{du}{dt} &= -\frac{u^2}{\ell(x)} \frac{\beta}{(1-x)(a+x)} \left(\frac{(1-x)(a+x)}{x} - \frac{\delta}{\beta} \right) \\ &= \frac{1}{x} \frac{u^2}{\ell(x)} \frac{\beta}{(1-x)(a+x)} \left(x + \frac{a}{x^*} \right) (x - x^*). \end{aligned}$$

Thus we reduce (3.1) to the following system:

$$(3.20) \quad \begin{aligned} \frac{dx}{dt} &= x(1-x) - \frac{x}{a+x} \frac{u}{\ell(x)}, \\ \frac{du}{dt} &= \frac{u^2 \beta}{x \ell(x) (1-x)(a+x)} \left(x + \frac{a}{x^*} \right) (x - x^*), \\ x(0) &> 0, \quad u(0) > 0. \end{aligned}$$

Consider the prey isocline of (3.20),

$$(3.21) \quad u = h(x) = (1-x)(a+x)\ell(x).$$

From (3.3), (3.19), and (3.21), it follows that

$$(3.22) \quad \begin{aligned} h'(x) &= \ell(x) \left[-2x - a + 1 - (1-x)(a+x) \cdot \frac{\delta}{x(1-x)} \right] \\ &= \frac{-\ell(x)}{x} P(x). \end{aligned}$$

Thus the prey isocline $u = h(x)$ has a local maximum and a local minimum at $x = \alpha_2$ and $x = \alpha_1$, respectively. Obviously $h(1) = 0$, $\lim_{x \rightarrow 0^+} h(x) = +\infty$, and $h'(x) > 0$ for $\alpha_1 < x < \alpha_2$ and $h'(x) < 0$ for $x \in (0, \alpha_1) \cup (\alpha_2, 1)$. Let \hat{x} satisfy $\hat{x} > 0$ and $h(\hat{x}) = h(\alpha_2)$. Then $0 < \hat{x} < \alpha_1$. (See Fig. 1.) Let

$$(3.23) \quad 0 < x^* < \hat{x};$$

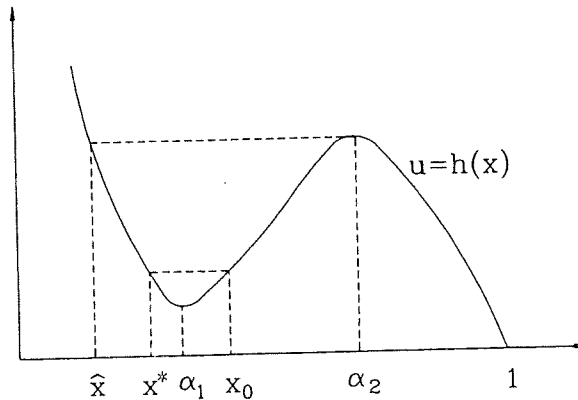


FIG. 1.

then it follows that

$$(3.24) \quad (x - x^*)(h(x) - u^*) < 0 \text{ for } 0 < x < 1, \quad x \neq x^*,$$

where $u^* = h(x^*)$. Construct the following Liapunov function

$$(3.25) \quad V(x, u) = \int_{x^*}^x \frac{\eta - x^*}{Q(\eta)} d\eta + \frac{1}{\beta} \int_{u^*}^u \frac{\eta - u^*}{\eta^2} d\eta,$$

where $Q(x) = x^2(1-x)/(x + \frac{a}{x^*})$.

Then an easy computation and (3.24) yield

$$\dot{V} = \frac{(x + \frac{a}{x^*})}{x(1-x)(a+x)\ell(x)} (x - x^*)(h(x) - u^*) \leq 0.$$

Then the global stability of the equilibrium (x^*, u^*) of (3.20) follows directly from LaSalle's invariance principle. We note that when we fix δ , then $\hat{x} = \hat{x}(\delta)$ is fixed. Thus $x^* = x^*(\beta)$ is a function of β satisfying $\lim_{\beta \rightarrow 0} x^*(\beta) = 0$ and, for $\beta > 0$ sufficiently small, $x^* < \hat{x}$. Thus (3.23) is satisfied, and we complete the proof of part (iii).

Remark 3.3. When $\hat{x} < x^* < \alpha_1$, the positive equilibrium $E^* = (x^*, u^*)$ of (3.20) is locally asymptotically stable. Unfortunately we are unable to establish the global stability of E^* . However, with the aid of the Liapunov function V in (3.25) we are able to estimate the domain of attraction of E^* . Let x_0 satisfy $\alpha_1 < x_0 < \alpha_2$, $h(x^*) = h(x_0)$ (see Fig. 1), and $c_0 = V(x_0, h(x_0))$. Then it is easy to verify that the set $\{(x, u) : 0 \leq V(x, u) \leq c_0\}$ is contained in the domain of attraction of $E^* = (x^*, u^*)$.

4. Model with type-3 functional response. In this section we discuss the global stability of the system (2.4),

$$(4.1) \quad \begin{aligned} \frac{dx}{dt} &= x(1-x) - \frac{x^2}{(a+x)(b+x)}y = f(x, y), \\ \frac{dy}{dt} &= y\left(\delta - \beta \frac{y}{x}\right) = g(x, y), \\ x(0) &> 0, \quad y(0) > 0. \end{aligned}$$

In Remark 2.4, we prove that if (i) $a+b \geq 1$ or (ii) $a+b < 1$ and $(1 - (a+b))^3 \leq 27ab$, then the positive equilibrium $E^* = (x^*, y^*)$ is globally asymptotically stable. Hence we restrict our attentions to the following case:

$$(4.2) \quad a+b < 1 \text{ and } (1 - (a+b))^3 > 27ab.$$

Under the assumption (4.2) the prey isocline $y = h(x) = \frac{(1-x)(a+x)(b+x)}{x}$ has one local minimum and one local maximum in the interval $[0,1]$ and $\lim_{x \rightarrow 0^+} h(x) = +\infty$, $h(1) = 0$. For the local stability of $E^* = (x^*, y^*)$, it suffices to check (2.7) and (2.8) with $h(x) = \frac{(1-x)(a+x)(b+x)}{x}$. It is easy to verify that (2.8) is satisfied and (2.7) can be rewritten as the following:

$$(4.3) \quad P(x^*) > 0,$$

where

$$(4.4) \quad P(x) = 2x^3 + (a+b-1+\delta)x^2 + (a+b)\delta x + ab(1+\delta).$$

LEMMA 4.1. *The equilibrium $E^* = (x^*, y^*)$ of (4.1) is locally asymptotically stable if (4.3) holds, and E^* is an unstable focus or node if $P(x^*) < 0$.*

To find a necessary and sufficient condition for (4.3), we consider $P(x)$ and

$$(4.5) \quad P'(x) = 6x^2 + 2(a+b-1+\delta)x + (a+b)\delta.$$

From (4.4), if

$$(4.6) \quad a+b-1+\delta \geq 0$$

then $P(x) \geq 0$ for all $0 \leq x \leq 1$. From (4.5), if

$$(4.7) \quad a+b-1+\delta < 0$$

and

$$(4.8) \quad D = (a+b-1+\delta)^2 - 6(a+b)\delta \leq 0$$

then $P'(x) \geq 0$ for $x > 0$, and hence $P(x) \geq 0$ for all $0 \leq x \leq 1$. If $D > 0$ and (4.7) holds, then from $P'(0) > 0$ and $P'(1) > 0$ it follows that $P'(x) = 0$ has two positive roots $0 < c_1 < c_2 < 1$, where

$$c_1 = \frac{-(a+b-1+\delta) - \sqrt{D}}{6}$$

and

$$(4.9) \quad c_2 = \frac{-(a+b-1+\delta) + \sqrt{D}}{6}.$$

If

$$(4.10) \quad P(c_2) \geq 0$$

then $P(x) \geq 0$ for all $0 < x < 1$. If

$$(4.11) \quad P(c_2) < 0$$

then $P(x) = 0$ has two positive roots α_1, α_2 satisfying $0 < c_1 < \alpha_1 < c_2 < \alpha_2 < 1$, and $P(x)$ can be written as

$$(4.12) \quad P(x) = 2(x + \alpha_0)(x - \alpha_1)(x - \alpha_2),$$

where $\alpha_0 > 0$. Under the assumption (4.11), the local asymptotic stability condition (4.3) can be formulated as

$$(4.13) \quad 0 < x^* < \alpha_1$$

or

$$(4.14) \quad \alpha_2 < x^* < 1.$$

We now state and prove our main results in this section.

THEOREM 4.2.

- (i) If $P(x) \geq 0$ for all $0 \leq x \leq 1$ then the equilibrium $E^* = (x^*, y^*)$ is globally asymptotically stable in the interior of the first quadrant.
- (ii) Let (4.11) and (4.14) hold. Then the conclusion of (i) holds.
- (iii) Let (4.11) hold. For $\beta > 0$ sufficiently small, $x^* = x^*(\beta)$ is sufficiently close to zero and (4.13) holds. Furthermore, the conclusion of (i) holds for $\beta > 0$ sufficiently small.
- (iv) If $\alpha_1 < x^* < \alpha_2$, then there exists a limit cycle of (4.1).

Proof. When $\alpha_1 < x^* < \alpha_2$, the equilibrium E^* is an unstable focus or node. Thus (iv) follows directly from the Poincaré-Bendixon theorem. As in Theorem 3.2 (i) and (ii), it suffices to construct a function $H(x, y)$ for Dulac's criterion.

Let

$$H(x, y) = (p(x))^{-1}y^{-2}, \quad x > 0, \quad y > 0,$$

where

$$p(x) = \frac{x^2}{(a+x)(b+x)}.$$

Then from (4.1) and the hypothesis in (i), an easy computation yields

$$\frac{\partial(fH)}{\partial x} + \frac{\partial(gH)}{\partial y} = H(x, y) \frac{-P(x)}{(a+x)(b+x)} \leq 0.$$

Hence we complete the proof of (i).

For part (ii), the proof is similar to that in part (ii) of Theorem 3.2. Let $H(x, y) = \ell(x)r(y)$, where

$$(4.15) \quad r(y) = y^{R-2}$$

for some $R > 0$ to be chosen, and $\ell(x)$ satisfies $\ell(x) > 0$,

$$(4.16) \quad \frac{\beta R}{x} + p'(x) + \frac{\ell'(x)}{\ell(x)}p(x) = 0,$$

where

$$(4.17) \quad p(x) = \frac{x^2}{(a+x)(b+x)}.$$

Then from (4.15) and (4.16)

$$\begin{aligned}
 \Delta &= \frac{\partial(fH)}{\partial x} + \frac{\partial(gH)}{\partial y} \\
 (4.18) \quad &= H(x, y) \left\{ 1 - \delta + R\delta - 2x + \frac{\ell'(x)}{\ell(x)}x(1-x) - y \left[\frac{\beta R}{x} + p'(x) + \frac{\ell'(x)}{\ell(x)}p(x) \right] \right\} \\
 &= H(x, y)I(x),
 \end{aligned}$$

where

$$(4.19) \quad I(x) = 1 - \delta + R\delta - 2x - \frac{1}{p(x)} \left(\frac{\beta R}{x} + p'(x) \right) x(1-x).$$

From (4.17), we have

$$(4.20) \quad p'(x) = \frac{(a+b)x^2 + 2abx}{(a+x)^2(b+x)^2}.$$

From (4.17), (4.20), and (4.4), a routine computation yields

$$\begin{aligned}
 (4.21) \quad I(x) &= R\delta - \beta R \frac{(a+x)(b+x)(1-x)}{x^2} + \frac{1}{(a+x)(b+x)} \\
 &\quad \cdot \{ ((1-\delta) - 2x)(x^2 + (a+b)x + ab) - [-(a+b)x^2 + x(-2ab + a + b) + 2ab] \} \\
 &= R\delta - \beta R \frac{(a+x)(b+x)(1+x)}{x^2} - \frac{P(x)}{(a+x)(b+x)}.
 \end{aligned}$$

From (4.1) and (4.12) we rewrite $I(x)$ in the following form:

$$\begin{aligned}
 I(x) &= R\beta \left[\frac{y^*}{x^*} - \frac{(a+x)(b+x)(1-x)}{x^2} \right] - \frac{2(x+\alpha_0)(x-\alpha_1)(x-\alpha_2)}{(a+x)(b+x)} \\
 &= R\beta \left[\frac{(a+x^*)(b+x^*)(1-x^*)}{(x^*)^2} - \frac{(a+x)(b+x)(1-x)}{x^2} \right] \\
 &\quad - 2 \frac{(x+\alpha_0)(x-\alpha_1)(x-\alpha_2)}{(a+x)(b+x)} \\
 &= R\beta \frac{(x-x^*)(x^2 + Ax + \frac{ab}{x^*})}{x^2} - \frac{2(x+\alpha_0)(x-\alpha_1)(x-\alpha_2)}{(a+x)(b+x)},
 \end{aligned}$$

where

$$A = \frac{1}{x^*} \left(ab \left(\frac{1}{x^*} - 1 \right) + (a+b) \right) > 0.$$

To make $I(x) \leq 0$ for $0 < x < 1$, we shall choose $R > 0$ satisfying

$$(4.22) \quad \frac{\beta R}{2} (a+x)(b+x) \left(x^2 + Ax + \frac{ab}{x^*} \right) (x-x^*) \leq x^2(x+\alpha_0)(x-\alpha_1)(x-\alpha_2).$$

Let

$$W(x) = \frac{x^2(x + \alpha_0)(x - \alpha_1)(x - \alpha_2)}{(a + x)(b + x)(x^2 + Ax + \frac{ab}{x^*})(x - x^*)}$$

and

$$Q(x) = \frac{x^2}{x^2 + Ax + \frac{ab}{x^*}} \frac{x + \alpha_0}{a + x} \frac{x - \alpha_1}{b + x}.$$

Then

$$(4.23) \quad W(x) = Q(x) + (x^* - \alpha_2) \frac{x^2(x + \alpha_0)(x - \alpha_1)}{(a + x)(b + x)(x^2 + Ax + \frac{ab}{x^*})(x - x^*)}.$$

For $x \in (0, \alpha_1) \cup (\alpha_2, x^*)$, (4.22) holds for any $R > 0$. From (4.23), the hypothesis $x^* > \alpha_2$, and the fact $Q(x)$ is increasing on $(\alpha_1, 1)$, it follows that

$$(4.24) \quad W(x) < Q(x) \leq Q(\alpha_2) \quad \text{for } \alpha_1 < x < \alpha_2.$$

Choose $R > 0$ such that $\frac{\beta R}{2} = Q(\alpha_2)$. Then for $x^* \leq x \leq 1$, we have

$$(4.25) \quad W(x) > Q(x) > Q(\alpha_2) = \frac{\beta R}{2}.$$

From (4.24) and (4.25), it follows that (4.22) holds. Thus we complete the proof of part (ii).

As we did in part (iii) of Theorem 3.2, we let $u = y\ell(x)$, where $\ell(x)$ satisfies (3.19) or $\ell(x) = (\frac{1-x}{x})^\delta$; then a routine computation shows that (4.1) can be reduced to the following system:

$$(4.26) \quad \begin{aligned} \frac{dx}{dt} &= x(1-x) - \frac{x^2}{(a+x)(b+x)} \frac{u}{\ell(x)}, \\ \frac{du}{dt} &= \frac{\beta u^2}{\ell(x)(1-x)(a+x)(b+x)} (x - x^*) \left(x^2 + Ax + \frac{ab}{x^*} \right), \\ x(0) &> 0, \quad u(0) > 0. \end{aligned}$$

Consider the prey isocline of (4.26),

$$(4.27) \quad u = H(x) = \frac{(1-x)(a+x)(b+x)\ell(x)}{x}.$$

From (3.19) and (4.4), an easy computation yields

$$(4.28) \quad \begin{aligned} H'(x) &= \frac{1}{x^2} \{ x\ell'(x)(1-x)(a+x)(b+x) + x\ell(x)[(1-x)(a+x)(b+x)]' \\ &\quad - (1-x)(a+x)(b+x)\ell(x) \} \\ &= \frac{\ell(x)}{x^2} \left\{ x(1-x)(a+x)(b+x) \left(\frac{-\delta}{x(1-x)} \right) + x[(1-x)(a+x)(b+x)]' \right. \\ &\quad \left. - (1-x)(a+x)(b+x) \right\} \\ &= -\frac{\ell(x)}{x^2} P(x). \end{aligned}$$

Thus the prey isocline $u = H(x)$ has a local maximum and local minimum at $x = \alpha_2$ and $x = \alpha_1$, respectively. Obviously, $H(1) = 0$, $\lim_{x \rightarrow 0^+} H(x) = +\infty$, and $H'(x) > 0$ for $\alpha_1 < x < \alpha_2$, and $H'(x) < 0$ for $x \in (0, \alpha_1) \cup (\alpha_2, 1)$. The proof of part (iii) follows directly by constructing a Liapunov function

$$V = \int_{x^*}^x \frac{\eta - x^*}{Q(\eta)} d\eta + \frac{1}{\beta} \int_{u^*}^u \frac{\eta - u^*}{\eta^2} d\eta,$$

where

$$Q(x) = \frac{x^2(1-x)}{x^2 + Ax + \frac{ab}{x}}.$$

As in Theorem 3.2 (iii), we complete the proof of part (iii).

Remark 4.3. Under the assumption (4.2), the prey isocline $h(x) = \frac{(1-x)(a+x)(b+x)}{x}$ has precisely one local minimum and one local maximum at x_1 and x_2 , $0 < x_1 < x_2 < 1$. We claim that under the assumption (4.11), we have $x_1 < \alpha_1 < \alpha_2 < x_2$, i.e., $h'(x) > 0$ for all $\alpha_1 \leq x \leq \alpha_2$. From (4.27) we have

$$(4.29) \quad xH(x) = h(x)\ell(x).$$

Differentiating with respect to x yields

$$(4.30) \quad xH'(x) + H(x) = h'(x)\ell(x) + h(x)\ell'(x).$$

Since $H(x)$ has a local minimum and a local maximum at $x = \alpha_1$ and $x = \alpha_2$, respectively, and $\ell(x) > 0$, $\ell'(x) < 0$ for $0 < x < 1$, from (4.30) it follows that

$$h'(\alpha_i) = \frac{H(\alpha_i) - h(\alpha_i)\ell'(\alpha_i)}{\ell(\alpha_i)} > 0$$

for $i = 1, 2$. Thus we complete the proof of the claim.

5. Discussion. In this paper we restrict our attention to the analysis of the predator-prey models (1.3),

$$(1.3) \quad \begin{aligned} \frac{dx}{dt} &= rx \left(1 - \frac{x}{K}\right) - \frac{mx}{A+x}y, \\ \frac{dy}{dt} &= y \left[s \left(1 - \frac{hy}{x}\right) \right], \\ x(0) &> 0, \quad y(0) > 0, \end{aligned}$$

and

$$(1.4) \quad \begin{aligned} \frac{dx}{dt} &= rx \left(1 - \frac{x}{K}\right) - \frac{mx^2}{(A+x)(B+x)}y, \\ \frac{dy}{dt} &= y \left[s \left(1 - \frac{hy}{x}\right) \right], \\ x(0) &> 0, \quad y(0) > 0. \end{aligned}$$

These models assume the prey (which is usually referred to as the herbivore [T]) grows logistically with intrinsic growth rate r and carrying capacity K in the absence of predation. The predator consumes the prey according to the functional response $p(x)$ and grows logistically with intrinsic growth rate s and carrying capacity proportional to the population size of the prey. The parameter h in the second equation of (1.3) and (1.4) is the number of herbivores (prey) required to support one predator at equilibrium when the predator density y equals x/h . The intrinsic growth rate s affects not only the potential increase of the predator population, but also its decrease. If y is greater than x/h , the predator population will decline, and the speed of its decline is directly proportional to the intrinsic growth rate s . Species of small body size and early maturity have high intrinsic growth rates. Frequently they also have low survival rates and short lives, and thus their population tends to both grow and decline rapidly [T]. The saturated predator functional response $p(x)$ used in model (1.3) is $\frac{mx}{A+x}$, which is of Michaelis-Menten type with half saturation constant A and maximal specific rate m . According to Holling's derivation, $A = 1/ct_h$ and $m = 1/t_h$ where t_h equals the handling time per prey item and c is the encounter rate per unit prey density [HO], [HHW2]. The functional response is called Holling's type-2 functional response, and it suits the predators which have only one type of prey to search. The saturated predator functional response $p(x)$ used in model (1.4) is Holling's type-3 functional response $\frac{mx^2}{(A+x)(B+x)}$. The type-3 curve suits the predators which show some form of learning behavior in which, below a certain level of threshold prey density, the predator will not utilize the prey for food at any great intensity. However, above that density level, the predators increase their feeding rates until some saturation level is reached. The sigmoidal functional response is typical for vertebrate predators with alternative prey available.

For the biological interpretations of Theorem 3.2 for model (1.3), there are three important parameters a , δ , and β . From (2.1), $a = A/K$ is the ratio of half-saturation constant and the carrying capacity of prey, and $\delta = \frac{s}{r}$ is the ratio of intrinsic rate of growth of predator and prey. The parameter β can be rewritten as $\beta = \delta \cdot \frac{hr}{m}$. Assuming that the growth of prey is not self-limited at equilibrium, hr is the number of prey to replace the individuals killed by one predator per unit time, while m is the maximal number of prey consumed by a predator per unit time [T]. The results in Theorem 3.2 can be classified into the following cases.

Case I. $a \geq 1$, i.e., $K \leq A$.

From Remark 2.3, if $a \geq 1$ then the prey isocline is monotone decreasing and the equilibrium E^* is globally asymptotically stable. Hence, for the small prey carrying capacity, the prey and predator approach constant values, and there is no limiting periodic behavior. We note that in this case the result is independent of the sizes of δ and β .

Case II. $a < 1$ and $a + \delta \geq 1$.

From Theorem 3.2(i) it follows that the equilibrium E^* is globally asymptotically stable when the prey carrying capacity K is greater than the half-saturation A , and the ratio s/r is larger than $1 - a$. Then the prey and predator approach equilibrium E^* , there is no limiting periodic behavior. In particular, when the intrinsic growth rate s of the predator is greater than the intrinsic growth rate r of the prey, there will be no limit cycle. We note that in this case, the result is independent of the size of β .

Case III. $a + \delta < 1$, $(1 - a - \delta)^2 - 8a\delta \leq 0$.

It is easy to verify that the necessary and sufficient condition for the above inequalities is $\delta_1 < \delta < 1 - a$ where $\delta_1 = 1 + 3a - \sqrt{8a^2 + 8a} > 0$. From Theorem 3.2(i),

the equilibrium E^* is globally asymptotically stable. Hence, when the ratio s/r is not too small, the prey and predator approach equilibrium E^* . We note that as in Case II, the result is independent of the size of β .

Case IV. $a + \delta < 1$, $(1 - a - \delta)^2 - 8a\delta > 0$.

Then δ satisfies $0 < \delta < \delta_1$. The numbers α_1, α_2 defined in §3 satisfy $0 < \alpha_1 < \alpha_2 < \frac{1-a}{2}$, and the prey isocline of the system (3.1), $y = (1-x)(a+x)$, attains its maximum at $x = \frac{1-a}{2}$. There are three subcases.

Subcase (i). $\alpha_2 < x^* < 1$, i.e., (3.7) holds.

The condition is equivalent to (3.7)', i.e., $\beta > \beta_2$ where $\beta_2 = \frac{\delta\alpha_2}{(1-\alpha_2)(a+\alpha_2)}$. Thus, if δ is sufficiently small ($\delta < \delta_1$) and β is sufficiently large, then the trajectory of (3.1) approaches the equilibrium E^* as $t \rightarrow \infty$. Since $\alpha_2 < x^* < 1$ and $\alpha_2 < \frac{1-a}{2}$ (thus, in particular, if the equilibrium E^* is at the right of the peak of the prey isocline), then E^* is globally asymptotically stable. We recall that $\delta = \frac{s}{r}$ and $\beta = \delta \cdot \frac{rh}{m}$. When the intrinsic growth rate of predator s is sufficiently smaller than that of prey, r and the maximal consumption rate m is sufficiently small, then the prey-predator system (1.3) has no limit cycle.

Subcase (ii). $0 < x^* < \alpha_1$, i.e., (3.8) holds.

The condition is equivalent to (3.8)', i.e., $0 < \beta < \beta_1$ where $\beta_1 = \frac{\delta\alpha_1}{(1-\alpha_1)(a+\alpha_1)}$. Thus if δ and β are both sufficiently small ($\delta < \delta_1, \beta < \beta_1$), the equilibrium E^* is a stable equilibrium. Hence, when the intrinsic growth rate of the predator is sufficiently smaller than that of the prey, and the maximal consumption rate is sufficiently large, the system (1.3) has no limit cycle.

Subcase (iii). $\alpha_1 < x^* < \alpha_2$, i.e., (3.9) holds.

The condition is equivalent to (3.9)', i.e., $\beta_1 < \beta < \beta_2$. From Theorem 3.2 (iv), there exists a limit cycle for the predator-prey system. Thus it is a necessary condition for the existence of the limit cycle that $\frac{s}{r}$ be sufficiently small. The condition $\beta_1 < \beta < \beta_2$ means that the maximal consumption rate cannot be too small or too large for the existence of the limit cycle.

The biological interpretations of Theorem 4.2 for model (1.4) with type-3 functional response are similar to those of model (1.3) with type-2 functional response. We note that the constants A and B in the type-3 functional response are obtained from the S-shaped curve by "curve fitting." The results in Theorem 4.2 can be classified into the following cases.

Case I. (i) $a + b \geq 1$ or (ii) $a + b < 1$ and $(1 - (a + b))^3 \leq 27ab$.

The prey isocline of (4.1) is monotone decreasing, and the global asymptotic stability of E^* follows directly from Remark 2.4. From (2.1), we have $a = \frac{A}{K}$ and $b = \frac{B}{K}$. Hence, for small prey carrying capacity K , the prey and predator approach constant values. The result in this case is independent of the sizes of δ and β .

Case II. $a + b < 1$ and $(1 - (a + b))^3 > 27ab$, $\delta \geq 1 - (a + b)$.

From Theorem 4.2 (i) it follows that the equilibrium E^* is globally asymptotically stable. Under the conditions $a + b < 1$ and $(1 - (a + b))^3 > 27ab$, i.e., the carrying capacity K of prey is sufficiently large, if the ratio s/r is larger than $1 - (a + b)$, then the prey and predator approach equilibrium E^* . In particular, when the intrinsic growth rate s of the predator is greater than the intrinsic growth rate r of the prey, there will be no limit cycle. We note that in this case, the result is independent of the size of β .

Case III. $a + b < 1$, $(1 - (a + b))^3 > 27ab$; $0 < \delta < 1 - (a + b)$; $(1 - (a + b) - \delta)^2 - 6(a + b)\delta \leq 0$.

As in Case III for model (1.3), the above conditions mean $0 < \tilde{\delta}_1 < \delta < 1 - (a + b)$, where $\tilde{\delta}_1 = 2(a + b) + 1 - \sqrt{3(a + b)((a + b) + 2)}$. From Theorem 4.2(i), the equilibrium E^* is globally asymptotically stable. Hence when the ratio s/r is not too small, the prey and predator approach equilibrium E^* . The result is independent of the size of β .

Case IV. $a + b < 1$, $(1 - (a + b))^3 > 27ab$; $0 < \delta < 1 - (a + b)$; $(1 - (a + b) - \delta)^2 - 6(a + b)\delta > 0$; $P(c_2) \geq 0$.

The condition (4.10), $P(c_2) \geq 0$, means the ratio δ is bounded away from zero. It is easy to verify that when $\delta = 0$, we have $c_2 = \frac{1-(a+b)}{3}$ and $P(c_2) = ab - \frac{1}{27}(1 - (a + b))^3 < 0$. The biological interpretation for this case is the same as in Case III above.

Case V. $a + b < 1$, $(1 - (a + b))^3 > 27ab$; $0 < \delta < 1 - (a + b)$; $(1 - (a + b) - \delta)^2 - 6(a + b)\delta > 0$; $P(c_2) < 0$.

From the analysis in §4, the condition for asymptotic stability of E^* is either (4.13) or (4.14). The condition $\alpha_1 < x^* < \alpha_2$ is the instability condition for E^* . From Remark 4.3, we have $h'(\alpha_i) > 0$, $i = 1, 2$, where $h(x) = \frac{(1-x)(a+x)(b+x)}{x}$ is the prey isocline of (4.1). Thus, in particular, if the equilibrium E^* is at the right of the peak of the prey isocline or at the left of the bottom of the prey isocline, then E^* is a stable equilibrium. The biological interpretations basically are the same as those of Case IV for the type-2 case. We omit them.

In §§3 and 4 we gave a global analysis of the asymptotic behavior of the well-known Holling-Tanner model (3.1) and the model (4.1) with a type-3 functional response. The mathematical results are by no means complete. In fact, we are unable to prove the global stability of the positive equilibrium E^* for the case (3.8), (4.13) in the model (3.1) and (4.1), respectively. However, with a change of variable in (3.17) we reduce (3.1), (4.1) to a Gause-type predator-prey system (3.20), (4.26), respectively. By constructing a Liapunov function, we show that for $\beta > 0$ sufficiently small, E^* is globally asymptotically stable.

There are two interesting problems that remain open. One is to prove the global stability of E^* for the case (3.8) and (4.13) for the model (3.1) and (4.1), respectively. The other is the problem of the uniqueness of the limit cycle for the case $\alpha_1 < x^* < \alpha_2$. We conjecture that the reduced system (3.20), (4.26) should play an important role in dealing with these problems.

Acknowledgments. The first author would like to thank Professor Yang Kuang of Arizona State University for introducing him to the global stability problem of the Holling-Tanner model.

REFERENCES

- [BHW] G. J. BUTLER, S. B. HSU, AND P. WALTMAN, *Coexistence of competing predators in a chemostat*, *J. Math. Biology*, 17(1983), pp. 133-151.
- [CHL] K. S. CHENG, S. B. HSU, AND S. S. LIN, *Some results on global stability of a predator-prey system*, *J. Math. Biology* 12(1981), pp. 115-126.
- [FM] H. I. FREEDMAN AND R. M. MATHSEN, *Persistence in predator-prey systems with ratio-dependence predation influence*, *Bull. Math. Biol.*, 55(1993), pp. 817-827.
- [G] B. S. GOH, *Global stability in many species systems*, *Emer. Natur.* 111(1977), pp. 135-143.
- [H] J. K. HALE, *Ordinary Differential Equations*, Wiley-Interscience, New York, 1969.
- [HHW1] S. B. HSU, S. P. HUBBELL, AND P. WALTMAN, *Competing predators*, *SIAM J. Appl. Math.*, 35(1978), pp. 525-617.
- [HHW2] ———, *A contribution to the theory of competing species*, *Ecological Monographs*, 48(1978), pp. 337-349.

- [HSU] S. B. HSU, *On global stability of a predator-prey system*, Math. Biosci., 39(1978), pp. 1-10.
- [HO] C. S. HOLLING, *The functional response of predators to prey density and its role in mimicry and population regulation*, Mem. Ent. Soc. Can., 46(1965), pp. 1-60.
- [K] Y. KUANG, *Global stability of Gause-type predator-prey systems*, J. Math. Biology, 28(1990), pp. 463-474
- [L] T. LINDSTRÖM, *Qualitative analysis of a predator-prey system with limit cycles*, J. Math. Biol., 31(1993), pp. 541-561.
- [LC] L. P. LIOU AND K. S. CHENG, *Global stability of a predator-prey system*, J. Math. Biol., 26(1988), pp. 26-71.
- [LG] P. H. LESLIE AND J. C. GOWER, *The properties of a stochastic model for the predator-prey type of interaction between two species*, Biometrika, 47(1960), pp. 219-234.
- [M] J. D. MURRAY, *Mathematical Biology*, Springer-Verlag, Berlin, 1989.
- [MAY] R. M. MAY, *Stability and Complexity in Model Ecosystems*, Princeton University Press, Princeton, NJ, 1974.
- [R] E. RENSHAW, *Modelling Biological Populations in Space and Time*, Cambridge University Press, Cambridge, U.K., 1991.
- [R1] L. A. REAL, *The kinetics of functional response*, American Naturalist, 111(1977), pp. 289-300.
- [S] J. MAYNARD SMITH, *Models in Ecology*, Cambridge University Press, Cambridge, U.K., 1974.
- [T] J. T. TANNER, *The stability and the intrinsic growth rates of prey and predator populations*, Ecology, 56(1975), pp. 855-867.