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# Global Stability for a Class of Predator-Prey Systems with Ratio-Dependence

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## Abstract

The main purpose of this paper is to study the global stability of the positive locally asymptotically stable rest point in a class of predator-prey systems with ratio-dependence. We apply the Poincaré-Bendixson theorem, Dulac's criterion, and the method of limit cycle stability analysis to establish sufficient conditions for the global stability.

**Keywords:** global stability, predator-prey system, ratio-dependence

## 1 Introduction

Continuous models, usually in the form of differential equations, have formed a large part of the traditional mathematical ecology literature. In such models, the key terms specifying the outcome of predator-prey interactions are the functional and numerical responses. The classical assumptions are that the functional and numerical responses depend on prey density only, so we call the traditional predation models as " prey-dependent " models. Interested readers may consult [2], [4], and [14].

Recently, traditional prey-dependent models have been challenged by several ecologists, on the grounds that the functional and numerical responses ought to depend on the ratio of prey/predator or predator/prey. However, the term "ratio-dependent predation" was first used by Arditi and Ginzburg [2] to describe situations in which the feeding rate of predators depends on the ratio of prey/predator (called ratio-dependent functional response in [4]) rather than on prey density alone.

An opposite pathway to ratio-driven predator-prey dynamics began with Leslie's [13] modification of the logistic equation to include a lower trophic level

$$\dot{y} = y[s(1-\beta\frac{y}{x})],$$

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and was called the logistic ratio-dependent predator equation by Berryman et al. in [4]. The functional responses of models [6] and [8] in Fig. 1 can be interpreted in the

$$\frac{mx}{b+ay+x}=\frac{mx/y}{b/y+a+x/y}.$$

Hence, Berryman et al. [4] consider these models to be ratio-dependent.

The merits of prey-dependent versus ratio-dependent models have been argued intensely. Arditi and Ginzburg [2] and Arditi et al. [3] give several examples of ecological systems in which ratio-dependence explains the dynamic and equilibrial properties of the systems better than the prey-dependence.

With regard to ratio-dependent functional response models [2], [6], [7], [8], [9], and [14] in Fig. 1, a model of general form appears in the works of Arditi and Ginzburg [2] and Freedman and Mathsen [7]. The authors [2] analyze the model by the isocline method and suggest that the ratio-dependent form of functional response is a simple way of accounting for many types of heterogeneity that occur in large scale natural systems, while the prey-dependent form may be more appropriate for homogeneous system like chemostats. In [7] the authors derive a criterion for persistence (that is, any solution with positive initial conditions never gets arbitrarily close to the axis).

Two special cases of model [2] in Fig. 1 have been studied by Lundberg and Fryxell [14] and Gutierrez [9]. The authors [14] discuss the local stability of the positive rest point by the Hartman-Grobman theorem, and use an Euler approximation to the differential equations. The ratio-dependent models predict that a rest point increases in both prey and predator density as productivity (carrying capacity, K) increases. Gutierrez [9] has a conclusion that ratio-dependent theory indicates the nature of the problem, and for some systems may provide sufficient detail.

Two particular models [6] and [8] in Fig. 1 have been discussed by some authors. In [6] DeAngelis et al. investigate model [6] by the isocline method, Kolmogorov's Criterion, and computer simulation. The analyses indicate that increases in maximum feeding rate may result in decreases in consumer population, and mutual interference between consumers is a major stabilizing factor in a nonlinear system. In [8] Getz proposes an ordinary differential equation formulation that is biologically more consistent than previous formulations, and the model [8] is obtained by this formulation.

With regard to the logistic ratio-dependent models [12] and [17] in Fig. 1, Hsu and Huang [12] apply Dulac's criterion and construct Liapunov functions to establish the global stability. The main purpose of this paper is to establish the global stability of the locally stable rest points of the ratio-dependent systems (2.1) and (2.2).

In section 2, we state models (2.1) and (2.2) with assumptions.

In section 3, we discuss the global stability of the general model (3.1) of (2.1) and (2.2) by Dulac's criterion.

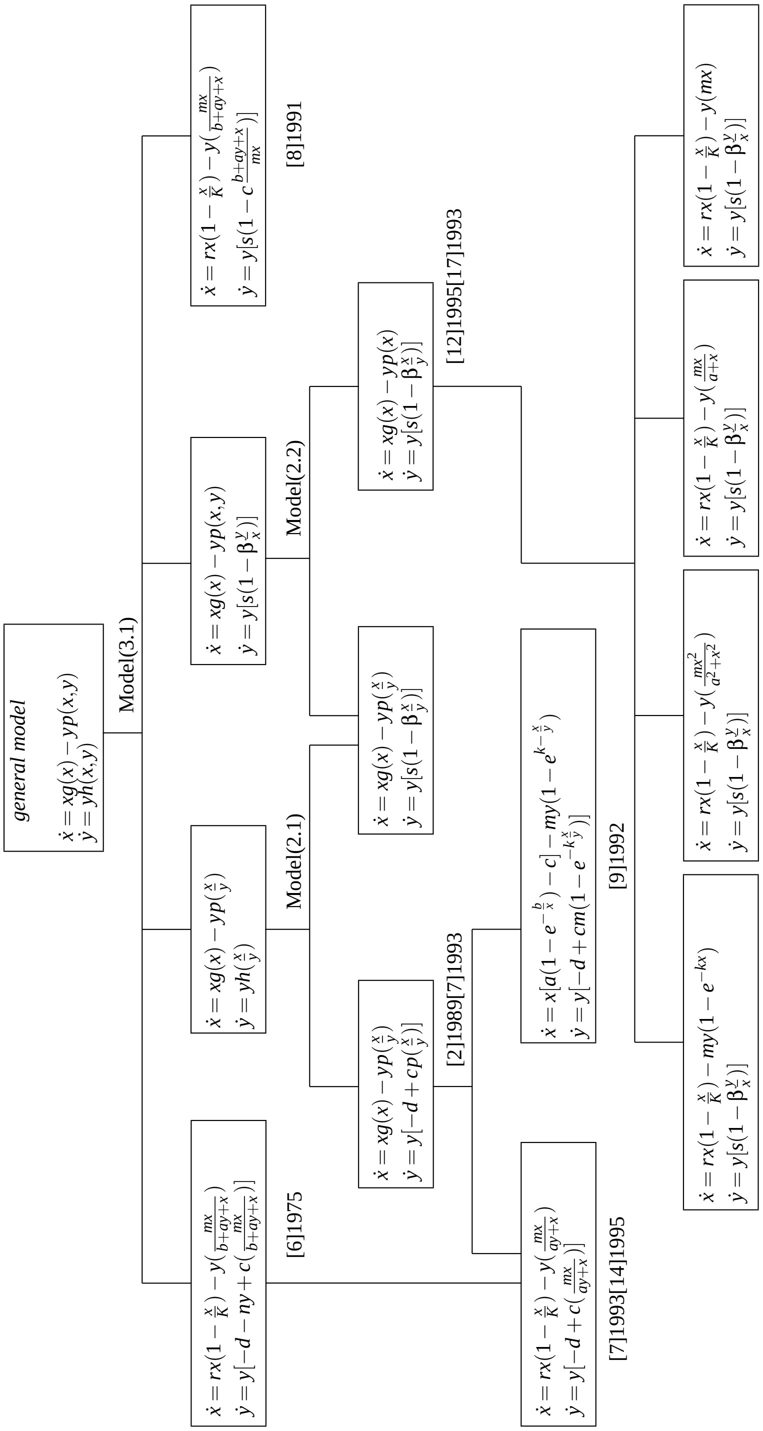

Figure 1: Ratio-dependent models where *x* denotes prey and *y* denotes predator.

Section 4 contains global stability properities of models (2.1) and (2.2) obtained either by the results of (3.1) or by performing limit cycle stability analysis.

In section 5, we present two examples to show the applicability of our theorems.

Section 6 is the conclusion.

## 2 The Models

We consider the following predator-prey systems with ratio-dependence

$$\begin{aligned}&\dot{x} = xg(x) - yp(\frac{x}{y}),\\ &\dot{y} = yh(\frac{x}{y}),\\ &x(0) > 0,\ \ y(0) > 0,\end{aligned} \tag{2.1}$$

and

$$\begin{aligned}&\dot{x} = xg(x) - yp(x,y),\\ &\dot{y} = y[s(1-\beta\frac{y}{x})],\\ &x(0) > 0,\ \ y(0) > 0,\end{aligned} \tag{2.2}$$

where "$\dot{}$" stands for $\frac{d}{dt}$ , $x$ represents the prey population (or density), and $y$ represents the predator population (or density). The specific growth rate, $g(x)$, governs the growth of the prey in the absence of predators. Several forms of $g(x)$ have been catalogued in [15] or [16]. For example, $g(x) = r(1-\frac{x}{K})$, $g(x) = \frac{r(K-x)}{K+\varepsilon x}$, or $g(x) = r[1-(\frac{x}{K})^{\delta}]$, $0 < \delta \leq 1$. $p(x,y)$ or $p(\frac{x}{y})$ is the predator response function (or feeding rate per predator) which has been much discussed in the literature. $h(\frac{x}{y})$ or $s(1-\beta\frac{y}{x})$ is the per capita numerical response function where $s$ is the intrinsic growth rate of the predator and $\beta$ is the number of prey required to support one predator at equilibrium when $y$ equals $x/\beta$.

The assumptions of system (2.1) on $g(x)$, $p(\frac{x}{y})$, and $h(\frac{x}{y})$ are :

(A1) $g \in C^1(R_+,R)$, $g(0) > 0$; there exists $K > 0$ such that $g(K) = 0$; $g'(x) < 0$ for all $x > 0$.

(A2) $p \in C^1(R_+,R_+)$, $p(0) = 0$; $p'(u) > 0$ for all $u > 0$.

(A3) $h \in C^1(R_+,R)$, $h(0) < 0$ or doesn't exist; there exists $L > 0$ such that $h(L) = 0$; $h'(u) > 0$ for all $u > 0$.

For convenience, we let

$$\begin{aligned}&f_1(x,y) = g(x) - \frac{y}{x}p(\frac{x}{y}),\\ &f_2(x,y) = h(\frac{x}{y}),\end{aligned}$$

that is,

$$\begin{aligned} xg(x) - yp(\frac{x}{y}) &= xf_1(x,y), \\ yh(\frac{x}{y}) &= yf_2(x,y). \end{aligned}$$

To express the fact that the two species have a predator-prey interaction, we have

$$\begin{aligned} -\frac{1}{x}[p(\frac{x}{y}) - \frac{x}{y}p'(\frac{x}{y})] &= \frac{\partial f_1}{\partial y}(x,y) < 0, \\ \frac{1}{y}h'(\frac{x}{y}) &= \frac{\partial f_2}{\partial x}(x,y) > 0. \end{aligned}$$

So we assume
(A4) $yp(\frac{x}{y}) - xp'(\frac{x}{y}) > 0$ for all $(x,y) \in R_+^2$.

For discussing the global stability of system (2.1), we will as sure that there is a unique positive rest point $E^* = (x^*, y^*)$ for system (2.1) under some conditions.
(A5) There exists a unique positive rest point $E^* = (x^*, y^*)$ for system (2.1) where $0 < x^* < K$ and $y^* > 0$ satisfies

$$x^* g(x^*) = y^* p(\frac{x^*}{y^*}) \tag{2.3}$$

and

$$h(\frac{x^*}{y^*}) = 0. \tag{2.4}$$

**Remark 2.1** In [7], [12], and [17], the numerical response $h(\frac{x}{y}) = s[1 - \frac{\beta}{x/y}] = s(1 - \beta\frac{y}{x})$. Hence $h(0)$ does not exist.

The assumptions of system (2.2) on $g(x)$ and $p(x,y)$ are :
(B1) $g \in C^1(R_+, R)$, $g(0) > 0$; there exists $K > 0$ such that $g(K) = 0$; $g'(x) < 0$ for all $x > 0$.
(B2) $p \in C^1(R_+^2, R_+)$, $p(0,y) = 0$ for all $y > 0$, $p(0,0) = 0$ or does not exist; $\frac{\partial p}{\partial x}(x,y) > 0$
and $\frac{\partial p}{\partial y}(x,y) \leq 0$ for all $(x,y) \in R_+^2$.

The respective similar hypotheses to (A4) and (A5) are
(B3) $p(x,y) + y\frac{\partial p}{\partial y}(x,y) > 0$ for all $(x,y) \in R_+^2$.
(B4) There exists a unique positive rest point $E^* = (x^*, y^*)$ for system (2.2) where $0 < x^* < K$ and $y^* > 0$ satisfies

$$\frac{g(x^*)}{p(x^*, y^*)} = \frac{y^*}{x^*} = \frac{1}{\beta}. \tag{2.5}$$

**Remark 2.2.** In [2], [7], [9], and [14], the functional responses $p(x,y) = p(\frac{x}{y})$ or $\frac{m(x/y)}{a+(x/y)} (= \frac{mx}{ay+x})$ or $m(1 - e^{-kx/y})$. Hence $p(0,0)$ does not exist.

In order to represent the merits of the ratio-dependent model, we can see the following Fig. 2 and Fig. 3 which were given by Arditi and Ginzburg [2]. Fig. 2 presents the observation of Katz (1985). From Fig. $2(a)$, we see that the number of prey eaten per predator depends not only on prey density, but also on predator density. When the data points align on a single curve, Fig. $2(b)$ is much better than Fig. $2(a)$. Hence, it is clear that the form $p(\frac{x}{y})$ represents the data much better than the form $p(x)$. Fig. 3 presents the results of an experiment using a predator-prey system in a complex environment (Bernstein, 1981). Open circles are the average of the number of prey eaten per predator where the prey density $x$ is fixed at a value with the constant ratio $x/y = 4$. When the numbers of prey and predators were changed with a ratio of $4 : 1$, the number of prey eaten per predator did not change significantly. Thus, the empirical data support the ratio-dependent functional response $p(\frac{x}{y})$.

It is not our purpose in this paper to discuss the ecological validity of such ratio-dependent models, but to note that such ratio-dependence does lead to some mathematical problems and therefore we study the global stability of such ratio-dependent models.

## 3 Global stability of a general model

For simplicity, we consider the following general model of (2.1) and (2.2)

$$\begin{aligned} \dot{x} &= xg(x) - yp(x,y), \\ \dot{y} &= yh(x,y), \\ x(0) &> 0, \;\; y(0) > 0, \end{aligned} \tag{3.1}$$

where $g(x)$, $p(x,y)$, and $h(x,y)$ satisfy

(H1) $g \in C^1(R_+, R)$, $g(0) > 0$; there exists $K > 0$ such that $g(K) = 0$; $g'(x) < 0$ for all $x > 0$.

(H2) $p \in C^1(R_+^2, R_+)$, $p(0,y) = 0$ for all $y > 0$, $p(0,0) = 0$ or does not exist; $\frac{\partial p}{\partial x}(x,y) > 0$ and $\frac{\partial p}{\partial y}(x,y) \leq 0$ for all $(x,y) \in R_+^2$.

(H3) $h \in C^1(R_+^2, R)$, $h(K,0) > 0$ or does not exist, $h(0,y) < 0$ or does not exist for all $y \geq 0$; there exists $L > 0$ such that $h(x, \frac{x}{L}) = 0$; $\frac{\partial h}{\partial x}(x,y) > 0$and $\frac{\partial h}{\partial y}(x,y) \leq 0$ for all $(x,y) \in R_+^2$.

The respective similar hypotheses to (A4) and (A5) are (H4) $p(x,y) + y\frac{\partial p}{\partial y}(x,y) > 0$ for all $(x,y) \in R_+^2$ .

(H5) There exists a unique positive rest point $E^* = (x^*, y^*)$ for system (3.1) where $0 < x^* < K$ and $y^* > 0$ satisfies

$$\frac{g(x^*)}{p(x^*,y^*)} = \frac{y^*}{x^*} \tag{3.2}$$

and

$$h(x^*,y^*) = 0. \tag{3.3}$$

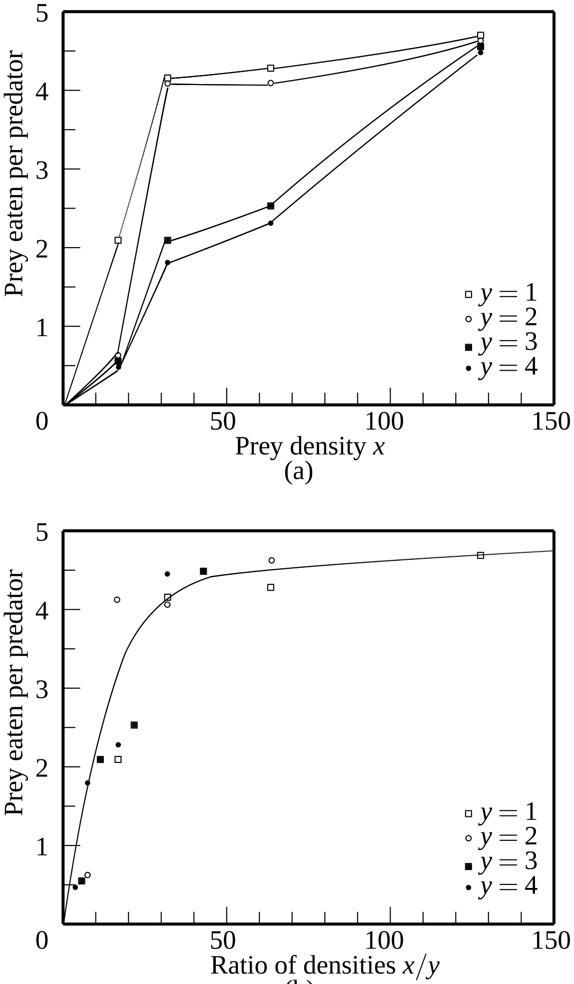

Figure 2: A marine system studied in the field. Number of prey (barnacles *Balanus balanoides*) eaten per predator (snails *Urosalpinx cinerea*) in 24·7 hr, at different prey densities $x$ and predator densities $y$. The data points align on a single curve much better when plotted against the ratio $x/y$ $(b)$ than when plotted against $x$ $(a)$ (data from Katz, 1985).

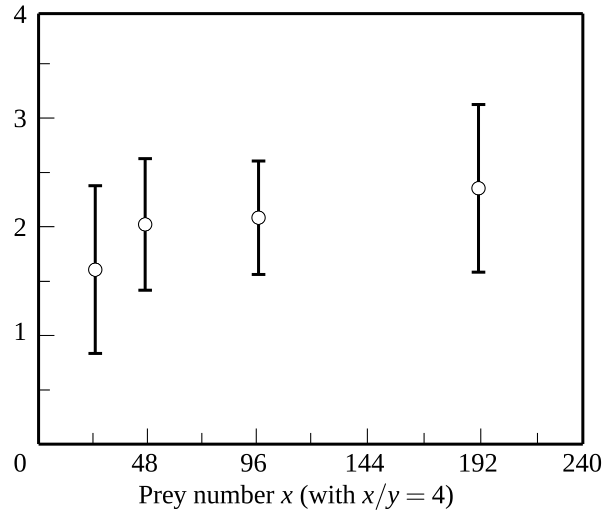

Figure 3: A mite system in a heterogeneous experimental environment. Number of prey (*Tetranychusurticae*) eaten per predator (*Phytoseiuluspersimilis*) in 24 hr, when prey and predator densities are varied in a constant ratio of 4 : 1. There is no significant difference (after Bernstein, 1981).

**Remark 3.1** (a). In [2], [7], [9], and [14], the functional responses $p(x,y) = p(\frac{x}{y})$ or $\frac{m(x/y)}{a+(x/y)}(= \frac{mx}{ay+x})$ or $m(1-e^{-kx/y})$ and the numerical responses $h(x,y) = -d + cp(\frac{x}{y})$ or $-d + c[\frac{m(x/y)}{a+(x/y)}]$ or $-d + cm(1-e^{-kx/y})$. Hence $p(0,0)$ and $h(K,0)$ do not exist and the $x$-axis is not in the domain of system (3.1). Similarly, in [8], [12], and [17], $h(0,y)$ does not exist for all $y > 0$ and the $y$-axis is not in the domain of (3.1), and in [2], [7], [8], [9], [12], [14], and [17], $h(0,0)$ does not exist and the $x$-axis or $y$-axis is not in the domain of (3.1). (b). Clearly system (3.1) may have rest points $E_0 = (0,0)$ when $p(0,0)$ and $h(0,0)$ exist and $E_1 = (K,0)$ when $h(K,0)$ exists.

In this section we restrict our attention to the global stability of the general model (3.1). Firstly, we study the local stability property of system (3.1) by the Hartman-Grobman theorem. Now we compute the variational matrix of system (3.1), denoted by A, and get

$$A = \begin{bmatrix} g(x) + xg'(x) - y\frac{\partial p}{\partial x}(x,y) & -p(x,y) - y\frac{\partial p}{\partial y}(x,y) \\ y\frac{\partial h}{\partial x}(x,y) & h(x,y) + y\frac{\partial h}{\partial y}(x,y) \end{bmatrix}.$$

The local stability of each rest point is determined by the eigenvalues $\lambda$ of matrix A.

At $E_0 = (0,0)$,

$$A(E_0) = \begin{bmatrix} g(0) & -p(0,0) \\ 0 & h(0,0) \end{bmatrix}.$$

From (H1), $g(0) > 0$. If $p(0,0)$ and $h(0,y)$ exist for all $y \geq 0$ then $p(0,0) = 0$ and $h(0,0) < 0$ by (H2) and (H3). Observably, $E_0$ is a saddle point with the positive $y$-axis as its stable manifold.

At $E_1 = (K,0)$,

$$A(E_1) = \begin{bmatrix} Kg'(K) & -p(K,0) \\ 0 & h(K,0) \end{bmatrix}.$$

From (H1), we have $g'(K) < 0$. If $h(K,0)$ exists then $h(K,0) > 0$ by (H3). Clearly, $E_1$ is a saddle point with the positive $x$-axis as its stable manifold.

At $E^* = (x^*,y^*)$,

$$\begin{aligned} A^* &\equiv A(E^*) \\ &= \begin{bmatrix} g(x^*) + x^*g'(x^*) - y^*\frac{\partial p}{\partial x}(x^*,y^*) & -p(x^*,y^*) - y^*\frac{\partial p}{\partial y}(x^*,y^*) \\ y^*\frac{\partial h}{\partial x}(x^*,y^*) & h(x^*,y^*) + y^*\frac{\partial h}{\partial y}(x^*,y^*) \end{bmatrix} \\ &= \begin{bmatrix} x^*g'(x^*) + \frac{y^*}{x^*}p(x^*,y^*) - y^*\frac{\partial p}{\partial x}(x^*,y^*) & -p(x^*,y^*) - y^*\frac{\partial p}{\partial y}(x^*,y^*) \\ y^*\frac{\partial h}{\partial x}(x^*,y^*) & y^*\frac{\partial h}{\partial y}(x^*,y^*) \end{bmatrix}. \end{aligned}$$

$A^*$ has eigenvalues $\lambda$ given by

$$\lambda^2 - (traceA^*)\lambda + detA^* = 0$$

where

$$\begin{aligned} detA^* = y^*\frac{\partial h}{\partial y}(x^*,y^*)[x^*g'(x^*) + \frac{y^*}{x^*}p(x^*,y^*) - y^*\frac{\partial p}{\partial x}(x^*,y^*)] + \\ y^*\frac{\partial h}{\partial x}(x^*,y^*)[p(x^*,y^*) + y^*\frac{\partial p}{\partial y}(x^*,y^*)] \end{aligned} \tag{3.4}$$

and

$$traceA^* = x^*g'(x^*) + \frac{y^*}{x^*}p(x^*,y^*) - y^*\frac{\partial p}{\partial x}(x^*,y^*) + y^*\frac{\partial h}{\partial y}(x^*,y^*) \tag{3.5}$$

For stability we require $Re\lambda < 0$ and so the necessary and sufficient conditions for locally asymptotical stability are

$$detA^* > 0 \quad \text{and} \quad traceA^* < 0.$$

According to above three results, we can get the following lemma.

**Lemma 3.2** *(i) If (H1)-(H4) hold and* $p(0,0)$ *and* $h(0,y)$ *exist for all* $y \geq 0$, *then the rest point* $E_0 = (0,0)$ *of system (3.1) is a saddle point with the positive y-axis as its stable manifold. (ii) If*

(H1)-(H4) *hold and* $h(K,0)$ *exists, then the rest point* $E_1 = (K,0)$ *of system (3.1) is a saddle point with the positive x-axis as its stable manifold. (iii) Let* (H1)-(H5) *hold. If the unique positive rest point* $E^* = (x^*, y^*)$ *of system (3.1) satisfies*

$$detA^* > 0 \quad and \quad traceA^* < 0,$$

*where* $detA^*$ *and* $traceA^*$ *are defined by equations (3.4) and (3.5) respectively, then* $E^*$ *is locally asymptotically stable.*

Next, the following lemma is a statement that system (3.1) is as ”well behaved” as an intuition from the biological problem.

**Lemma 3.3** *Under assumptions* (H1)-(H5)*, solutions of system* (3.1) *are positive and bounded, and furthermore, there exists* $\tau > 0$ *such that* $x(t) < K$ *for all* $t \geq \tau$*.*

**Proof:** By Lemma 3.2(i)(ii), if $h(K,0)$ exists ($p(0,0)$ and $h(0,y)$ exist for all $y \geq 0$) then the rest point $E_1 = (K,0)$ ($E_0 = (0,0)$) is a saddle point with the positive $x$-axis ($y$-axis) as its stable manifold. If solutions $(x(t), y(t))$ of system (3.1) enter the positive $x$-axis ($y$-axis) from the first quadrant, then $(x(t), y(t))$ will approach $E_1$ ($E_0$). This implies that the stable manifold of $E_1$ ($E_0$) is not unique. So it is impossible that solutions $(x(t), y(t))$ of system (3.1) enter the positive $x$-axis or $y$-axis from the first quadrant. Thus, if $x(0) > 0$ and $y(0) > 0$ then solutions of system (3.1) are positive.

Firstly, we claim that $x(t)$ is bounded for all $t \geq 0$. We consider the following two cases : (I) $x(0) < K$ , or (II) $x(0) \geq K$. We discuss them as follows.

(I) If $x(0) < K$ then $x(t) < K$ for all $t \geq 0$, otherwise, there is $t_1 > 0$ such that $x(t_1) = K$ and $\dot{x}(t_1) \geq 0$. From the first equation of (3.1), (H1), and (H2), it follows that

$$\dot{x}(t_1) = -y(t_1)p(x(t_1), y(t_1)) < 0.$$

This contradicts $\dot{x}(t_1) \geq 0$. That is, if $x(0) < K$ then $x(t) < K$ for all $t \geq 0$.

(II) From the first equation of (3.1), (H1), and (H2), we have $\dot{x} < 0$ for all $x \geq K,\ y > 0$. That is, $x$ is strictly decreasing for all $x \geq K$ , $y > 0$. Therefore, if $x(0) \geq K$ then either $x(t)$ decreases to $\hat{x} \geq K$, or there exists $\tau > 0$ such that $x(\tau) < K$, which yields that $x(t) < K$ for all $t \geq \tau$, by using the same discussion as case (I). Hence $x(t) < M \equiv max\{K, x(0)\}$ for all $t \geq 0$.

Next, we claim that $y(t)$ is bounded for all $t \geq 0$. We consider the following two cases : (III) $y(0) < ML^{-1}$, or (IV) $y(0) \geq ML^{-1}$. We discuss them as follows.

(III) If $y(0) < ML^{-1}$ then $y(t) < ML^{-1}$ for all $t \geq 0$, otherwise, there is $t_2 > 0$ such that $y(t_2) = ML^{-1}$ and $\dot{y}(t_2) \geq 0$. From the second equation of (3.1) and (H3), it follows that

$$\begin{aligned}\dot{y}(t_2) &= y(t_2)h(x(t_2), y(t_2)) \\ &= \frac{M}{L}h(x(t_2), \frac{M}{L}) < \frac{M}{L}h(M, \frac{M}{L}) = 0.\end{aligned}$$

This contradicts to $\dot{y}(t_2) \geq 0$. That is, if $y(0) < ML^{-1}$ then $y(t) < ML^{-1}$ for all $t \geq 0$.

(IV) From the second equation of (3.1) and (H3), we have $h(x,y) < 0$ for all $0 < x < M,\ y \geq ML^{-1}$, which implies $\dot{y} < 0$ for all $0 < x < M,\ y \geq ML^{-1}$. Therefore, if $y(0) \geq ML^{-1}$ then either $y(t)$ decreases to $\bar{y} \geq ML^{-1}$, or there exists $s > 0$ such that $y(s) < ML^{-1}$, which yields that $y(t) < ML^{-1}$ for all $t \geq s$, by using the same discussion as case (III). Hence $y(t) < N \equiv max\{ML^{-1}, y(0)\}$ for all $t \geq 0$.

Finally, we want to show that it is impossible that $x(t)$ decreases to $\hat{x} \geq K$, and hence we have the result that there exists $\tau > 0$ such that $x(t) < K$ for all $t \geq \tau$. Suppose that $x(t)$ decreases to $\hat{x} \geq K$. Since $x(t)$ and $y(t)$ are positive and bounded, according to the Poincaré-Bendixson theorem, solutions $(x(t), y(t))$ of system (3.1) will approach a positive rest point $(\hat{x}, \hat{y})$, where $\hat{y} > 0$. This contradicts (H5), and we complete the proof. □

**Remark 3.4**
Lemma 2.1 in [12] is a special case of Lemma 3.3.

Finally, we have the following theorem by applying Dulac's criterion.

**Theorem 3.5** *Let* (H1)-(H5) *hold. If* $detA^* > 0$ *and*

$$xg'(x) + \frac{y}{x}p(x,y) - y\frac{\partial p}{\partial x}(x,y) + y\frac{\partial h}{\partial y}(x,y) < 0 \tag{3.6}$$

*for all* $(x,y) \in R^2_+$*, where* $detA^*$ *is defined by equations (3.4), then the rest point* $E^* = (x^*, y^*)$ *of system (3.1) is globally asymptotically stable in the first quadrant.*

**Proof:** Let

$$\begin{aligned} f_1(x,y) &= xg(x) - yp(x,y), \\ f_2(x,y) &= yh(x,y). \end{aligned}$$

We construct

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

An easy computation yields

$$\begin{aligned} &\frac{\partial(f_1H)}{\partial x} + \frac{\partial(f_2H)}{\partial y} \\ &= H\left(\frac{\partial f_1}{\partial x} + \frac{\partial f_2}{\partial y}\right) + f_1\frac{\partial H}{\partial x} + f_2\frac{\partial H}{\partial y} \\ &= x^{-1}y^{-1}[g(x) + xg'(x) - y\frac{\partial p}{\partial x}(x,y) + h(x,y) + y\frac{\partial h}{\partial y}(x,y)] - \\ &\quad x^{-2}y^{-1}[xg(x) - yp(x,y)] - x^{-1}y^{-2}[yh(x,y)] \\ &= x^{-1}y^{-1}[xg'(x) + \frac{y}{x}p(x,y) - y\frac{\partial p}{\partial x}(x,y) + y\frac{\partial h}{\partial y}(x,y)] \quad < 0 \end{aligned}$$

whenever

$$xg'(x)+\frac{y}{x}p(x,y)-y\frac{\partial p}{\partial x}(x,y)+y\frac{\partial h}{\partial y}(x,y) \quad < 0 \ \text{ for all } \ (x,y)\in R^2_+.$$

Hence, if (3.6) holds then there is no periodic orbit in the first quadrant by Dulac's criterion. From Lemma 3.2 (iii) and $detA^* > 0$, if (3.6) holds then $E^*$ is locally asymptotically stable. By Lemma 3.3 and the Poincaré-Bendixson theorem, it suffices to show that the unique positive rest point $E^*$ is globally asymptotically stable in the first quadrant. □

**Remark 3.6**

(a). Since

$$xg'(x)+\frac{y}{x}p(x,y)-y\frac{\partial p}{\partial x}(x,y)=x\frac{\partial f}{\partial x},$$

Theorem 3.5 says that if (3.1) is a self-regulating predator-prey system (that is, $\frac{\partial f}{\partial x} < 0$, $\frac{\partial h}{\partial y} < 0$ in $R^2_+$) then the rest point $E^* = (x^*, y^*)$ is globally asymptotically stable in the first quadrant.

(b). Consider the following Leslie-Gower model [12] and [17]

$$\begin{aligned} \dot{x} &= rx(1-\frac{x}{K})-y(mx) \\ \dot{y} &= y[s(1-\beta\frac{y}{x})] \\ x(0) &> 0, y(0) > 0, \end{aligned} \tag{3.7}$$

where the functional response $p(x,y) = mx$ is of Holling-Type 1. System (3.7) is exactly a self-regulating predator-prey system. Hence, by (a) the rest point $E^*$ of (3.7) is globally asymptotically stable in the first quadrant. Remark 2.3 in [12] had the same conclusion by constructing a Liapunov function.

(c). The Kolmogorov model [1], [5], and [11]

$$\begin{aligned} \dot{x} &= xf(x,y), \\ \dot{y} &= yh(x,y), \\ x(0) &> 0, y(0) > 0, \end{aligned}$$

is a general model of (3.1), and Theorem 3.5 looks like a special case of Theorem 3 in [5]. Cheng et al. proved Theorem 3 in [5] by the method of limit cycle stability analysis. However, the assumptions for system (3.1) are different from the assumptions needed in Theorem 3 of [5] and we get Theorem 3.5 by applying Dulac's criterion.

## 4 Global stability of ratio-dependent models

In this section we state the principal results of the paper. Firstly, we restrict our attention to the global stability of system (2.1). We are trying to do this by using Theorem 3.5. Here,

$p(x,y) = p(\frac{x}{y}) \equiv p(u)$ and $h(x,y) = h(\frac{x}{y}) \equiv h(u)$, so

$$\begin{aligned} F(x,y) &\equiv xg'(x) + \frac{y}{x}p(x,y) - y\frac{\partial p}{\partial x}(x,y) + y\frac{\partial h}{\partial y}(x,y) \\ &= xg'(x) + \frac{p(u)}{u} - p'(u) - uh'(u) \end{aligned}$$

and by (3.4), we get

$$detA^* = -x^*u^*g'(x^*)h'(u^*)$$

where

$$u^* = \frac{x^*}{y^*}.$$

Assume

$$\frac{p(u)}{u} - p'(u) - uh'(u) \leq 0,$$

that is,

$$[\frac{p(u)}{u} + h(u)]' \geq 0$$

for all $u > 0$. Thus, from (A1) and (A3), we have

$$detA^* > 0$$

and

$$F(x,y) < 0 \text{ for all } (x,y) \in R_+^2.$$

Hence we obtain the following theorem by Theorem 3.5.

**Theorem 4.1** *Let* (A1)-(A5) *hold. If*

$$[\frac{p(u)}{u} + h(u)]' \geq 0 \tag{4.1}$$

*for all* $u > 0$, *then the rest point* $E^*$ *of system (2.1) is globally asymptotically stable in the first quadrant.*

**Remark 4.2** As an intuition from the biological problem, Theorem 4.1 is a statement that, for any ratio $u$ (prey/predator), if the sum of “the average rate of change of the feeding rate per predator” and “the predator growth rate” is nondecreasing as $u$ increases, then the rest point $E^*$ of system (2.1) is globally asymptotically stable in the first quadrant.

Next, we study the global stability of system (2.2) by using the method of limit cycle stability analysis. Here, $h(x,y) = s(1 - \beta\frac{y}{x})$. From (2.5) and (3.4)-(3.5), we obtain

$$detA^* = -s\{x^*g'(x^*) - y^*[\frac{\partial p}{\partial x}(x^*,y^*) + \frac{1}{\beta}\frac{\partial p}{\partial y}(x^*,y^*)]\} \tag{4.2}$$

and

$$traceA^* = [xg(x)]'|_{x=x^*} - y^* \frac{\partial p}{\partial x}(x^*, y^*) - s. \tag{4.3}$$

Hence, by Lemma 3.2(iii), we have the following lemma.

**Lemma 4.3** *Let* (B1)-(B4) *hold. If* $detA^* > 0$ *and*

$$[xg(x)]'|_{x=x^*} \leq s,$$

*where* $detA^*$ *is defined by equation* (4.2), *then the rest point* $E^*$ *of the system* (2.2) *is locally asymptotically stable.*

We can combine Lemma 4.3 and the method of limit cycle stability analysis to get the following theorem.

**Theorem 4.4** *Let (B1)-(B4) hold. If* $detA^* > 0$ *and*

$$[xg(x)]' \leq s \tag{4.4}$$

*for all* $x > 0$, *where* $detA^*$ *is defined by equation* (4.2), *then the rest point* $E^*$ *of system* (2.2) *is globally asymptotically stable in the first quadrant.*

**Proof:** It suffices to show that system (2.2) has no closed orbit in the first quadrant. Suppose there is a $T-$periodic orbit $\Gamma = \{(x(t), y(t)) |\ 0 \leq t \leq T\}$.
Compute

$$\begin{aligned}\Delta =& \int_0^T \{\frac{\partial}{\partial x}[p(x,y)(\frac{xg(x)}{p(x,y)} - y)] + \\ & \frac{\partial}{\partial y}[p(x,y)(\frac{sy}{p(x,y)}(1-\beta\frac{y}{x}))]\}\Big|_{\substack{x=x(t)\\ y=y(t)}} dt \\ =& \int_0^T \{[\frac{xg(x)}{p(x,y)} - y]\frac{\partial p}{\partial x}(x,y) + \\ & p(x,y)\frac{\partial}{\partial x}[\frac{xg(x)}{p(x,y)}] + \\ & [\frac{sy}{p(x,y)}(1-\beta\frac{y}{x})]\frac{\partial p}{\partial y}(x,y) + \\ & p(x,y)\frac{\partial}{\partial y}[\frac{sy}{p(x,y)}(1-\beta\frac{y}{x})]\}\Big|_{\substack{x=x(t)\\ y=y(t)}} dt.\end{aligned}$$

From (2.2), and

$$\frac{dp(x,y)}{dt} = \frac{\partial p}{\partial x}(x,y)\frac{dx}{dt} + \frac{\partial p}{\partial y}(x,y)\frac{dy}{dt}$$

it follows that

$$\begin{aligned}0=&\int_0^T \frac{1}{p(x(t),y(t))}dp(x(t),y(t))\\ =&\int_0^T \{[\frac{xg(x)}{p(x,y)}-y]\frac{\partial p}{\partial x}(x,y)+\\ &[\frac{sy}{p(x,y)}(1-\beta\frac{y}{x})]\frac{\partial p}{\partial y}(x,y)\}\Big|_{\substack{x=x(t)\\ y=y(t)}}\,dt\end{aligned}$$

and

$$0=\int_0^T \frac{1}{y(t)}dy(t)=\int_0^T s(1-\beta\frac{y}{x})\Big|_{\substack{x=x(t)\\ y=y(t)}}\,dt.$$

Hence we have

$$\begin{aligned}\Delta=&\int_0^T \{p(x,y)\frac{\partial}{\partial x}[\frac{xg(x)}{p(x,y)}]+\\ &p(x,y)\frac{\partial}{\partial y}[\frac{sy}{p(x,y)}(1-\beta\frac{y}{x})]\}\Big|_{\substack{x=x(t)\\ y=y(t)}}\,dt\\ =&\int_0^T \{g(x)+xg'(x)-[\frac{xg(x)}{p(x,y)}]\frac{\partial p}{\partial x}(x,y)-s+\\ &2s(1-\beta\frac{y}{x})-[\frac{sy}{p(x,y)}(1-\beta\frac{y}{x})]\frac{\partial p}{\partial y}(x,y)\}\Big|_{\substack{x=x(t)\\ y=y(t)}}\,dt \qquad (4.5)\\ =&\int_0^T \{[xg(x)]'-y\frac{\partial p}{\partial x}(x,y)-s\}\Big|_{\substack{x=x(t)\\ y=y(t)}}\,dt.\end{aligned}$$

From (B2) and (4.4), it follows that

$$\Delta<0.$$

This indicates that all periodic orbits of system (2.2) in the first quadrant are orbitally stable. Since every periodic orbit is orbitally stable then there is a unique stable limit cycle in the first quadrant. That is, $E^*$ is unstable. However, by (4.4), $detA^*>0$, and Lemma 4.3, $E^*$ is locally asymptotically stable. Thus, there is no periodic orbit in the first quadrant. By Lemma 3.3 and the Poincaré-Bendixson theorem, it suffices to show that the unique positive rest point $E^*$ is globally asymptotically stable in the first quadrant. □

**Remark 4.5** Theorem 4.4 says that, for any locally asymptotically stable rest point $E^*$ of (2.2), if the instantaneous rate of change of the recruitment rate (or harvesting rate) of the prey in the absence of predators with respect to prey density $x$ is not greater than the intrinsic growth rate $s$ of the predator, then $E^*$ is globally asymptotically stable in the first quadrant.

For the system (2.2) with $p(x,y) = p(x)$, (4.2) and (4.3) becomes

$$detA^* = -s[x^*g'(x^*) - y^*p'(x^*)] > 0$$

and

$$traceA^* = p(x^*)\left[\frac{xg(x)}{p(x)}\right]'\Bigg|_{x=x^*} - s$$

respectively, and we have the following corollary by (4.5).

**Corollary 4.6** *Consider the system* (2.2) *with* $p(x,y) = p(x)$ *and let* (B1)-(B4) *hold. If*

$$Q(x) \leq 0 \ \textit{ for all } \ x > 0,$$

*where*

$$Q(x) = p(x)\left[\frac{xg(x)}{p(x)}\right]' - s$$

*and* $Q(x)$ *is not identically zero, then the rest point* $E^*$ *is globally asymptotically stable in the first quadrant.*

**Remark 4.7** In [12], Hsu and Huang analyzed the global stability of system (2.2) with $p(x) = \frac{mx}{A+x}$ or $\frac{mx^2}{(A+x)(B+x)}$ by Dulac's criterion, $H(x,y) = (\frac{mx}{A+x})^{-1}y^{-2}$ or $[\frac{mx^2}{(A+x)(B+x)}]^{-1}y^{-2}$ and got Theorem 3.2(i) and Theorem 4.2(i) in [12] which are special cases of Corollary 4.6 (The more detailed statement will be given in Remark 5.4).

**Remark 4.8** When we consider system (2.2) and construct

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

as we did in Theorem 3.5, we have the same result as Theorem 4.4.

## 5 Examples

We now illustrate the above results by means of two examples.

**Example 5.1** Consider the ratio-dependent functional response model in [7] and [14]

$$\begin{aligned}
&\dot{x} = rx(1-\frac{x}{K}) - y(\frac{mx}{ay+x}),\\
&\dot{y} = y[-d + c(\frac{mx}{ay+x})],\\
&x(0) > 0, y(0) > 0,
\end{aligned} \tag{5.1}$$

which is a special case of system (2.1). We note that hypotheses (A1)-(A4) are satisfied when

$$cm - d > 0.$$

From (2.3) and (2.4), it follows that

$$\begin{aligned}
x^* &= \frac{(acr - cm + d)K}{acr},\\
y^* &= \frac{(cm-d)(acr - cm + d)K}{a^2cdr}.
\end{aligned}$$

We observe that (A5) holds when

$$acr - cm + d > 0.$$

We can get the global stability property of (5.1) by Theorem 4.1. Since $p(u) = \frac{mu}{a+u}$ and $h(u) = -d + c(\frac{mu}{a+u})$, (4.1) becomes

$$G(u) \geq 0,$$

where

$$G(u) = \frac{m(ac-1)}{(a+u)^2}.$$

We note that $G(u) \geq 0$ for all $u > 0$ if and only if

$$ac \geq 1.$$

On the other hand, if we construct

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

then, as we did in Theorem 4.1, we get the following sufficient condition (5.2) which is different from the condition (4.1)

$$-r + \frac{2p(u)}{u} - p'(u) - uh'(u) < 0. \tag{5.2}$$

We can verify that (5.2) is satisfied for the model (5.1) if and only if

$$ar - m \geq 0$$

Hence we have the following property.

**Remark 5.2**
(a). Sufficient conditions for the global stability of (5.1) are : Suppose $cm-d>0$, $acr-cm+d>0$, and one of the following three conditions is satisfied: (i) $ac\geq 1$, (ii) $ar-m\geq 0$,
Then the rest point $E^*$ of model (5.1) is globally asymptotically stable in the first quadrant.
(b). The local stability analysis of the rest point $E^*$ of model (5.1) was done in [14]. In [7] the authors showed that if $acr+d>cm$ then model (5.1) is persistent.

**Example 5.3** Consider the logistic ratio-dependent model in [7], [12], and [17]

$$\begin{aligned}&\dot{x}=rx(1-\frac{x}{K})-y(\frac{mx}{a+x}),\\&\dot{y}=y[s(1-\beta\frac{y}{x})],\\&x(0)>0,y(0)>0,\end{aligned}\tag{5.3}$$

which is a special case of system (2.2). It is easy to verify that (B1)-(B4) are satisfied.
Hence, as we did in Example 5.1, we obtain the following property by Corollary 4.6.

**Remark 5.4** (a). Sufficient conditions for the global stability of model (5.3) are :
If either

(i) $ar+Ks-Kr\geq 0$

or

(ii) $ar+Ks-Kr<0$ and $(ar+Ks-Kr)^2-8aKrs\leq 0$,

then the rest point $E^*$ of model (5.3) is globally asymptotically stable in the first quadrant.
(b). The local stability analysis of the rest point $E^*$ of model (5.3) was done in [12] and [17]. Furthermore, the authors [12] analyzed the global stability property of model (5.3) by Dulac's criterion $(H(x,y)=(\frac{mx}{a+x})^{-1}y^{-2})$ and got the same conclusion as (a). In [7] the authors showed that model (5.3) is persistent.

# 6 Conclusion

In this paper, we have focused on predator-prey systems with ratio-dependence. It is our main purpose to obtain the global stability properties of such ratio-dependent models (2.1) and (2.2).

It is a well-know fact that the local stability of a rest point in a predator-prey system does not necessarily imply its global stability. We have presented sufficient conditions for the global stability of (2.1) and (2.2) by the application of Dulac's criterion or the method of limit cycle stability analysis . The ecological reasons for incorporating ratio-dependence into predator-prey systems have been argued elsewhere. It is not our purpose to enforce these arguments, but rather to give sufficient conditions under which each unique positive rest point of such systems is globally asymptotically stable in the first quadrant when they are used.

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# 具有比率相關之捕食系統的整體穩定性

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## 摘　要

本篇論文主要在研究具有比率相關之捕食系統的整體穩定性。我們利用 Poinecaré-Bendixson 定理及 Dulac 準則、極限環穩定分析法等兩種方法，得到上述系統的整體穩定性之充分條件。

關鍵詞：整體穩定性、捕食系統、比率相關。

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