

DYNAMICS OF TWO PREDATOR-PREY MODELS WITH POWER LAW RELATION

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Abstract In this paper, we propose a predator-prey model with power law relation based on the model in [Hatton et al, *The predator-prey power law: Biomass scaling across terrestrial and aquatic biomes*, *Science* 349(2015), aac6284], and analyze the global dynamics of both models. We obtain that Hatton's model is persistent for power less than 1, and there exists a separatrix near the origin such that solutions of the model above it are driven to the origin and the ones below it are far away from origin for power greater than 1. However, our model is persistent for all power and has the same singularity as that of Hatton's model at the origin for power greater than 1, which indicate that the prey and predator will coexist or extinct eventually. Furthermore, in our model, the prey will be stable at its carrying capacity and the predator will be extinct for power less than 1, and the prey will be stable at its carrying capacity or both the prey and predator will be extinct for power greater than 1.

Keywords Predator-prey model, power law, equilibrium, stability, Hopf bifurcation.

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1. Introduction

Since Lotka-Volterra predator-prey model was proposed to study the problems in chemical reactions and fishes with predator-prey relation [24, 35], the predator-prey models are always the focus in mathematical biology. Generally, the predator-prey model can be given by ordinary differential equations ([7], Chapter 5)

$$\begin{cases} \frac{dX}{dt} = F(X, Y), \\ \frac{dY}{dt} = G(X, Y), \end{cases} \quad (1.1)$$

where X and Y are biomass, and $F(X, Y)$ and $G(X, Y)$ are the growth rates of the prey and predator species at time t , respectively. Many classical predator-prey models are special cases of (1.1), for example, Kolmogorov predator-prey model and Lotka-Volterra predator-prey model. However, it makes model (1.1) difficult to study since there are few techniques. Therefore, according to biological meaning, model (1.1) can be written into different forms, such as, predator functional

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responses models [11, 15, 17, 26, 30, 34, 42] and ratio-dependent functional responses models [2, 4, 12, 18, 20, 21, 36–38, 40]. Reference [5] gave a detailed introduction to predator functional responses and ratio-dependent functional responses in the predator-prey models.

Recently, predator-prey models were studied to describe herd [1, 8–10, 32] and spatiotemporal [33, 39, 43] behaviors, and influence of stochastic perturbation [19, 22, 25, 28, 29, 41]. The responses of these models are functions of predator and prey with exponent, and we call them *exponential functional response*. The models with exponential functional response have singularities at the origin, which can not be discussed with the method of linearization. However, the singularities of the origin deserve to be discussed by developing various methods. The model with exponent response was also considered in [23].

All of the above literatures assumed that the intrinsic growth rate of prey is $\frac{dX}{dt} = rX$, i.e., the intrinsic growth rate of prey is in proportion to its biomass, where r is the intrinsic average growth rate of prey. In fact, the linear intrinsic growth only provides advantage in analysis of the models. Obviously, it has shortcoming in describing real population problems.

In 2015, the empirical findings of Hatton et al [14] showed that biomass of prey and predator have power law relation near the steady state. They proposed a predator-prey model

$$\begin{cases} \frac{dX}{dt} = rX^k - XY, \\ \frac{dY}{dt} = gXY - mY, \end{cases} \quad (1.2)$$

where X and Y are biomass of prey and predator at time t , respectively, r is the intrinsic growth rate of prey, g is the growth efficiency of predator in converting prey into offspring of predator, m is the mortality rate of predator, and $r > 0$, $g > 0$, $m > 0$, $k > 0$. Furthermore, their empirical findings also showed that the exponent k is near $\frac{3}{4}$ for most predator and prey relation in terrestrial and aquatic biomes, whereas the exponent k is close to 1 or $k > 1$ for some piscivore and fish relation. A generalization of model (1.2) can be written as

$$\begin{cases} \frac{dX}{dt} = P(X) - Q(X, Y), \\ \frac{dY}{dt} = gQ(X, Y) - mH(Y), \end{cases} \quad (1.3)$$

where $P(X)$ is the prey production, $Q(X, Y)$ is the prey consumption by predator, $H(Y)$ is the predator death. If prey production is assumed to be $P(X) = rX^k$, and model (1.3) has a positive equilibrium, then the prey and the predator have power law relation near the steady state. Based on model (1.2), a pest control predator-prey model is proposed in [31].

The growth of prey rX^k in model (1.2) is an exponential function with exponent k . The expressional forms of the right side in model (1.2) are similar to those of the exponential functional response models. Therefore, model (1.2) also has the similar singularities at the origin, which is one of our goal in this paper.

The Lotka-Volterra predator-prey model is the case of model (1.2) for $k = 1$, which is usually regarded as unrealistic model for the unbounded prey in the absence of predator and structural stability although it explain a real fishing problem in the Adriatic perfectly. Accordingly, model (1.2) has the same problem, i.e., the prey

in absence of the predator will be infinity, which is a contradiction to the limited environmental resource in the sense of biology. Although more than two thousands of data sets for the predator and prey relation support the results in [14], model (1.2) is too simple to be realistic for describing real relation of predator and prey. The other one problem is that the conclusion of [14] shows that the growth of community is density-dependent, but model (1.2) is not the density-dependent growth in the expressional forms. It will be more suitable to consider a density-dependent growth in proposing a mathematical model. Another shortcoming of model (1.2) is that both the predator and the prey in model (1.2) will be unbounded for $k > 1$. This contradicts to the density-dependent growth and limited environmental resources.

Motivated by the above, in this paper, we intend to adapt model (1.2) to obtain a more biological meaningful model. Therefore, considering the logistic density dependence of the prey, we propose a predator-prey model with power law relation as follows

$$\begin{cases} \frac{dX}{dt} = rX^k \left(1 - \frac{X}{K}\right) - XY, \\ \frac{dY}{dt} = gXY - mY, \end{cases} \tag{1.4}$$

where K is the carrying capacity of the prey in an environment and model (1.4) has the density-dependent growth.

Apparently, interspecies competition is linear and intraspecies competition is nonlinear and asymmetric in model (1.4). These characteristics are similar to those of Gilpin-Ayala competition model proposed in [3, 13],

$$\begin{cases} \frac{dX_1}{dt} = r_1 X_1 \left[1 - \left(\frac{X_1}{K_1}\right)^{\theta_1} - a_{12} \frac{X_2}{K_2}\right], \\ \frac{dX_2}{dt} = r_2 X_2 \left[1 - \left(\frac{X_2}{K_2}\right)^{\theta_2} - a_{21} \frac{X_1}{K_1}\right], \end{cases} \tag{1.5}$$

where X_i and r_i are the density and the intrinsic growth rate of the i th species, respectively; K_i is the carrying capacity of the i th species in the absence of the j th species, a_{ij} is the reduction of the growth rate of the i th species by the j th species, θ_i is the asymmetry growth of the i th species, $i, j = 1, 2$. Model (1.5) is Lotka-Volterra competition model when $\theta_1 = \theta_2 = 1$. In fact, Gilpin and Ayala [3, 13] gave eleven competition models, among which model (1.5) was regarded as the best one for fitting to the experimental data and received much attention since then. The above mentioned papers [1, 8–10, 23, 32, 33, 39, 43] studied nonlinear models with the nonlinear interspecies competition and linear intraspecies competition.

In Section 3, we will show that model (1.4) has power law relation near the steady state, and it is persistent for all $k > 0$. Therefore, any solution of model (1.4) is bounded, and model (1.4) is more suitable for describing the predator and prey relation in an ecological environment.

We also analyze the global behaviors of models (1.2) and (1.4) in this paper. Our main results are illustrated by some simulations of examples in Section 4. In Section 5, our conclusions and some discussions are given.

2. Dynamics of model (1.2)

In this section, we analyze model (1.2) in $R_+^2 = \{(X, Y) | X \geq 0, Y \geq 0\}$. It is easy to get that model (1.2) has a boundary equilibrium $E^0 = (0, 0)$ and a positive equilibrium $E^* = (X^*, Y^*)$, where

$$X^* = \frac{m}{g}, \quad Y^* = r \left(\frac{m}{g} \right)^{k-1}.$$

Apparently, $Y^* = \frac{gr}{m}(X^*)^k$, showing the existence of a power law relation for the positive equilibrium. The Jacobi matrix of model (1.2) is

$$J = \begin{bmatrix} rkX^{k-1} - Y & -X \\ gY & gX - m \end{bmatrix}.$$

2.1. Stability of boundary equilibrium

Model (1.2) without predator is

$$\frac{dX}{dt} = rX^k. \quad (2.1)$$

$X = 0$ is a solution of (2.1). Solution of equation (2.1) with initial value $X(t_0) = X_0 \neq 0$ is

$$X^{1-k} = (1-k)r(t-t_0) + X_0^{1-k}$$

for $k \neq 1$, and

$$X = X_0 e^{r(t-t_0)}$$

for $k = 1$. Therefore, we know that $X \rightarrow +\infty$ as $t \rightarrow +\infty$ for $0 < k \leq 1$, and $X \rightarrow +\infty$ as

$$t \rightarrow \left[\frac{1}{r(k-1)X_0^{k-1}} + t_0 \right]^-$$

for $k > 1$. For $k > 1$, this means that the population of prey diverges in finite time, which does not seem true in the sense of biology.

On the other hand, model (1.2) without prey is

$$\frac{dY}{dt} = -mY, \quad (2.2)$$

so the solution of equation (2.2) with initial value $Y(t_0) = Y_0$ is $Y = Y_0 e^{-m(t-t_0)}$, accordingly $Y \rightarrow 0$ as $t \rightarrow +\infty$.

Furthermore, we can prove the following result regarding the stability of E^0 .

Theorem 2.1. *If $0 < k \leq 1$, then E^0 is a saddle. If $k > 1$, then there exists a separatrix, and solutions of (1.2) above it are driven to E^0 and the ones below it are far away from E^0 .*

Proof. If $k = 1$, then the eigenvalues of Jacobi matrix at E^0 are $r > 0$ and $-m < 0$. Accordingly, E^0 is a saddle.

If $0 < k < 1$, the Jacobi matrix at E^0 is not determined. The above discussions show that solutions of (1.2) with initial on x -axis are always on x -axis and tend

to infinity as $t \rightarrow +\infty$, and solutions of (1.2) with initial on y -axis are always on y -axis and tend to origin as $t \rightarrow +\infty$. By the method of [8], for $X \ll 1$ and $Y \ll 1$, model (1.2) can be approximated by

$$\begin{cases} \frac{dX}{dt} = rX^k, \\ \frac{dY}{dt} = -mY. \end{cases} \quad (2.3)$$

The solution of (2.3) with initial value $(X(t_0), Y(t_0)) = (X_0, Y_0)$ is

$$Y = Y_0 e^{-\frac{m}{(1-k)r}(X^{1-k} - X_0^{1-k})}.$$

If

$$Y_0 = e^{-\frac{m}{(1-k)r}X_0^{1-k}},$$

then the solution of (2.3) with initial value (X_0, Y_0) is along the curve

$$Y = e^{-\frac{m}{(1-k)r}X^{1-k}}.$$

Thus, all solutions of (1.2) with positive initial value (X_0, Y_0) near the origin will be very close to the above curve. Accordingly, E^0 is a saddle.

If $k > 1$, for $X \ll 1$ and $Y \ll 1$, model (1.2) may be approximated by

$$\begin{cases} \frac{dX}{dt} = rX^k - XY, \\ \frac{dY}{dt} = -mY. \end{cases} \quad (2.4)$$

The first equation of (2.4) can be rewritten as

$$X^{-k} \frac{dX}{dt} = r - X^{1-k}Y.$$

Let $Z = X^{1-k}$, then the above equation is

$$\frac{dZ}{dt} = (1-k)r - (1-k)ZY.$$

Substituting the solution $Y = Y_0 e^{-m(t-t_0)}$ of the second equation of (2.4) with initial value $Y(t_0) = Y_0$, we get

$$\frac{dZ}{dt} + (1-k)Y_0 e^{-m(t-t_0)}Z = (1-k)r,$$

which is a linear differential equation, and its solution with initial value $Z(t_0) = Z_0$ is

$$\begin{aligned} Z &= e^{(k-1)Y_0 \int_{t_0}^t e^{-m(s-t_0)} ds} \left[(1-k)r \int_{t_0}^t e^{-(k-1)Y_0 \int_{t_0}^w e^{-m(s-t_0)} ds} dw + Z_0 \right] \\ &= e^{-\frac{k-1}{m}Y} \left[\frac{(k-1)r}{m} \int_{-\frac{k-1}{m}Y_0}^{-\frac{k-1}{m}Y} \frac{e^{-u}}{u} du + Z_0 e^{\frac{k-1}{m}Y_0} \right] \\ &= e^{-\frac{k-1}{m}Y} \left[\frac{(k-1)r}{m} Ei \left(\frac{k-1}{m}Y \right) - \frac{(k-1)r}{m} Ei \left(\frac{k-1}{m}Y_0 \right) + Z_0 e^{\frac{k-1}{m}Y_0} \right], \end{aligned}$$

where

$$Ei(s) = - \lim_{\varepsilon \rightarrow 0^+} \left(\int_{-s}^{-\varepsilon} \frac{e^{-t}}{t} dt + \int_{\varepsilon}^{\infty} \frac{e^{-t}}{t} dt \right)$$

is the Cauchy principle value of the exponential integral for $s > 0$ [6]. So

$$X^{1-k} = e^{-\frac{k-1}{m}Y} \left[\frac{(k-1)r}{m} Ei\left(\frac{k-1}{m}Y\right) - \frac{(k-1)r}{m} Ei\left(\frac{k-1}{m}Y_0\right) + X_0^{1-k} e^{\frac{k-1}{m}Y_0} \right]$$

is a solution of (2.4) with initial value $(X(t_0), Y(t_0)) = (X_0, Y_0)$. If

$$X_0^{k-1} = \frac{me^{\frac{k-1}{m}Y_0}}{(k-1)rEi\left(\frac{k-1}{m}Y_0\right)},$$

then the solution of (2.4) with initial value (X_0, Y_0) is driven to E^0 along the curve

$$X^{k-1} = \frac{me^{\frac{k-1}{m}Y}}{(k-1)rEi\left(\frac{k-1}{m}Y\right)},$$

which is a separatrix. Solutions of (2.4) above the separatrix are driven to E^0 and the ones below it are far away from E^0 . Therefore, for $X \ll 1$ and $Y \ll 1$, the solutions of model (1.2) near E^0 have the same property. This completes our proof. \square

Remark 2.1. The singularity of E^0 is showed in Figure 3 in Section 4. It is clear that the first quadrant is divided by a separatrix Γ into two parts D_1 and D_2 . The solutions above the separatrix Γ are driven to E^0 and the ones below it are far away from E^0 .

2.2. Stability of positive equilibrium

The Jacobi matrix at E^* is

$$J^* = \begin{bmatrix} r\left(\frac{m}{g}\right)^{k-1}(k-1) - \frac{m}{g} & \\ gr\left(\frac{m}{g}\right)^{k-1} & 0 \end{bmatrix},$$

and its characteristic polynomial is

$$f(\lambda) = \lambda^2 - a(k-1)\lambda + am,$$

where $a = r\left(\frac{m}{g}\right)^{k-1} > 0$. $f(\lambda)$ has two roots $\frac{a(k-1) \pm \sqrt{a^2(k-1)^2 - 4am}}{2}$. Then, there are three cases to discuss:

Case 1. For $0 < k < 1$, if $a^2(k-1)^2 - 4am \geq 0$, i.e., $a \geq \frac{4m}{(k-1)^2}$, the two roots of $f(\lambda)$ both are negative numbers, and E^* is a stable node. If $a^2(k-1)^2 - 4am < 0$, i.e., $a < \frac{4m}{(k-1)^2}$, the two roots of $f(\lambda)$ both are imaginary numbers with negative real parts, and E_* is a stable focus.

Case 2. For $k = 1$, model (1.2) is the Lotka-Volterra predator-prey model. E^* is a center ([27], P79–81).

Case 3. For $k > 1$, if $a \geq \frac{4m}{(k-1)^2}$, then the two roots of $f(\lambda)$ both are positive numbers, and E^* is an unstable node. If $a < \frac{4m}{(k-1)^2}$, then the two roots of $f(\lambda)$ both are imaginary numbers with positive real parts, and E_* is an unstable focus.

The above discussions lead to the following results.

Theorem 2.2. For $0 < k < 1$, if $a \geq \frac{4m}{(k-1)^2}$, then E^* is a local stable node; if $a < \frac{4m}{(k-1)^2}$, then E^* is a local stable focus. For $k = 1$, E^* is a center. For $k > 1$, if $a \geq \frac{4m}{(k-1)^2}$, then E^* is an unstable node; if $a < \frac{4m}{(k-1)^2}$, then E^* is an unstable focus.

By Bendixson-Dulac criterion, it is easy to show that there is no periodic solution in the first quadrant.

Theorem 2.3. For $k \neq 1$, model (1.2) has no periodic solution in the first quadrant.

Proof. Using Dulac function in ([16], P162). Let

$$h(X, Y) = X^{-1}Y^{-1}, \quad H_1(X, Y) = rX^k - XY, \quad H_2(X, Y) = gXY - mY,$$

then

$$\Delta = \frac{\partial[H_1(X, Y)h(X, Y)]}{\partial X} + \frac{\partial[H_2(X, Y)h(X, Y)]}{\partial Y} = r(k-1)X^{k-2}Y^{-1}.$$

Thus, $\Delta > 0$ for $k > 1$, and $\Delta < 0$ for $0 < k < 1$ in $\text{int}R_+^2$. The Bendixson-Dulac criterion completes our proof. \square

By Theorems 2.1, 2.2 and 2.3, we have the global dynamics of model (1.2).

Theorem 2.4. For $0 < k < 1$, E^0 is a saddle, and if $a \geq \frac{4m}{(k-1)^2}$, then E^* is a globally asymptotically stable node; if $a < \frac{4m}{(k-1)^2}$, then E^* is a globally asymptotically stable focus. For $k = 1$, E^0 is a saddle, and E^* is a center. For $k > 1$, if $a \geq \frac{4m}{(k-1)^2}$, then E^* is an unstable node; if $a < \frac{4m}{(k-1)^2}$, then E^* is an unstable focus; furthermore, there exists a separatrix, and solutions of (1.2) above it are driven to E^0 and the ones below it are far away from E^0 .

Remark 2.2. Theorem 2.4 means that the predator and the prey in model (1.2) coexist for $0 < k \leq 1$, and will be extinct or diverged for $k > 1$. Therefore, model (1.2) is permanent for $0 < k \leq 1$ and not persistent for $k > 1$.

3. Dynamics of model (1.4)

In this section, we analyze model (1.4) in R_+^2 . It is easy to check that model (1.4) has two boundary equilibria $E_0 = (0, 0)$, $E_K = (K, 0)$ and a positive equilibrium $E_* = (X_*, Y_*)$, where

$$X_* = \frac{m}{g}, \quad Y_* = r \left(\frac{m}{g}\right)^{k-1} \left(1 - \frac{m}{gK}\right).$$

$Y_* = \frac{gr}{m} \left(1 - \frac{m}{gK}\right) X_*^k$ shows that there is a power law relation for E_* . $Y_* > 0$ if and only if $K > \frac{m}{g}$. Therefore, we get the condition for the existence of positive equilibrium of model (1.4).

Theorem 3.1. *If $K > \frac{m}{g}$, then model (1.4) has a positive equilibrium E_* .*

Model (1.4) without predator is

$$\frac{dX}{dt} = rX^k \left(1 - \frac{X}{K}\right). \quad (3.1)$$

It is easy to know that equation (3.1) has two equilibria 0 and K , and any positive solution of equation (3.1) tends to K as $t \rightarrow +\infty$. Model (1.4) without prey is (2.2). Next, we discuss the boundedness of model (1.4).

Theorem 3.2. *Any solution of model (1.4) with positive initial value is positive and bounded for all $k > 0$.*

Proof. It is obvious that any solution of model (1.4) with positive initial value is positive. From the first equation of model (1.4), we get that for all $X > 0$ and $Y > 0$

$$\frac{dX}{dt} \leq rX^k \left(1 - \frac{X}{K}\right).$$

The above discussion shows that $X = K$ is a solution of equation (3.1) which is globally attractive. It follows the differential inequality theorem that there exists a $T_1 > t_0$ for any $\varepsilon > 0$ and some t_0 such that for $t > T_1$

$$X < K + \varepsilon.$$

Let $Z = gX + Y$, then

$$\begin{aligned} \frac{dZ}{dt} &= g \frac{dX}{dt} + \frac{dY}{dt} = g \left[rX^k \left(1 - \frac{X}{K}\right) - XY \right] + gXY - mY \\ &= grX^k \left(1 - \frac{X}{K}\right) + gmX - m(gX + Y) \leq g(rX^k + mX) - mZ. \end{aligned}$$

Thus, for $t > T_1$

$$\frac{dZ}{dt} + mZ \leq g[r(K + \varepsilon)^k + m(K + \varepsilon)].$$

We have

$$\limsup_{t \rightarrow +\infty} Z \leq \frac{g}{m} [r(K + \varepsilon)^k + m(K + \varepsilon)],$$

i.e.

$$\limsup_{t \rightarrow +\infty} (gX + Y) \leq \frac{g}{m} [r(K + \varepsilon)^k + m(K + \varepsilon)].$$

This completes our proof. \square

3.1. Stability of boundary equilibria

By a similar proof of Theorem 2.1, it is easy to get the following result.

Theorem 3.3. *If $0 < k \leq 1$, then E_0 is a saddle. If $k > 1$, then there exists a separatrix, and solutions of (1.2) above it are driven to E_0 and the ones below it are far away from E_0 .*

Remark 3.1. The singularity of E_0 will be showed by Figures 2 and 5 in Section 4. It is clear that the solutions above the separatrix are driven to E_0 and the ones below it are far away from E_0 .

The Jacobi matrix of model (1.4) is

$$J = \begin{bmatrix} rkX^{k-1} - \frac{r(k+1)}{K}X^k - Y & -X \\ gY & gX - m \end{bmatrix}.$$

The Jacobi matrix at E_K is

$$J_K = \begin{bmatrix} -rK^{k-1} & -K \\ 0 & gK - m \end{bmatrix},$$

and its two eigenvalues are $-rK^{k-1}$ and $gK - m$.

Theorem 3.4. *For all $k > 0$, if $K \leq \frac{m}{g}$, then E_K is a local stable node; if $K > \frac{m}{g}$, then E_K is a saddle.*

Proof. If $K < \frac{m}{g}$ and $K > \frac{m}{g}$, then the results follow the two eigenvalues of Jacobi matrix at E_K directly. If $K = \frac{m}{g}$, then it is easy to know that E_K is a local stable node by the analysis of the vector fields of (1.4). This completes our proof. \square

3.2. Stability of positive equilibrium

The Jacobi matrix at the positive equilibrium E_* is

$$J_* = \begin{bmatrix} r(\frac{m}{g})^{k-1}(k - 1 - \frac{mk}{Kg}) - \frac{m}{g} \\ gr(\frac{m}{g})^{k-1}(1 - \frac{m}{gK}) & 0 \end{bmatrix},$$

and its characteristic polynomial is

$$f(\lambda) = \lambda^2 - ab\lambda + amc,$$

where $a = r(\frac{m}{g})^{k-1} > 0$, $b = k - 1 - \frac{mk}{Kg} > -1$ and $c = 1 - \frac{m}{gK} > 0$. $f(\lambda)$ has two roots $\frac{ab \pm \sqrt{a^2b^2 - 4amc}}{2}$.

For $-1 < b < 0$, if $ab^2 \geq 4mc$, then both roots of $f(\lambda)$ are negative numbers, and E_* is a local stable node; if $ab^2 < 4mc$, then both roots of $f(\lambda)$ are imaginary numbers with negative real parts, and E_* is a local stable focus.

For $b = 0$, then both roots of $f(\lambda)$ are the pure imaginary numbers $\pm 2\sqrt{amc}$. Let $\lambda = \alpha(b) \pm i\beta(b)$ be the two roots, then $\alpha(0) = 0$, $\beta(0) = r(\frac{K}{k})^k \frac{g}{K} (k - 1)^k > 0$, and $\frac{d(Re\lambda)}{db}|_{b=0} = \frac{r}{2}(\frac{K}{k})^{k-1}(k - 1)^{k-1} > 0$ for $k > 1$. Therefore, the Hopf bifurcation occurs from E_* when b passes through 0 for $k > 1$.

For $b > 0$, if $ab^2 \geq 4mc$, then both roots of $f(\lambda)$ are positive numbers, and E_* is a local unstable node; if $ab^2 < 4mc$, then both roots of $f(\lambda)$ are imaginary numbers with positive real parts, and E_* is a local unstable focus.

For $0 < k \leq 1$, there must be $b < 0$. For $k > 1$, b can be negative, 0 or positive. Therefore, from the above discussions, we get the following results.

Theorem 3.5. *For $0 < k \leq 1$, E_* is local stable. Furthermore, if $ab^2 \geq 4mc$, then E_* is a local stable node; if $ab^2 < 4mc$, then E_* is a local stable focus.*

Theorem 3.6. For $k > 1$,

- (i) if $b < 0$, then E_* is a local stable node when $ab^2 \geq 4mc$, and E_* is a local stable focus when $ab^2 < 4mc$.
- (ii) if $b = 0$, then Hopf bifurcation occurs from E_* for model (1.4).
- (iii) if $b > 0$, then E_* is a local unstable node when $ab^2 \geq 4mc$, and E_* is a local unstable focus when $ab^2 < 4mc$.

By Bendixson-Dulac criterion, we determine the fact that there is no periodic solution in the first quadrant for model (1.4) when $0 < k \leq 1$.

Theorem 3.7. For $0 < k \leq 1$, model (1.4) has no periodic solution in the first quadrant.

Proof. Let

$$h_1(X, Y) = X^\alpha Y^\beta, \quad H_3(X, Y) = rX^k \left(1 - \frac{X}{K}\right) - XY, \quad H_4(X, Y) = gXY - mY,$$

then

$$\begin{aligned} \Delta &= \frac{\partial[H_3(X, Y)h_1(X, Y)]}{\partial X} + \frac{\partial[H_4(X, Y)h_1(X, Y)]}{\partial Y} \\ &= r \left[(\alpha + k)X^{\alpha+k-1} - \frac{\alpha + k + 1}{K}X^{\alpha+k} \right] Y^\beta - (\alpha + 1)X^\alpha Y^{\beta+1} \\ &\quad + (\beta + 1)(gX^{\alpha+1} - mX^\alpha Y^\beta). \end{aligned}$$

Let $\alpha = -k$ and $\beta = -1$, then $\Delta < 0$ for $0 < k \leq 1$ in the first quadrant. This indicates that there is no periodic solution in the first quadrant for $0 < k \leq 1$. The Bendixson-Dulac criterion completes our proof. \square

3.3. Global dynamics

By Theorems 3.1, 3.3, 3.4, 3.5 and 3.7, we get the global dynamics of model (1.4) for $0 < k \leq 1$.

Theorem 3.8. For $0 < k \leq 1$, boundary equilibrium E_0 is a saddle. If $K \leq \frac{m}{g}$, then there is no positive equilibrium, and boundary equilibrium E_K is a globally asymptotically stable node. If $K > \frac{m}{g}$, then there is a unique positive equilibrium E_* , which is globally asymptotically stable, and boundary equilibrium E_K is a saddle.

Remark 3.2. Theorem 3.8 means that the prey survives and will be stable at its carrying capacity whereas the predator will extinct for $K \leq \frac{m}{g}$, and the predator and prey coexist for $K > \frac{m}{g}$. It is apparent that model (1.4) is permanent for $0 < k < 1$ and $K > \frac{m}{g}$.

For $k > 1$, from Theorem 3.1, we know that model (1.4) has no positive equilibrium, which means that there is no periodic solution of model (1.4) in the first quadrant, and boundary equilibrium E_K is a stable node for $K \leq \frac{m}{g}$. Moreover, from Theorems 3.3 and 3.4, we know that the positive solutions of model (1.4) are bounded and have singularity at E_0 . So, we get the following result from the above analysis.

Theorem 3.9. *For $k > 1$, if $K \leq \frac{m}{g}$, then model (1.4) has no positive equilibrium and boundary equilibrium E_K is a stable node. Moreover, there exists a separatrix, and solutions of (1.4) above it are driven to E_0 and the ones below it are driven to E_K .*

Remark 3.3. In the conditions of Theorem 3.9, the prey survives and will be stable at its carrying capacity whereas the predator will be extinct, or the predator and prey are both extinct.

Similarly, we have the following result from Theorems 3.1, 3.4, 3.6 and 3.7.

Theorem 3.10. *For $k > 1$, there exists a separatrix, and solutions of (1.4) above it are driven to E_0 and the ones below it are far away from E_0 . If $K > \frac{m}{g}$, then boundary equilibrium E_K is a saddle, and there is a unique positive equilibrium E_* , which is local stable for $b < 0$ and unstable for $b > 0$, and from which Hopf bifurcation occurs for $b = 0$.*

4. Simulations

In this section, we give some examples to illustrate our main results by numerical simulations.

First, we consider model (1.2) satisfying Theorem 2.4. Figure 1 shows the dynamical behavior of (1.2) for $k = 0.75$. The positive equilibrium $(2, 0.8 \times 2^{-0.25})$ is a globally asymptotically stable focus and the origin is a saddle in Figure 1. In Figure 3, the dynamical behavior of (1.2) for $k = 1.5$ is given. It is clear that there exists a separatrix, which comes from the origin and solutions of (1.2) with initial value on it are driven to the origin along it, and solutions of (1.2) above it are driven to the origin and the ones below it are far away from the origin in Figure 3. Furthermore, the positive equilibrium in Figure 3(a) is an unstable node, and the positive equilibrium in Figure 3(b) is an unstable focus.

Then, we consider model (1.4) satisfying Theorems 3.8 and 3.10. The dynamical behavior of (1.4) for $k = 0.75$ is showed in Figure 4. The boundary equilibrium $(0.8, 0)$ is a globally asymptotically stable node, and the origin is a saddle in Figure 4(a). The positive equilibrium $(2, 0.5 \times 2^{-0.25})$ is a globally asymptotically stable focus, and the boundary equilibria $(0, 0)$ and origin are saddles in Figure 4(b). Figures 2 and 5 give the dynamical behavior of (1.4) for $k = 1.5$, in which there exists a separatrix, which comes from the origin and solutions of (1.4) with initial value on it are driven to the origin along it, and solutions of (1.4) above it are driven to the origin and the ones below it are far away from the origin. Furthermore, the boundary equilibrium $(2, 0)$ is a saddle and the positive equilibrium $(\frac{1}{2}, \frac{2.1}{8} \times \sqrt{2})$ is an unstable focus in Figure 2, there is no positive equilibrium and the boundary equilibrium $(0.6, 0)$ is a stable node in Figure 5(a), and the boundary equilibrium $(4, 0)$ is a saddle and the positive equilibrium $(\frac{13}{6}, \frac{19}{8} \times \sqrt{\frac{13}{6}})$ is a stable focus in Figure 5(b).

5. Conclusions and discussions

In this section, we give our main conclusions and discussions.

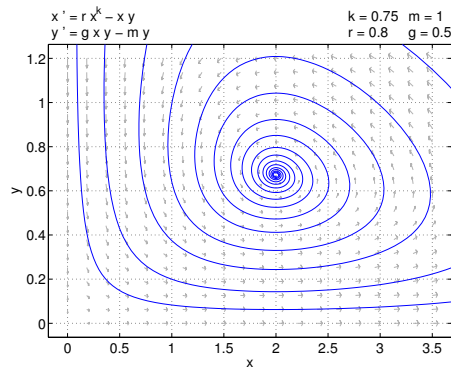


Figure 1. Dynamical behavior of (1.2) for $k = 0.75$, $r = 0.8$, $g = 0.5$, $m = 1$.

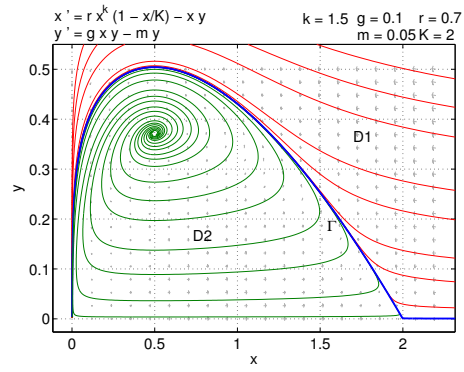
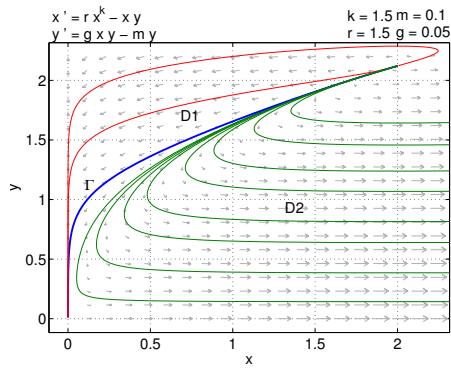
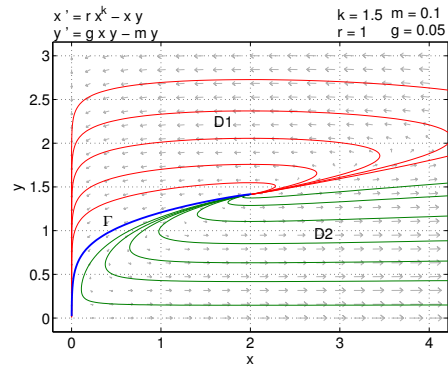


Figure 2. Dynamical behavior of (1.4) with $k = 1.5$, $r = 0.7$, $K = 2$, $g = 0.1$, $m = 0.05$.

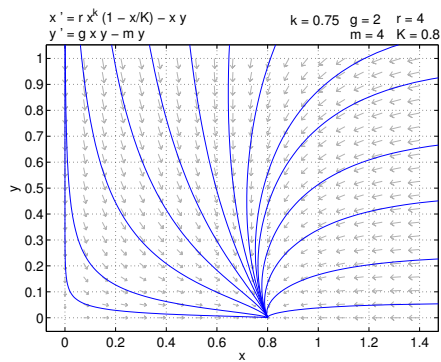


(a) $r = 1.5$, $g = 0.05$, $m = 0.1$.

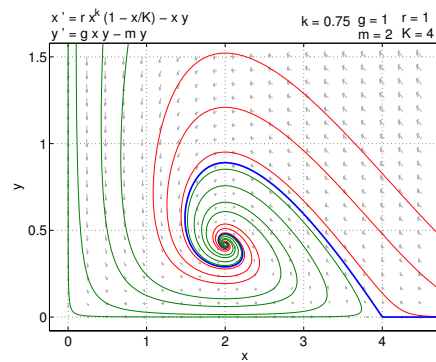


(b) $r = 1$, $g = 0.05$, $m = 0.1$.

Figure 3. Dynamical behavior of (1.2) for $k = 1.5$. There exists a separatrix, which comes from the origin. Solutions of (1.2) with initial value on it are driven to the origin along it, and solutions of (1.2) above it are driven to the origin and the ones below it are far away from the origin.



(a) $r = 4$, $K = 0.8$, $g = 2$, $m = 4$.



(b) $r = 1$, $K = 4$, $g = 1$, $m = 2$.

Figure 4. Dynamical behavior of (1.4) for $k = 0.75$.

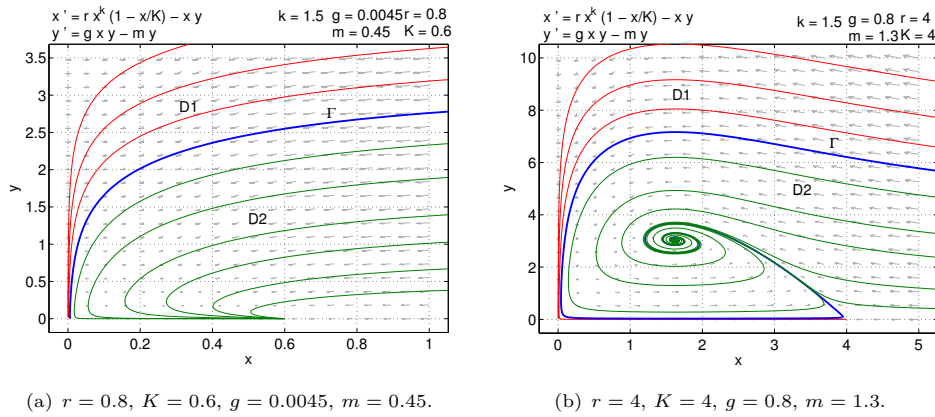


Figure 5. Dynamical behavior of (1.4) for $k = 1.5$. There exists a separatrix, which comes from the origin. Solutions of (1.4) with initial value on it are driven to the origin along it, and solutions of (1.4) above it are driven to the origin and the ones below it are far away from the origin.

By the qualitative theory of ordinary differential equation, we easily get the stability of positive equilibrium and prove that there is no periodic solution in the first quadrant for model (1.2). However, boundary equilibrium E^0 has singularity and its stability can not be analyzed by the linearization method, because the linearization matrix of model (1.2) at E^0 does not exist for $0 < k < 1$ and has 0 as one of its eigenvalues for $k > 1$. Using the approximate method, we get that E^0 is a saddle for $0 < k < 1$, and there exists a separatrix such that solutions of (1.2) above it are driven to E^0 and the ones below it are far away from E^0 for $k > 1$. The results show that the predator and prey coexist for $0 < k < 1$, and will be extinct or diverged for $k > 1$. The dynamics of model (1.2) is well known for $k = 1$, which is the Lotka-Volterra predator-prey model. From our analysis, it is easy to know that model (1.2) is persistent for $0 < k \leq 1$ and unbounded for $k > 1$.

Model (1.4) has the same singularity as that of model (1.2) at the origin for $k > 1$. Since model (1.4) is bounded for all $k > 0$, the singularity at the origin implies that three cases could occur: the prey will survive whereas the predator will be extinct, the predator and prey will be extinct or coexist ultimately. We give sufficient conditions for the stability of boundary equilibrium E_K and positive equilibrium E_* , which show that the prey survives only and predator and prey coexist respectively. The dynamics of model (1.4) is more complicated for $k > 1$, because Hopf bifurcation occurs at E_* besides the singularity at the origin.

For $0 < k \leq 1$, the prey and predator in model (1.2) coexist stably, and the prey survives and the predator will be extinct in model (1.4) besides they coexist. For $k > 1$, model (1.2) is not persistent and model (1.4) is bounded. Model (1.2) has two situations: both the prey and predator will be extinct or unbounded. Model (1.4) has three situations: both the prey and predator will be extinct, the prey survives and the predator will be extinct, or the prey and predator coexist stably.

From our results, it is clear that both the prey and predator in model (1.2) will be extinct in certain conditions for $k > 1$. But, the data results of [14] showed that the predator-prey relation of some fishes coexist stably for $k > 1$. This contradiction means that capture ability of the predator in model (1.2) is too strong. Because the higher capture ability of predator will decrease the amounts of the prey, accordingly

decrease itself. In order to eliminate the contradiction, we use Y^σ ($\sigma < 1$) to replace Y in the consumption function XY in the right sides of model (1.2), which means that capture ability of the predator is decreased for large amount of predator. This modification may result in stable coexist. Otherwise, we use the functional responses to replace the consumption function, and may get stable coexistence.

From our discussion, it is clear that model (1.4) is the density-dependent and bounded for all $k > 0$. So, model (1.4) is an improvement of model (1.2). However, model (1.4) is not persistent for $k > 1$, because both the prey and predator will be extinct in certain conditions. Therefore, in order to get that model (1.4) is persistent, we modify the consumption function of model (1.4) by the same manners as these of above discussions for model (1.2).

Furthermore, there are some interesting problems that deserve to be discussed further for model (1.4). For example, there is a heteroclinic cycle in Figure 2, which consists of two boundary equilibria, $(0, 0)$ and $(2, 0)$, and two connecting heteroclinic orbits, the separatrix and the x -axis between the two boundary equilibria. So, model (1.4) must exist a heteroclinic cycle for $k > 1$. However, the conditions for existence of a heteroclinic cycle still need further study.

References

- [1] V. Ajraldi, M. Pittavino and E. Venturino, *Modeling herd behavior in population systems*, Nonlinear Anal.: Real World Appl., 2011, 12(4), 2319–2338.
- [2] R. Arditi and L. R. Ginzburg, *Coupling in predator-prey dynamics: ratio-dependence*, J. Theor. Biol., 1989, 139(3), 311–326.
- [3] F. J. Ayala, M. E. Gilpin and J. G. Ehrenfeld, *Competition between species: Theoretical models and experimental tests*, Theor. Popul. Biol., 1973, 4(3), 331–356.
- [4] F. S. Berezovskaya, A. S. Novozhilov and G. P. Karev, *Population models with singular equilibrium*, Math. Biosci., 2007, 208(1), 270–299.
- [5] A. A. Berryman, *The origins and evolution of predator-prey theory*, Ecology, 1992, 73(5), 1530–1535.
- [6] K. Boyadzhiev and V. H. Moll, *The integrals in Gradshteyn and Ryzhik, Part 26: The exponential integral*, SCIENTIA Series A: Mathematical Sciences, 2015, 26, 19–30.
- [7] F. Brauer and C. Castillo-Chavez, *Mathematical Models in Population Biology and Epidemiology*, Springer, New York, 2012.
- [8] P. A. Braza, *Predator-prey dynamics with square root functional responses*, Nonlinear Anal.: Real World Appl., 2012, 13(4), 1837–1843.
- [9] J. Chattopadhyay, S. Chatterjee and E. Venturino, *Patchy agglomeration as a transition from monospecies to recurrent plankton blooms*, J. Theor. Biol., 2008, 253(2), 289–295.
- [10] L. Chen and F. Chen, *Dynamical analysis of a predator-prey model with square root functional response*, J. Nonlinear Funct. Anal., 2015, Article ID 8.
- [11] L. Chen, F. Chen and L. Chen, *Qualitative analysis of a predator-prey model with Holling type II functional response incorporating a constant prey refuge*, Nonlinear Anal.: Real World Appl., 2010, 11(1), 246–252.

- [12] P. Feng, *Analysis of a delayed predator-prey model with ratio-dependent functional response and quadratic harvesting*, J. Appl. Math. Comput., 2014, 44(1–2), 251–262.
- [13] M. E. Gilpin and F. J. Ayala, *Global models of growth and competition*, Proc. Natl. Acad. Sci. USA, 1973, 70(12), 3590–3593.
- [14] I. A. Hatton, K. S. McCann, J. M. Fryxell, T. J. Davies, M. S. merlak, A. R. E. Sinclair and M. Loreau, *The predator-prey power law: Biomass scaling across terrestrial and aquatic biomes*, Science, 2015, 349(6252), aac6284.
- [15] C. S. Holling, *The functional response of invertebrate predators to prey density*, Memoirs of the Entomological Society of Canada, 1966, 98(48), 5–86.
- [16] S. B. Hsu, *Ordinary Differential Equations with Applications (2nd Edition)*, World Scientific, Singapore, 2013.
- [17] S. B. Hsu and T. Huang, *Global stability for a class of predator-prey systems*, SIAM J. Appl. Math., 1995, 55(3), 763–783.
- [18] S. B. Hsu, T. Huang and Y. Kuang, *Global analysis of the Michaelis-Menten-type ratio-dependent predator-prey system*, J. Math. Biol., 2001, 42(6), 489–506.
- [19] C. Ji, D. Jiang and Y. Zhao, *Qualitative analysis of stochastic ratio-dependent predator-prey systems*, J. Appl. Anal. Comput., 2019, 9(2), 475–500.
- [20] C. Jost, O. Arino and R. Arditi, *About deterministic extinction in ratio-dependent predator-prey models*, Bull. Math. Biol., 1999, 61(1), 19–32.
- [21] Y. Kuang and E. Beretta, *Global qualitative analysis of a ratio-dependent predator-prey system*, J. Math. Biol., 1998, 36(4), 389–406.
- [22] Q. Liu, D. Jiang, T. Hayat and A. Alsaedi, *Dynamics of a stochastic predator-prey model with distributed delay and Markovian switching*, Phys. A, 2019, 527, 121264.
- [23] X. Liu and Y. Lou, *Global dynamics of a predator-prey model*, J. Math. Anal. Appl., 2010, 371(1), 323–340.
- [24] A. J. Lotka, *Contribution to the theory of periodic reaction*, J. Phys. Chem., 1910, 14(3), 271–274.
- [25] J. Lv, X. Zou and Y. Li, *Dynamical properties of a stochastic predator-prey model with functional response*, J. Appl. Anal. Comput., 2020, 10(4), 1242–1255.
- [26] X. Meng, R. Liu, L. Liu and T. Zhang, *Evolutionary analysis of a predator-prey community under natural and artificial selections*, Appl. Math. Model., 2015, 39(2), 574–585.
- [27] J. D. Murray, *Mathematical Biology I: An Introduction (Third Edition)*, Springer, New York, 2002.
- [28] C. E. H. Pimentel, P. M. Rodriguez and L. A. Valencia, *A note on a stage-specific predator-prey stochastic model*, Phys. A, 2020, 553, 124575.
- [29] H. Qi and X. Meng, *Threshold behavior of a stochastic predator-prey system with prey refuge and fear effect*, Appl. Math. Lett., 2021, 113, 106846.
- [30] E. Sáez and E. González-Olivares, *Dynamics of a predator-prey model*, SIAM J. Appl. Math., 1999, 59(5), 1867–1878.

- [31] K. Sun, T. Zhang and Y. Tian, *Theoretical study and control optimization of an integrated pest management predator-prey model with power growth rate*, Math. Biosci., 2016, 279, 13–26.
- [32] X. Tang, Y. Song and T. Zhang, *Turing-Hopf bifurcation analysis of a predator-prey model with herd behavior and cross-diffusion*, Nonlinear Dyn., 2016, 86(1), 73–89.
- [33] E. Venturino and S. Petrovskii, *Spatiotemporal behavior of a prey-predator system with a group defense for prey*, Ecol. Complex., 2013, 14, 37–47.
- [34] C. Viberti and E. Venturino, *An ecosystem with Holling type II response and predators' genetic variability*, Math. Model. Anal., 2014, 19(3), 371–394.
- [35] V. Volterra, *Variazioni e fluttuazioni del numero d'individui in specie animali conviventi*, Memorie Royal Accademia Nazionale dei Lincei, 1926, 2, 31–113.
- [36] D. Xiao and L. S. Jennings, *Bifurcations of a ratio-dependent predator-prey system with constant rate harvesting*, SIAM J. Appl. Math., 2005, 65(3), 737–753.
- [37] D. Xiao and S. Ruan, *Global dynamics of a ratio-dependent predator-prey system*, J. Math. Biol., 2001, 43(3), 268–290.
- [38] M. Xiao and J. Cao, *Hopf bifurcation and non-hyperbolic equilibrium in a ratio-dependent predator-prey model with linear harvesting rate: Analysis and computation*, Math. Comput. Model., 2009, 50(3–4), 360–379.
- [39] C. Xu, S. Yuan and T. Zhang, *Global dynamics of a predator-prey model with defence mechanism for prey*, Appl. Math. Lett., 2016, 62, 42–48.
- [40] Y. Yang and T. Zhang, *Dynamic analysis of a modified stochastic predator-prey system with general ratio-dependent functional response*, Bull. Korean Math. Soc., 2016, 53(1), 103–117.
- [41] S. Zhang, T. Zhang and S. Yuan, *Dynamics of a stochastic predator-prey model with habitat complexity and prey aggregation*, Ecol. Complex., 2021, 45, 100889.
- [42] T. Zhang, W. Ma, X. Meng and T. Zhang, *Periodic solution of a prey-predator model with nonlinear state feedback control*, Appl. Math. Comput., 2015, 266, 95–107.
- [43] T. Zhang, Y. Xing, H. Zang and M. Han, *Spatio-temporal dynamics of a reaction-diffusion system for a predator-prey model with hyperbolic mortality*, Nonlinear Dyn., 2014, 78(1), 265–277.