

A PREY-PREDATOR MODEL WITH HOLLING II FUNCTIONAL RESPONSE AND THE CARRYING CAPACITY OF PREDATOR DEPENDING ON ITS PREY*

Hanwu Liu^{1,†}, Ting Li^{1,2} and Fengqin Zhang¹

Abstract One prey-predator model is formulated and the global behavior of its solution is analyzed. In this model, the carrying capacity of predator depends on the amount of its prey, and the Holling II functional response is involved. This model may have four classes of positive equilibriums and limit cycle. The positive equilibriums may be stable, or a saddle-node, or a saddle, or a degenerate singular point. In alpine meadow ecosystem, the dynamics of vegetation and plateau pika can be described by this model. Through simulating with virtual parameters, the cause of alpine meadow degradation and effective recovery strategy is investigated. Increasing grazing rate or decreasing plateau pika mortality may cause alpine meadow degradation. Correspondingly, reducing grazing rate and increasing plateau pika mortality may recover the degraded alpine meadow effectively.

Keywords Prey-predator model, density-dependent, global behavior, Holling II functional response.

MSC(2010) 34D20, 34C60, 92D25.

1. Introduction

In ecosystem, predation is an important relationship among populations. A lot of predator-prey models have been investigated [14, 16]. Taking into account the digestive saturation of predator, Holling proposed three functional response functions in 1965 [6], and the Holling II functional response is incorporated in many models [4, 7, 8, 17] thereafter. In general, the growth of predator is assumed to be density-dependent [4, 8, 18, 19], and the carrying capacity is assumed to be constant [1, 9, 11, 15]. However, due to the complicated relationships in ecosystem, the carrying capacity of predator may be influenced by the amount of its prey. For example, in alpine meadow ecosystem, plateau pika feeds on vegetation, at the same time, vegetation is also the main component of plateau pika living environment.

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*The authors were supported by National Natural Science Foundation of China (11371313, 61573016), Research Project Supported by Shanxi Scholarship Council of China (2017-111) and Project of Yuncheng University (swsx201604).

Because the higher vegetation prevents plateau pika from finding its natural enemy, so environment with higher vegetation is not suitable for plateau pika to live in. Liu [10] indicates that the carrying capacity of plateau pika increases firstly and then decreases with vegetation heightening. There are few research considering model in which the carrying capacity of predator depends on the amount of its prey. Falcone etc [5] proposed the model (1.1)

$$\begin{cases} x' = rx - \alpha xy, \\ y' = -dy + \beta xy - f(x)y^2, \end{cases} \quad (1.1)$$

where, $x(t)$ and $y(t)$ are the number of prey and predator at time t respectively. Prey population grows exponentially with growth rate $r > 0$. In the absence of prey, the mortality rate of predator is $d > 0$. Parameter $\alpha > 0$ is predation rate of predator and $\beta > 0$ is the conversion rate. The growth of predator is density-dependent, and its carrying capacity is $\frac{1}{f(x)}$ which depends on the amount of its prey. However, there was not theoretical analysis in [5], Falcone and Israel [4] analyzed model (1.1) preliminarily, Chu and Ding [2] and Tedeschini-Lalli [13] studied model (1.1) numerically to show the intertwined attractive basins of two sinks.

In second section, we formulate a prey-predator model and analyze its global behavior. In this model, the carrying capacity of predator depends on the amount of its prey, and the Holling type II functional response is involved. The third section provides four examples and corresponding numerical simulation. In section 4, we analyze the reason of alpine meadow degradation and explore the effective recovery strategies. Section 5 is a discussion.

2. Model formulation and analysis

When the growth of predator population is density-dependent, density may affect the actual mortality or the actual birth rate, more likely affect both of them at the same time in different degree. Here, assume that only the actual birth rate of predator population is affected by its density. Assume that the carrying capacity of predator population is a function of its prey density x , and denote it as $\varphi(x)$. Thus, according to model (1.1), one can formulate model (2.1).

$$\begin{cases} x' = rx(1 - \frac{x}{K}) - \frac{\alpha xy}{p+x} - \mu x, \\ y' = -dy + \frac{\beta xy}{p+x}(1 - \frac{y}{\varphi(x)}). \end{cases} \quad (2.1)$$

Here, $K > 0$ is the carrying capacity of prey, and $\mu > 0$ is the loss rate of prey that is irrelevant to predator. The predation rate is Holling II type, that is, $\frac{\alpha x}{p+x}$, where α is the maximum predation rate, and predation rate is half maximal at $x = p$. Parameter β is the maximum birth rate of predator. Assume that $\varphi(x)$ is sufficiently smooth, and when $x \geq 0$, $\varphi(x) > 0$ holds. Here, only the isolated equilibriums of model (2.1) are considered.

Theorem 2.1. *Model (2.1) always has trivial equilibrium $O(0, 0)$. When $r > \mu$, model (2.1) has predator-only equilibrium $E(\frac{K(r-\mu)}{r}, 0)$, and when $r - \mu > \frac{rdp}{K(\beta-d)} > 0$, model (2.1) has positive equilibrium.*

Proof. The existence of trivial equilibrium and predator-only equilibrium is obvious. Denote $f(x) \triangleq \frac{-r}{\alpha K}(x + p)[x - \frac{K(r-\mu)}{r}]$, $g(x) \triangleq (\frac{\beta-d}{\beta} - \frac{dp}{\beta x})\varphi(x)$, then the positive equilibrium of model (2.1) satisfies

$$\begin{cases} y = f(x), \\ y = g(x). \end{cases}$$

Obviously, $f(\frac{K(r-\mu)}{r}) = 0, g(\frac{K(r-\mu)}{r}) > 0$ and when $r-\mu > \frac{rdp}{K(\beta-d)} > 0, f(\frac{dp}{\beta-d}) > 0$ and $g(\frac{dp}{\beta-d}) = 0$ hold. So, there exists solution of $f(x) = g(x)$ between $\frac{dp}{\beta-d}$ and $\frac{K(r-\mu)}{r}$, thus, model (2.1) has positive equilibrium. \square

Through observing and analyzing the images of function $y = f(x)$ and $y = g(x)$, one can know that the positive equilibrium (x^*, y^*) of model (2.1) may fall into four classes: A, B, C, D, and the A class positive equilibrium must exist (Figure 1). In Figure 1, the downward parabola is image of $y = f(x)$, and the rest curves are image of $y = g(x)$. The characteristics of these four classes of positive equilibrium are:

- Class A: $g'(x^*) > f'(x^*)$,
- Class B: $g'(x^*) < f'(x^*)$,
- Class C: $g'(x^*) = f'(x^*), g''(x^*) < f''(x^*)$,
- Class D: $g'(x^*) = f'(x^*), g''(x^*) > f''(x^*)$.

One can know that there may exist positive equilibrium satisfying $g'(x^*) = f'(x^*)$ and $g''(x^*) = f''(x^*)$. This kind of positive equilibrium is similar to class C or class D and is omitted.

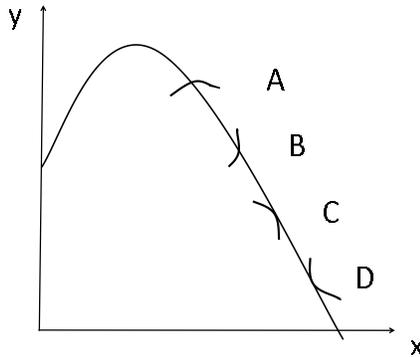


Figure 1. Model (2.1) may have four classes of positive equilibrium.

Theorem 2.2. When $r < \mu$, the trivial equilibrium O of model (2.1) is locally asymptotically stable, otherwise, O is unstable. When $0 < r - \mu < \frac{rdp}{K(\beta-d)}$, the predator-only equilibrium E of model (2.1) is locally asymptotically stable, otherwise, E doesn't exist or is unstable.

Proof. The Jacobian matrix of model (2.1) at O is

$$J_O = \begin{pmatrix} r - \mu & 0 \\ 0 & -d \end{pmatrix}.$$

Its eigenvalues are $r - \mu, -d$. So when $r < \mu$, both eigenvalues are less than zero and O is locally asymptotically stable.

The Jacobian matrix of model (2.1) at E is

$$J_E = \begin{pmatrix} \mu - r & \frac{-\alpha K(r-\mu)}{rp+K(r-\mu)} \\ 0 & \frac{-rdp+K(\beta-d)(r-\mu)}{rp+K(r-\mu)} \end{pmatrix}.$$

Its eigenvalues are $\mu - r, \frac{-rdp+K(\beta-d)(r-\mu)}{rp+K(r-\mu)}$. So when $0 < r - \mu < \frac{rdp}{K(\beta-d)}$, both eigenvalues are less than zero and E is locally asymptotically stable. \square

Theorem 2.3. Denote $h(x) \triangleq 2rx^2 + [rp + K(\beta + \mu - r - d)]x - pdK$.

(i) When $r - \mu > \frac{rdp}{K(\beta-d)} > 0, h(x^*) > 0$, the positive equilibrium of class A is locally asymptotically stable, and the positive equilibrium of class B is a saddle.

(ii) When $r - \mu > \frac{rdp}{K(\beta-d)} > 0, h(x^*) < 0$, the positive equilibrium of class A is unstable, and the positive equilibrium of class B is a saddle.

Proof. The Jacobian matrix of model (2.1) at positive equilibrium $P(x^*, y^*)$ is

$$J_P = \begin{pmatrix} \frac{-rx^*}{K} + \frac{\alpha x^* y^*}{(x^*+p)^2} & \frac{-\alpha x^*}{x^*+p} \\ \frac{pdy^*}{x^*(x^*+p)} + \frac{\beta x^* (y^*)^2 \varphi'(x^*)}{(x^*+p)\varphi^2(x^*)} & \frac{-\beta x^* y^*}{(x^*+p)\varphi(x^*)} \end{pmatrix}.$$

The characteristic equation of J_P is $\lambda^2 + a_1\lambda + a_2 = 0$, where $a_1 = \frac{h(x^*)}{K(x^*+p)}, a_2 = \frac{-\alpha\beta(x^*)^2 y^*}{(x^*+p)^2 \varphi(x^*)} (g'(x^*) - f'(x^*))$.

For the positive equilibrium of class A, $a_2 > 0$ holds, and condition $h(x^*) > 0$ implies $a_1 > 0$. So both eigenvalues have negative real parts and the positive equilibrium is locally asymptotically stable.

For the other cases, the proof is similar. \square

Theorem 2.4. When $h(x^*) \neq 0$, the positive equilibrium of class C or D is a saddle-node.

Proof. It is easy to know that the Jacobian matrix of model (2.1) at class C or D positive equilibrium has one and only one 0 eigenvalue.

Making transformations $dt = (x + p)\varphi(x)d\tilde{t}, \begin{cases} \tilde{x} = x - x^* \\ \tilde{y} = y - y^* \end{cases}$ and

$$\begin{cases} \tilde{x} = \alpha\tilde{x} + \alpha\tilde{y}, \\ \tilde{y} = (r - \mu - \frac{rp}{K} - \frac{2rx^*}{K})\tilde{x} + (\beta - d - \frac{pd}{x^*})\tilde{y}, \end{cases}$$

in turn, one can transform model (2.1) into model (2.2). At the same time, the positive equilibrium (x^*, y^*) of model (2.1) changes to the trivial equilibrium $\bar{O}(0, 0)$

of model (2.2).

$$\left\{ \begin{aligned} \frac{d\bar{x}}{d\bar{\tau}} &= -\frac{\alpha^2 K x^* y^*}{h(x^*)} \left(\frac{\beta x^* y^* \varphi''(x^*)}{2\varphi(x^*)} + \frac{pd\varphi'(x^*)}{x^*} - \frac{dp\varphi(x^*)}{(x^*)^2} + \frac{r\beta x^*}{\alpha K} \right) \bar{x}^2 \\ &\quad - \left[\frac{K x^* y^*}{h(x^*)} \left(\frac{\alpha^2 \beta x^* y^* \varphi''(x^*)}{2\varphi(x^*)} + \frac{2\alpha^2 dp\varphi'(x^*)}{x^*} - \frac{2\alpha^2 dp\varphi(x^*)}{(x^*)^2} + \frac{2r\alpha\beta x^*}{K} \right) \right. \\ &\quad \left. - \beta x^* \left(r - \mu - \frac{rp}{K} - \frac{2rx^*}{K} \right) - \alpha\beta y^* \right] \bar{x}\bar{y} \\ &\quad - \left\{ \frac{K x^* y^*}{h(x^*)} \left[\frac{\alpha^2 \beta x^* y^* \varphi''(x^*)}{2\varphi(x^*)} - (\beta - d)\alpha^2 \varphi'(x^*) - \frac{\alpha\beta^2 y^*}{\varphi(x^*)} + \frac{r\alpha\beta x^*}{K} \right] \right. \\ &\quad \left. + \alpha\beta y^* + \frac{\alpha\beta x^* y^* \varphi'(x^*)}{\varphi(x^*)} - \frac{\beta^2 x^* y^*}{\varphi(x^*)} \right\} \bar{y}^2 + o(\rho^2), \\ \frac{d\bar{y}}{d\bar{\tau}} &= -\frac{\varphi(x^*)h(x^*)}{K} \bar{y} + \left[-\frac{\alpha^2 K x^* y^*}{h(x^*)} \left(\frac{\beta x^* y^* \varphi''(x^*)}{2\varphi(x^*)} + \frac{pd\varphi'(x^*)}{x^*} - \frac{dp\varphi(x^*)}{(x^*)^2} \right) \right. \\ &\quad \left. - \frac{\alpha(x^*)^2 \varphi(x^*)}{h(x^*)} \left(\frac{2rx^*}{K} + \mu - r + \frac{rp}{K} \right) \right] \bar{x}^2 \\ &\quad + \left[(\beta x^* - \frac{\alpha^2 K x^* y^*}{h(x^*)}) \left(\frac{2rx^*}{K} + \frac{rp}{K} \mu - r \right) \right. \\ &\quad \left. + \frac{K x^* y^*}{h(x^*)} \left(\frac{\alpha^2 \beta x^* y^* \varphi''(x^*)}{2\varphi(x^*)} + \frac{2\alpha^2 dp\varphi'(x^*)}{x^*} - \frac{2\alpha^2 dp\varphi(x^*)}{(x^*)^2} - \frac{\alpha\beta h(x^*)}{K x^*} \right) \right] \bar{x}\bar{y} \\ &\quad + \left\{ \frac{K x^* y^*}{h(x^*)} \left[\frac{\alpha^2 \beta x^* y^* \varphi''(x^*)}{2\varphi(x^*)} + (\beta - d)\alpha^2 \varphi'(x^*) - \frac{\alpha\beta^2 y^*}{\varphi(x^*)} \right] - \frac{\beta^2 x^* y^*}{\varphi(x^*)} \right. \\ &\quad \left. - \frac{\alpha x^*}{h(x^*)} \left(\frac{2rx^*}{K} + \frac{rp}{K} - r + \mu \right) (h(x^*)\varphi'(x^*) + rx^*\varphi(x^*) + \frac{\varphi(x^*)h(x^*)}{x^*}) \right\} \bar{y}^2 \\ &\quad + o(\rho^2). \end{aligned} \right. \tag{2.2}$$

Let $L_0 \triangleq -\frac{\varphi(x^*)h(x^*)}{K}$, then transformation $d\bar{\tau} = L_0 d\tau$ transforms model (2.2) into model (2.3).

$$\left\{ \begin{aligned} \frac{d\bar{x}}{d\bar{\tau}} &= a_{20}\bar{x}^2 + a_{11}\bar{x}\bar{y} + a_{02}\bar{y}^2 + o(\rho^2) \triangleq \Phi(\bar{x}, \bar{y}), \\ \frac{d\bar{y}}{d\bar{\tau}} &= \bar{y} + b_{20}\bar{x}^2 + b_{11}\bar{x}\bar{y} + b_{02}\bar{y}^2 + o(\rho^2) \triangleq \bar{y} + \Psi(\bar{x}, \bar{y}). \end{aligned} \right. \tag{2.3}$$

Setting $\bar{y} = c_2\bar{x}^2 + o(\bar{x}^2)$ and substituting it into $\bar{y} + \Psi(\bar{x}, \bar{y}(\bar{x})) = 0$, one can get $c_2\bar{x}^2 + b_{20}\bar{x}^2 + o(\bar{x}^2) = 0$. Thus, $c_2 = -b_{20}$, that is, $\bar{y} = -b_{20}\bar{x}^2 + o(\bar{x}^2)$. Substituting this relation into $\Phi(\bar{x}, \bar{y}(\bar{x}))$, one can obtain $\Phi(\bar{x}, \bar{y}) = a_{20}\bar{x}^2 + o(\bar{x}^2)$. The fact that $a_{20} = \frac{\alpha^2 \beta K^2 (x^*)^2 y^*}{2\varphi(x^*)h^2(x^*)} (g''(x^*) - f''(x^*)) \neq 0$. implies that the trivial equilibrium $\bar{O}(0, 0)$ of model (2.2) is a saddle-node [3]. That is, the positive equilibrium of class C or D of model (2.1) is a saddle-node. \square

Theorem 2.5. *When $h(x^*) = 0$, the positive equilibrium of class A may be a center or a focus, the positive equilibrium of class B is a saddle, the positive equilibrium of class C or D is a degenerate singular point.*

Proof. When $h(x^*) = 0$, the Jacobian matrix of model (2.1) at the positive equilibrium $P(x^*, y^*)$ is

$$J_P = \begin{pmatrix} \frac{\beta x^* y^*}{(x^*+p)\varphi(x^*)} & \frac{-\alpha x^*}{x^*+p} \\ \frac{\beta x^* y^* g'(x^*)}{(x^*+p)\varphi(x^*)} & \frac{-\beta x^* y^*}{(x^*+p)\varphi(x^*)} \end{pmatrix}.$$

Its characteristic equation is $\lambda^2 = \frac{\alpha\beta(x^*)^2 y^* (f'(x^*) - g'(x^*))}{(x^*+p)^2 \varphi(x^*)} \triangleq \Lambda$. For the positive equilibrium of class A, $\Lambda < 0$ and J_P has a pair of pure imaginary characteristic roots. Hence, the positive equilibrium may be a center or a focus, one can use formal series method to analyze furthermore. For the positive equilibrium of class B, $\Lambda > 0$

and J_P has a positive and a negative eigenvalue, so the positive equilibrium is a saddle.

For the positive equilibrium of class C or D, $\Lambda = 0$ and J_P has a double characteristic root 0. Making transformations $dt = (x + p)\varphi(x)d\tilde{\tau}$,

$$\begin{cases} \tilde{x} = x - x^*, \\ \tilde{y} = y - y^*, \end{cases} \text{ and}$$

$$\begin{cases} \tilde{x} = \frac{\alpha\varphi(x^*)}{\beta y^*}\bar{x} + \frac{\alpha\varphi(x^*)}{\beta^2 x^* (y^*)^2}\bar{y}, \\ \tilde{y} = \bar{x}, \end{cases}$$

in turn, one can transform model (2.1) into model (2.4), and transform the positive equilibrium (x^*, y^*) of model (2.1) into the trivial equilibrium $\tilde{O}(0, 0)$ of model (2.4).

$$\begin{cases} \frac{d\bar{x}}{d\tilde{\tau}} = \bar{y} + \alpha\varphi(x^*)[-1 + \frac{\alpha(\beta-d)\varphi(x^*)\varphi'(x^*)}{\beta^2 y^*} + \frac{\alpha x^* \varphi''(x^*)}{2\beta}] \bar{x}^2 \\ \quad + \frac{\alpha\varphi(x^*)}{\beta x^*} [-1 + \frac{2\alpha(\beta-d)\varphi(x^*)\varphi'(x^*)}{\beta^2 y^*} + \frac{\alpha x^* \varphi''(x^*)}{\beta y^*} + \frac{\beta x^*}{\alpha y^* \varphi(x^*)}] \bar{x}\bar{y} \\ \quad + \frac{\alpha^2 \varphi^2(x^*)}{2\beta^3 x^* (y^*)^2} (\frac{2\varphi(x^*)\varphi'(x^*)}{\beta x^* y^*} + \varphi''(x^*)) \bar{y}^2 + o(\rho^2) \\ \quad \triangleq \bar{y} + \varphi(\bar{x}, \bar{y}), \\ \frac{d\bar{y}}{d\tilde{\tau}} = -\alpha x^* \varphi(x^*) [-\beta y^* + \frac{rx^* \varphi(x^*)}{K} + \frac{\alpha(\beta-d)\varphi(x^*)\varphi'(x^*)}{\beta} + \frac{\alpha x^* y^* \varphi''(x^*)}{2}] \bar{x}^2 \\ \quad + [\alpha\varphi(x^*) + \alpha y^* \varphi(x^*) + \alpha x^* \varphi'(x^*) - \beta x^* \\ \quad - \frac{2r\alpha x^* \varphi^2(x^*)}{K\beta y^*} - \frac{2\alpha^2(\beta-d)\varphi^2(x^*)\varphi'(x^*)}{\beta^2} - \frac{\alpha^2 x^* \varphi(x^*)\varphi''(x^*)}{\beta}] \bar{x}\bar{y} \\ \quad + \frac{\alpha\varphi(x^*)}{\beta x^* y^*} (1 + \frac{x\varphi'(x^*)}{\varphi(x^*)} - \frac{rx^*}{K\beta y^*} - \frac{\alpha\varphi(x^*)\varphi'(x^*)}{\beta^2 y^*} - \frac{\alpha x^* \varphi''(x^*)}{2\beta}) + o(\rho^2) \\ \quad \triangleq \psi(\bar{x}, \bar{y}). \end{cases} \tag{2.4}$$

Rewrite model (2.4) as model (2.5),

$$\begin{cases} \frac{d\bar{x}}{d\tilde{\tau}} = \bar{y} + A_{20}\bar{x}^2 + A_{11}\bar{x}\bar{y} + A_{02}\bar{y}^2 + o(\rho^2) \triangleq \bar{y} + \Psi(\bar{x}, \bar{y}), \\ \frac{d\bar{y}}{d\tilde{\tau}} = B_{20}\bar{x}^2 + B_{11}\bar{x}\bar{y} + B_{02}\bar{y}^2 + o(\rho^2) \triangleq \Phi(\bar{x}, \bar{y}). \end{cases} \tag{2.5}$$

Letting $\bar{y} = a_2\bar{x}^2 + a_3\bar{x}^3 + \dots$ and substituting it into $\bar{y} + \Psi(\bar{x}, \bar{y}) = 0$, one can obtain $a_2 = -A_{20}$, $a_3 = A_{11}A_{20}$, that is, $\bar{y} = -A_{20}\bar{x}^2 + A_{11}A_{20}\bar{x}^3 + \dots$. Using this relation, one can obtain $\Phi(\bar{x}, \bar{y}) = B_{20}\bar{x}^2 + o(\bar{x}^3)$, $\Psi'_x(\bar{x}, \bar{y}) + \Phi'_y(\bar{x}, \bar{y}) = (2A_{20} + B_{11})\bar{x} + o(\bar{x}^2)$ and $B_{20} = \frac{-\alpha^2(x^*)^2\varphi^2(x^*)}{2} \neq 0$. Hence, the positive equilibrium of class C or D of model (2.1) is degenerate singular point [3]. \square

3. Examples and simulation

In this section, we give some examples of $\varphi(x)$ and perform corresponding numerical simulation. In simulation, the parameter values are $r = 1, K = 150, \alpha = 0.6, \mu = 0.02, d = 0.1, \beta = 0.2, p = 50$, and at this time, $r - \mu = 0.98 > \frac{1}{3} = \frac{r\mu p}{K(\beta - d)}$. In Figure 2, 3, 4, 5, the solid lines are the trajectories of model (2.1), the dashed lines are the images of $y = f(x) = -\frac{1}{90}(x^2 - 97x - 7350)$ or $y = g(x) = (\frac{1}{2} - \frac{25}{x})\varphi(x)(y \geq 0)$, and

the intersections of $y = f(x)$ and $y = g(x)$ are the positive equilibria of model (2.1).

If $\varphi(x) = 200$, the carrying capacity of predator is constant. Model (2.1) has only one positive equilibrium D , which is class A and is globally asymptotically stable (Figure 2).

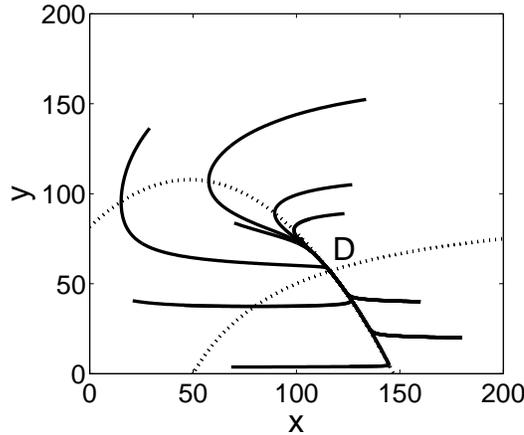


Figure 2. When $\varphi(x) = 200$, the positive equilibrium of model (2.1) and its stability.

If $\varphi(x) = 2x + 1$, the carrying capacity of predator increases linearly with the number of its prey increasing, model (2.1) has only one positive equilibrium F , which is class A and is globally stable (Figure 3).

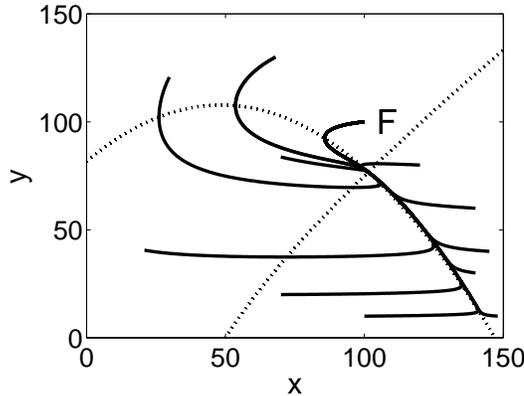


Figure 3. When $\varphi(x) = 2x + 1$, the positive equilibrium of model (2.1) and its stability.

If $\varphi(x) = (x-90)^2+427.4$, model (2.1) has one positive equilibrium of class A, $G1$ and one positive equilibrium of class D, $G2$ (Figure 4). The positive equilibrium $G2$ is a saddle-node, its separatrix (the dot line in Figure 4) divides the first quadrant into two parts, the smaller part is the attraction domain of $G1$, and the larger part is the attraction domain of $G2$.

If $\varphi(x) = 180 \sin(x/12.5) + 200$, the carrying capacity of predator changes with period 25π , model (2.1) has two positive equilibria of class A, $H1$ and $H3$ and

one positive equilibrium of class B, $H2$ (Figure 5). The two dot lines in Figure 5 are the trajectories that enter into saddle $H2$, they divide the first quadrant into two parts, and this two parts are attraction domain of $H1$ and $H3$ respectively.

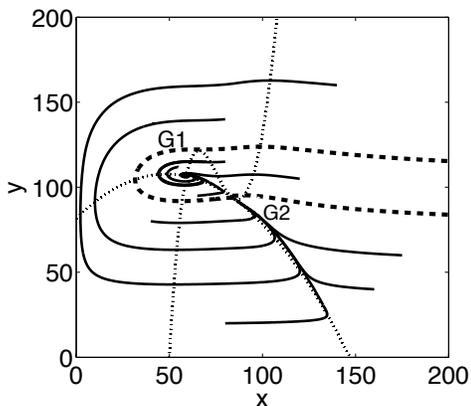


Figure 4. When $\varphi(x) = (x - 90)^2 + 427.4$, the positive equilibriums of model (2.1) and their stability.

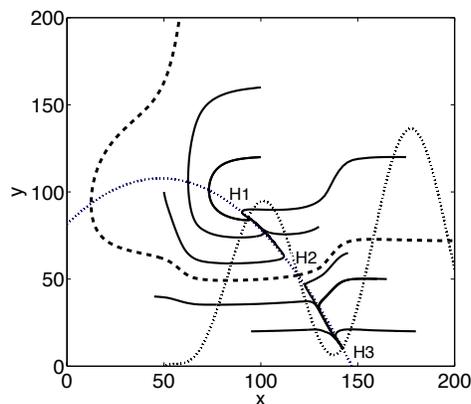


Figure 5. When $\varphi(x) = 180 \sin(x/12.5) + 200$, the positive equilibriums of model (2.1) and their stability.

When $h(x^*) < 0$, the positive equilibrium of class A is unstable, and there may exist limit cycle around it (Figure 6). In Figure 6, the parameter values are $r = 0.9$, $K = 100$, $\alpha = 0.75$, $\mu = 0.02$, $d = 0.5$, $\beta = 5.5$, $p = 12$ and $\varphi(x) = 200$. This time, the unique positive equilibrium is unstable, $h(x^*) = -361.77 < 0$, and a limit cycle appears.

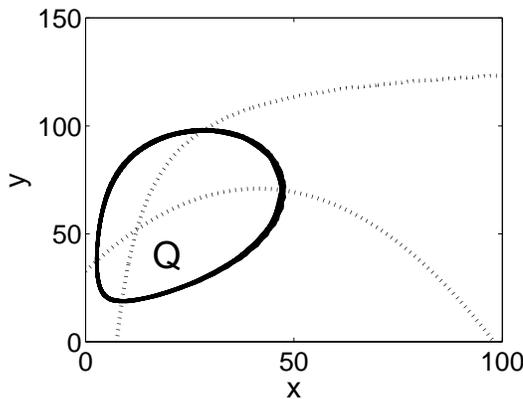


Figure 6. When $h(x^*) < 0$, there exists limit cycle around class A positive equilibrium.

4. Application

The alpine meadow is an important ecosystem in China that provides important ecological services. Over the past few decades, it has been observed that many alpine meadows have been degraded resulting in severe consequences in the ecology,

environment and economy. In alpine meadow, plateau pika feeds on vegetation, that is, plateau pika is predator and vegetation is prey. At the same time, the carrying capacity of plateau pika is influenced by the amount of vegetation also. So the relations between plateau pika and vegetation can be described by model (2.1). Next, we try to explore why alpine meadow degraded and how recover it with the help of model (2.1).

All parameters in model (2.1) are chosen on the basis of 1 ha of alpine meadow, and we use year as the time unit. We take $p = 2000\text{kg}$ empirically, and determine other parameter values basing on [12] and references therein. The values of r , d , K are 0.227, 0.95, 4000kg respectively. One plateau pika consumes 0.36kg vegetation, and assume that it happens at $x = 2000\text{kg}$, that is, $\frac{\alpha x}{p+x} = \frac{\alpha \times 2000}{2000+2000} = 0.36$, so we take $\alpha = 0.72$. Similarly, the birth rate of plateau pika is 2.625, and assume that it happens at $x = 2000\text{kg}$, that is, $\frac{\beta x}{p+x} = \frac{\beta \times 2000}{2000+2000} = 2.625$, so we take $\beta = 5.25$. The carrying capacity of plateau pika is $\varphi(x) = \frac{4 \times 265 \times 1297^3 (x+1)}{3 \times 1297^4 + (x+1)^4}$ which increases firstly and then decreases with x increasing. And $\varphi(x)$ attains its maximum value 265 at $x = 1296$. Other than plateau pika, vegetation may reduce owing to grazing, and μ is the grazing rate.

The images of $y = f(x)$ and $y = g(x)$ in Figure 7 shows that model (2.1) has only one positive equilibrium which belongs to class A and is stable. When μ increases, curve $y = f(x)$ moves leftward and the positive equilibrium moves leftward along curve $y = g(x)$. If μ is smaller, then with μ increasing the positive equilibrium moves left-upward, it results in vegetation decreasing and plateau pika increasing. This phenomenon is consistent with the reality of alpine meadow degrading. Hence, μ increasing, that is, overgrazing is the cause of alpine meadow degradation. When μ is larger, then with μ increasing the positive equilibrium moves left-downward, it results in both vegetation and plateau pika decreasing. This time, alpine meadow loss its function severely. When μ is greater than 0.2145 (namely the value of $\frac{rdp}{K(\beta-d)}$), the positive equilibrium disappears, plateau pika becomes extinct, vegetation is less, and the alpine meadow system is incomplete.

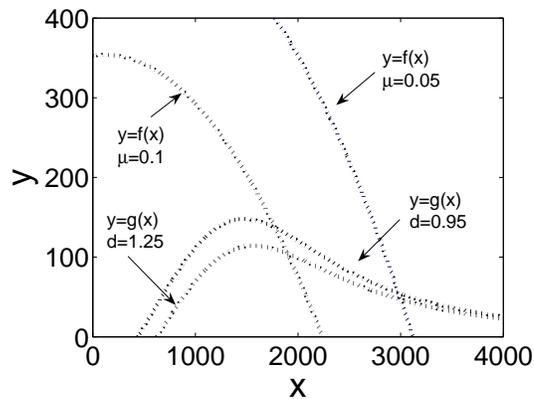


Figure 7. The influence of μ and d on positive equilibrium of (2.1).

On the other hand, due to irrational hunting, the natural enemies of plateau pika decreased heavily, and the mortality of plateau pika reduced. As shown in Figure 7, when d decreases, the curve $y = g(x)$ expands left-upward, and the positive

equilibrium moves left-upward. This time, plateau pika increases and vegetation decreases. Hence, decreasing of plateau pika mortality is also a cause of alpine meadow degrading.

Up to now, we have known that both grazing rate increasing and plateau pika mortality decreasing are the cause of alpine meadow degrading. Thus, we can recover the degraded alpine meadow through decreasing grazing rate and increasing plateau pika mortality correspondingly. From Figure 7, one can know that decreasing μ and increasing d would result in the positive equilibrium moving right-downward, that is, vegetation increasing, plateau pika decreasing and even becoming extinct. Although reducing grazing rate and increasing plateau pika mortality seem to have the same effect, but they are different obviously. Reducing grazing rate can increase vegetation significantly, even near to its carrying capacity. Whereas, through increasing plateau pika mortality, the recovery of vegetation is limited. When $\mu = 0.1$, vegetation only can recover to 2600kg approximately through increasing d . Therefore, decreasing grazing rate is the fundamental strategy to recover degraded alpine meadow.

5. Discussion

Because of the complicated relations in ecological system, the carrying capacity of predator may be determined by the amount of its prey. Considering this phenomenon, this paper formulated a prey-predator model with Holling II functional response and analyzed its global behavior. This model may have positive equilibrium or limit cycle, and the positive equilibrium may be stable, or a saddle-node, or a saddle, or a degenerate singular point. The global behavior of this model may alter with the relation between carrying capacity of predator and amount of its prey changing. Thus, before studying or managing populations, it is needed to understand the relations among populations fully.

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