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Fear effect exerted by carnivore in grassland ecosystem

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A four-dimensional mathematical model is formulated to explore the fear effect exerted by large carnivore in the grassland ecosystem. The model depicts the interactions among herbage, domestic herbivore, wild herbivore and large carnivore, which incorporates both direct predation and anti-predator mechanisms. The dynamic properties of the model are analytically investigated, including the dissipativity of solutions, and the existence and stability of different equilibria. Some numerical simulations are also presented to exhibit rich dynamical behaviors, such as various types of bistabilities, periodic oscillation and chaotic oscillation. The study reveals that the appropriate level of fear factors can stabilize the system and increase the density of herbage and domestic herbivore. The fear effect plays an important role in maintaining the balance of the grassland ecosystem and promoting the economy of human society.

Keywords: Fear effect; grassland ecosystem; food chain model; bifurcation; chaotic dynamics.

Mathematics Subject Classification 2020: 92D25, 92D40, 34C05

1. Introduction

Grassland ecosystem is the main and important component of the terrestrial ecosystems in China, which has a significant role and value in developing animal husbandry, protecting biodiversity and maintaining ecological balance [14, 47]. In recent

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years, due to the combined impacts of human activities and global climate changes, the desertification of grassland is very serious, causing great damage to the natural environment, and directly affecting the human economy [16]. Therefore, management/control strategies are needed to protect the grassland ecosystem.

There is an increasing body of significant research on the impact of human activities, climate change, abiotic/biotic factors on the dynamics of the grassland ecosystem. In particular, many modeling studies have been conducted to improve our understanding of this important ecosystem. For example, Sun and Mu [48] developed a theoretical model to investigate the impact of climate change on the grassland ecosystem, Chen *et al.* [5] presented a model analysis of the grazing effect on the above-ground biomass and net primary production of a Mongolian grassland ecosystem, Zhao *et al.* [58] explored the spatial variability of soil properties affected by the grazing intensity in Inner Mongolia grassland, Chen *et al.* [4] investigated the impact of both climate change and anthropogenic activities on alpine grasslands over the Qinghai-Tibet Plateau, Miller *et al.* [27] emphasized the significance of large carnivore in maintaining healthy and balanced ecosystems, highlighting the importance of conservation efforts aimed at safeguarding these critical species.

Large carnivore is an ecologically important group of species in the grassland ecosystem, e.g. coyotes *Canis latrans* in North America [56], mountain lions *Felis concolor* ssp. in South America [26] and lions *Panthera leo* in Africa [33]. They often prey on livestock, especially, if the local wild prey population decreases, then the intensity of predation on livestock by large carnivore will continue to increase [1].

The increasing economic losses lead to frequent conflicts between human and carnivore [1, 15, 17], which stimulate humans to kill large carnivore to reduce their population size [42]. However, the absence of large carnivore such as wolves can lead to ecosystem simplification or degradation [41, 46] and may have further ecological consequences. It is thus important to understand large carnivore's impact on vegetation communities to balance the biodiversity and human economy.

Predation, as a direct effect of the large carnivore, has received a lot of attention because it is easily observed in many situations [24, 43]. It has been extensively studied by many researchers from the perspective of dynamic modeling (see, e.g. [13] and the references therein). However, more and more biologists have realized that the relationship between predator and prey cannot be simply described only as direct killing. When a predator is present, the prey can perceive the risk of predation and thus alter their behavior, reproduction and foraging time/pattern [2, 9, 22, 34, 35, 38–41, 50]. Therefore, these anti-predator behaviors may play a considerably important role in predator–prey interaction [57].

There is also increasing evidence that indirect effects (e.g. fear effect) are more potent than direct predation [12, 23, 49, 57]. Zanette *et al.* [57] conducted an experiment during the entire reproduction period of the prey population. They prevented direct predation by isolating the prey (song sparrow) with an electric fence and manipulated the predation risk by using the playbacks of predator sounds. Their results suggested that the number of offspring of song sparrows dropped by about 40% per year due to the presence of predation risk. Suraci *et al.* [49] assessed predation risk by using month-long playbacks of large carnivore's vocalizations. Their results showed that the fear effect led to a reduction in the foraging activity of raccoons even without direct predation, which was good for the prey of raccoons. It indicated that the fear effect can cause a trophic cascade that affects the evolution of system diversity and community structure. Therefore, the indirect effect should not be ignored in predator–prey interactions.

The indirect effect has also attracted great attention from mathematical biologists and some mathematical models have been proposed to explore the fear effect in predator–prey interactions. These models have been fully investigated from both theoretical and numerical perspectives and rich results have been yielded. Wang *et al.* [51] first formulated a mathematical model that incorporates the cost of fear on prey reproduction and compared it with the classical predator–prey model. Their results showed that the fear effect can alter the predator–prey system from population oscillations to a stable state. Furthermore, the cost of fear not only affects the existence of Hopf bifurcation but also alters the Hopf bifurcation's direction from supercritical to subcritical as the level of fear increases. Panday *et al.* [30] first considered the fear effect in a tri-trophic food chain model. They found that the fear effect plays an important role in stabilizing the system, and the system patterns changed from chaos to a stable state through periodic oscillations. In addition, many different predator–prey systems also incorporate aspects of the fear effect [6, 7, 10, 11, 19, 20, 29, 31, 32, 44, 52–55]. To our knowledge, the mechanism of the fear effect exerted by large carnivore on both vegetation communities and the human economy has not been well investigated and documented. This motivates the principal aim of this paper: to develop a mechanistic model to describe the interactions between large carnivore, domestic herbivore, wild herbivore and herbage, and then, explore the impact of the fear effect on the community structure of grassland and the human economy.

The rest of the paper is organized as follows. In Sec. 2, a new four-species food chain model (2.2) is proposed to describe the fear effect on predation and reproduction. In Sec. 3, the dynamics of the model are investigated, including the dissipativity of solutions, the existence and stability of equilibria. The theoretical results are illustrated by numerical simulations in Sec. 4. The numerical analyses show that the model admits many different dynamical behaviors compared to the classical model. In Sec. 5, the impact of the fear effect is deliberately explored by numerical studies. The paper ends with Sec. 6 where some conclusions and further discussions are presented.

2. Model Formulation

Consider a grassland ecosystem consisting of four species: herbage, domestic herbivore, wild herbivore and large carnivore, whose biomass densities are denoted by

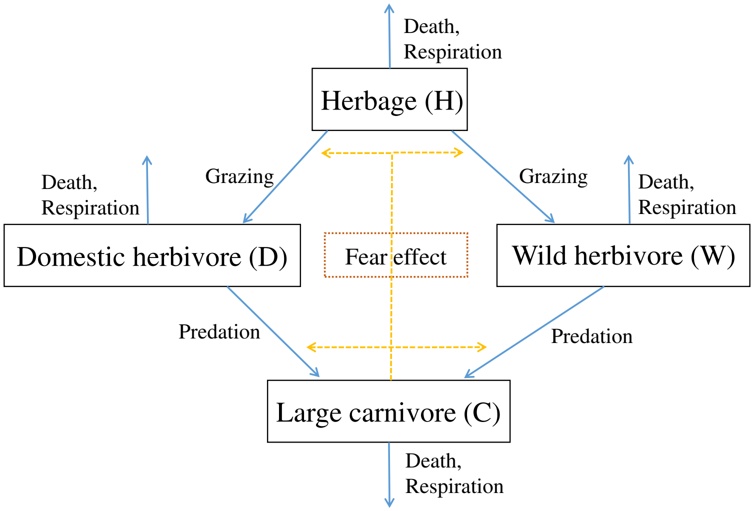


Fig. 1. Schematic diagram of interactions in ecosystems consisting of four species.

H, D, W and C, respectively. The anti-predator response is assumed to manifest itself in the form of the fear effect. The interactions including the fear effect among the four species are shown in the schematic diagram in Fig. 1. In the absence of the anti-predator response, the following model describes the interactions of the four species

$$\begin{aligned}
\frac{dH}{dt} &= rH\left(1-\frac{H}{K}\right) - g_1(H)D - g_2(H)W,\\
\frac{dD}{dt} &= e_1 g_1(H)D - g_3(D)C - d_1 D,\\
\frac{dW}{dt} &= e_2 g_2(H)W - g_4(W)C - d_2 W,\\
\frac{dC}{dt} &= (c_1 g_3(D) + c_2 g_4(W))C - d_3 C.
\end{aligned} \tag{2.1}$$

Here, K and r represent the environmental carrying capacity and the intrinsic growth rate of herbage; e_1 and e_2 denote the conversion efficiency from herbage to domestic herbivore and wild herbivore, respectively; c_1 and c_2 denote the conversion efficiency from domestic herbivore and wild herbivore to large carnivore, respectively; $d_i (i = 1, 2, 3)$ denote the natural death rate of domestic herbivore, wild herbivore and large carnivore, respectively; $g_i(i = 1, 2, 3, 4)$ represent the prey-dependent functional response.

In order to incorporate the anti-predator mechanism into the model properly, we suppose that T is the total time spent by a domestic herbivore for gathering food from the herbage. Then it can be divided into two main parts:

- T_{dsh} is the time spent by a domestic herbivore for searching herbage;
- T_{dwc} is the time wasted by a domestic herbivore for interfering with the large carnivore due to the anti-predator response.

Let

- α_{dsh} be the encounter rate between domestic herbivore and herbage;
- α_{dec} be the encounter rate between domestic herbivore and large carnivore.

Assume that the number of herbage consumed per domestic herbivore is proportional to the searching time and the density of herbage. Then the total number of herbage consumed by per domestic herbivore is described by

$$N_{\mathrm{dh}} = \alpha_{\mathrm{dsh}} H T_{\mathrm{dsh}}.$$

Similarly, assume the number of large carnivores encountered per domestic herbivore be proportional to the searching time and the density of large carnivore. Thus, the number of large carnivores encountered reads

$$N_{\mathrm{dc}} = \alpha_{\mathrm{dec}} C T_{\mathrm{dsh}}.$$

When a domestic herbivore encounters a large carnivore, the wasted time due to the interference is denoted by t_{dwc}. Then T_{dwc} is given by the product of the number of encounters between large carnivores N_{dc} and the time wasted per encounter t_{dwc}. Suppose the domestic herbivore moves randomly, then T_{dwc} can be expressed as follows:

$$T_{\mathrm{dwc}} = \alpha_{\mathrm{dec}} t_{\mathrm{dwc}} C T_{\mathrm{dsh}}.$$

Combining the above assumptions and analyses, one can conclude that

$$T = T_{\mathrm{dsh}} + T_{\mathrm{dwc}} = T_{\mathrm{dsh}} + \alpha_{\mathrm{dec}} t_{\mathrm{dwc}} C T_{\mathrm{dsh}}.$$

With this consideration, the prey-dependent only functional response $g_1(H)$ in (2.1) is replaced by $g_1(H, C)$ with

$$g_1(H, C) = \frac{N_{\mathrm{dh}}}{T} = \frac{\alpha_{\mathrm{dsh}} H}{1 + \alpha_{\mathrm{dec}} t_{\mathrm{dwc}} C} =: \frac{a_1 H}{1 + \beta_1 C},$$

where $a_1 = \alpha_{\mathrm{dsh}}$, $\beta_1 = \alpha_{\mathrm{dec}} t_{\mathrm{dwc}}$. Here, the factor $1/(1 + \beta_1 C)$ reflects the fear effect exerted by the carnivore on the domestic herbivore's preying behavior and consequence. It represents a cost to the domestic herbivore since its predation rate is decreased.

By a similar derivation under similar assumptions as above, second prey-dependent only functional response $g_2(D)$ is replaced by

$$g_2(H, C) = \frac{a_2 H}{1 + \beta_2 C},$$

where the factor $1/(1 + \beta_2 C)$ accounts for a cost to the wild herbivore caused by the fear effect exerted by the carnivore on the wild herbivore's preying behavior and consequence.

In addition to the cost described above for the herbivores, their anti-predation responses should also have some benefits. The main benefit is that the responses would reduce the risk of predation by the carnivore [8]. Hence, the benefit should be incorporated into the functional response $g_3(D)$ and $g_4(W)$. To avoid making the model too complicated, we adopt linear functional responses $g_3(D) = b_1D$ and $g_4(W) = b_2W$ and incorporate only constant parameters m_1, $m_2 \in (0, 1]$ to reflect the benefits. Combining all the above preparation, we arrive at the following model system:

$$\begin{aligned}
\frac{dH}{dt} &= rH\left(1 - \frac{H}{K}\right) - \frac{a_1DH}{1+\beta_1C} - \frac{a_2WH}{1+\beta_2C} =: f_1(H, D, W, C),\\
\frac{dD}{dt} &= \frac{e_1a_1HD}{1+\beta_1C} - m_1b_1CD - d_1D =: f_2(H, D, W, C),\\
\frac{dW}{dt} &= \frac{e_2a_2HW}{1+\beta_2C} - m_2b_2CW - d_2W =: f_3(H, D, W, C),\\
\frac{dC}{dt} &= c_1m_1b_1DC + c_2m_2b_2WC - d_3C =: f_4(H, D, W, C),
\end{aligned} \tag{2.2}$$

where a_1 and a_2 denote the foraging rate of domestic herbivore and wild herbivore on herbage, respectively; b_1 and b_2 denote the predation rate of large carnivore on domestic herbivore and wild herbivore, respectively; β_1 and β_2 denote the fear effect coefficient; $m_1, m_2 \in (0, 1]$ are the ratio of the searching efficiency due to fear effect. This model is demonstrated in the schematic diagram in Fig. 1.

Considering the biological background, we assume that all the parameters in (2.2) are positive and the system is associated with the following positive initial values in $\mathbb{R}^4_+$:

$$H(0) > 0, \quad D(0) > 0, \quad W(0) > 0, \quad C(0) > 0.$$

3. Model Analysis

In this section, we investigate the existence and stability of boundary and positive equilibria. We first introduce an important lemma.

Lemma 3.1. *System* (2.2) *is dissipative with respect to the region*

$$\Omega = \left\{(H, D, W, C) \in \mathbb{R}^4_+ \middle|\, 0 \le \mu_1H + D + W + \frac{1}{\mu_2}C \le Q\right\},$$

where

$$Q = \frac{\mu_1K(r+\mu)^2}{4r}, \quad \mu_1 = \max\{e_1, e_2\}, \quad \mu_2 = \max\{c_1, c_2\}, \quad \mu = \min\{d_1, d_2, d_3\}.$$

Proof. It is clear that system (2.2) has a uniquely global solution for any initial condition and the interior of $\mathbb{R}^4_+$ is a positive invariant with respect to the model

(2.2). Note that

$$\frac{dH}{dt} \le rH\left(1 - \frac{H}{K}\right),$$

which implies that

$$\limsup_{t\to\infty} H(t) \le K. \tag{3.1}$$

Let

$$M(t) = \mu_1 H(t) + D(t) + W(t) + \frac{1}{\mu_2}C(t).$$

A direct calculation gives

$$\begin{aligned}\frac{dM}{dt} &\le \frac{\mu_1 r}{K}H(K-H) - d_1 D - d_2 W - \frac{d_3}{\mu_2}C\\ &\le \frac{\mu_1 r}{K}H(K-H) + \mu\mu_1 H - \mu\left(\mu_1 H + D + W + \frac{1}{\mu_2}C\right),\end{aligned}$$

then

$$\begin{aligned}\frac{dM}{dt} + \mu M &\le \mu_1 H\left(r + \mu - \frac{r}{K}H\right)\\ &= -\frac{\mu_1 r}{K}\left(H - \frac{(r+\mu)K}{2r}\right)^2 + \frac{\mu_1 K(r+\mu)^2}{4r} \le \frac{\mu_1 K(r+\mu)^2}{4r}.\end{aligned}$$

This leads to

$$M(t) \le \frac{\mu_1 K(r+\mu)^2}{4r}(1 - e^{-\mu t}) + M(0)e^{-\mu t},$$

therefore,

$$\limsup_{t\to\infty} M(t) \le \frac{\mu_1 K(r+\mu)^2}{4r}.$$

The proof is complete. □

The possible nonnegative equilibria of (2.2) are listed below. The extinction equilibrium $E_0 = (0,0,0,0)$; herbage-only equilibrium $E_h = (K,0,0,0)$; two-species coexistence equilibria

- $E_{\text{hd}} = (H_1^*, D_1^*, 0, 0)$, where

  $$H_1^* = \frac{d_1}{e_1 a_1}, \quad D_1^* = \frac{r}{a_1}\left(1 - \frac{d_1}{e_1 a_1 K}\right)$$

  are derived from

  $$r\left(1 - \frac{H_1^*}{K}\right) - a_1 D_1^* = 0, \quad e_1 a_1 H_1^* - d_1 = 0;$$

- $E_{\mathrm{hw}} = (H_2^*, 0, W_2^*, 0)$, where

$$H_2^* = \frac{d_2}{e_2 a_2}, \quad W_2^* = \frac{r}{a_2}\left(1 - \frac{d_2}{e_2 a_2 K}\right)$$

  are derived from

$$r\left(1 - \frac{H_2^*}{K}\right) - a_1 W_2^* = 0, \quad e_2 a_2 H_2^* - d_2 = 0;$$

three-species coexistence equilibria are

- the wild herbivore-free equilibrium $E_{\mathrm{hdc}} = (H_3^*, D_3^*, 0, C_3^*)$, where H_3^*, D_3^* and C_3^* satisfy

$$\begin{aligned} &r\left(1 - \frac{H_3^*}{K}\right) - \frac{a_1 D_3^*}{1 + \beta_1 C_3^*} = 0, \quad \frac{e_1 a_1 H_3^*}{1 + \beta_1 C_3^*} - m_1 b_1 C_3^* - d_1 = 0, \\ &c_1 m_1 b_1 D_3^* - d_3 = 0; \end{aligned} \tag{3.2}$$

- the domestic herbivore-free equilibrium $E_{\mathrm{hwc}} = (H_4^*, 0, W_4^*, C_4^*)$, where H_4^*, W_4^* and C_4^* satisfy

$$\begin{aligned} &r\left(1 - \frac{H_4^*}{K}\right) - \frac{a_2 W_4^*}{1 + \beta_2 C_4^*} = 0, \quad \frac{e_2 a_2 H_4^*}{1 + \beta_2 C_4^*} - m_2 b_2 C_4^* - d_2 = 0, \\ &c_2 m_2 b_2 W_4^* - d_3 = 0; \end{aligned} \tag{3.3}$$

the interior equilibrium $E_{\mathrm{hdwc}} = (H_5^*, D_5^*, W_5^*, C_5^*)$, where H_5^*, D_5^*, W_5^* and C_5^* satisfy

$$\begin{aligned} &r\left(1 - \frac{H_5^*}{K}\right) - \frac{a_1 D_5^*}{1 + \beta_1 C_5^*} - \frac{a_2 W_5^*}{1 + \beta_2 C_5^*} = 0, \quad \frac{e_1 a_1 H_5^*}{1 + \beta_1 C_5^*} - m_1 b_1 C_5^* - d_1 = 0, \\ &\frac{e_2 a_2 H_5^*}{1 + \beta_2 C_5^*} - m_2 b_2 C_5^* - d_2 = 0, \quad c_1 m_1 b_1 D_5^* + c_2 m_2 b_2 W_5^* - d_3 = 0. \end{aligned} \tag{3.4}$$

Theorem 3.2.

(i) E_0 *always exists and is unstable*;
(ii) E_h *always exists. If*

$$d_1 > e_1 a_1 K \quad \textit{and} \quad d_2 > e_2 a_2 K, \tag{3.5}$$

then E_h *is globally asymptotically stable.*

Proof. For E_0, one has

$$J(E_0) = \begin{pmatrix} r & 0 & 0 & 0 \\ 0 & -d_1 & 0 & 0 \\ 0 & 0 & -d_2 & 0 \\ 0 & 0 & 0 & -d_3 \end{pmatrix},$$

which implies that E_0 is unstable.

The Jacobian matrix at E_h is

$$J(E_h) = \begin{pmatrix} -r & -a_1K & -a_2K & 0 \\ 0 & e_1a_1K - d_1 & 0 & 0 \\ 0 & 0 & e_2a_2K - d_2 & 0 \\ 0 & 0 & 0 & -d_3 \end{pmatrix}.$$

If (3.5) holds, then the four eigenvalues of characteristic equation of $J(E_h)$ have negative real parts. Whence, E_h is locally asymptotically stable. From (3.1), for any $\varepsilon > 0$, there exists a T such that $H(t) < K + \varepsilon$ when $t > T$, then

$$\frac{dD}{dt} = \frac{e_1a_1DH}{1+\beta_1C} - m_1b_1CD - d_1D < (e_1a_1(K+\varepsilon) - d_1)D,$$

$$\frac{dW}{dt} = \frac{e_2a_2WH}{1+\beta_2C} - m_2b_2CW - d_2W < (e_2a_2(K+\varepsilon) - d_2)W.$$

It follows that $D(t) \to 0$ and $W(t) \to 0$ as $t \to \infty$ if (3.5) holds. By the theory of asymptotical autonomous systems [28], (2.2) reduces to a limiting system

$$\frac{dH}{dt} = rH\left(1 - \frac{H}{K}\right),$$

which means that $H(t) \to K$ as $t \to \infty$, then E_h is globally attractive. This means that E_h is globally asymptotically stable. □

Theorem 3.2(i) implies that the extinction equilibrium E_0 is always unstable and the four species cannot become extinct at the same time; Theorem 3.2(ii) implies that (2.2) can have the only herbage being stable at its carrying capacity K when the death rates of domestic herbivore and wild herbivore are large.

Theorem 3.3. *If*

$$e_1a_1K\left(1 - \frac{a_1d_3}{c_1m_1b_1r}\right) < d_1 < e_1a_1 \min\left\{\frac{d_2}{e_2a_2}, K\right\}, \tag{3.6}$$

then E_{hd} *exists and is locally asymptotically stable. Furthermore, if*

$$d_2 > e_2a_2K \quad \textit{and} \quad d_3 > c_1m_1b_1Q, \tag{3.7}$$

then E_{hd} *is globally asymptotically stable.*

Proof. It is clear that E_{hd} always exists if $d_1 < e_1a_1K$. Note that

$$J(E_{\text{hd}}) = \begin{pmatrix} -\frac{rH_1^*}{K} & -a_1H_1^* & -a_2H_1^* & \beta_1a_1D_1^*H_1^* \\ e_1a_1D_1^* & 0 & 0 & -e_1a_1\beta_1H_1^*D_1^* - m_1b_1D_1^* \\ 0 & 0 & e_2a_2H_1^* - d_2 & 0 \\ 0 & 0 & 0 & c_1m_1b_1D_1^* - d_3 \end{pmatrix},$$

which means that E_{hd} is locally asymptotically stable if (3.6) holds.

We now prove the global stability of E_{hd}. From (3.1), for any $\varepsilon > 0$, there exists a T such that $H(t) < K + \varepsilon$ when $t > T$, then

$$\frac{dW}{dt} < (e_2 a_2 (K + \varepsilon) - d_2)W.$$

If $e_2 a_2 K < d_2$, then $W(t) \to 0$ as $t \to \infty$. For any $\varepsilon' > 0$, there exists a T' such that $D(t) < Q + \varepsilon'$ when $t > T'$. Hence

$$\frac{dC}{dt} < (c_1 m_1 b_1 (Q + \varepsilon') - d_3)C.$$

If $c_1 m_1 b_1 Q < d_3$, then $C(t) \to 0$ as $t \to \infty$. According to the theory of asymptotical autonomous systems [28], (2.2) reduces to a limiting system

$$\begin{aligned} \frac{dH}{dt} &= rH\left(1 - \frac{H}{K}\right) - a_1 DH =: F_1(H, D), \\ \frac{dD}{dt} &= e_1 a_1 HD - d_1 D =: F_2(H, D). \end{aligned} \tag{3.8}$$

When (3.6) holds, let $B(H, D) = 1/(HD)$. For any solution (H, D),

$$\left.\frac{\partial(F_1 B)}{\partial H} + \frac{\partial(F_2 B)}{\partial D}\right|_{(3.8)} = -\frac{r}{KD} < 0.$$

Therefore, system (3.8) has no periodic orbit in $(0, \infty) \times (0, \infty)$ by using the Dulac–Bendixson theorem [37]. Moreover, if $d_1 < e_1 a_1 K$ holds, then (H_1^*, D_1^*) is the unique interior equilibrium of (3.8), so every positive solution will tend to (H_1^*, D_1^*). This together with the condition for the local stability of (H_1^*, D_1^*) implies that (H_1^*, D_1^*) is globally asymptotically stable with respect to (3.8). Note that $W(t) \to 0$ and $C(t) \to 0$ as $t \to \infty$ if (3.7) holds. Therefore, E_{hd} is globally asymptotically stable. The proof is now complete. □

Theorem 3.3 provides sufficient conditions for the existence and stability of E_{hd}, which implies that both the herbage and the domestic herbivore can stably coexist at the equilibrium E_{hd} if the death rate of domestic herbivore d_1 is intermediate large while the death rates of wild herbivore (d_2) and carnivore (d_3) are properly large.

By carrying out arguments similar to those of Theorem 3.3, one can explore the existence and stability of E_{hw} and reaches the following conclusions.

Theorem 3.4. *If*

$$e_2 a_2 K\left(1 - \frac{a_2 d_3}{c_2 m_2 b_2 r}\right) < d_2 < e_2 a_2 \min\left\{\frac{d_1}{e_1 a_1}, K\right\},$$

then E_{hw} exists and is locally asymptotically stable. Furthermore, if

$$d_1 > e_1 a_1 K \quad \textit{and} \quad d_3 > c_2 m_2 b_2 Q,$$

then E_{hw} is globally asymptotically stable.

Theorem 3.4 provides sufficient criteria for the existence and stability of E_{hw}, from which it follows that both the herbage and the wild herbivore can stably coexist at the equilibrium E_{hw} if the death rate of wild herbivore d_2 has intermediate values while the death rates of domestic herbivore (d_1) and carnivore (d_3) are suitably large.

For the wild herbivore-free equilibrium E_{hdc}, by (3.2), a direct calculation gives

$$\begin{cases} D_3^* = \dfrac{d_3}{c_1 m_1 b_1}, \quad H_3^* = \dfrac{(d_1 + m_1 b_1 C_3^*)(1+\beta_1 C_3^*)}{e_1 a_1}, \\ (1+\beta_1 C_3^*)(-m_1 b_1 \beta_1 C_3^{*2} - (d_1\beta_1 + m_1 b_1) C_3^* + (e_1 a_1 K - d_1)) = \dfrac{e_1 a_1^2 d_3 K}{r c_1 m_1 b_1} =: A. \end{cases}$$

Let

$$f(C) = (1+\beta_1 C)(-m_1 b_1 \beta_1 C^2 - (d_1\beta_1 + m_1 b_1)C + (e_1 a_1 K - d_1)),$$

then

$$f'(C) = -3\beta_1^2 m_1 b_1 C^2 - 2\beta_1(2m_1 b_1 + \beta_1 d_1)C + (\beta_1 e_1 a_1 K - 2\beta_1 d_1 - m_1 b_1).$$

A sufficient and necessary condition for $f(C) = 0$ to have positive roots is $d_1 < e_1 a_1 K$. Moreover, if $\beta_1 e_1 a_1 K - 2\beta_1 d_1 - m_1 b_1 > 0$, then $f'(0) > 0$ and $f'(C) = 0$ has a positive root $\hat{C}$. Conversely, if $\beta_1 e_1 a_1 K - 2\beta_1 d_1 - m_1 b_1 < 0$, then $f'(0) < 0$.

Consider the parabola s and the straight line l represented by

$$s : y = f(C), \quad l : y = A,$$

then the key idea of the proof of the existence of E_{hdc} is to explore the number of intersections of s and l in $\mathbb{R}_+^2$. We now obtain the following theorem by a detailed analysis of the relative position relationship between s and l.

Theorem 3.5. *Let* $\gamma = (\beta_1 e_1 a_1 K - m_1 b_1)/2\beta_1$, $f(0) = e_1 a_1 K - d_1$. *The following statements hold.*

(i) *If* $d_1 < \gamma$ *and* $f(\hat{C}) < A$ (*see Fig.* 2(a)), *or* $d_1 > \max\{\gamma, e_1 a_1 K - A\}$, *then* E_{hdc} *does not exist*;

(ii) *if* $d_1 < \gamma$ *and* $f(0) < A < f(\hat{C})$, *then* (2.2) *has two wild-herbivore-free equilibria* E_{hdc} *and* E'_{hdc} (*see Fig.* 2(b)), *in particular, if* $f(\hat{C}) = A$, *then* $E_{\mathrm{hdc}} = E'_{\mathrm{hdc}}$;

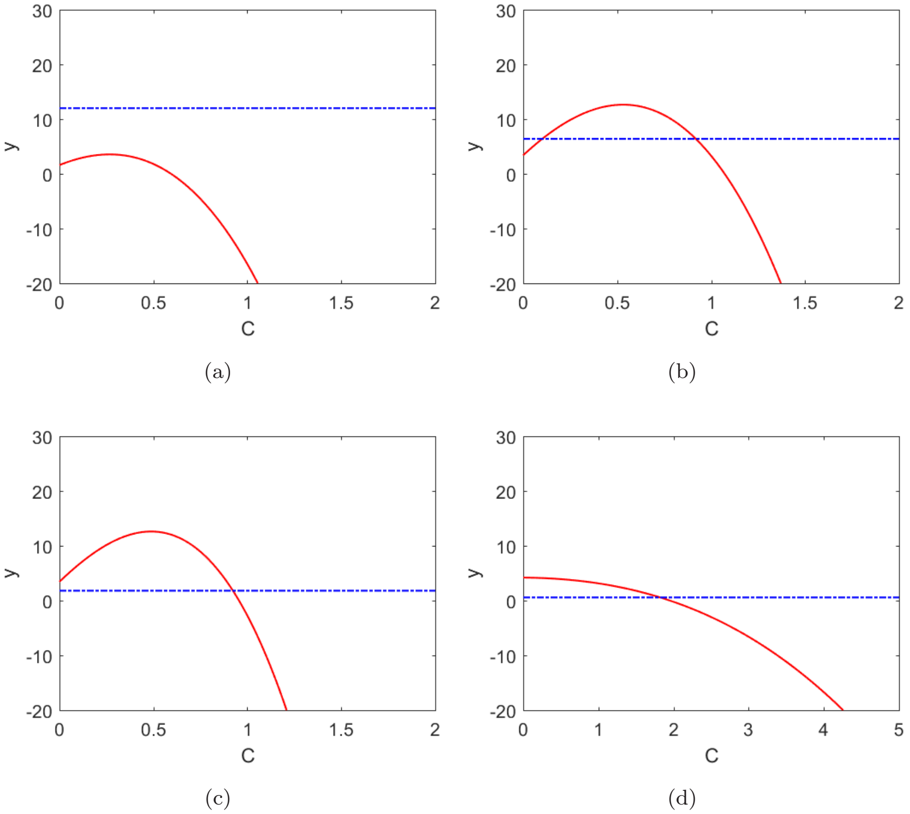
(iii) *if* $\gamma < d_1 < e_1 a_1 K - A$ *or* $d_1 < \min\{\gamma, e_1 a_1 K - A\}$, *then the wild herbivore-free equilibrium* E_{hdc} *exists and is unique* (*see Figs.* 2(c) *and* 2(d)).

Let $E_{\mathrm{hdc}} = (H_3^*, D_3^*, 0, C_3^*)$ be a wild herbivore-free equilibrium of (2.2).

Theorem 3.6. *If*

$$d_2 > \frac{e_2 a_2 H_3^*}{1+\beta_2 C_3^*} - m_2 b_2 C_3^* \quad \text{and} \quad b_1 > \frac{e_1 a_1 \beta_1 (K - 2H_3^*)}{m_1 (1+\beta_1 C_3^*)^2}, \tag{3.9}$$

then E_{hdc} *is locally asymptotically stable.*



(a) (b)

(c) (d)

Fig. 2. Schematic illustration of the relative position of parabola s and straight line l.

Proof. The Jacobian matrix of system (2.2) at E_{hdc} is

$$J(E_{\mathrm{hdc}}) = \begin{pmatrix} -a_{11} & -a_{12} & -a_{13} & a_{14} \\ a_{21} & 0 & 0 & -a_{24} \\ 0 & 0 & a_{33} & 0 \\ 0 & a_{42} & a_{43} & 0 \end{pmatrix},$$

where

$$a_{11} = \frac{rH_3^*}{K}, \quad a_{12} = \frac{a_1 H_3^*}{1+\beta_1 C_3^*}, \quad a_{13} = \frac{a_2 H_3^*}{1+\beta_2 C_3^*}, \quad a_{14} = \frac{\beta_1 a_1 D_3^* H_3^*}{(1+\beta_1 C_3^*)^2},$$

$$a_{21} = \frac{e_1 a_1 D_3^*}{1+\beta_1 C_3^*}, \quad a_{24} = \frac{e_1 a_1 \beta_1 H_3^* D_3^*}{(1+\beta_1 C_3^*)^2} + m_1 b_1 D_3^*,$$

$$a_{33} = \frac{e_2 a_2 H_3^*}{1+\beta_2 C_3^*} - m_2 b_2 C_3^* - d_2, \quad a_{42} = c_1 m_1 b_1 C_3^*, \quad a_{43} = c_2 m_2 b_2 C_3^*.$$

Then a_{33} is one of the eigenvalues of characteristic equation of $J(E_{\text{hdc}})$ and the other three eigenvalues satisfy

$$\lambda^3 + a_{11}\lambda^2 + (a_{12}a_{21} + a_{24}a_{42})\lambda + a_{42}(a_{11}a_{24} - a_{14}a_{21}) = 0.$$

A simple calculation gives

$$a_{11}(a_{12}a_{21} + a_{24}a_{42}) > a_{42}(a_{11}a_{24} - a_{14}a_{21}).$$

By Routh–Hurwitz criterion, if $a_{11}a_{24} - a_{14}a_{21} > 0$ and $a_{33} < 0$, then E_{hdc} is locally asymptotically stable. The proof is complete. □

Theorem 3.7. *If*

$$d_i > e_i a_i H_3^* - \frac{c_i e_i m_i b_i C_3^*}{\mu_1\mu_2}\ (i = 1, 2) \quad \textit{and} \quad \frac{\mu_1\mu_2 m_1 b_1 D_3^*}{e_1} < d_3 < \frac{\mu_1\mu_2\rho}{C_3^*}, \tag{3.10}$$

where

$$\rho = rH_3^* - \frac{d_1 D_3^*}{e_1} - \frac{r}{4K}\left(H_3^* + K - \frac{a_1 K D_3^*}{r(1 + Q\beta_1)}\right)^2,$$

and Q, μ_1 *and* μ_2 *are defined in Lemma* 3.1, *then* E_{hdc} *is globally asymptotically stable.*

Proof. Consider

$$V_3 = \left(H - H_3^* - H_3^* \ln\frac{H}{H_3^*}\right) + \frac{1}{e_1}\left(D - D_3^* - D_3^* \ln\frac{D}{D_3^*}\right) + \frac{1}{e_2}W + \frac{1}{\mu_1\mu_2}\left(C - C_3^* - C_3^* \ln\frac{C}{C_3^*}\right).$$

Differentiating V along solutions of (2.2) with respect to t, one has

$$\begin{aligned}\frac{dV_3}{dt} &= (H - H_3^*)\left(r\left(1 - \frac{H}{K}\right) - \frac{a_1 D}{1 + \beta_1 C} - \frac{a_2 W}{1 + \beta_2 C}\right) + (D - D_3^*) \\ &\quad \times \left(\frac{a_1 H}{1 + \beta_1 C} - \frac{m_1 b_1}{e_1}C - \frac{d_1}{e_1}\right) + \left(\frac{a_2 HW}{1 + \beta_2 C} - \frac{m_2 b_2}{e_2}CW - \frac{d_2}{e_2}W\right) \\ &\quad + (C - C_3^*)\left(\frac{c_1 m_1 b_1}{\mu_1\mu_2}D + \frac{c_2 m_2 b_2}{\mu_1\mu_2}W - \frac{d_3}{\mu_1\mu_2}\right) \\ &\le rH\left(1 - \frac{H}{K}\right) - rH_3^* + \frac{rH_3^* H}{K} + a_1 H_3^* D + a_2 H_3^* W + \frac{m_1 b_1 D_3^* C}{e_1} - \frac{d_1 D}{e_1} \\ &\quad + \frac{d_1 D_3^*}{e_1} - \frac{a_1 D_3^* H}{1 + \beta_1 Q} - \frac{d_2 W}{e_2} - \frac{d_3 C}{\mu_1\mu_2} + \frac{d_3 C_3^*}{\mu_1\mu_2} - \frac{c_1 m_1 b_1 C_3^* D}{\mu_1\mu_2} - \frac{c_2 m_2 b_2 C_3^* W}{\mu_1\mu_2} \\ &\le -\frac{r}{K}\left(H - \frac{H_3^* + K - a_1 K D_3^*/r(1 + Q\beta_1)}{2}\right)^2\end{aligned}$$

$$
\begin{aligned}
&\quad + \frac{r(H_3^* + K - a_1 K D_3^*/r(1+Q\beta_1))^2}{4K} - rH_3^* + a_1 H_3^* D + a_2 H_3^* W \\
&\quad + \frac{m_1 b_1 D_3^* C}{e_1} - \frac{d_1 D}{e_1} + \frac{d_1 D_3^*}{e_1} - \frac{d_2 W}{e_2} - \frac{d_3 C}{\mu_1\mu_2} \\
&\quad + \frac{d_3 C_3^*}{\mu_1\mu_2} - \frac{c_1 m_1 b_1 C_3^* D}{\mu_1\mu_2} - \frac{c_2 m_2 b_2 C_3^* W}{\mu_1\mu_2} \\
&\le \frac{r(H_3^* + K - a_1 K D_3^*/r(1+Q\beta_1))^2}{4K} + \left(a_1 H_3^* - \frac{d_1}{e_1} - \frac{c_1 m_1 b_1 C_3^*}{\mu_1\mu_2}\right) D \\
&\quad + \left(\frac{m_1 b_1 D_3^*}{e_1} - \frac{d_3}{\mu_1\mu_2}\right) C + \left(a_2 H_3^* - \frac{d_2}{e_2} - \frac{c_2 m_2 b_2 C_3^*}{\mu_1\mu_2}\right) W - rH_3^* \\
&\quad + \frac{d_1 D_3^*}{e_1} + \frac{d_3 C_3^*}{\mu_1\mu_2}.
\end{aligned}
$$

It is observed that if (3.10) holds, then $dV_3/dt \le 0$, and $dV_3/dt = 0$ if and only if $(H, D, W, C) \equiv (H_3^*, D_3^*, 0, C_3^*)$. By using the Lyapunov–Lasalle's invariance principle [21], E_{hdc} is globally asymptotically stable if (3.10) holds. □

Theorems 3.5–3.7 present sufficient criteria for the existence and stability for E_{hdc}, which implies that the herbage, domestic herbivore and carnivore can coexist if the death rate of domestic herbivore d_1 satisfies the theorem condition.

When (2.2) has two wild-herbivore-free equilibria $E_{\text{hdc}} = (H_3^*, D_3^*, 0, C_3^*)$ and $E'_{\text{hdc}} = (H_3^{'*}, D_3^{'*}, 0, C_3^{'*})$; since those two equilibria have similar expressions, the proof is very similar and the details are omitted.

From (3.3), for the domestic herbivore-free equilibrium $E_{\text{hwc}} = (H_4^*, 0, W_4^*, C_4^*)$, we have

$$
\begin{cases}
W_4^* = \dfrac{d_3}{c_2 m_2 b_2}, \quad H_4^* = \dfrac{(d_2 + m_2 b_2 C_4^*)(1+\beta_2 C_4^*)}{e_2 a_2}, \\
(1+\beta_2 C_4^*)(-m_2 b_2 \beta_2 C_4^{*2} - (d_2\beta_2 + m_2 b_2) C_4^* + (e_2 a_2 K - d_2)) \\
\qquad = \dfrac{e_2 a_2^2 d_3 K}{r c_2 m_2 b_2} =: A'.
\end{cases}
$$

The Jacobian matrix at E_{hwc} is $J(E_{\text{hwc}})$=

$$
\begin{pmatrix}
-\dfrac{rH_4^*}{K} & -\dfrac{a_1 H_4^*}{1+\beta_1 C_4^*} & -\dfrac{a_2 H_4^*}{1+\beta_2 C_4^*} & \dfrac{\beta_2 a_2 W_4^* H_4^*}{(1+\beta_2 C_4^*)^2} \\
0 & \dfrac{e_1 a_1 H_4^*}{1+\beta_1 C_4^*} - m_1 b_1 C_4^* - d_1 & 0 & 0 \\
\dfrac{e_2 a_2 W_4^*}{1+\beta_2 W_4^*} & 0 & 0 & -\dfrac{e_2 a_2 \beta_2 H_4^* W_4^*}{(1+\beta_2 C_4^*)^2} - m_2 b_2 W_4^* \\
0 & c_1 m_1 b_1 C_4^* & c_2 m_2 b_2 C_4^* & 0
\end{pmatrix}.
$$

Let $g(C) = (1+\beta_2 C)(-m_2 b_2 \beta_2 C^2 - (d_2\beta_2 + m_2 b_2)C + (e_2 a_2 K - d_2))$, $\gamma' = (\beta_2 e_2 a_2 K - m_2 b_2)/2\beta_2$. If $\beta_2 e_2 a_2 K - 2\beta_2 d_2 - m_2 b_2 > 0$, then $g'(0) > 0$ and

$g'(C) = 0$ has a positive root $\hat{C}'$. Similar to the proof of Theorems 3.5–3.7, the following theorem can be derived.

Theorem 3.8.

(i) *If* $d_2 < \gamma'$ *and* $g(\hat{C}') < A'$, *or* $d_2 > \max\{\gamma', e_2a_2K - A'\}$, *then* E_{hwc} *does not exist*;

(ii) *if* $d_2 < \gamma'$ *and* $g(0) < A' < g(\hat{C}')$, *then* (2.2) *has two domestic herbivore-free equilibria* E_{hwc} *and* E'_{hwc}, *in particular, if* $g(\hat{C}') = A'$, *then* $E_{\mathrm{hwc}} = E'_{\mathrm{hwc}}$;

(iii) *if* $\gamma' < d_2 < e_2a_2K - A'$ *or* $d_2 < \min\{\gamma', e_2a_2K - A'\}$, *then the domestic-herbivore-free equilibrium* E_{hwc} *exists and is unique.*

Theorem 3.9. *If*

$$d_1 > \frac{e_1a_1H_4^*}{1+\beta_1C_4^*} - m_1b_1C_4^* \quad \text{and} \quad b_2 > \frac{e_2a_2\beta_2(K-2H_4^*)}{m_2(1+\beta_2C_4^*)^2}, \tag{3.11}$$

then E_{hwc} *is locally asymptotically stable.*

Theorem 3.10. *If*

$$d_i > e_ia_iH_4^* - \frac{c_ie_im_ib_iC_4^*}{\mu_1\mu_2}\ (i=1,2) \quad \text{and} \quad \frac{\mu_1\mu_2m_2b_2W_4^*}{e_2} < d_3 < \frac{\mu_1\mu_2\rho'}{C_4^*}, \tag{3.12}$$

where

$$\rho' = rH_4^* - \frac{d_2W_4^*}{e_2} - \frac{r}{4K}\left(H_4^* + K - \frac{a_2KW_4^*}{r(1+Q\beta_2)}\right)^2,$$

and Q, μ_1 *and* μ_2 *are defined in Lemma* 3.1, *then* E_{hwc} *is globally asymptotically stable.*

Theorems 3.8–3.10 characterize the existence and stability of E_{hwc}, which implies that the herbage, the wild herbivore and large carnivore can coexist if the death rate of wild herbivore d_2 satisfies some suitable conditions.

For the interior equilibrium $E_{\mathrm{hdwc}} = (H_5^*, D_5^*, W_5^*, C_5^*)$, from (3.4), H_5^*, D_5^*, W_5^* and C_5^* are given by

$$\begin{cases} H_5^* = \dfrac{(1+\beta_1C_5^*)(d_1+m_1b_1C_5^*)}{e_1a_1} = \dfrac{(1+\beta_2C_5^*)(d_2+m_2b_2C_5^*)}{e_2a_2}, \\[2ex] D_5^* = \dfrac{d_3 - c_2m_2b_2W_5^*}{c_1m_1b_1}, \\[2ex] W_5^* = \dfrac{\begin{array}{c}(1+\beta_2C_5^*)(c_1m_1b_1r(1+\beta_1C_5^*)(Ke_1a_1 - (1+\beta_1C_5^*) \\ \times (d_1+m_1b_1C_5^*)) - Ke_1a_1^2d_3)\end{array}}{Ke_1a_1\big(a_2c_1m_1b_1(1+\beta_1C_5^*) - a_1c_2m_2b_2(1+\beta_2C_5^*)\big)}. \end{cases} \tag{3.13}$$

Let

$$\begin{aligned} h(C) &= (e_2a_2m_1b_1\beta_1 - e_1a_1m_2b_2\beta_2)C^2 + (e_2a_2(d_1\beta_1 + m_1b_1) \\ &\quad - e_1a_1(d_2\beta_2 + m_2b_2))C + e_2a_2d_1 - e_1a_1d_2, \\ \Lambda &= (e_2a_2(d_1\beta_1 + m_1b_1) - e_1a_1(d_2\beta_2 + m_2b_2))^2 - 4(e_2a_2m_1b_1\beta_1 - e_1a_1m_2b_2\beta_2) \\ &\quad \times (e_2a_2d_1 - e_1a_1d_2), \\ w(C) &= \frac{\begin{array}{c}(1+\beta_2C)(c_1m_1b_1r(1+\beta_1C)(Ke_1a_1 - (1+\beta_1C) \\ \times (d_1 + m_1b_1C)) - Ke_1a_1^2d_3)\end{array}}{Ke_1a_1(a_2c_1m_1b_1(1+\beta_1C) - a_1c_2m_2b_2(1+\beta_2C))}, \end{aligned}$$

solving the first and third equations of (3.13) leads to $h(C_5^*) = 0$ and $w(C_5^*) = W_5^*$.

Lemma 3.11. *For $h(C) = 0$, the following claims hold.*

(i) *If*

$$(e_2a_2d_1 - e_1a_1d_2)(e_2a_2m_1b_1\beta_1 - e_1a_1m_2b_2\beta_2) < 0,$$

then $h(C) = 0$ has a unique positive root C_0;

(ii) *if*

$$(e_2a_2d_1 - e_1a_1d_2)(e_2a_2m_1b_1\beta_1 - e_1a_1m_2b_2\beta_2) > 0, \quad \Lambda \geq 0,$$
$$(e_2a_2(d_1\beta_1 + m_1b_1) - e_1a_1(d_2\beta_2 + m_2b_2))(e_2a_2m_1b_1\beta_1 - e_1a_1m_2b_2\beta_2) < 0,$$

then $h(C) = 0$ has two positive roots C_1 and C_2.

Lemma 3.11 gives the conditions for the existence of C_5^*. Then the following theorem shows the existence of the interior equilibrium.

Theorem 3.12. (i) *If* (i) in Lemma 3.11 holds and $0 < w(C_0) < d_3/c_2m_2b_2$, then (2.2) has a unique interior equilibrium;

(ii) if (ii) in Lemma 3.11 holds and $0 < w(C_i) < d_3/c_2m_2b_2 (i = 1, 2)$, then (2.2) has two interior equilibria.

Let $E_{\text{hdwc}} = (H_5^*, D_5^*, W_5^*, C_5^*)$ be an interior equilibrium of (2.2).

Theorem 3.13. *If*

$$\sigma_2, \sigma_3 > 0 \quad \textit{and} \quad N_{11}\sigma_1\sigma_2 > \sigma_2^2 + N_{11}^2\sigma_3, \tag{3.14}$$

where $\sigma_i (i = 1, 2, 3)$ and N_{11} are defined in (3.15) *and* (3.16), *then E_{hdwc} is locally asymptotically stable.*

Proof. The Jacobian matrix at E_{hdwc} reads

$$J(E_{\text{hdwc}}) = \begin{pmatrix} -N_{11} & -N_{12} & -N_{13} & N_{14} \\ N_{21} & 0 & 0 & -N_{24} \\ N_{31} & 0 & 0 & -N_{34} \\ 0 & N_{42} & N_{43} & 0 \end{pmatrix},$$

where

$$\begin{aligned} &N_{11} = \frac{rH_5^*}{K}, \quad N_{12} = \frac{a_1 H_5^*}{1+\beta_1 C_5^*}, \quad N_{13} = \frac{a_2 H_5^*}{1+\beta_2 C_5^*}, \\ &N_{14} = \frac{\beta_1 a_1 D_5^* H_5^*}{(1+\beta_1 C_5^*)^2} + \frac{\beta_2 a_2 W_5^* H_5^*}{(1+\beta_2 C_5^*)^2}, \quad N_{21} = \frac{e_1 a_1 D_5^*}{1+\beta_1 C_5^*}, \\ &N_{24} = \frac{e_1 a_1 \beta_1 H_5^* D_5^*}{(1+\beta_1 C_5^*)^2} + m_1 b_1 D_5^*, \quad N_{31} = \frac{e_2 a_2 W_5^*}{1+\beta_2 C_5^*}, \\ &N_{34} = \frac{e_2 a_2 \beta_2 H_5^* W_5^*}{(1+\beta_2 C_5^*)^2} + m_2 b_2 W_5^*, \\ &N_{42} = c_1 m_1 b_1 C_5^*, \quad N_{43} = c_2 m_2 b_2 C_5^*. \end{aligned} \tag{3.15}$$

The characteristic equation of $J(E_{\text{hdwc}})$ is

$$\lambda^4 + N_{11}\lambda^3 + \sigma_1\lambda^2 + \sigma_2\lambda + \sigma_3 = 0,$$

where

$$\begin{aligned} \sigma_1 &= N_{12}N_{21} + N_{13}N_{31} + N_{24}N_{42} + N_{34}N_{43} > 0, \\ \sigma_2 &= N_{11}(N_{24}N_{42} + N_{34}N_{43}) - N_{14}(N_{31}N_{43} + N_{21}N_{42}), \\ \sigma_3 &= N_{21}N_{34}(N_{12}N_{43} - N_{13}N_{42}) + N_{24}N_{31}(N_{13}N_{42} - N_{12}N_{43}). \end{aligned} \tag{3.16}$$

By Routh–Hurwitz criterion and (3.14), E_{hdwc} is locally asymptotically stable. □

Theorem 3.14. *If*

$$d_i > \mu_1 a_i H_5^* - \frac{c_i m_i b_i C_5^*}{\mu_2} \ (i = 1, 2), \quad \mu_2(m_1 b_1 D_5^* + m_2 b_2 W_5^*) < d_3 < \frac{\zeta\mu_2}{C_5^*}, \tag{3.17}$$

where $\zeta = \mu_1 r H_5^* - \mu_1 r(H_5^* + K - P)^2/4K - d_1 D_5^* - d_2 W_5^*$, *then* E_{hdwc} *is globally asymptotically stable.*

Proof. Let

$$P = \frac{K}{\mu_1 r}\left(\frac{e_1 a_1 D_5^*}{1+\beta_1 Q} + \frac{e_2 a_2 W_5^*}{1+\beta_2 Q}\right),$$

where Q is defined in Lemma 3.1. Consider the Lyapunov function defined by

$$\begin{aligned} V_5 &= \mu_1\left(H - H_5^* - H_5^* \ln\frac{H}{H_5^*}\right) + \left(D - D_5^* - D_5^* \ln\frac{D}{D_5^*}\right) \\ &\quad + \left(W - W_5^* - W_5^* \ln\frac{W}{W_5^*}\right) + \frac{1}{\mu_2}\left(C - C_5^* - C_5^* \ln\frac{C}{C_5^*}\right). \end{aligned}$$

Differentiating V along solutions of (2.2) with respect to t leads to

$$\begin{aligned} \frac{dV_5}{dt} &= \mu_1(H - H_5^*)\left(r\left(1 - \frac{H}{K}\right) - \frac{a_1 D}{1+\beta_1 C} - \frac{a_2 W}{1+\beta_2 C}\right) + (D - D_5^*) \\ &\quad \times \left(\frac{e_1 a_1 H}{1+\beta_1 C} - m_1 b_1 C - d_1\right) + (W - W_5^*)\left(\frac{e_2 a_2 H}{1+\beta_2 C} - m_2 b_2 C - d_2\right) \\ &\quad + \frac{(C - C_5^*)}{\mu_2}(c_1 m_1 b_1 D + c_2 m_2 b_2 W - d_3) \\ &\le \mu_1 r H\left(1 - \frac{H}{K}\right) - \mu_1 H_5^*\left(r\left(1 - \frac{H}{K}\right) - \frac{a_1 D}{1+\beta_1 C} - \frac{a_2 W}{1+\beta_2 C}\right) \\ &\quad - d_1(D - D_5^*) - D_5^*\left(\frac{e_1 a_1 H}{1+\beta_1 C} - m_1 b_1 C\right) - d_2(W - W_5^*) \\ &\quad - W_5^*\left(\frac{e_2 a_2 H}{1+\beta_2 C} - m_2 b_2 C\right) - \frac{d_3}{\mu_2}(C - C_5^*) - \frac{C_5^*}{\mu_2}(c_1 m_1 b_1 D + c_2 m_2 b_2 W) \\ &\le -\frac{\mu_1 r}{K}\left(H - \frac{H_5^* + K - P}{2}\right)^2 + \frac{\mu_1 r(H_5^* + K - P)^2}{4K} \\ &\quad + \left(\mu_1 a_1 H_5^* - d_1 - \frac{c_1 m_1 b_1 C_5^*}{\mu_2}\right) D + \left(\mu_1 a_2 H_5^* - d_2 - \frac{c_2 m_2 b_2 C_5^*}{\mu_2}\right) W \\ &\quad + \left(m_1 b_1 D_5^* + m_2 b_2 W_5^* - \frac{d_3}{\mu_2}\right) C - \mu_1 r H_5^* + d_1 D_5^* + d_2 W_5^* + \frac{d_3 C_5^*}{\mu_2}. \end{aligned}$$

It is observed that if (3.17) holds, then $dV_5/dt \le 0$, and $dV_5/dt = 0$ if and only if $(H, D, W, C) \equiv (H_5^*, D_5^*, W_5^*, C_5^*)$. By Lyapunov–Lasalle's invariance principle [21], E_{hdwc} is globally asymptotically stable if (3.17) holds. □

Theorems 3.12–3.14 explore the existence and stability of the interior equilibrium E_{hdwc}. It reveals that all species (the herbage, the domestic and wild herbivore and large carnivore) can coexist if some sufficient conditions hold.

In order to clarify the relationship between the existence and stability of different equilibria, the sufficient criteria for the existence, uniqueness and stability of the equilibria are summarized in Table 1. It is observed in Table 1 that if $d_1 > e_1 a_1 K$ and $d_2 > e_2 a_2 K$, then E_h is globally asymptotically stable; if $d_1 < e_1 a_1 K$ or $d_2 < e_2 a_2 K$, then E_h loses its stability and E_{hd} or E_{hw} uniquely exists.

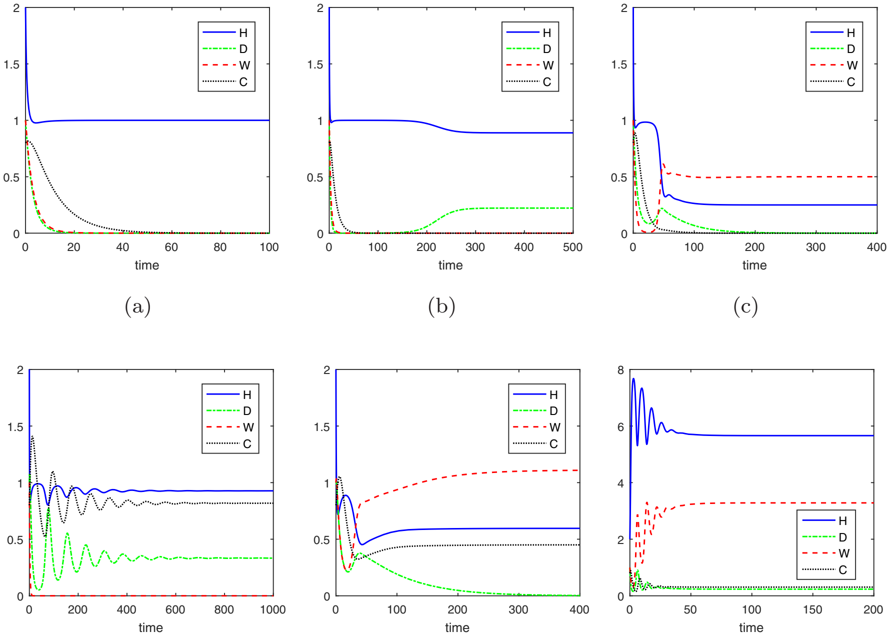
Table 1. Existence, uniqueness and stability of equilibria of (2.2).

Equilibria	Existence and uniqueness	Local stability	Globally stable
E_0	Always	Unstable	Unstable
E_h	Always	$d_1 > e_1a_1K, d_2 > e_2a_2K$	$d_1 > e_1a_1K, d_2 > e_2a_2K$
E_{hd}	$d_1 < e_1a_1K$	$e_1a_1K - A < d_1$ $< e_1a_1 \min\left\{\frac{d_2}{e_2a_2}, K\right\}$	$d_2 > e_2a_2K, d_3 > c_1m_1b_1Q$
E_{hw}	$d_2 < e_2a_2K$	$e_2a_2K - A' < d_2$ $< e_2a_2 \min\left\{\frac{d_1}{e_1a_1}, K\right\}$	$d_1 > e_1a_1K, d_3 > c_2m_2b_2Q$
E_{hdc}	$\gamma < d_1 < e_1a_1K - A$ or $d_1 < \min\{\gamma, e_1a_1K - A\}$	$d_2 > \frac{e_2a_2H_3^*}{1+\beta_2C_3^*} - m_2b_2C_3^*$, $b_1 > \frac{e_1a_1\beta_1(K-2H_3^*)}{m_1(1+\beta_1C_3^*)^2}$	$d_i > e_ia_iH_3^* -$ $\frac{c_ie_im_ib_iC_3^*}{\mu_1\mu_2}$ $(i = 1, 2)$, $\frac{\mu_1\mu_2m_1b_1D_3^*}{e_1} < d_3 < \frac{\mu_1\mu_2\rho}{C_3^*}$
E_{hwc}	$\gamma' < d_2 < e_2a_2K - A'$, $d_2 < \min\{\gamma', e_2a_2K - A'\}$	$d_1 > \frac{e_1a_1H_4^*}{1+\beta_1C_4^*} - m_1b_1C_4^*$, $b_2 > \frac{e_2a_2\beta_2(K-2H_4^*)}{m_2(1+\beta_2C_4^*)^2}$	$d_i > e_ia_iH_4^* -$ $\frac{c_ie_im_ib_iC_4^*}{\mu_1\mu_2}$ $(i = 1, 2)$, $\frac{\mu_1\mu_2m_2b_2W_4^*}{e_2} < d_3 < \frac{\mu_1\mu_2\rho'}{C_4^*}$
E_{hdwc}	$(e_2a_2m_1b_1\beta_1 - e_1a_1m_2b_2\beta_2)\times$ $(e_2a_2d_1 - e_1a_1d_2) < 0$, $0 < w(C_0) < d_3/c_2m_2b_2$,	$\sigma_2, \sigma_3 > 0$, $N_{11}\sigma_1\sigma_2 > \sigma_2^2 + N_{11}^2\sigma_3$	$d_i > \mu_1a_iH_5^* -$ $\frac{c_im_ib_iC_5^*}{\mu_2}(i = 1, 2)$, $\mu_2(m_1b_1D_5^* + m_2b_2W_5^*)$ $< d_3 < \frac{\zeta\mu_2}{C_5^*}$

4. Numerical Analyses

The theorems established in the previous section reveal the complex dynamics of the system (2.2). In this section, some numerical simulations are carried out to well illustrate and supplement the previous theoretical analyses. More biologically interesting findings will be presented below.

Theorem 3.2 indicates that all four species will never be simultaneously extinct because E_0 is unstable. When d_1 and d_2 are large enough, E_h is globally asymptotically stable, and the herbage tends to its carrying capacity when there are no species D, W and C (see Fig. 3(a)). By Theorem 3.3, when d_2 and d_3 are large enough and d_1 is within an appropriate range, E_{hd} is globally asymptotically stable. This means that species W and C eventually become extinct, and the other two species coexist stably (see Fig. 3(b)). Figure 3(c) verifies the existence and stability of E_{hw} (Theorem 3.4) and shows that species D and C eventually tend to become extinct and the other two species coexist stably. Figure 3(d) verifies the conditions of Theorems 3.5–3.7, here E_{hdc} is an attractor, which implies species H, D and C coexist at this equilibrium, only the species W becomes extinct. As shown in Fig. 3(e), E_{hwc} is an attractor, where species H, W and C coexist at this equilibrium, and only one species D becomes extinct. Theorems 3.12–3.14 provide



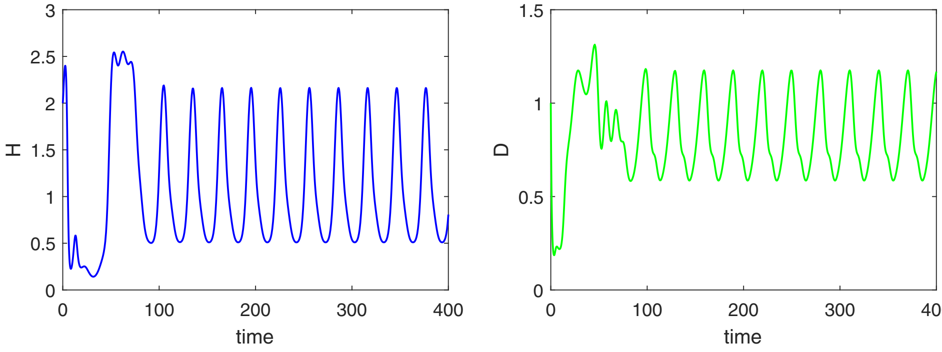
(a) (b) (c)

(d) (e) (f)

Fig. 3. Possible attractors of system (2.2). (a) E_h, (b) $E_{\rm hd}$, (c) $E_{\rm hw}$, (d) $E_{\rm hdc}$, (e) $E_{\rm hwc}$ and (f) $E_{\rm hdwc}$. Parameter values are listed in Table 2 and all the solutions start at (2, 1, 1, 0.8).

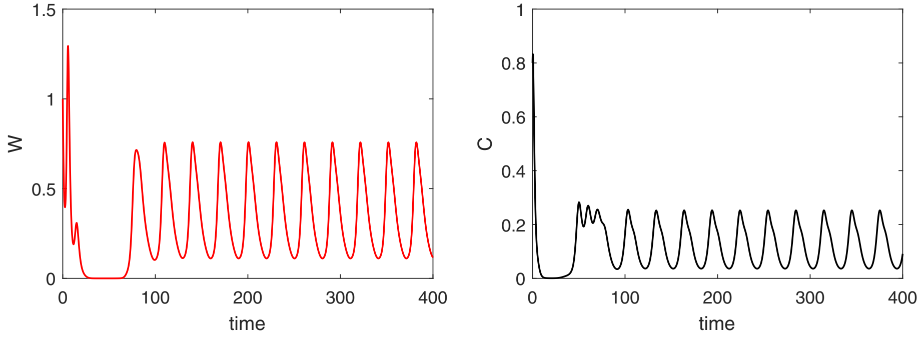
sufficient criteria for the global coexistence of four species, here interior equilibrium $E_{\rm hdwc}$ is an attractor, four species coexist together at $E_{\rm hdwc}$ (see Fig. 3(f)).

In addition to the above equilibrium dynamics, the existence of periodic solutions to (2.2) can be seen in Fig. 4, while the four species coexist cyclically.



(a) (b)

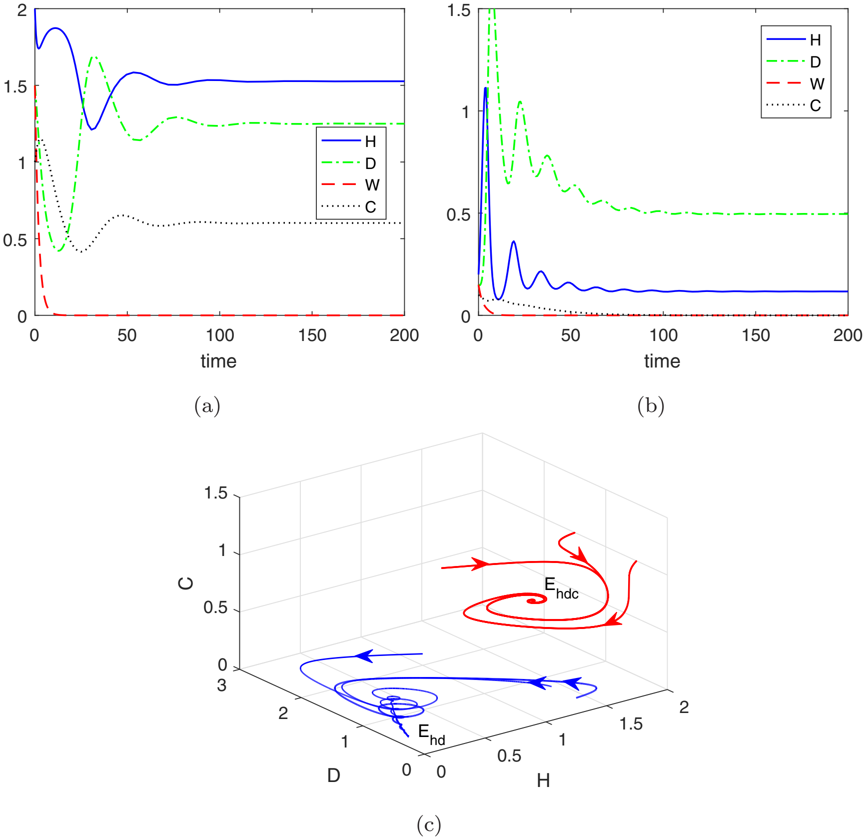
Fig. 4. Cyclic coexistence of H, D, W and C. Here, $K = 3, r = 1, a_1 = 0.9, e_1 = 0.7, b_1 = 1, c_1 = 0.9, d_1 = 0.1, d_3 = 0.8, e_2 = 0.9, a_2 = 2, d_2 = 0.8, c_2 = 0.8, b_2 = 0.2, \beta_1 = 16, \beta_2 = 10, m_1 = 1, m_2 = 1$.



(c)

(d)

Fig. 4. (*Continued*)

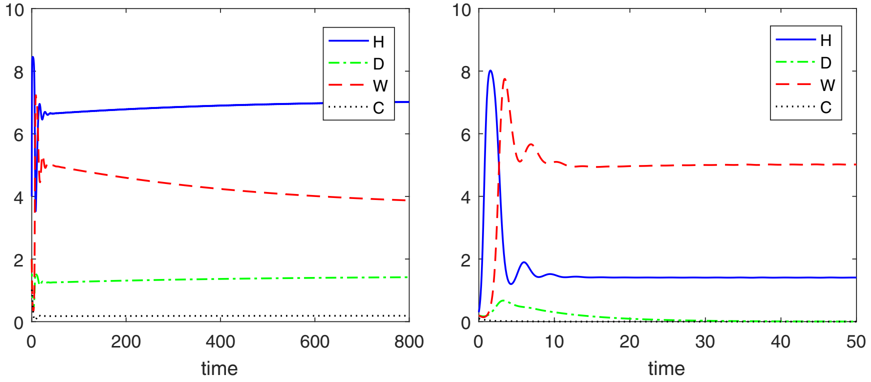


(a)

(b)

(c)

Fig. 5. Bistable scenarios of system (2.2). (a) and (b) Different solutions are attracted by $E_{\rm hdc}$ and $E_{\rm hd}$, respectively. (c) Phase space diagram for the system excluding species W, the solution trajectories originating from six different initial conditions converge to $E_{\rm hdc}$ or $E_{\rm hd}$. Here, $K = 2$, $r = 1, a_1 = 1.9, e_1 = 0.9, b_1 = 0.1, c_1 = 0.8, d_1 = 0.2, d_3 = 0.1, e_2 = 0.6, a_2 = 0.4, d_2 = 0.4$, $c_2 = 0.6, b_2 = 0.1, \beta_1 = 15, \beta_2 = 20, m_1 = 1, m_2 = 1$.



(a) (b)

Fig. 6. Bistable scenario of system (2.2). Different solutions are attracted by E_{hdwc} and E_{hw}, respectively. Here, $K = 8.6, r = 4.8, a_1 = 0.5, e_1 = 0.4, b_1 = 0.5, c_1 = 0.8, d_1 = 0.4, d_3 = 0.8, \beta_1 = 9.8, \beta_2 = 20.7, e_2 = 0.8, a_2 = 0.8, d_2 = 0.9, c_2 = 0.6, b_2 = 0.1, m_1 = 1, m_2 = 1$.

Bistability means that, for a fixed set of parameter values, multiple attractors coexist in a given system. By further analyzing the conditions for the existence and stability of equilibria, we find that (2.2) may admit different kinds of bistable scenarios. For example, Figs. 5(a) and 5(b) show a bistability between E_{hdc} and E_{hd}. In Fig. 5(c), we draw three-dimensional phase portraits of the model (2.2) excluding species W, it can also be seen that the system has two different attractors corresponding to different initial values. Similarly, Fig. 6 shows the bistable phenomena between E_{hdwc} and E_{hw}, where E_{hdwc} and E_{hw} are both stable attractors. In short, with different values of system parameters and initial population size, system (2.2) shows stable and oscillating coexistence of the populations and bistable phenomena.

5. Fear Effect

The anti-predator mechanism plays some important roles in predation. The effect of fear is twofold: one is to interfere with the foraging of domestic and wild herbivores, while the other is to prevent predation of the herbivore by the large carnivore, these are represented as the cost and benefit of the fear effect, respectively. In this section, we expound the twofold of fear effect exerted by the large carnivore in a grassland ecosystem through numerical simulations. In the formulation of the model (2.2), the cost of fear effect is denoted by β_1 and β_2, and the benefit of fear effect is represented by m_1 and m_2.

In the grassland ecosystem, the level of defense of herbivores may change due to altered predation risk. β_1, β_2, m_1 and m_2 also characterize the anti-predator response level, thus those parameters may strongly influence the dynamical behaviors of our model.

Table 2. Parameter values for attractors of (2.2) presented in Fig. 3.

Figures	Parameters	Attractors
Fig. 3(a)	$K = 1, r = 1, a_1 = 0.5, e_1 = 0.5, b_1 = 0.1, c_1 = 0.8,$ $d_1 = 0.3, d_3 = 0.1, \beta_1 = 10, \beta_2 = 15, e_2 = 0.6,$ $a_2 = 0.4, d_2 = 0.25, c_2 = 0.6, b_2 = 0.1, m_1 = 1, m_2 = 1$	E_h is an attractor, where D, W, C become extinct.
Fig. 3(b)	$K = 1, r = 1, a_1 = 0.5, e_1 = 0.9, b_1 = 0.1, c_1 = 0.8,$ $d_1 = 0.4, d_3 = 0.1, \beta_1 = 10, \beta_2 = 15, e_2 = 0.6,$ $a_2 = 0.4, d_2 = 0.25, c_2 = 0.6, b_2 = 0.1, m_1 = 1, m_2 = 1$	E_{hd} is an attractor, where W, C become extinct.
Fig. 3(c)	$K = 1, r = 1, a_1 = 0.5, e_1 = 0.6, b_1 = 0.1, c_1 = 0.9,$ $d_1 = 0.1, d_3 = 0.1, \beta_1 = 10, \beta_2 = 15, e_2 = 0.8,$ $a_2 = 1.5, d_2 = 0.3, c_2 = 0.9, b_2 = 0.1, m_1 = 1, m_2 = 1$	E_{hw} is an attractor, where D, C become extinct.
Fig. 3(d)	$K = 1, r = 1, a_1 = 2, e_1 = 0.9, b_1 = 0.1, c_1 = 0.9,$ $d_1 = 0.1, d_3 = 0.03, \beta_1 = 10, \beta_2 = 15, e_2 = 0.6,$ $a_2 = 0.4, d_2 = 0.4, c_2 = 0.6, b_2 = 0.1, m_1 = 1, m_2 = 1$	E_{hdc} is an attractor, where H, D, C coexist at equilibrium.
Fig. 3(e)	$K = 1, r = 1, a_1 = 2, e_1 = 0.6, b_1 = 0.1, c_1 = 0.9,$ $d_1 = 0.1, d_3 = 0.1, \beta_1 = 10, \beta_2 = 10, e_2 = 0.9,$ $a_2 = 2, d_2 = 0.15, c_2 = 0.9, b_2 = 0.1, m_1 = 1, m_2 = 1$	E_{hwc} is an attractor, where H, W, C coexist at equilibrium.
Fig. 3(f)	$K = 8, r = 2, a_1 = 0.9, e_1 = 0.7, b_1 = 1.3, c_1 = 0.9,$ $d_1 = 0.1, d_3 = 0.8, \beta_1 = 20, \beta_2 = 16, e_2 = 0.9,$ $a_2 = 1, d_2 = 0.8, c_2 = 0.8, b_2 = 0.2, m_1 = 1, m_2 = 1$	The interior equilibrium E_{hdwc} is an attractor, the solution of (2.2) tends to a steady state.

Numerical simulations are carried out to explore the dynamic behavior by varying the four fear parameters. These simulations are implemented by the ode45 and ode23 functions in MATLAB. In the following numerical simulations, the initial values are set to be $H(0) = 2$, $D(0) = 1$, $W(0) = 1$, $C(0) = 0.8$, and parameter values are selected as

$$\begin{gathered} a_1 = 0.9, \quad a_2 = 1.3, \quad K = 8.6, \quad r = 1, \quad e_1 = 0.7, \quad b_1 = 1, \quad b_2 = 0.2, \\ c_1 = 0.9, \quad c_2 = 0.8, \quad d_1 = 0.1, \quad d_2 = 0.8, \quad d_3 = 0.8, \quad e_2 = 0.9. \end{gathered} \tag{5.1}$$

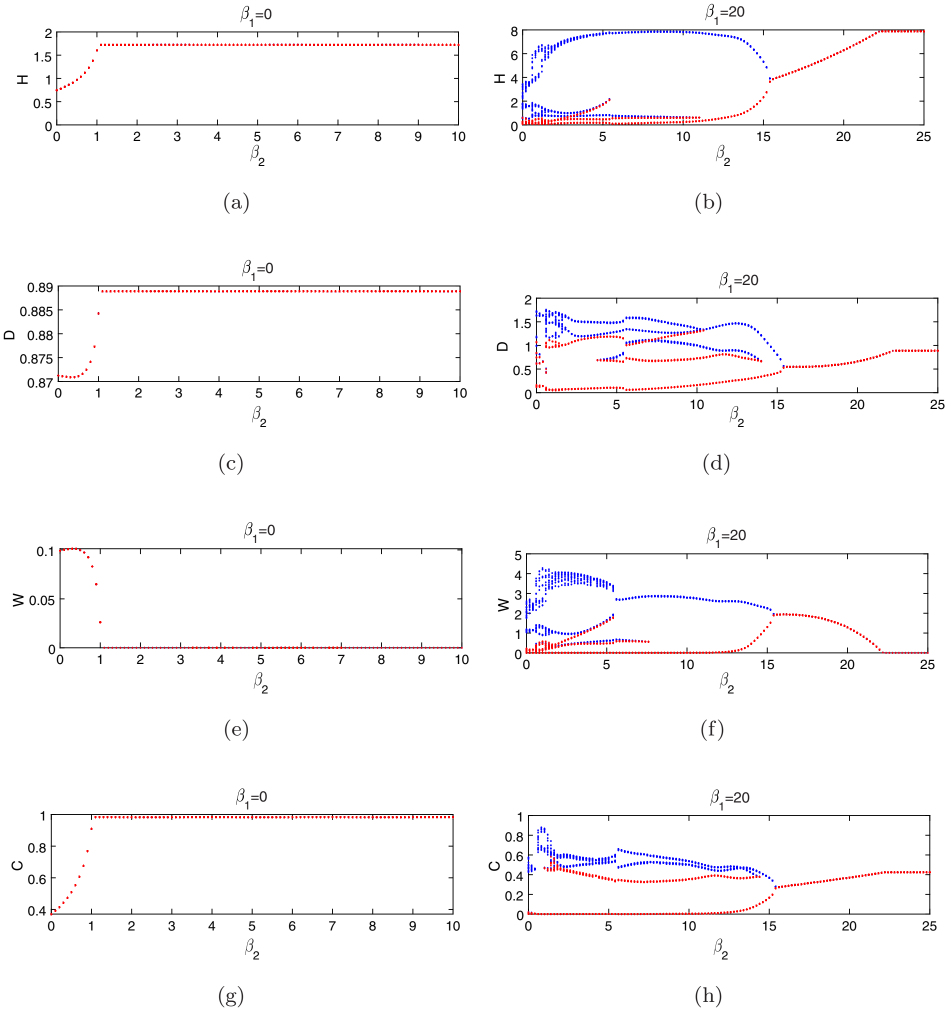
5.1. *Cost of fear effect on herbivore (β_1 and β_2)*

Now we investigate the impact of the cost of fear effect, here the benefit of fear effect on herbivore is not considered (i.e. $m_1 = m_2 = 1$). We consider two cases: (i) the domestic herbivore has no anti-predator response (i.e. $\beta_1 = 0$) and (ii) the domestic herbivore has the anti-predator response (i.e. $\beta_1 = 20$). In order to do this, we draw the bifurcation diagrams with β_2 being the bifurcation parameter (see Fig. 7).

First, we consider the case (i). From Figs. 7(a), 7(c), 7(e) and 7(g), it is observed that, when the value of the fear coefficient β_2 is small, the solution of the system (2.2) converges to an interior equilibrium. As the value of β_2 increases further, the densities of species H, D and C increase, the density of wild herbivore decreases, and eventually species W becomes extinct and the remaining three species coexist. In conclusion, when species D has no anti-predator response, the solutions of system

(2.2) shift from the interior equilibrium to the wild herbivore-free equilibrium as the value of β_2 increases.

Next, we consider the case (ii). We investigate the bifurcation dynamics of the system by varying the fear coefficient β_2. Figures 7(b), 7(d), 7(f) and 7(h) show that when the fear coefficient β_2 is small, system (2.2) shows chaotic behavior. As the value of β_2 increases, the system experiences a bifurcation path of chaotic → periodic → equilibrium. When β_2 is mediate large, the solution of the system converges to a coexistence equilibrium, where the four species coexist at some steady states. When β_2 continues to increase, the densities of species H, D and C increase



(a) (b)

(c) (d)

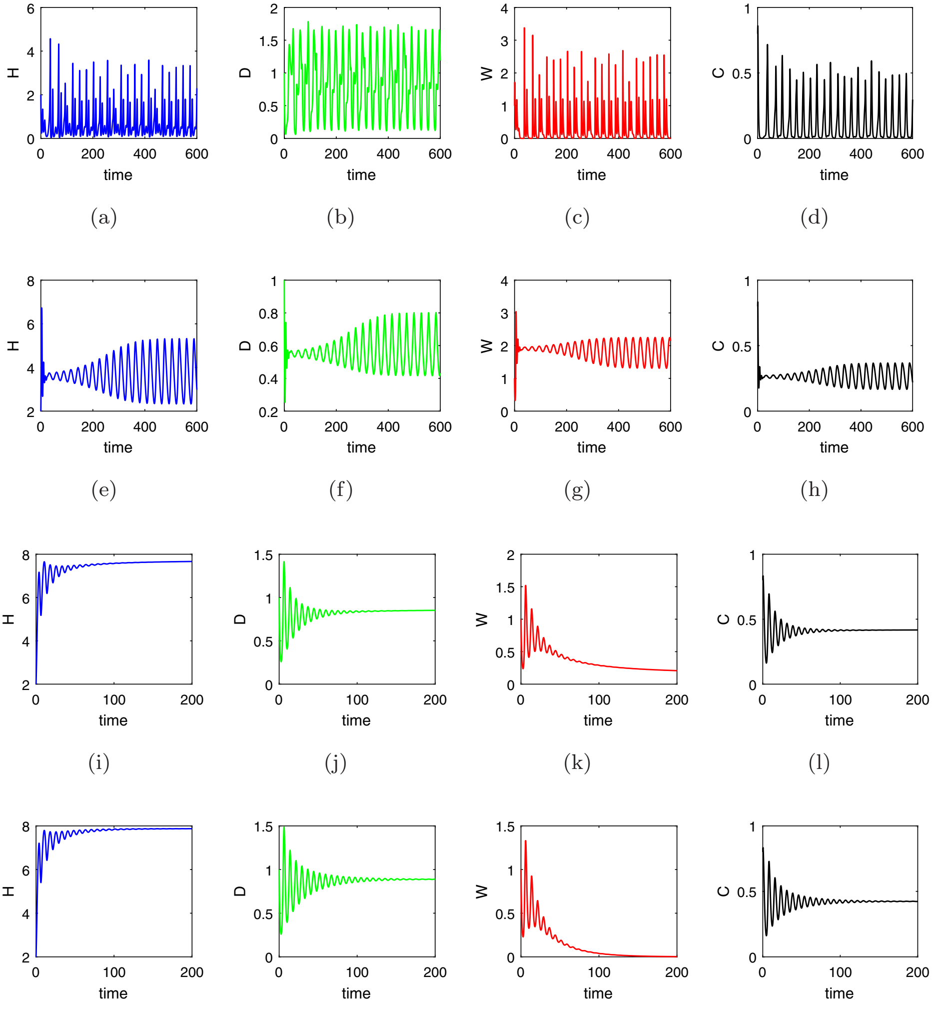
(e) (f)

(g) (h)

Fig. 7. Bifurcation diagrams of (2.2) with β_2 being the bifurcation parameter for different β_1. Here $m_1 = m_2 = 1$, other parameters are defined in (5.1).

and the three species eventually coexist. Note that the density of the wild herbivore decreases and eventually becomes extinct.

For case (ii), in order to better visualize the solutions of system (2.2), we draw the time-series solutions of the system by choosing four different values of β_2 (see Fig. 8), which demonstrate different dynamical behaviors. Figures 8(a)–8(d) correspond to the case that wild herbivore has no anti-predator response (i.e. β_2=0), and shows the chaotic oscillations. Figures 8(e)–8(h) exhibit limit cycle oscillations



(a) (b) (c) (d)

(e) (f) (g) (h)

(i) (j) (k) (l)

(m) (n) (o) (p)

Fig. 8. Time-series solutions of system (2.2) for different values of β_2. Here $\beta_1 = 20$, $m_1 = m_2 = 1$ and other parameter values are defined in (5.1). (a)–(d) show the chaotic behavior for $\beta_2 = 0$, (e)–(h) show the limit cycle oscillation for $\beta_2 = 15$, (i)–(l) and (m)–(p) show the equilibrium for $\beta_2 = 22$ and $\beta_2 = 23$, respectively.

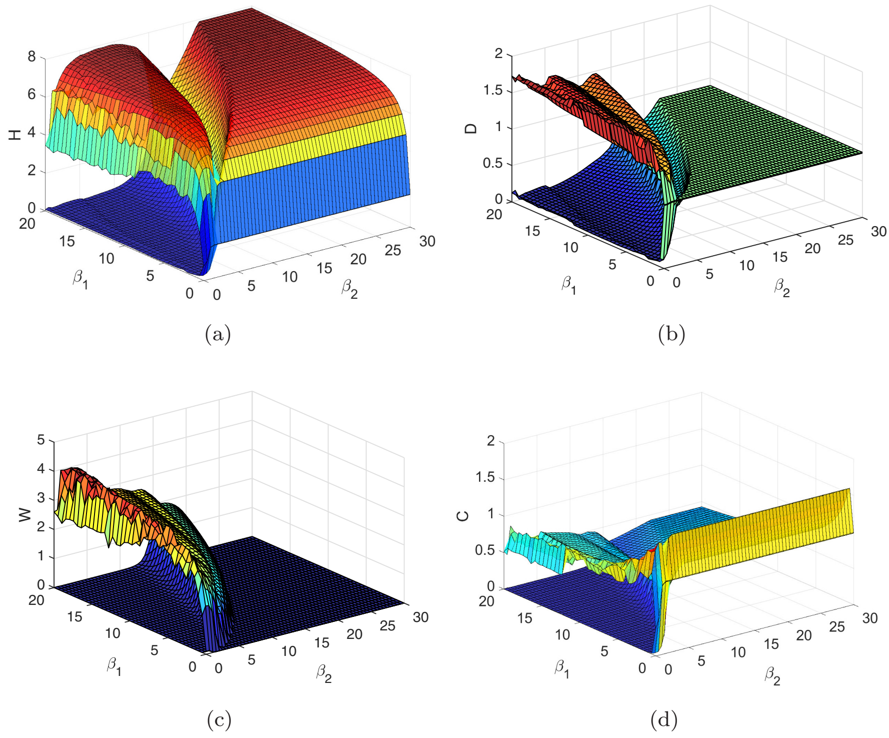


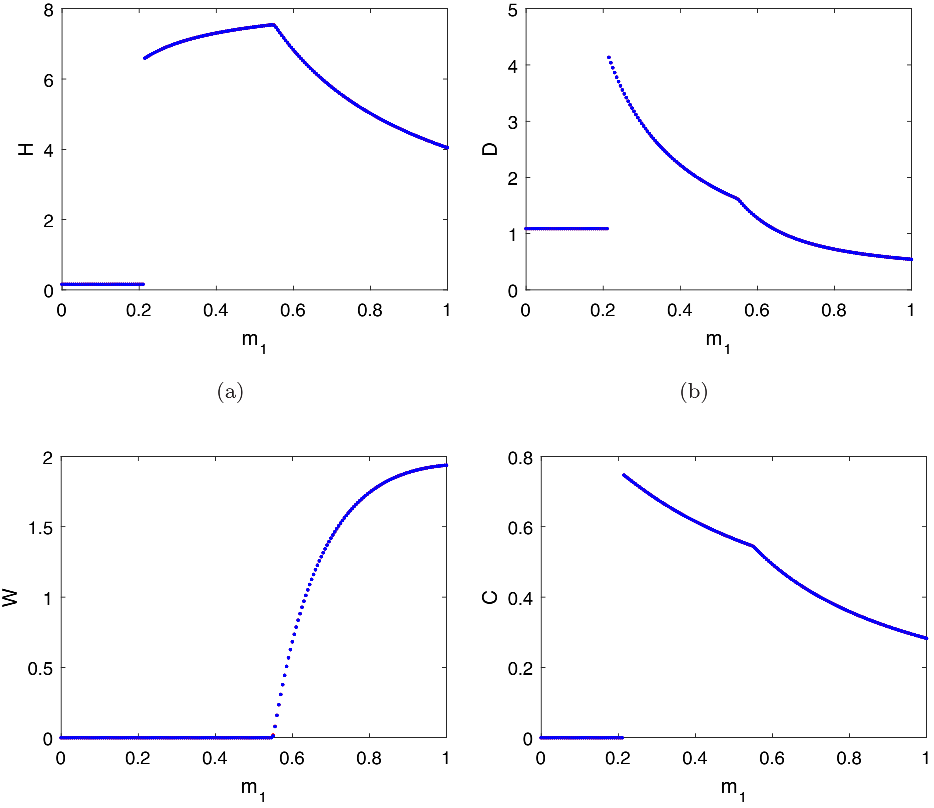
Fig. 9. Bifurcation surfaces of (2.2) with β_1 and β_2 being the bifurcation parameters. Here $m_1 = m_2 = 1$, other parameters are defined in (5.1).

at $\beta_2 = 15$, while four species H, D, W and C cyclically coexist. From Figs. 8(i)–8(l), the system has a stable interior equilibrium when $\beta_2 = 22$. Figures 8(m)–8(p) depict the solution of system (2.2) is transferred from an interior equilibrium to a wild herbivore-free equilibrium (i.e. $\beta_2 = 23$).

To better investigate the joint effect of the two fear factors β_1 and β_2, the bifurcation surfaces of system (2.2) for varying β_1 and β_2 are given. From Fig. 9, one observes that, for small values of β_2 and large values of β_1, the system shows chaotic dynamics. Then as the values of β_2 increase, we observe that the system regains stability from periodic oscillations. Given the above analysis, it is observed that the large fear effect level on wild herbivore can transform system (2.2) from chaotic dynamics to stable dynamics. It also indicates that the presence of fear effect does contribute to the recovery of grazing and the increase of the domestic herbivore's density, but excessive fear levels are sometimes detrimental to the diversity of the system because they can cause wild herbivore to become extinct.

5.2. *Benefit of fear effect on herbivore* (m_1 *and* m_2)

In addition to the cost in the foraging of herbivore, it is also interesting to examine the role that the benefit of the fear effect plays in dynamics evolution of the model.



(a)

(b)

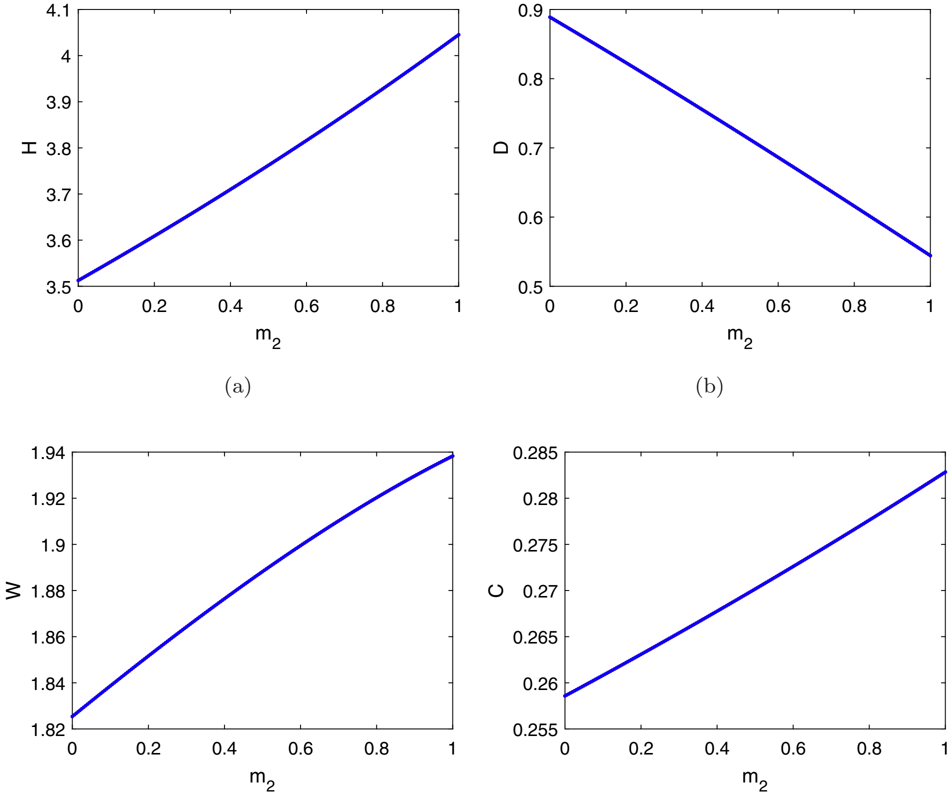
(c)

(d)

Fig. 10. Bifurcation diagrams of (2.2) with m_1 being the bifurcation parameter. Here, $\beta_1 = 20$, $\beta_2 = 16$, $m_2 = 1$ and other parameters are defined in (5.1).

In this subsection, we explore the effect of different levels of the parameters m_1 and m_2, which represent the decrease in predation efficiency of domestic and wild herbivores by the large carnivore due to the fear effect.

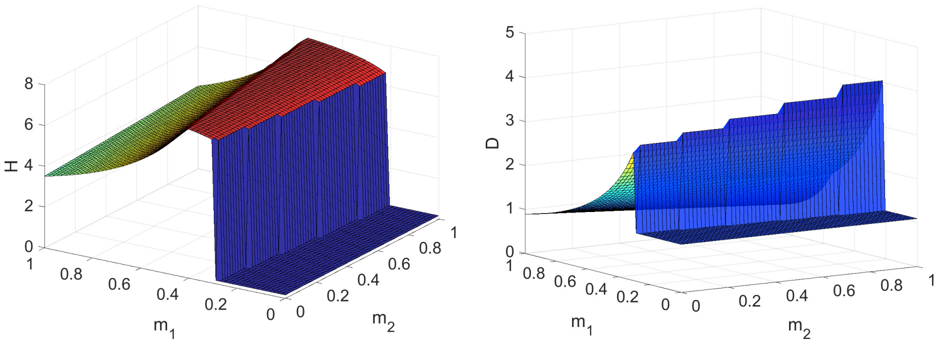
First, the bifurcation diagrams with m_1 being the bifurcation parameter are helpful to our observation (see Fig. 10). From Fig. 10, one can see that if the species W has no benefit of fear effect (i.e. $m_2 = 1$), when $m_1 \in (0, 0.21]$, (2.2) converges to the boundary equilibrium E_{hd}; when $m_1 \in (0.21, 0.55)$, as m_1 increases, the density of H increases and the densities of D and C decrease, W is still extinct; when $m_1 \in [0.55, 1]$, with the increase of m_1, the density of W begins to increase and the densities of other three species decrease. Therefore, in mathematics, $m_1 = 0.21$ and $m_1 = 0.55$ are the thresholds where the system experiences a bifurcation path from the boundary equilibrium E_{hd} to the boundary equilibrium E_{hdc} and then to the internal equilibrium as m_1 increases; in ecology, it is revealed that the predation of C on D is much more difficult when the benefit of the fear effect is larger (i.e. m_1 is smaller), which is detrimental to the coexistence of the species in (2.2).



(a) (b)

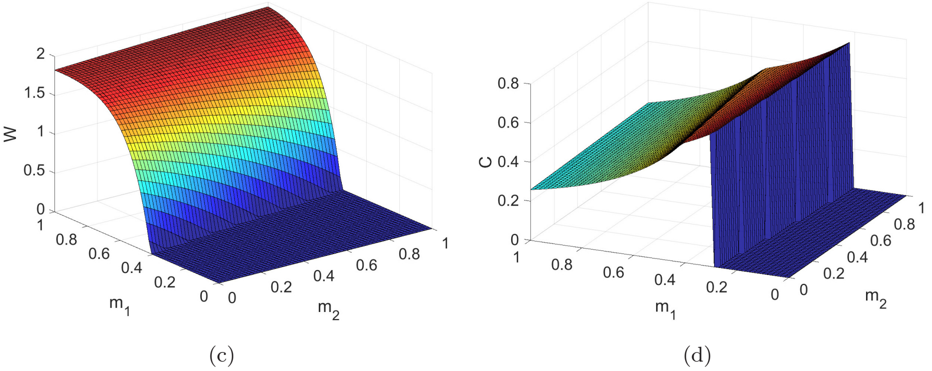
(c) (d)

Fig. 11. Bifurcation diagrams of (2.2) with m_2 being the bifurcation parameter. Here $\beta_1 = 20$, $\beta_2 = 16$, $m_1 = 1$ and other parameters are defined in (5.1).



(a) (b)

Fig. 12. Bifurcation surfaces of (2.2) with m_1 and m_2 being the bifurcation parameters. Here, $\beta_1 = 20$, $\beta_2 = 16$ and other parameters are defined in (5.1).



(c) (d)

Fig. 12. (*Continued*)

We now consider the case that species D has no benefit of fear effect (i.e. $m_1 = 1$). In Fig. 11, the bifurcation diagrams with m_2 being the bifurcation parameter reveals that H, W and C all show a significant positive response as m_2 increases, while D has a significant negative response. In this case, (2.2) always has an interior equilibrium. We also draw the bifurcation surfaces with m_1 and m_2 being bifurcation parameters to explore the joint effect (see Fig. 12). One observes the dynamic evolution of system (2.2) and the density variation of species H, D, W and C. If the fear factor m_1 is small enough, then the species W and C are extinct and the species H and D coexist. In this case, it can be seen that the change of m_2 has no perceptible effect on the system. On the contrary, when the fear factor m_2 is in the appropriate range ($0 < m_2 < 1$) and m_1 is large, the change of m_1 will have a significant impact on the population dynamics of all four species. Given the above analysis, we conclude that the parameters m_1 and m_2 play a significant role in the variation of population density.

6. Conclusion and Discussion

In the grassland ecosystem, the impact of the fear effect is a new and debatable topic. Herbivore will perceive predation risk and adopt the anti-predator strategy in the presence of large carnivore. The anti-predator strategy is an important obstacle factor for the foraging of herbivore while it plays a positive role in reducing the predation risk. This phenomenon, combined with recent studies on the fear effect, prompts us to theoretically explore the mechanisms of how the anti-predator strategy affects the structure and function of the grassland ecosystem. In this study, we develop a four-dimensional model (2.2) to investigate the fear effect. The model describes the interactions among herbage, domestic herbivore, wild herbivore and large carnivore. Both the cost and benefit of the fear effect are explicitly incorporated into the model, and four parameters β_1, β_2, m_1 and m_2 are introduced to characterize the fear effect.

Theoretical and numerical results show that model (2.2) displays rich and complex dynamic behaviors, such as stable coexistence, cyclic phenomenon, bistable scenarios and chaotic dynamics. The numerical study reveals that the fear effect plays an important role in determining the long-term population dynamics in the grassland ecosystem. For example, with the fear factor β_1 being constant, the fear factor β_2 can control the chaotic dynamics. As β_2 increases, species H, D and C show a significant positive response and W shows a negative response, and when β_2 exceeds a certain value, W becomes extinct. It is worth noting that the fear factor does not always transform the ecosystem from a chaotic state to a stable state, such as β_1 in this paper. The benefit of the anti-predator response is also important and we explore this effect by drawing the bifurcation diagrams/surfaces. These findings demonstrate that the fear effect coefficients m_1 and m_2 have an important contribution to the changes in population densities of species H, D, W and C.

Our results provide some beneficial management/control strategies for maintaining biodiversity. Previous studies have focused on the harm of predation on livestock by the large carnivore. But the retaliatory persecution of large carnivore by humans presents a grave threat to the grassland system. An interesting application of this study is to simulate the illusion of the presence of large carnivore by imitating their sounds in the areas where wild herbivore exists. Even if there is no direct predation, the fear effect can alleviate the pressure on the grassland ecosystem. In addition, it can promote an increase in domestic herbivore density and enhance the economic benefits for people. In summary, although large carnivore has been reintroduced in some areas [41, 45], applying fear effects in the grassland ecosystem is another possible protection strategy.

It can be seen from the above discussion that, if fear level exceeds a certain value, then species W will become extinct. This means that, in the application, the fear should be kept at some appropriate level. Here, we attempt to explore the impact of fear effect on the grassland ecosystem and obtain some interesting results. But there are still some problems to be solved. For example, in the derivation of the functional response for herbivore (D/W), we only consider the time wasted by each herbivore due to the disturbance by large carnivore in the process of predation (i.e. $\beta_1 C/\beta_2 C$), but ignore the wasted time due to interference between herbivores (i.e. $\gamma_1 D + \gamma_2 W$). It is expected to possibly produce more complex population dynamics, and it is also very interesting but challenging in mathematics.

Finally, one thing that should be pointed out is that the modeling idea and the model can be applied to other ecosystems. For example, consider the system consisting of one phytoplankton species, two zooplankton species and one fish species in aquatic ecosystems [3, 18, 36], the cascade effect of fear on phytoplankton is significant in the ecological environment because of the frequent outbreaks of phytoplankton bloom; in coral reef ecosystems, the most important measure to save the coral reef is to control the overgrowth rate of algae, when predator species is present, the prey can sense some vibrations and hide in the reef [25].

Acknowledgments

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