

ON MECHANISMS OF TROPHIC CASCADE CAUSED BY ANTI-PREDATION RESPONSE IN FOOD CHAIN SYSTEMS

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ABSTRACT. Motivated by a recent field study [Nat. Commun. 7(2016), 10698] on the impact of fear of large carnivores on the populations in a cascading ecosystem of food chain type with the large carnivores as the top predator, in this paper we propose two model systems in the form of ordinary differential equations to mechanistically explore the cascade of such a fear effect. The models are of the Lotka-Volterra type, one is three dimensional and the other four dimensional. The 3-D model only considers the cost of the anti-predation response reflected in the decrease of the production, while the 4-D model considers also the benefit of the response in reducing the predation rate, in addition to the cost by reducing the production. We perform a thorough analysis on the dynamics of the two models. The results reveal that the 3-D model and 4-model demonstrate opposite patterns for trophic cascade in terms of the dependence of population sizes for each species at the co-existence equilibrium on the anti-predation response level parameter, and such a difference is attributed to whether or not there is a benefit for the anti-predation response by the meso-carnivore species.

1. INTRODUCTION

Predator-prey interactions have attracted the great attention of both ecologists and mathematical biologists, not only because of their vast existence in nature but also because of their diversified forms and rich consequences in the real world. Mathematically, if only considering direct interaction through predation, a classic predator-prey model can be generally described by a system of ordinary differential equations of the form:

$$\begin{cases} \frac{du}{dt} = f_1(u(t)) - p(u(t), v(t))v(t), \\ \frac{dv}{dt} = f_2(v(t)) + cp(u(t), v(t))v(t). \end{cases} \quad (1.1)$$

See, e.g., [16, 17, 28, 29]. Here $u(t)$ and $v(t)$ are the populations of the prey and predator respectively, $f_1(u)$ and $f_2(v)$ denote growth functions of the prey and the predator respectively, $p(u, v)$ is the functional response which accounts for the predation rate and biomass transfer from the prey to the predator after predation, and the constant c explains the efficiency in biomass transfer.

Predator-prey ODE models of the above form only consider interactions of two species with direct effect reflected by the predation term. However, since 1990s, more and more ecologists have realized the existence of indirect effects (e.g., fear effect), and observed impact of such effects; see, e.g. [1, 14, 21, 26]. Recent field experiments have found the presence of predator itself, can have significant influence on prey's population through changes in reproduction [15, 35], habitat selection [4, 27] and physiology [3, 5, 34]. In contrast, as far as mathematical modeling is concerned, indirect effects have been largely (if

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not all) ignored in those existing models describing predator-prey interactions and those on conservation and management of the ecosystem.

Motivated by the field study in [35] which observed an as high as 40% decrease in prey's reproduction rate when the prey perceived a risk of predator coming from the playback of the predator's voice, [30] formulated a mathematical model in the form of the following ordinary differential equations

$$\begin{cases} \frac{du}{dt} = f(k, v(t)) r_0 u(t) - d u(t) - a u^2(t) - p(u(t)) v(t), \\ \frac{dv}{dt} = c p(u(t)) v(t) - m v(t). \end{cases} \quad (1.2)$$

Here u is the population of the prey species and v is the population of predator species, and the prey's growth follows a logistic growth with the intrinsic growth rate being split into the net growth rate r_0 and natural death rate d , given by $r_0 - d$. To mimic the scenario of the field experimental study in [35] in which predation actually did not occur due to the use of electronic fence, in (1.2) the fear effect is only incorporated into the production term by the function $f(k, v(t))$ accounting for a cost. The term $au^2 = (au)u$ reflects the self-limiting mechanism of u (due to intra-species competition) and c is the biomass transform efficiency constant. The function $p(u)$ is the functional response which is assumed to depend on the prey population only. Analysis of (1.2), both analytical and numerical, have revealed some interesting dynamics that would have not occurred without considering the fear effect.

Since [30], there have been some follow-up modelling works that extend the model (1.2) to accommodate various aspects of fear effect. For example, [31] considered *age structure* and discussed different impacts of fear effect on different age stages; [32] explored the fear effect reflected through the *dispersals* and its impact on the pattern formation. [8] incorporated an extra food source for the predator in (1.2) and also added a white noise to the death rates of the prey and predator, and analyzed the resulting stochastic model. [18] further considered a digestion delay in addition to the cost of fear, white noise in the death rates, and extra food for the predator but ignored the benefit of the anti-predation response. More recently, in addition to a digestion delay and a cost in prey's production due to the anti-predation response, [33] further incorporated a benefit term from the anti-predation response, and explored the joint impact of the fear effect and the digestion delay on the population dynamics for both predator and prey.

In the real world, it is quite common that a species can predate on one species and in the mean time, it can be a prey of other species. This leads to occurrence of food chains between multiple species, consisting of cascading predator-prey interactions. One may naturally ask how a fear effect arising from one or more species in the chain will affect the dynamics of the whole cascaded populations? In a more recent field experimental study [25], the authors tested a meso-predator cascade by manipulating the large carnivores playback, which resulted in a decrease in the population of meso-carnivore and increase in the population of its prey. That is, the fear effect on the top species in that chain of three species actually affects every species in the ecosystem explicitly or implicitly.

To better understand the above mentioned propagation of the fear effect from top layer to the bottom layer in that food chain ecosystem reported in [25], we incorporate a fear effect on the top species into a Lotka-Volterra type food chain model, formulated by the following system of ordinary differential equations

$$\begin{cases} \frac{dN_1}{d\tau} = N_1 (R_1 - a_{11}N_1 - a_{12}N_2), \\ \frac{dN_2}{d\tau} = N_2 (R_2 - a_{22}N_2 - a_{23}N_3 + a_{21}N_1), \\ \frac{dN_3}{d\tau} = N_3 (B(\alpha) - D - a_{33}N_3 + a_{32}N_2), \\ N_1(0) \geq 0, \quad N_2(0) \geq 0, \quad N_3(0) \geq 0. \end{cases} \quad (1.3)$$

Here, N_3 is the population of the meso-carnivore (e.g., racoon) which is affected by the large carnivore's (e.g., wolf, bear) *playback*; N_2 is the prey (e.g., crab) of the meso-carnivore N_3 , and N_1 is the prey of N_2 . Each species is assumed to follow a logistic growth with growth rates R_1 , R_2 and $B(\alpha) - D$ respectively. The population of the large carnivores does not appear in the system because in the field study [25], only their voices are played, and hence they only have fear (indirect) effect on the meso-carnivores represented by $B(\alpha)$, where the net birth (production) rate $B(\alpha)$ depends on a parameter α standing for the meso-carnivore's anti-predation response level. By its biological meaning, $B(\alpha)$ is assumed to satisfy

$$B'(\alpha) < 0, \quad B(0) = B_3 > 0 \quad \text{and} \quad \lim_{\alpha \rightarrow \infty} B(\alpha) = 0. \quad (1.4)$$

The constant D is the natural death rate of N_3 , a_{ii} ($i = 1, 2, 3$) are the intra-species competition coefficients. a_{12} and a_{23} are the predation rates, while a_{21} and a_{32} are the conversion rate of the biomass from N_1 to N_2 and from N_2 to N_3 respectively; thus, a_{12}/a_{21} and a_{23}/a_{32} actually account for the efficiency of biomass transfer from the predations. We point out that this type of three dimensional food chain models have been intensive and extensively studied by some researchers, see, e.g., [9, 11, 12, 13] and the references therein. As far as fear effect in food chains is concerned, two recent papers [19, 20] have also followed line of [30] to consider fear effect in food chain of three species; their scenario is different from ours: they considered other types of functional responses, they incorporated fear effects in the bottom and middle species, and they assumed that the top and middle species are specialist predators. The *first goal* of this paper is to explore the dynamics of (1.3), particularly, the impact of the meso-carnivore's anti-predation response level α on the dynamics.

In (1.3), only the cost for the meso-carnivore's anti-predation response is considered. For such a response, in addition to cost, there should also be a benefit (see, e.g., [6, 26]), typically reflected by the decrease in the chance of being predated. A response strategy is expected to seek balance between cost and benefit to achieve certain optimality. In order to also add the benefit into the interplay in the above model system (1.3), we need the term of predation on the meso-carnivore by a large carnivore, which inevitably requires us to add the the population of that large carnivore into the system. This leads to the following four dimensional food chain model

$$\begin{cases} \frac{dN_1}{d\tau} = N_1 (R_1 - a_{11}N_1 - a_{12}N_2), \\ \frac{dN_2}{d\tau} = N_2 (R_2 - a_{22}N_2 - a_{23}N_3 + a_{21}N_1), \\ \frac{dN_3}{d\tau} = N_3 (B(\alpha, N_4) - D_3 - a_{33}N_3 + a_{32}N_2 - a_{34}(\alpha)N_4), \\ \frac{dN_4}{d\tau} = N_4 (-D_4 + \bar{c}a_{34}(\alpha)N_3), \\ N_1(0) \geq 0, \quad N_2(0) \geq 0, \quad N_3(0) \geq 0, \quad N_4(0) \geq 0, \end{cases} \quad (1.5)$$

where N_4 is the population of the restored top predator (large carnivore) which is assumed to be a specialist predator with the mortality rate D_4 . Now the net growth function of N_3 depends not only

on the anti-predation response level α but also on the population of its predator N_4 . The function $a_{34}(\alpha)$ denotes the encounter rate between N_3 and N_4 which is affected by the protective behaviours of N_3 species characterized by its dependence on the anti-predation response level α . By their biological meanings of $B(\alpha, N_4)$ and $a_{34}(\alpha)$, they are assumed to satisfy the following conditions:

$$\begin{cases} B(\alpha, N_4) \text{ is decreasing in } \alpha \text{ and } N_4, & B(0, N_4) = B(\alpha, 0) = B_3 > 0, \\ \lim_{\alpha \rightarrow \infty} B(\alpha, N_4) = \lim_{N_4 \rightarrow \infty} B(\alpha, N_4) = 0, \end{cases} \quad (1.6)$$

and

$$a_{34}(\alpha) \text{ is decreasing, } a_{34}(0) = a_0 > 0, \quad \lim_{\alpha \rightarrow \infty} a_{34}(\alpha) = 0. \quad (1.7)$$

Finally, \bar{c} is the efficiency of biomass transform. So in this model, we consider both the complex multi-trophic predator-prey structure and the trade-off from anti-predation response.

The remainder of this paper is organized as follows. In Section 2, we analyze the model system (1.3). We establish the well-posedness of system (1.3) and find the condition for existence and stability for all its equilibrium solutions. We also discuss the relationship between the anti-predation level and the final population size. In the end, some numerical examples, together with some discussions, are given to demonstrate our results. In Section 3, we investigate the dynamics of the four dimension model (1.5), including the existence and stability of equilibria as well as the continuously dependence between the final population size with respect to the anti-predation level. We also discuss the difference of the results from those for (1.3) in Section 2. In addition, we also present some numerical examples to illustrate that different functional response functions may lead to slightly different dynamical behaviour of the solution. In Section 4, we summarize our main results and discuss their biological implications. We also discuss some possible future projects along this direction of anti-predation response in predator-prey interactions.

2. ANALYSIS OF THE MODEL WITHOUT LARGE CARNIVORES

In this section, we analyze the three-species model (1.3). We first show the well-posedness of the system (1.3). Then we find all equilibrium solutions and discuss their stability in terms of the parameter values and anti-predation strategy level. As we mentioned in last section, this kind of food chain models have been studied in literatures, and thus, some technical results can be found in existing researches, e.g., [9, 11, 12, 13] and their references. But we need to associate the results to the new parameter α , the anti-predation response level of the species N_3 to shy light on influence of the fear effect for this model.

2.1. Preliminaries. For mathematical simplification, we first non-dimensionalize the model (1.3). Let

$$t = R_1\tau, \quad x = \frac{a_{11}N_1}{R_1}, \quad y = \frac{a_{12}N_2}{R_1}, \quad z = \frac{a_{23}N_3}{R_1},$$

then model (1.3) becomes

$$\begin{cases} \frac{dx}{dt} = x(1 - x - y), \\ \frac{dy}{dt} = y(k - d_1y - z + \beta_1x), \\ \frac{dz}{dt} = z(f(\alpha) - d_2z + \beta_2y), \end{cases} \quad (2.1)$$

where

$$k = \frac{R_2}{R_1}, \quad d_1 = \frac{a_{22}}{a_{12}}, \quad d_2 = \frac{a_{33}}{a_{23}}, \quad \beta_1 = \frac{a_{21}}{a_{11}}, \quad \beta_2 = \frac{a_{32}}{a_{12}},$$

$$f(\alpha) = \frac{B(\alpha) - D}{R_1}, \quad f(0) = \frac{B_3 - D}{R_1}, \quad \lim_{\alpha \rightarrow \infty} f(\alpha) = -\frac{D}{R_1}.$$

By the basic theory of ODE systems, we can easily show that the initial value problem for (2.1) has a unique solution; moreover, the solution is nonnegative (positive) with nonnegative (positive) initial conditions because each equation in (2.1) is of Gaussian type. Now we show that the solution to system (2.1) is bounded.

From the first equation in system (2.1) and by the non-negativity of $y(t)$, we have

$$\frac{dx}{dt} = x(1 - x - y) \leq x(1 - x).$$

By the comparison theorem [24], we can obtain $\lim_{t \rightarrow \infty} \sup x(t) \leq 1$. Therefore, for any $\epsilon_1 > 0$, there holds $x(t) \leq 1 + \epsilon_1$ for large t . Incorporating this estimate for large t into the second equation in (2.1) results in

$$\frac{dy}{dt} = y(k - d_1y - z + \beta_1x) \leq y(k + \beta_1(1 + \epsilon_1) - d_1y), \quad \text{for large } t.$$

Applying the comparison theorem again, we then obtain

$$\limsup_{t \rightarrow \infty} y(t) \leq \frac{k + \beta_1(1 + \epsilon_1)}{d_1}.$$

Since $\epsilon_1 > 0$ is arbitrary small, the above inequality actually implies

$$\limsup_{t \rightarrow \infty} y(t) \leq \frac{k + \beta_1}{d_1}.$$

Incorporating the above inequality into the third equation in (2.1) and by the same argument, we can obtain

$$\limsup_{t \rightarrow \infty} z(t) \leq \max \left(\frac{f(\alpha)d_1 + \beta_2(k + \beta_1)}{d_1d_2}, 0 \right).$$

Combining the above, we have proved that the solution $(x(t), y(t), z(t))$ to (2.1) is bounded.

2.2. Existence and Stability of the boundary equilibria. In this section, we find all **boundary** equilibrium solutions and give the condition for their existence and stability. For the result to be biologically meaningful, we are only interested in equilibria with nonnegative components.

An equilibrium of (2.1) solves the following system

$$\begin{cases} x(1 - x - y) = 0, \\ y(k - d_1y - z + \beta_1x) = 0, \\ z(f(\alpha) - d_2z + \beta_2y) = 0. \end{cases}$$

There are seven boundary equilibrium solutions. $E_0 = (0, 0, 0)$ is the trivial equilibrium solution which always exists. $E_1 = (1, 0, 0)$, $E_2 = (0, k/d_1, 0)$ and $E_3 = (0, 0, f(\alpha)/d_2)$ are the equilibria representing the scenario that only one species survives; E_1 and E_2 always exist, while E_3 exists only when $f(\alpha) > 0$.

There are also other three *possible* equilibria corresponding to the scenario of two species coexisting, and they are given by

$$\begin{aligned} E_{12} &= \left(1 - \frac{k + \beta_1}{d_1 + \beta_1}, \frac{k + \beta_1}{d_1 + \beta_1}, 0\right), \\ E_{13} &= \left(1, 0, \frac{f(\alpha)}{d_2}\right), \\ E_{23} &= \left(0, \frac{d_2 k - f(\alpha)}{d_1 d_2 + \beta_2}, k - \frac{d_1 d_2 k - d_1 f(\alpha)}{d_1 d_2 + \beta_2}\right). \end{aligned}$$

By the nonnegative requirement, E_{12} exists when $k < d_1$, E_{13} exists when $f(\alpha) > 0$ and E_{23} exists when $d_2 k > f(\alpha) > -\beta_2 k / d_1$.

The local stability of an equilibrium is obtained by linearization at the equilibrium. The Jacobian matrix at equilibrium (x^*, y^*, z^*) is given by

$$J(E = (x^*, y^*, z^*)) = \begin{pmatrix} 1 - 2x^* - y^* & -x^* & 0 \\ \beta_1 y^* & k - 2d_1 y^* + \beta_1 x^* - z^* & -y^* \\ 0 & \beta_2 z^* & f(\alpha) - 2d_2 z^* + \beta_2 y^* \end{pmatrix}. \quad (2.2)$$

At $E_0 = (0, 0, 0)$, the Jacobian is given by

$$J(E_0) = \begin{pmatrix} 1 & 0 & 0 \\ 0 & k & 0 \\ 0 & 0 & f(\alpha) \end{pmatrix},$$

therefore E_0 is unstable, as there are positive eigenvalues $\lambda_1 = 1$ and $\lambda_2 = k$.

Similarly, at $E_1 = (1, 0, 0)$, the Jacobian is given by

$$J(E_1) = \begin{pmatrix} -1 & -1 & 0 \\ 0 & k + \beta_1 & 0 \\ 0 & 0 & f(\alpha) \end{pmatrix},$$

therefore E_1 is unstable, as there is a positive eigenvalue $\lambda = k + \beta_1$.

At $E_2 = (0, k/d_1, 0)$, the Jacobian is given by

$$J(E_2) = \begin{pmatrix} 1 - \frac{k}{d_1} & 0 & 0 \\ \frac{\beta_1 k}{d_1} & -k & -\frac{k}{d_1} \\ 0 & 0 & f(\alpha) + \frac{\beta_2 k}{d_1} \end{pmatrix},$$

therefore E_2 is asymptotically stable if and only if $1 - k/d_1 < 0$ and $f(\alpha) < -\beta_2 k / d_1$.

At $E_3 = (0, 0, f(\alpha)/d_2)$, the Jacobian is given by

$$J(E_3) = \begin{pmatrix} 1 & 0 & 0 \\ 0 & k - \frac{f(\alpha)}{d_2} & 0 \\ 0 & \frac{\beta_2 f(\alpha)}{\alpha_2} & -f(\alpha) \end{pmatrix},$$

hence, E_3 is unstable since there is a positive eigenvalue $\lambda = 1$.

At E_{12} , the Jacobian becomes

$$J(E_{12}) = \begin{pmatrix} \frac{k + \beta_1}{d_1 + \beta_1} - 1 & \frac{k + \beta_1}{d_1 + \beta_1} - 1 & 0 \\ \frac{\beta_1 k + \beta_1^2}{d_1 + \beta_1} & -\frac{d_1 k + d_1 \beta_1}{d_1 + \beta_1} & -\frac{k + \beta_1}{d_1 + \beta_1} \\ 0 & 0 & f(\alpha) + \frac{\beta_2 k + \beta_2 \beta_1}{d_1 + \beta_1} \end{pmatrix},$$

thus, E_{12} is asymptotically stable if and only if $f(\alpha) < -\frac{\beta_2 k + \beta_2 \beta_1}{d_1 + \beta_1}$.

At $E_{13} = (1, 0, f(\alpha)/d_2)$, the Jacobian reduces to

$$J(E_{13}) = \begin{pmatrix} -1 & -1 & 0 \\ 0 & k + \beta_1 - \frac{f(\alpha)}{d_2} & 0 \\ 0 & \frac{\beta_2 f(\alpha)}{\alpha_2} & -f(\alpha) \end{pmatrix},$$

therefore E_{13} is asymptotically stable if and only if $f(\alpha) > d_2(k + \beta_1)$.

At $E_{23} = \left(0, \frac{d_2 k - f(\alpha)}{d_1 d_2 + \beta_2}, k - \frac{d_1 d_2 k - d_1 f(\alpha)}{d_1 d_2 + \beta_2}\right)$, the Jacobian is given by

$$J(E_{23}) = \begin{pmatrix} 1 - \frac{d_2 k - f(\alpha)}{d_1 d_2 + \beta_2} & 0 & 0 \\ \frac{\beta_1 d_2 k - \beta_1 f(\alpha)}{d_1 d_2 + \beta_2} & -\frac{d_1 d_2 k - d_1 f(\alpha)}{d_1 d_2 + \beta_2} & -\frac{d_2 k - f(\alpha)}{d_1 d_2 + \beta_2} \\ 0 & \beta_2 k - \frac{\beta_2 d_1 d_2 k - \beta_2 d_1 f(\alpha)}{d_1 d_2 + \beta_2} & -d_2 k + \frac{d_1 d_2^2 k - d_1 d_2 f(\alpha)}{d_1 d_2 + \beta_2} \end{pmatrix},$$

therefore E_{23} is asymptotically stable if and only if $f(\alpha) > d_2 k - d_1 d_2 - \beta_2$.

We summarize the above analysis in the following proposition.

Proposition 2.1. For system (2.1), the following statement hold.

- (i) Equilibrium E_0 and E_1 always exist and are unstable.
- (ii) Equilibrium E_2 always exists; it is asymptotically stable if and only if $k > d_1$ and $f(\alpha) < -\beta_2 k/d_1$.

- (iii) When $f(\alpha) > 0$, E_3 exists; it is unstable. E_{13} exists and is asymptotically stable if and only if $f(\alpha) > d_2(k + \beta_1)$.
- (iv) When $k < d_1$, E_{12} exists; it is asymptotically stable if and only if $f(\alpha) < -\beta_2(k + \beta_1)/(d_1 + \beta_1)$.
- (v) When $d_2k > f(\alpha) > -\beta_2k/d_1$, E_{23} exists; it is asymptotically stable if and only if $f(\alpha) < d_2k - d_1d_2 - \beta_2$.

2.3. Existence and stability of a positive equilibrium solution. There is a unique positive equilibrium solution $E^* = (x^*, y^*, z^*)$ if

$$d_2(k + \beta_1) > f(\alpha) > \max\left(d_2k - d_1d_2 - \beta_2, \frac{-\beta_2(k + \beta_1)}{d_1 + \beta_1}\right). \quad (2.3)$$

Indeed, $E^* = (x^*, y^*, z^*)$ is given by

$$\begin{cases} x^* = 1 - y^*, \\ y^* = \frac{d_2(k + \beta_1) - f(\alpha)}{d_2(d_1 + \beta_1) + \beta_2}, \\ z^* = k + \beta_1 - (d_1 + \beta_1)y^*. \end{cases} \quad (2.4)$$

The conditions in (2.3) directly comes from the formulas in (2.4).

The Jacobian matrix at the positive equilibrium can be simplified as

$$J(E^*) = \begin{pmatrix} -x^* & -x^* & 0 \\ \beta_1 y^* & -d_1 y^* & -y^* \\ 0 & \beta_2 z^* & -d_2 z^* \end{pmatrix},$$

Thus, the corresponding characteristic equation is

$$\begin{aligned} \lambda^3 + (d_1 y^* + d_2 z^* + x^*)\lambda^2 + (d_1 d_2 y^* z^* + \beta_1 x^* y^* + \beta_2 y^* z^* + d_1 x^* y^* + d_2 x^* z^*)\lambda \\ + (\beta_1 d_2 + d_1 d_2 + \beta_2)x^* y^* z^* = 0. \end{aligned}$$

where

$$\begin{cases} a_1 = d_1 y^* + d_2 z^* + x^* > 0, \\ a_2 = d_1 d_2 y^* z^* + \beta_1 x^* y^* + \beta_2 y^* z^* + d_1 x^* y^* + d_2 x^* z^* > 0, \\ a_3 = (\beta_1 d_2 + d_1 d_2 + \beta_2)x^* y^* z^* > 0, \end{cases}$$

and

$$\begin{aligned} a_1 a_2 - a_3 = d_1^2 d_2 (y^*)^2 z^* + d_1 d_2^2 y^* (z^*)^2 + \beta_1 d_1 x^* (y^*)^2 + \beta_2 d_1 (y^*)^2 z^* + \beta_2 d_2 y^* (z^*)^2 \\ + d_1^2 x^* (y^*)^2 + 2d_1 d_2 x^* y^* z^* + d_2^2 x^* (z^*)^2 + \beta_1 (x^*)^2 y^* + d_1 (x^*)^2 y^* + d_2 (x^*)^2 z^* > 0. \end{aligned}$$

By Routh-Hurwitz criterion, the positive equilibrium is locally asymptotically stable. Moreover, we can prove that it is actually globally asymptotically stable as long as it exists (i.e., (2.3) holds).

Theorem 2.1. If (2.3) holds, then the positive equilibrium E^* is globally asymptotically stable.

Proof. Consider the Lyapunov function

$$V(x, y, z) = \beta_1 \beta_2 (x - x^* - x^* \ln \frac{x}{x^*}) + \beta_2 (y - y^* - y^* \ln \frac{y}{y^*}) + (z - z^* - z^* \ln \frac{z}{z^*}),$$

then

$$\frac{dV}{dt} = -\beta_1 \beta_2 (x - x^*)^2 - \beta_2 (y - y^*)^2 - (z - z^*)^2 \leq 0$$

and $\frac{dV}{dt} = 0$ if and only if $(x, y, z) = (x^*, y^*, z^*)$. By LaSalle’s Invariant Principle, we conclude E^* is globally asymptotically stable. \square

For readers’ convenience, we summarize the analytical results on the dynamics of the model (2.1) obtained above in the following Table 1.

TABLE 1. Condition of existence and stability of the equilibria in model (2.1)

Equilibrium solution	Existence	Stability
E_0	Always	Unstable
E_1	Always	Unstable
E_2	Always	$d_1 < k$ and $f(\alpha) < -\beta_2 k/d_1$
E_3	$f(\alpha) > 0$	Unstable
E_{12}	$d_1 > k$	$f(\alpha) < -\beta_2(k + \beta_1)/(d_1 + \beta_1)$
E_{13}	$f(\alpha) > 0$	$f(\alpha) > d_2(k + \beta_1)$
E_{23}	$d_2 k > f(\alpha) > -\beta_2 k/d_1$	$f(\alpha) < d_2 k - d_1 d_2 - \beta_2$
E^*	$d_2(k + \beta_1) > f(\alpha) > \max\left(d_2 k - d_1 d_2 - \beta_2, -\frac{\beta_2(k + \beta_1)}{d_1 + \beta_1}\right)$	GAS

From Theorem 2.1 , we know that the positive equilibrium is always globally asymptotically stable as long as it exists (i.e., (2.3) holds), implying that the populations of all three species will converge to co-existence state at the respect levels x^* , y^* and z^* . Thus, it is worthwhile to investigate how the response strength α will affect these levels. Indeed, direct calculations give

$$\begin{cases} \frac{dy^*}{d\alpha} = \frac{-f'(\alpha)}{d_2(d_1 + \beta_1) + \beta_2} > 0, \\ \frac{dx^*}{d\alpha} = -\frac{dy^*}{d\alpha} < 0, \\ \frac{dz^*}{d\alpha} = -(d_1 + \beta_1)\frac{dy^*}{d\alpha} < 0. \end{cases}$$

That is, within the range of α that guarantees (2.3), with the increase of the anti-predation response strength α , the final population sizes of the meso-carnivore, its prey and the prey’s prey will decrease, increase and decrease respectively, demonstrating an alternative pattern for the fear effect in the cascade, which was observed in the field study [25]. Therefore, the model (1.3) does provide a mechanism that can explain the phenomenon of trophic cascade caused by a fear of large carnivores reported in [25].

2.4. Numerical simulations. In this subsection, we present some numerical simulations to illustrate the analytical results obtained above. For this purpose, we choose a particular form for the function $B(\alpha)$ given by

$$B(\alpha) = \frac{R_3}{1 + c\alpha},$$

and this sends (1.3) to the following system:

$$\begin{cases} \frac{dN_1}{d\tau} = N_1 (R_1 - a_{11}N_1 - a_{12}N_2), \\ \frac{dN_2}{d\tau} = N_2 (R_2 - a_{22}N_2 - a_{23}N_3 + a_{21}N_1), \\ \frac{dN_3}{d\tau} = N_3 \left(\frac{R_3}{1 + c\alpha} - D - a_{33}N_3 + a_{32}N_2 \right), \\ N_1(0) \geq 0, \quad N_2(0) \geq 0, \quad N_3(0) \geq 0, \end{cases} \quad (2.5)$$

We fix the parameters

$$\begin{aligned} R_1 = 1, \quad a_{11} = 1, \quad a_{12} = 0.4, \quad R_2 = 1, \quad a_{22} = 0.2, \quad a_{23} = 0.5, \quad a_{21} = 0.5, \\ R_3 = 3, \quad D = 1, \quad a_{33} = 0.5, \quad a_{32} = 0.05, \quad c = 0.4, \end{aligned} \quad (2.6)$$

and demonstrate how α impacts the population dynamics. In this case, $k = R_2/R_1 = 1$ and $d_1 = a_{22}/a_{12} = 1/2$ so $k > d_1$. According to Proposition 2.1, there are three threshold values for α , denoted by α_1^* , α_2^* and α_3^* , which are given by

$$\begin{cases} f(\alpha_1^*) = d_2(k + \beta_1), \\ f(\alpha_2^*) = d_2k - d_1d_2 - \beta_2, \\ f(\alpha_3^*) = -\frac{\beta_2k}{d_1}. \end{cases}$$

Using the parameter values in (2.6), we obtain $\alpha_1^* = 0.5$, $\alpha_2^* \approx 2.954545455$ and $\alpha_3^* = 7.5$. By Proposition 2.1, when $0 < \alpha < 0.5$, the equilibrium E_{13} is stable (as demonstrated in Figure 1-(a) for $\alpha = 0.4$); when $0.5 < \alpha < 2.954545455$, the coexistence equilibrium E^* is stable (as demonstrated in Figure 1-(b) for $\alpha = 2$); when $2.954545455 < \alpha < 7.5$ (destroying (2.3), hence E^* no longer exists), the equilibrium E_{23} is stable (as demonstrated in Figure 1-(c) for $\alpha = 5$); when $\alpha > 7.5$, the equilibrium E_2 is stable (as demonstrated in Figure 1-(d) for $\alpha = 10$). The bifurcation diagram with respect to α is given in Figure 2.

Now, we change R_1 to $R_1 = 3$ and a_{33} to $a_{33} = 0.1$ and keep other parameters the same as in (2.6). Then $k = R_2/R_1 = 1/3$ and $d_1 = a_{22}/a_{12} = 1/2$ leading to the scenario of $k < d_1$. According to Proposition 2.1, there are two threshold values for α , denoted by $\bar{\alpha}_1$ and $\bar{\alpha}_2$, which are given by

$$\begin{cases} f(\bar{\alpha}_1) = d_2(k + \beta_1), \\ f(\bar{\alpha}_2) = -\frac{\beta_2(k + \beta_1)}{d_1 + \beta_1}. \end{cases}$$

Using the parameter values in (2.6), we obtain $\bar{\alpha}_1 = 2.5$ and $\bar{\alpha}_2 \approx 8.409090911$. By Proposition 2.1, when $0 < \alpha < 2.5$, the equilibrium E_{13} is stable (as demonstrated in Figure 3-(a) for $\alpha = 2$); when $2.5 < \alpha < 8.409090911$, the coexistence equilibrium E^* is stable (as demonstrated in Figure 3-(b) for $\alpha = 6$); when $\alpha > 8.409090911$, the equilibrium E_{12} is stable (as demonstrated in Figure 3-(c) for $\alpha = 10$). The bifurcation diagram with respect to α is given in Figure 4.

We find that depending on the difference between k and d_1 , we have two kinds of bifurcation. In both cases, when the anti-predation response α passes a threshold, it leads to a transcritical bifurcation and we can always observe a meso-predator cascade inside the coexistence region when increasing α : the population of meso-predator is decreasing, the population of its prey is increasing and the population of the prey's prey (bottom prey) is decreasing. However, this pattern will be dramatically changed when we restore large carnivores instead of only manipulating their playback to induce fear. In the next section, we will model the case when we also introduce the large carnivores back into the food chain, leading to a 4-D model.

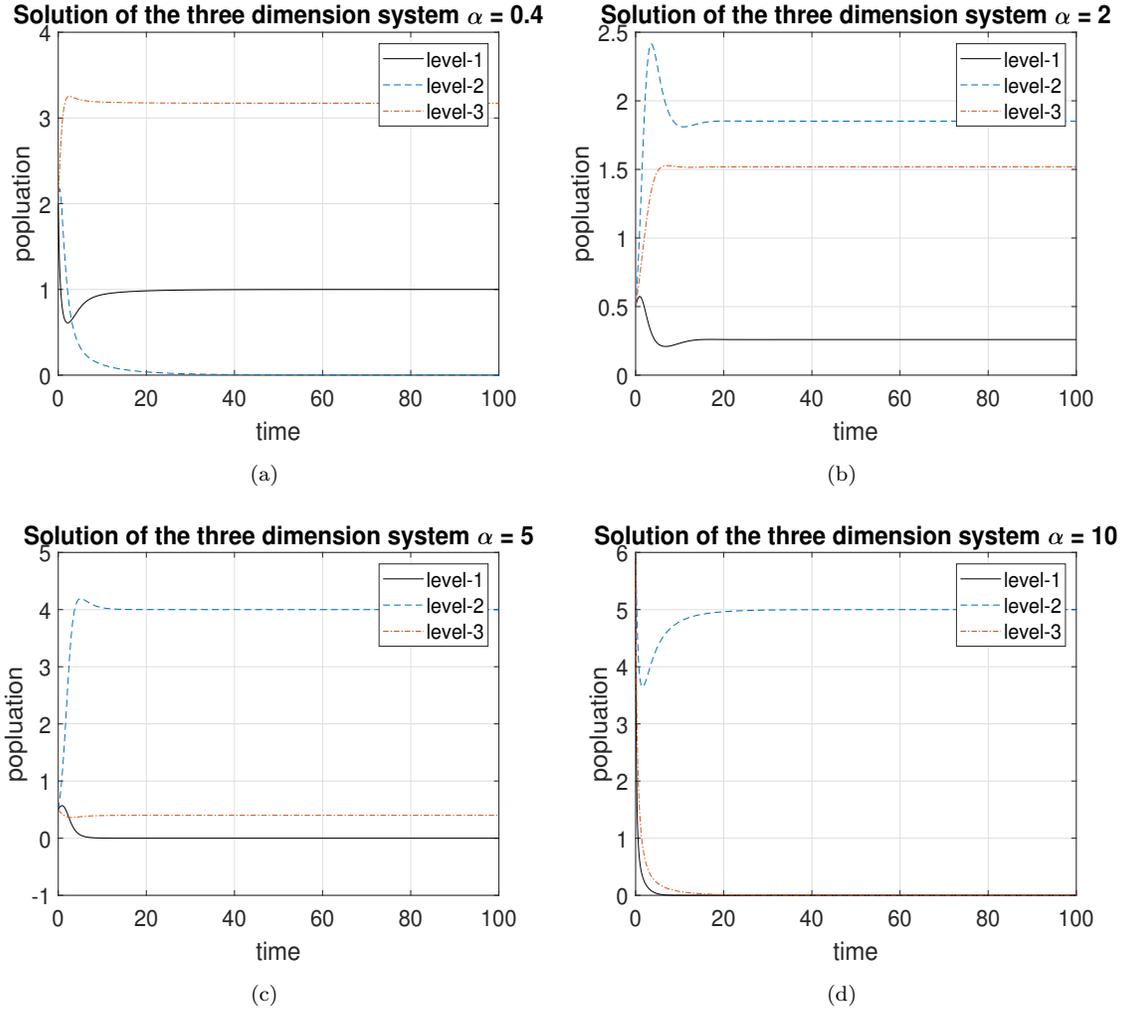


FIGURE 1. Population dynamics of (2.5) when $d_1 < k$. (a) When $0 < \alpha = 0.4 < 0.5$, the equilibrium E_{13} is stable, (b) $0.5 < \alpha = 2 < 2.954545455$, the coexistence equilibrium E^* is stable, (c) when $2.954545455 < \alpha = 5 < 7.5$, the equilibrium E_{23} is stable, (d) when $\alpha = 10 > 7.5$, the equilibrium E_2 is stable.

3. MODEL WITH RESTORING LARGE CARNIVORES

In this section, we analyze (1.5) which has the population of large carnivores incorporated together with a benefit in preventing predation of the meso-carnivore by the large carnivores, in addition to the cost in the meso-carnivore's production. Parallel to Section 2, we first establish the well-posedness of the 4-D model (1.5), discuss all possible equilibrium solutions and find the condition for their existence and stability in terms of the parameter values and anti-predation strategy level.

3.1. Well-posedness. For mathematical simplification, we still apply non-dimensionalization for our model (1.5) which is a natural expansion of the non-dimensionalization for (1.3) in Section 2, given by

$$t = R_1\tau, \quad x = \frac{a_{11}N_1}{R_1}, \quad y = \frac{a_{12}N_2}{R_1}, \quad z = \frac{a_{23}N_3}{R_1}, \quad w = \frac{a_0N_4}{R_1},$$

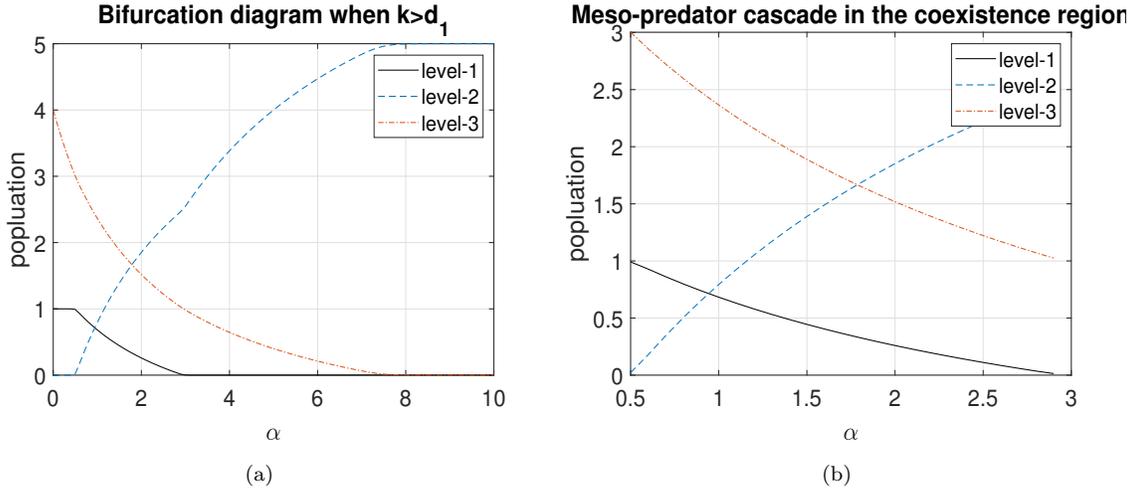


FIGURE 2. (a) Bifurcation diagram of (2.5) when $k > d_1$, (b) In the region when the coexistence equilibrium E^* is stable, we can observe a meso-predator cascade.

with $a_0 = a_{34}(0)$. Then model (1.5) becomes

$$\begin{cases} \frac{dx}{dt} = x(1 - x - y), \\ \frac{dy}{dt} = y(k - d_1 y - z + \beta_1 x), \\ \frac{dz}{dt} = z(f(\alpha, w) - d_2 z + \beta_2 y - p(\alpha)w), \\ \frac{dw}{dt} = w(-m + cp(\alpha)z) \end{cases} \quad (3.1)$$

where

$$k = \frac{R_2}{R_1}, \quad d_1 = \frac{a_{22}}{a_{12}}, \quad d_2 = \frac{a_{33}}{a_{23}}, \quad \beta_1 = \frac{a_{21}}{a_{11}}, \quad \beta_2 = \frac{a_{32}}{a_{12}}, \quad m = \frac{D_4}{R_1}, \quad c = \frac{\bar{c}a_0}{a_{23}}.$$

For the transformed and rescaled functions $f(\alpha, w)$ and $p(\alpha)$, the conditions (1.6) and (1.7) are transformed to

$$\begin{cases} f(\alpha, w) = \frac{B(\alpha, N_4) - D_3}{R_1}, \\ f(\alpha, 0) = f(0, w) = f_0 = \frac{B_3 - D_3}{R_1}, \\ \frac{\partial f}{\partial \alpha} < 0, \quad \frac{\partial f}{\partial w} < 0, \\ \lim_{\alpha \rightarrow \infty} f(\alpha, w) = \lim_{w \rightarrow \infty} f(\alpha, w) = \frac{-D_3}{R_1}, \\ p(\alpha) = \frac{a_{34}(\alpha)}{a_0}, \\ \frac{dp}{d\alpha} < 0, \\ p(0) = 1 \quad \text{and} \quad \lim_{\alpha \rightarrow \infty} p(\alpha) = 0. \end{cases} \quad (3.2)$$

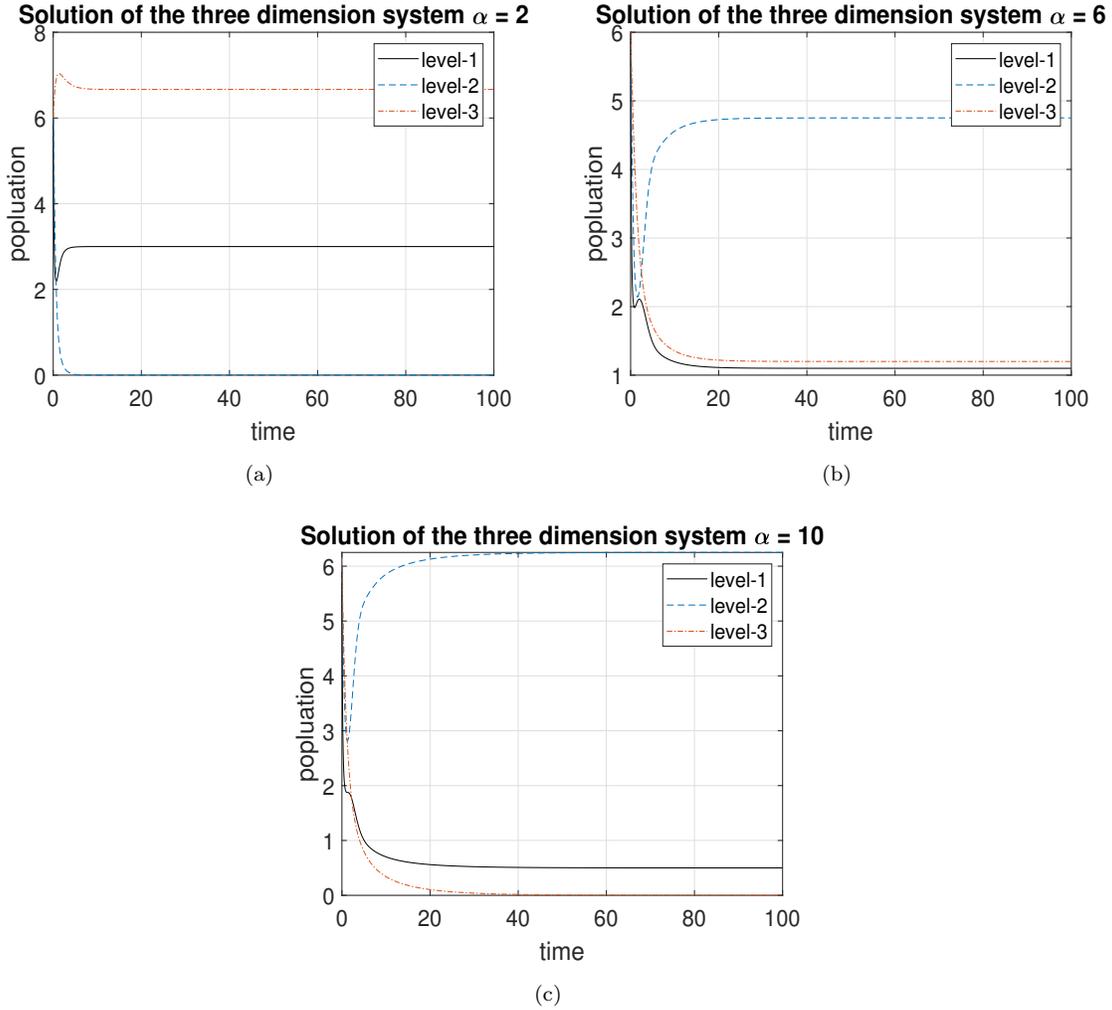


FIGURE 3. Population dynamics of (2.5) when $d_1 > k$. (a) When $0 < \alpha = 2 < 2.5$, the equilibrium E_{13} is stable, (b) $2.5 < \alpha = 6 < 8.409090911$, the coexistence equilibrium E^* is stable, (c) when $8.409090911 < \alpha = 10$, the equilibrium E_{12} is stable.

By the fundamental theory of ODEs, we easily see that the initial value problem associated with (3.1) has a unique solution; moreover, the solution is nonnegative (positive) with nonnegative (positive) initial conditions. Next we show that the solution to system (3.1) is bounded.

Firstly, by the same argument as in subsection 2.2, we can obtain the same estimates for $x(t)$ and $y(t)$:

$$\limsup_{t \rightarrow \infty} x(t) \leq 1 \quad \text{and} \quad \limsup_{t \rightarrow \infty} y(t) \leq \frac{k + \beta_1}{d_1}.$$

For z and w , we consider $P = cz + w$. Then we have

$$\frac{dP}{dt} = cz(f(\alpha, w) - d_2z + \beta_2y) - mw.$$

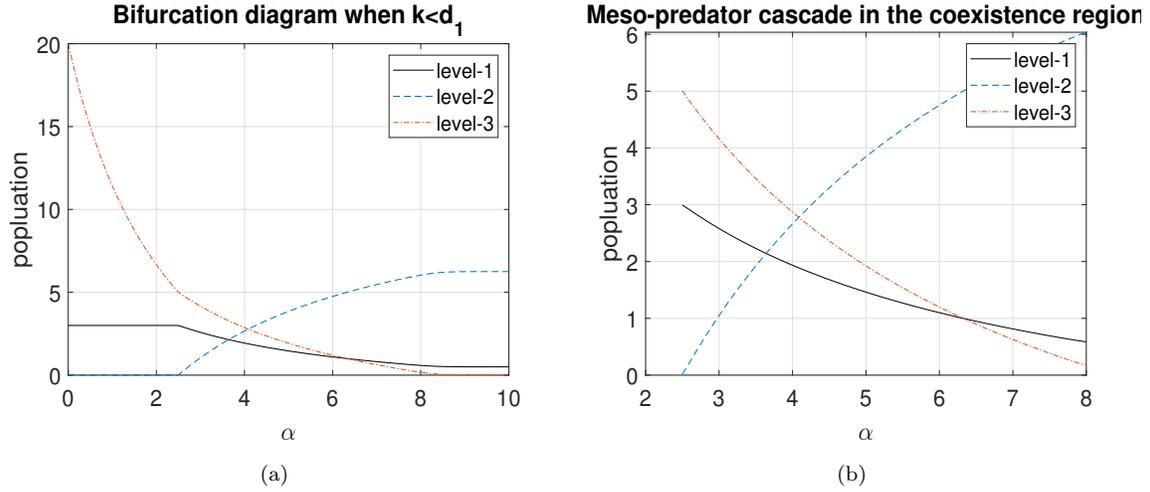


FIGURE 4. (a) Bifurcation diagram of (2.5) when $d_1 > k$, (b) In the region when the coexistence equilibrium E^* is stable, we can observe a meso-predator cascade.

Now for any given $\epsilon > 0$, there holds $y(t) \leq (k + \beta_1)(1 + \epsilon)/d_1$ for large t . Then for some $\mu \in (0, m)$ and large t , we have

$$\begin{aligned} \frac{dP}{dt} + \mu P &= cz(\mu + f(\alpha, w) - d_2z + \beta_2y) - (m - \mu)w, \\ &\leq cz \left(\mu + f_0 + \frac{\beta_2(k + \beta_1)(1 + \epsilon)}{d_1} - d_2z \right) \\ &=: cz(\bar{K} - d_2z) \end{aligned} \quad (3.3)$$

where

$$\bar{K} = \mu + f_0 + \frac{\beta_2(k + \beta_1)(1 + \epsilon)}{d_1}.$$

If $\bar{K} \leq 0$, since $z(t) \geq 0$, we can conclude that

$$\frac{dP}{dt} + \mu P \leq 0,$$

leading to $P \leq P_0 e^{-\mu t}$, where $P_0 = cz_0 + w_0$ comes from the initial condition. Thus,

$$\limsup_{t \rightarrow \infty} P(t) \leq 0.$$

If $\bar{K} > 0$, then

$$\frac{dP}{dt} + \mu P \leq \frac{c\bar{K}^2}{4d_2}.$$

By the comparison theorem [24], we can obtain

$$P \leq P_0 e^{-\mu t} + (1 - e^{-\mu t}) \frac{c\bar{K}^2}{4\mu d_2}.$$

which implies

$$\limsup_{t \rightarrow \infty} P(t) \leq \frac{c\bar{K}^2}{4\mu d_2}.$$

Thus, in both cases, P is bounded, implying that z and w are both bounded. Therefore, all four components of the solution are bounded.

3.2. Existence and Stability of the boundary equilibrium solutions. As in Section 2, we first analyze the boundary equilibria of the model (3.1). Again, we are only interested in the equilibria with nonnegative components.

By solving the system

$$\begin{cases} x(1 - x - y) = 0, \\ y(k - d_1y - z + \beta_1x) = 0, \\ z(f(\alpha, w) - d_2z + \beta_2y - p(\alpha)w) = 0, \\ w(-m + cp(\alpha)z) = 0, \end{cases}$$

we find that there are eleven possible boundary equilibria and they are described below. $E_0 = (0, 0, 0, 0)$ is the trivial equilibrium solution which always exists, $E_1 = (1, 0, 0, 0)$, $E_2 = (0, k/d_1, 0, 0)$ and $E_3 = (0, 0, f_0/d_2, 0)$ are the equilibria that correspond to the case of only one species surviving: E_1 and E_2 are always exist while E_3 exists only when $f_0 > 0$. There are also four possible equilibria accounting for the scenario of two species coexisting and they are

$$\begin{aligned} E_{12} &= \left(\frac{d_1 - k}{d_1 + \beta_1}, \frac{k + \beta_1}{d_1 + \beta_1}, 0, 0 \right), \\ E_{13} &= \left(1, 0, \frac{f_0}{d_2}, 0 \right), \\ E_{23} &= \left(0, \frac{d_2k - f_0}{d_1d_2 + \beta_2}, \frac{k\beta_2 + d_1f_0}{d_1d_2 + \beta_2}, 0 \right), \\ E_{34} &= \left(0, 0, \frac{m}{cp(\alpha)}, \bar{w} \right) \end{aligned}$$

where \bar{w} satisfies the equation

$$f(\alpha, \bar{w}) - \frac{d_2m}{cp(\alpha)} - p(\alpha)\bar{w} = 0. \tag{3.4}$$

Due to the requirement of non-negativity, E_{12} exists when $k < d_1$, E_{13} exists when $f_0 > 0$, and E_{23} exists when $d_2k > f_0 > -\beta_2k/d_1$. For the existence and uniqueness of E_{34} , we denote

$$F_1(w) = f(\alpha, w) - \frac{d_2m}{cp(\alpha)} - p(\alpha)w.$$

Then it is obvious that $F_1(w)$ is a decreasing function with respect to w and $\lim_{w \rightarrow \infty} F_1(w) = -\infty$. Thus, the sufficient and necessary condition for E_{34} to exist is $F_1(0) > 0$, that is $f_0 > d_2m/cp(\alpha)$.

There are three possible equilibria for the case of three species coexisting, given by

$$\begin{aligned} E_{123} &= \left(\frac{d_1d_2 - d_2k + \beta_2 + f_0}{\beta_1d_2 + d_1d_2 + \beta_2}, \frac{\beta_1d_2 + d_2k - f_0}{\beta_1d_2 + d_1d_2 + \beta_2}, \frac{\beta_1\beta_2 + \beta_1f_0 + \beta_2k + d_1f_0}{\beta_1d_2 + d_1d_2 + \beta_2}, 0 \right), \\ E_{134} &= \left(1, 0, \frac{m}{cp(\alpha)}, \bar{w} \right), \\ E_{234} &= \left(0, \frac{cp(\alpha)k - m}{d_1cp(\alpha)}, \frac{m}{cp(\alpha)}, \hat{w} \right), \end{aligned}$$

where \bar{w} is as in (3.4) and \hat{w} satisfies the equation

$$f(\alpha, \hat{w}) - \frac{d_2m}{cp(\alpha)} + \frac{\beta_2cp(\alpha)k - \beta_2m}{d_1cp(\alpha)} - p(\alpha)\hat{w} = 0. \tag{3.5}$$

Thus, E_{123} exists when

$$d_2(k + \beta_1) > f_0 > \max \left(d_2k - d_1d_2 - \beta_2, -\frac{\beta_2(k + \beta_1)}{d_1 + \beta_1} \right),$$

The condition for E_{134} to exist is the same as for the existence of E_{34} , that is, when $f_0 > d_2m/cp(\alpha)$. Condition for E_{234} to exist is $cp(\alpha)k - m > 0$ and

$$f_0 > \frac{d_2m}{cp(\alpha)} - \frac{\beta_2cp(\alpha)k - \beta_2m}{d_1cp(\alpha)}.$$

In order to discuss the local stability, we calculate the Jacobian matrix at equilibrium $E = (x^*, y^*, z^*, w^*)$ as

$$J(E) = \begin{pmatrix} 1 - 2x^* - y^* & -x^* & 0 & 0 \\ \beta_1y^* & k - 2d_1y^* + \beta_1x^* - z^* & -y^* & 0 \\ 0 & \beta_2z^* & J_{33} & J_{34} \\ 0 & 0 & cp(\alpha)w^* & -m + cp(\alpha)z^* \end{pmatrix}, \quad (3.6)$$

where

$$J_{33} = f(\alpha, w^*) - 2d_2z^* + \beta_2y^* - p(\alpha)w^*,$$

and

$$J_{34} = z^* \left. \frac{\partial f(\alpha, w)}{\partial w} \right|_{w=w^*} - p(\alpha)z^* < 0 \quad \text{for } z^* > 0, \quad w^* > 0.$$

At $E_0 = (0, 0, 0, 0)$, the Jacobian becomes

$$J(E_0) = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & k & 0 & 0 \\ 0 & 0 & f_0 & 0 \\ 0 & 0 & 0 & -m \end{pmatrix},$$

thus, E_0 is unstable.

At $E_1 = (1, 0, 0, 0)$, the Jacobian reduces to

$$J(E_1) = \begin{pmatrix} -1 & -1 & 0 & 0 \\ 0 & k + \beta_1 & 0 & 0 \\ 0 & 0 & f_0 & 0 \\ 0 & 0 & 0 & -m \end{pmatrix},$$

hence E_1 is unstable.

At $E_2 = (0, k/d_1, 0, 0)$, the Jacobian is given by

$$J(E_2) = \begin{pmatrix} 1 - \frac{k}{d_1} & 0 & 0 & 0 \\ \frac{\beta_1 k}{d_1} & -k & -\frac{k}{d_1} & 0 \\ 0 & 0 & f_0 + \frac{\beta_2 k}{d_1} & 0 \\ 0 & 0 & 0 & -m \end{pmatrix},$$

so E_2 is asymptotically stable if and only if $1 - k/d_1 < 0$ and $f_0 < -\beta_2 k/d_1$.

At $E_3 = (0, 0, f_0/d_2, 0)$, the Jacobian is now

$$J(E_3) = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & k - \frac{f_0}{d_2} & 0 & 0 \\ 0 & \frac{\beta_2 f_0}{\alpha_2} & -f_0 & J_{34} \\ 0 & 0 & 0 & -m + \frac{cp(\alpha)f_0}{d_2} \end{pmatrix},$$

therefore E_3 is unstable.

At E_{12} , the Jacobian is reduced to

$$J(E_{12}) = \begin{pmatrix} \frac{k - d_1}{d_1 + \beta_1} & \frac{k - d_1}{d_1 + \beta_1} & 0 & 0 \\ \frac{\beta_1 k + \beta_1^2}{d_1 + \beta_1} & -\frac{d_1 k + d_1 \beta_1}{d_1 + \beta_1} & -\frac{k + \beta_1}{d_1 + \beta_1} & 0 \\ 0 & 0 & f_0 + \frac{\beta_2 k + \beta_2 \beta_1}{d_1 + \beta_1} & 0 \\ 0 & 0 & 0 & -m \end{pmatrix},$$

therefore E_{12} is asymptotically stable if and only if

$$f_0 < \frac{-(\beta_2 k + \beta_2 \beta_1)}{d_1 + \beta_1}.$$

At E_{13} , the Jacobian is

$$J(E_{13}) = \begin{pmatrix} -1 & -1 & 0 & 0 \\ 0 & k + \beta_1 - \frac{f_0}{d_2} & 0 & 0 \\ 0 & \frac{\beta_2 f_0}{\alpha_2} & -f_0 & J_{34} \\ 0 & 0 & 0 & -m + \frac{cp(\alpha)f_0}{d_2} \end{pmatrix},$$

consequently, E_{13} is asymptotically stable if and only if

$$\frac{md_2}{cp(\alpha)} > f_0 > d_2(k + \beta_1).$$

At E_{23} , the Jacobian is given by

$$J(E_{23}) = \begin{pmatrix} 1 - \frac{d_2 k - f_0}{d_1 d_2 + \beta_2} & 0 & 0 & 0 \\ \frac{\beta_1 d_2 k - \beta_1 f_0}{d_1 d_2 + \beta_2} & -\frac{d_1 d_2 k - d_1 f_0}{d_1 d_2 + \beta_2} & -\frac{d_2 k - f_0}{d_1 d_2 + \beta_2} & 0 \\ 0 & \frac{k\beta_2^2 + d_1 f_0 \beta_2}{d_1 d_2 + \beta_2} & -\frac{k\beta_2 d_2 + d_1 f_0 d_2}{d_1 d_2 + \beta_2} & J_{34} \\ 0 & 0 & 0 & -m + \frac{cp(\alpha)(k\beta_2 + d_1 f_0)}{d_1 d_2 + \beta_2} \end{pmatrix},$$

therefore E_{23} is asymptotically stable if and only if

$$f_0 > d_2 k - d_1 d_2 - \beta_2 \quad \text{and} \quad p(\alpha) < \frac{m(d_1 d_2 + \beta_2)}{c(k\beta_2 + d_1 f_0)}.$$

At $E_{34} = \left(0, 0, \frac{m}{cp(\alpha)}, \bar{w}\right)$, the Jacobian becomes

$$J(E_{34}) = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & k - \frac{m}{cp(\alpha)} & 0 & 0 \\ 0 & \frac{\beta_2 m}{cp(\alpha)} & \frac{-d_2 m}{cp(\alpha)} & J_{34} \\ 0 & 0 & cp(\alpha)\bar{w} & 0 \end{pmatrix},$$

therefore E_{34} is unstable.

At $E_{123} = (X_1, Y_1, Z_1, 0)$, the Jacobian is given by

$$J(E_{123}) = \begin{pmatrix} -X_1 & -X_1 & 0 & 0 \\ \beta_1 Y_1 & -d_1 Y_1 & -Y_1 & 0 \\ 0 & \beta_2 Z_1 & -d_2 Z_1 & 0 \\ 0 & 0 & 0 & -m + cp(\alpha)Z_1 \end{pmatrix},$$

where X_1 , Y_1 and Z_1 denote the three positive components in E_{123} . In Section 2, for the three dimensional model (2.1), we have proved the principle 3×3 sub-matrix of $J(E_{123})$ only has negative eigenvalues. Therefore E_{123} is asymptotically stable if and only if $-m + cp(\alpha)Z_1 < 0$, that is

$$p(\alpha) < \frac{m(\beta_1 d_2 + d_1 d_2 + \beta_2)}{c(\beta_1 \beta_2 + \beta_1 f_0 + \beta_2 k + d_1 f_0)}.$$

At $E_{134} = \left(1, 0, \frac{m}{cp(\alpha)}, \bar{w}\right)$, the Jacobian is given by

$$J(E_{134}) = \begin{pmatrix} -1 & -1 & 0 & 0 \\ 0 & k + \beta_1 - \frac{m}{cp(\alpha)} & 0 & 0 \\ 0 & \frac{\beta_2 m}{cp(\alpha)} & -\frac{d_2 m}{cp(\alpha)} & J_{34} \\ 0 & 0 & cp(\alpha)\bar{w} & 0 \end{pmatrix},$$

Since $J_{34} < 0$, E_{123} is asymptotically stable if and only if $k + \beta_1 - m/cp(\alpha) < 0$, that is $p(\alpha) < m/c(k + \beta_1)$.

At E_{234} , the Jacobian becomes

$$J(E_{234}) = \begin{pmatrix} 1 - \frac{cp(\alpha)k - m}{d_1 cp(\alpha)} & 0 & 0 & 0 \\ \frac{\beta_1 (cp(\alpha)k - m)}{d_1 cp(\alpha)} & -\frac{d_1 (cp(\alpha)k - m)}{d_1 cp(\alpha)} & -\frac{cp(\alpha)k - m}{d_1 cp(\alpha)} & 0 \\ 0 & \frac{\beta_2 m}{cp(\alpha)} & -\frac{d_2 m}{cp(\alpha)} & J_{34} \\ 0 & 0 & cp(\alpha)\hat{w} & 0 \end{pmatrix},$$

the lower 3×3 principle sub-matrix can be written as

$$A = \begin{pmatrix} -d_1 Y_2 & Y_2 & 0 \\ \beta_2 Z_2 & -d_2 Z_2 & J_{34} \\ 0 & cp(\alpha)\hat{w} & 0 \end{pmatrix},$$

where

$$Y_2 = \frac{cp(\alpha)k - m}{d_1 cp(\alpha)} \quad \text{and} \quad Z_2 = \frac{m}{cp(\alpha)}.$$

Then the characteristic polynomial of matrix A is

$$\lambda^3 + (d_1 Y_2 + d_2 Z_2) \lambda^2 + (-cp(\alpha) \hat{w} J_{34} + d_2 Z_2 d_1 Y_2 + \beta_2 Z_2 Y_2) \lambda - cp(\alpha) J_{34} d_1 \hat{w} Y_2 = 0,$$

where

$$\begin{cases} a_1 = d_1 Y_2 + d_2 Z_2 > 0, \\ a_2 = -cp(\alpha) \hat{w} J_{34} + d_2 Z_2 d_1 Y_2 + \beta_2 Z_2 Y_2 > 0, \\ a_3 = cp(\alpha) - J_{34} d_1 \hat{w} Y_2 > 0, \end{cases}$$

and

$$a_1 a_2 - a_3 = -cp(\alpha) J_{34} d_2 \hat{w} Z_2 + d_1^2 d_2 Y_2^2 Z_2 + d_1 d_2^2 Y_2 Z_2^2 + \beta_2 d_1 Y_2^2 Z_2 + \beta_2 d_2 Y_2 Z_2^2 > 0.$$

Therefore, by the Routh-Hurwitz criterion, the sub-matrix A only has negative eigenvalues. Thus, E_{234} is asymptotically stable if and only if

$$1 - \frac{cp(\alpha)k - m}{d_1 cp(\alpha)} < 0.$$

3.3. Existence and stability of the positive equilibrium. By solving the system

$$\begin{cases} 1 - x - y = 0, \\ k - d_1 y - z + \beta_1 x = 0, \\ f(\alpha, w) - d_2 z + \beta_2 y - p(\alpha) w = 0, \\ -m + cp(\alpha) z = 0, \end{cases} \quad (3.7)$$

we can find the expression of the possible positive equilibrium solution $E^* = (x^*, y^*, z^*, w^*)$ where

$$\begin{cases} x^* = \frac{cp(\alpha)(d_1 - k) + m}{cp(\alpha)(\beta_1 + d_1)}, \\ y^* = \frac{cp(\alpha)(\beta_1 + k) - m}{cp(\alpha)(\beta_1 + d_1)}, \\ z^* = \frac{m}{cp(\alpha)}, \end{cases}$$

and w^* is given by the equation

$$f(\alpha, w^*) - d_2 z^* + \beta_2 y^* - p(\alpha) w^* = 0.$$

Therefore, there exists a unique positive equilibrium if and only if the following inequalities hold

$$\begin{cases} cp(\alpha)(d_1 - k) + m > 0 \\ cp(\alpha)(\beta_1 + k) - m > 0, \\ f_0 - \frac{d_2 m}{cp(\alpha)} + \frac{cp(\alpha)\beta_2(\beta_1 + k) - \beta_2 m}{cp(\alpha)(\beta_1 + d_1)} > 0, \end{cases} \quad (3.8)$$

The Jacobian of the positive equilibrium is given by

$$J(E^*) = \begin{pmatrix} -x^* & -x^* & 0 & 0 \\ \beta_1 y^* & -d_1 y^* & -y^* & 0 \\ 0 & \beta_2 z^* & -d_2 z^* & J_{34} \\ 0 & 0 & cp(\alpha)w^* & 0 \end{pmatrix},$$

The corresponding characteristic equation is

$$\lambda^4 + a_1 \lambda^3 + a_2 \lambda^2 + a_3 \lambda + a_4 = 0,$$

where

$$\begin{cases} a_1 = d_1 y^* + d_2 z^* + x^* > 0, \\ a_2 = -J_{34} cp(\alpha)w^* + d_1 d_2 y^* z^* + \beta_1 x^* y^* + \beta_2 y^* z^* + d_1 x^* y^* + d_2 x^* z^* > 0, \\ a_3 = -J_{34} cp(\alpha) d_1 w^* y^* - J_{34} cp(\alpha) w^* x^* + \beta_1 d_2 x^* y^* z^* + d_1 d_2 x^* y^* z^* + \beta_2 x^* y^* z^* > 0, \\ a_4 = -J_{34} \beta_1 cp(\alpha) w^* x^* y^* - J_{34} cp(\alpha) d_1 w^* x^* y^* > 0. \end{cases}$$

Calculation gives

$$\begin{aligned} a_1 a_2 - a_3 &= -J_{34} cp(\alpha) d_2 w^* z^* + d_1^2 d_2 (y^*)^2 z^* + d_1 d_2^2 y^* (z^*)^2 + \beta_1 d_1 x^* (y^*)^2 + \beta_2 d_1 (y^*)^2 z^* + \beta_2 d_2 y^* (z^*)^2 \\ &+ d_1^2 x^* (y^*)^2 + 2d_1 d_2 x^* y^* z^* + d_2^2 x^* (z^*)^2 + \beta_1 (x^*)^2 y^* + d_1 (x^*)^2 y^* + d_2 (x^*)^2 z^* > 0 \end{aligned}$$

and

$$\begin{aligned} a_1 a_2 a_3 - a_1^2 a_4 - a_3^2 &= d_2 x^* z^* (cp(\alpha)w^* J_{34} + \beta_1 x^* y^*)^2 + d_1 d_2 y^* z^* (\beta_1 x^* y^* + cp(\alpha)w^* J_{34})^2 + \text{positive terms} > 0. \end{aligned}$$

Therefore, by the Routh-Hurwitz criterion, the positive equilibrium is locally asymptotically stable.

For readers' convenience, we summarize the results obtained above about the existence and stability of all the equilibria in Table 2.

As was done to rescaled model (1.5) in Section 2, we can also examine the relationship how the population size for each species at the stable positive equilibrium depends on the anti-predation level α . Indeed, we can calculate to obtain

$$\frac{dz^*}{d\alpha} = \frac{-m}{cp^2(\alpha)} \frac{dp}{d\alpha} > 0.$$

By using implicit differentiation on the system (3.7), we can also determine $\frac{dx^*}{d\alpha} > 0$ and $\frac{dy^*}{d\alpha} < 0$.

However, we are not able to determine the sign of $\frac{dw^*}{d\alpha}$.

From the above discussion, we see that after incorporating the benefit obtained by the meso-predator's anti-predation response in reducing the predation by the large carnivores, the final population sizes of the meso-predator, its prey and its prey's prey are increasing, decreasing, and increasing respectively with respect to the response strength α . This alternating pattern is totally opposite to the one obtained in Section 2 on this context.

TABLE 2. Condition of existence and stability of the equilibria in model (3.1)

Equilibrium solution	Existence	Stability
E_0	Always	Unstable
E_1	Always	Unstable
E_2	Always	$1 - k/d_1 < 0$ and $f_0 < -\beta_2 k/d_1$
E_3	$f_0 > 0$	Unstable
E_{12}	$k < d_1$	$f_0 < -\frac{\beta_2 k + \beta_2 \beta_1}{d_1 + \beta_1}$
E_{13}	$f_0 > 0$	$\frac{md_2}{cp(\alpha)} > f_0 > d_2(k + \beta_1)$
E_{23}	$d_2 k > f_0 > -\beta_2 k/d_1$	$f_0 > d_2 k - d_1 d_2 - \beta_2$ and $p(\alpha) < \frac{m(d_1 d_2 + \beta_2)}{c(k\beta_2 + d_1 f_0)}$
E_{34}	$f_0 > d_2 m/cp(\alpha)$	Unstable
E_{123}	$d_2(k + \beta_1) > f_0 > \max\left(d_2 k - d_1 d_2 - \beta_2, -\frac{\beta_2(k + \beta_1)}{d_1 + \beta_1}\right)$	$p(\alpha) < \frac{m(\beta_1 d_2 + d_1 d_2 + \beta_2)}{c(\beta_1 \beta_2 + \beta_1 f_0 + \beta_2 k + d_1 f_0)}$
E_{134}	$f_0 > d_2 m/cp(\alpha)$	$p(\alpha) < \frac{m}{c(k + \beta_1)}$
E_{234}	$cp(\alpha)k - m > 0$ and $f_0 > \frac{d_2 m}{cp(\alpha)} - \frac{\beta_2 cp(\alpha)k - \beta_2 m}{d_1 cp(\alpha)}$	$1 - \frac{cp(\alpha)k - m}{d_1 cp(\alpha)} < 0$
E^*	Condition (3.8)	Stable

3.4. **Numerical simulations.** In this part, we present some numerical simulations to illustrate the analytical results obtained above. To this end, we choose

$$B(\alpha, N_4) = \frac{R_3}{1 + c_1 \alpha N_4} \quad \text{and} \quad a_{34}(\alpha) = \frac{1}{1 + c_2 \alpha}$$

in (1.5), leading to the following system

$$\begin{cases} \frac{dN_1}{d\tau} = N_1 (R_1 - a_{11}N_1 - a_{12}N_2), \\ \frac{dN_2}{d\tau} = N_2 (R_2 - a_{22}N_2 - a_{23}N_3 + a_{21}N_1), \\ \frac{dN_3}{d\tau} = N_3 \left(\frac{R_3}{1 + c_1 \alpha N_4} - D_3 - a_{33}N_3 + a_{32}N_2 - \frac{N_4}{1 + c_2 \alpha} \right), \\ \frac{dN_4}{d\tau} = N_4 \left(-D_4 + \frac{cN_3}{1 + c_2 \alpha} \right), \\ N_1(0) \geq 0, \quad N_2(0) \geq 0, \quad N_3(0) \geq 0, \quad N_4(0) \geq 0, \end{cases} \quad (3.9)$$

We fix the parameters

$$\begin{aligned} R_1 = 3, \quad a_{11} = 1, \quad a_{12} = 0.4, \quad R_2 = 1, \quad a_{22} = 0.2, \quad a_{23} = 0.5, \quad a_{21} = 0.5, \\ R_3 = 3, \quad D_3 = 1, \quad a_{33} = 0.5, \quad a_{32} = 0.05, \quad c_1 = 0.4, \quad D_4 = 0.1, \quad c = 0.5, \quad c_2 = 0.2, \end{aligned} \quad (3.10)$$

and illustrate how α impacts the population dynamics.

For the above set of parameter values, $k = 1/3 < d_1 = 1/2$, the bifurcation diagram with respect to α is given in Figure 5. There is a transcritical bifurcation between E^* and E_{123} where the critical value α^* is given by

$$f_0 - \frac{d_2 m}{cp(\alpha^*)} + \frac{cp(\alpha^*)\beta_2(\beta_1 + k) - \beta_2 m}{cp(\alpha^*)(\beta_1 + d_1)} = 0.$$

Using the parameter values in (3.10), we can solve this equation to obtain $\alpha^* \approx 97.77777780$. We can observe a trophic cascade in Figure 5 inside the coexistence region with respect to increment of

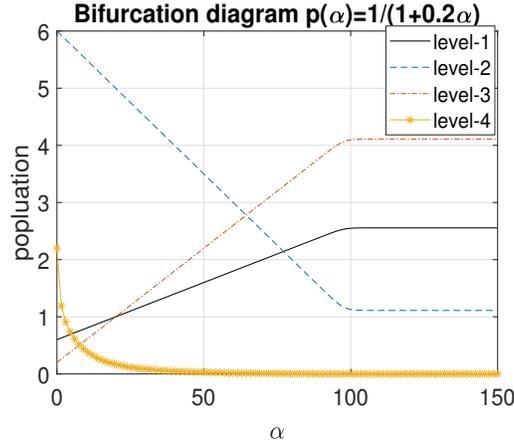


FIGURE 5. Bifurcation diagram of (3.9) when $k < d_1$.

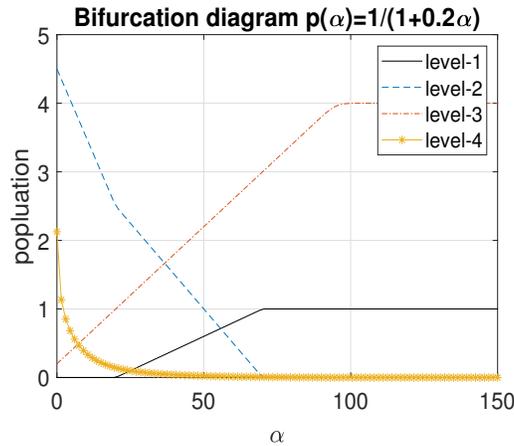


FIGURE 6. Bifurcation diagram of (3.9) when $k > d_1$.

α . Contrary to the previous section, this cascade shows an increasing population in odd level and decreasing population in even level.

Next, we change R_1 from $R_1 = 3$ to $R_1 = 1$ in (3.10) and keep the same values for other parameters. We then have $k = R_2/R_1 = 1$ and $d_1 = a_{22}/a_{12} = 1/2$ so that $k > d_1$. For this case, we observe more complicated dynamical behaviours: there are three critical values for α , denoted by $\bar{\alpha}_1$, $\bar{\alpha}_2$ and $\bar{\alpha}_3$, which are given by

$$\begin{cases} cp(\bar{\alpha}_1)(d_1 - k) + m = 0 \\ cp(\bar{\alpha}_2)(\beta_1 + k) - m = 0, \\ \frac{md_2}{cp(\bar{\alpha}_3)} = f_0. \end{cases}$$

Using the parameter values in (3.10), we obtain $\bar{\alpha}_1 = 20$, $\bar{\alpha}_2 = 70$ and $\bar{\alpha}_3 = 95$. In figure 6, when $0 < \alpha < \bar{\alpha}_1$, E_{234} is stable; when $\bar{\alpha}_1 < \alpha < \bar{\alpha}_2$, E^* is stable; when $\bar{\alpha}_2 < \alpha < \bar{\alpha}_3$, E_{134} is stable; when $\bar{\alpha}_3 < \alpha$, E_{13} is stable. We can also observe trophic cascade in this case as is shown in Figure 6.

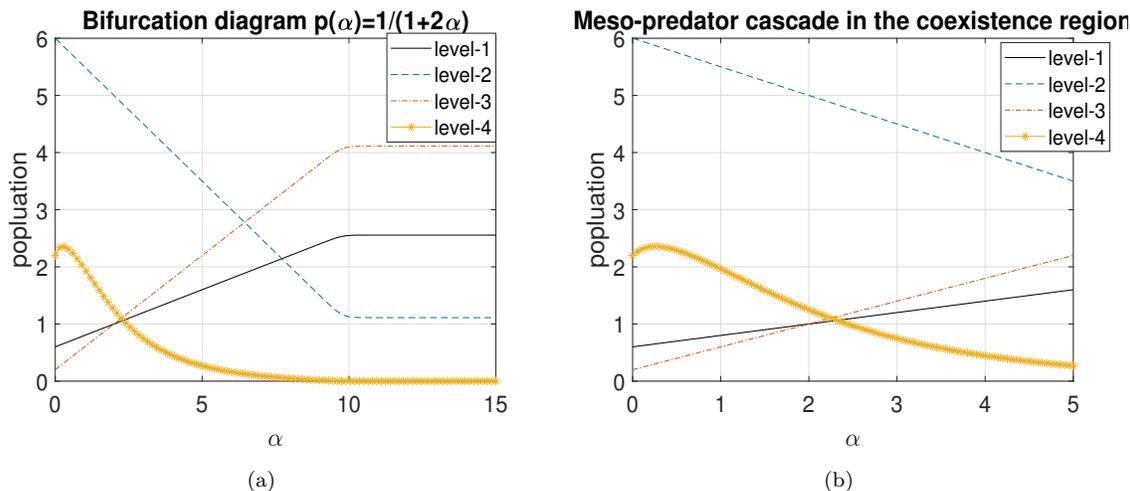


FIGURE 7. (a) Bifurcation diagram of (3.9) when $c_2 = 2$, (b) In the region when the coexistence equilibrium E^* is stable, we can observe a meso-predator cascade with non-monotonically change on top predator.

In the last two cases, we can see that population size of large carnivores at the positive equilibrium is monotonically decreasing. We point out that this is dependent on the choice of the benefit reflecting term $p(\alpha) = a_{34}(\alpha)/a_0$. To see this, we change c_2 from 0.2 to 2 (corresponding to a more significant benefit to N_3 and disadvantage to N_4), then, as is shown in Figure 7-(a), we can see a transcritical bifurcation from E^* to E_{123} at threshold value $\tilde{\alpha} = 10.43750000$, and before this value, $w^*(\alpha)$ is not monotone: it increases first and then decreases. Figure 7-(b) is an enlargement of (a) in which, one can more clearly see that while the lower trophic still follow the cascade, the top predator (w^*) increases first and then decreases with respect to the increment of α . Thus, the response function $p(\alpha)$ has an impact of the trophic cascade.

4. CONCLUSION AND DISCUSSIONS

A recent experimental study [25] in fields observed a phenomenon of trophic cascade in a food chain population system consisting of three species, i.e., meso-carnivore on top, its prey in the middle and the prey's prey in the bottom, caused by the fear of virtual large carnivores which is implemented by playback of the large carnivores. This phenomenon, together with some recent works on fear effect in two species predator-prey models, has motivated us to theoretically explore the mechanisms for such trophic cascade in this paper. To this end, we have proposed two models, (1.3) and (1.5), with (1.3) directly corresponding to the scenario of field study in [25], and (1.5) being an extension to include a benefit in the meso-carnivore from the anti-predation response, in addition to a cost, as in (1.3). In order to incorporate the benefit term into the model, we have to add the population of the large carnivores into the interplay, making (1.5) a 4-D system.

We have thoroughly analyzed the two models, using the approach of dynamical systems. For each of the two models, we have obtained complete structure of the equilibria, and established their stability/instability in terms of the model parameters, in the form of thresholds for certain parameters. For model (1.3) our results show that an anti-predation response *at lower level* is *beneficial* to the top and

bottom species (N_3 and N_1); while *at higher level*, it is *beneficial* to the middle species (N_2) but *disadvantageous* to N_3 and N_1 , confirming the phenomenon of trophic cascade reported in that experimental study. For model (1.5), our results show that there are now three threshold values for the response level α , distinguishing ranges for α accounting for various combinations of co-existence among the four species. Particularly, within certain range of parameters, the model also demonstrates the phenomenon of trophic cascade but with an opposite alternating pattern for the three species (the meso-carnivore, its prey and its prey's prey): increasing the response level α is *beneficial* to N_3 and N_1 but *disadvantageous* to N_2 . This change is attributed to the effect of the benefit of the anti-predation response in reducing the predation and its balance with cost of such a response.

Our results can have ecological implications as they may suggest practical strategies of management/control for maintaining biodiversity. For example, in some ecosystems, populations of some meso-predators have been observed to increase significantly due to the loss/extinction of larger carnivores, and this has in turn put some pressure on the meso-predators' preys for their survivals. Our results on model (1.3) suggest that by creating certain virtual situations (e.g. vocal) mimicking the large carnivore predators, one may expect to reduce the populations of the meso-predators, and consequently relax the pressure on the meso-predators' preys. On the other hand, if the large (top) predators of the meso-predators are present, their predation on the meso-predators poses a major threat to the meso-predators. In such a case, by our results on model (1.5), creating the aforementioned virtual situations may stimulate the meso-predators to increase their anti-predation response level, which will then reduce the predation risk by the top predators. This way, the *benefit* of anti-predation response of the meso-predators in reducing the predation risk may outplay the *cost* in production, and thus, enhance the survival probability of the meso-predators. Such a net benefit in the meso-predators can then be passed on to the lower level species in an alternating fashion. Therefore, the risk events such as fear effect in some species in an ecosystem may actually offer a management tool in shifting the structure of ecosystem and help conserve the biodiversity.

Note that in our model, we have used the mass action or Holling Type I functional responses as the predation mechanism. For some species between which the predation involves foraging, this mechanism is not suitable and other types of functional responses should be adopted. It would be interesting and worthwhile to investigate the population dynamics in models like (1.3) and (2.1) with such replaced functional responses. We also point out that in our models, we have only considered fear effect of meso-carnivore species N_3 against the large carnivores N_4 . Such fear effect may also exist in N_2 against N_3 and in N_1 against N_2 . Modeling fear effect in those or in all levels would also be interesting but would be very challenging mathematically.

We remark that for predator-prey interactions between *two species only*, the recent works mentioned in the introduction may also suggest some possible extensions and expansions of the two models in this paper. For example, one may also incorporate age structure, spatial structure, digestion delay, extra food, stochastic noise, as was done in [8, 18, 31, 32, 33]. Efforts on all these lines will greatly enhance our understanding of predator-prey interactions, and enrich the theory in this area.

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