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# A diffusive one-prey and two-competing-predator system with a ratio-dependent functional response: I, long time behavior and stability of equilibria

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ABSTRACT

We study a ratio-dependent reaction–diffusion system incorporating one prey and two competing predator species under homogeneous Neumann boundary conditions. In this paper, we examine the global attractor and persistence of the system, which characterize the long time behavior of the time-dependent solution, and the stability of all non-negative equilibria of the system. We classify the relations between two competing predators into four categories via domination of one predator over another and weak/strong competition states. These competition states will be the criteria which influence the outcomes of the system. The results include total extinction, competitive exclusion, behavior of a predator driving the extinction of another predator and its prey, behavior of a predator saving its competing predator and prey on the verge of extinction.



## 1. Introduction

In this paper, we study the following reaction–diffusion system with a ratio-dependent functional response:

$$\begin{cases} u_t - d_1\Delta u = u\left(1 - u - \dfrac{c_1 v}{u+\alpha_1 v+\beta_1 w} - \dfrac{c_2 w}{u+\alpha_2 v+\beta_2 w}\right) & \\ v_t - d_2\Delta v = v\left(\dfrac{m_1 u}{u+\alpha_1 v+\beta_1 w} - b_1\right) & \\ w_t - d_3\Delta w = w\left(\dfrac{m_2 u}{u+\alpha_2 v+\beta_2 w} - b_2\right) & \text{in } (0,\infty)\times\Omega, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = \dfrac{\partial w}{\partial \nu} = 0 & \text{on } (0,\infty)\times\partial\Omega, \\ u(0,x) = u_0(x), \qquad v(0,x) = v_0(x), \qquad w(0,x) = w_0(x) & \text{in } \Omega, \end{cases} \tag{MP}$$

where $\Omega \subseteq \mathbb{R}^N$ is a bounded spatial region with a smooth boundary $\partial\Omega$; $\nu$ is the outward unit normal vector of the boundary $\partial\Omega$; the given coefficients $c_i$, $m_i$, $b_i$, $\alpha_i$, $\beta_i$ and $d_i$ are positive constants; the initial values $u_0$, $v_0$ and $w_0$ are non-negative smooth functions which are not identically zero. Throughout this article, we assume that $\Omega$ and $N$ are fixed.

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Model (MP) describes the population dynamics of three species which disperse by diffusion in the habitat area $\Omega$. $u$, $v$ and $w$ stand for the densities of the prey and two predators, respectively. The interaction between prey and predator species is based on a ratio-dependent functional response, that is, the rate at which an individual predator species consumes an individual prey species and two predators compete for single prey. Thus system (MP) is the so-called food web model with one prey and two competing predators. The parameters $c_i$ are the capturing (or catching efficiency) rates of the predators; $m_i$ are the conversion rates (or maximum growth rates); $b_i$ are the death rates; $\beta_1$ and $\alpha_2$ can be regarded as the relative competition efficiency of the other predator species, $w$, and the prey species, $v$, for the prey species, respectively. $\alpha_1$ and $\beta_2$ can be also regarded as the relative competition efficiency of the same predator species $v$ and the prey species, $w$, respectively. $d_i$ are the diffusion rates of the corresponding species (the single prey, first and second predators). The homogeneous Neumann boundary condition means that (MP) is self-contained and has no population flux across the boundary $\partial\Omega$.

In order to illustrate a set of candidate coupled differential equations which will govern the population dynamics of the multi-species system, we present the following ODE system:

$$\frac{dx_i}{dt} = r_i x_i - b_i \frac{r_i}{K_i} x_i^2 + m x_i \sum_j f_{ij} - \sum_j x_j f_{ji}, \tag{1.1}$$

which can be obtained by slightly modifying or generalizing the models proposed in [1–3]. Here $x_i$ is the population size of species $i$, and $f_{ij}$ are the functional responses dependent on the population sizes. The given coefficients are all constants which have following meanings: $m$ is the ecological efficiency; $r_i$ is a positive intrinsic growth rate for basal species (those that have no resources) or a negative death rate for other species; $K_i$ is the carrying capacity; $b_i$ is equal to 1 for basal species or 0 for other species. Thus $m$ and $K_i$ are positive constants; $r_i$ is a positive or negative constant. For more biological background information, see [1–4]. Until very recently, the most well-known and widely used forms of the functional response $f_{ij}$ were the Lotka–Volterra, Holling type II (or Michaelis–Menten), Beddington–DeAngelis and the ratio-dependent type—see [5,1–3,6–10,4] and references therein for ODE systems; [11–22] for PDE systems with homogeneous Neumann boundary conditions.

In particular, among the above functional responses, there has been much debate about the predator–prey model with the Holling type II functional response that exhibits the highly controversial "paradox of enrichment", which means that enriching a predator–prey system (by increasing the carrying capacity) causes an increase in the equilibrium density of the predator but not in that of the prey and destabilizes the positive equilibrium [6–8,10]. After careful consideration of this problem, Arditi and Ginzburg [5] proposed the $2 \times 2$ predator–prey model with a ratio-dependent type functional response, wherein the extinction of the prey species can be observed. Since then, it has been strongly championed by researchers in numerous fields and supported by laboratory experiments and observations. These observations show that in many situations when predators have to search, share and compete for their resources, a suitable functional response should be ratio-dependent. These ratio-dependent models display the richest dynamics (e.g., total extinction), while the others show the least in dynamical behavior [6,7,10]. Further, for multi-species interactions, Arditi and Michalski [1] proposed the following generalized ratio-dependent functional response:

$$f_{ij} = \frac{a_{ij} x_j^{r(i)}}{x_i + \sum\limits_{k \in R(i)} b_{ik} x_k^{r(i)}}$$

with the self-consistent conditions

$$x_j^{r(i)} = \frac{\beta_{ji} x_i^{C(j)} x_j}{\sum\limits_{k \in C(j)} \beta_{jk} x_k^{C(j)}} \quad \text{and} \quad x_k^{C(i)} = \frac{h_{jk} x_j^{r(k)} x_k}{\sum\limits_{l \in R(k)} h_{lk} x_l^{r(k)}},$$

where $a_{ij}$ is the coupling constant; $b_{ik}$ is the handling time of predator species $i$ for prey species $k$; $\beta_{ij}$ is the efficiency of predator $i$ for prey $j$; $h_{jk}$ is the relative preference of predator $j$ for prey $k$; $R(i)$ are the prey species for predator $i$; $C(i)$ are the predator species on prey $i$; $x_j^{r(i)}$ is the part of species $j$ that is currently being accessed as resource by species $i$; $x_k^{C(j)}$ is the part of species $k$ that is currently acting as predator of species $j$.

Among the specific examples which can be derived from (1.1) with a ratio-dependent functional response $f_{ij}$, the models qualitatively studied are the two-species predator–prey system in [6,10], and a simple food-chain ODE system in [8]. Furthermore, by using deep mathematical analysis, the long-time behavior and emergence of stationary pattern in their corresponding reaction–diffusion systems were also investigated under homogeneous Neumann boundary conditions; see [19] for a diffusive ratio-dependent predator–prey system, [15,21] for a ratio-dependent simple food-chain model with diffusion.

Regarding our topic, we consider a food-web (1.1) consisting of three species, a prey(basal) $x_1$, two predators $x_2$ and $x_3$ (which eat $x_1$). Then, using the obvious fact that $x_2^{C(x_1)} = x_2$ and $x_3^{C(x_1)} = x_3$, we can derive

$$x_1^{r(x_2)} = \frac{\beta_{12} x_1 x_2}{\beta_{12} x_2 + \beta_{13} x_3} \quad \text{and} \quad x_1^{r(x_3)} = \frac{\beta_{13} x_1 x_3}{\beta_{12} x_2 + \beta_{13} x_3},$$