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A Michaelis–Menten type food chain model with strong Allee effect on the prey

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ABSTRACT

Dynamical behaviours of a tritrophic food chain model with strong Allee effect in the prey are studied in this paper. Positivity and boundedness of the system are discussed. Some global results on extinction of the species are derived. Stability analysis of the equilibrium points is presented. The effect of discrete time-delay is studied, where the delay may be regarded as the gestation period of the superpredator. Numerical simulations are carried out to validate our analytical findings. Implications of our analytical and numerical findings are discussed critically.

1. Introduction

The study of *food chains* is a central part of ecology, and mathematical modelling of food chains has played an important role in driving progress in modern ecology research. Charles Sutherland Elton has coined the term ‘food chain’ in his classical book “Animal Ecology” [16]. The concept of *trophic level* was introduced by Raymond L. Lindeman [23]. The first mathematical model of food chain was developed independently by Alfred James Lotka (a US physical chemist) and Vito Volterra (an Italian mathematician) [24,37]. Subsequently many modifications of the Lotka–Volterra model have been done. The study of the dynamics of tritrophic models has been started in the late seventies of the twentieth century. For a historical account of the theoretical works on food chain models, see references [7,26].

The trophic level of an organism is the position it occupies in a food chain. In case of three-species (or tri-trophic) food chains, we usually call the species at trophic level 1 as *prey*, the species at trophic level 2 as the *middle predator*, and the species at trophic level 3 as the *top predator* or *superpredator*. Behaviour of the entire community is assumed to arise from the coupling of these interacting species, where Z prey on Y and only on Y and Y prey on X (see Fig. 1). Also a distinct feature of these food chains is the so called *domino effect*: if one species dies out, all the species at higher trophic level die out as well.

It has long been recognised that the famous *logistic growth function* has the capability of describing individual population growth. The function is introduced in 1838 by the Belgian mathematician Pierre Francois Verhulst [36] and later it is rediscovered in 1920 by American biologists Reymon Pearl and Lowell Reed [30]. If $X(T)$ denotes the population density at

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Prey
↓
Predator
↓
Superpredator

Fig. 1. The feeding relationship in the food chain.

time T, then the logistic growth equation is given by

$$\frac{dX}{dT} = rX\left(1 - \frac{X}{K}\right), \tag{1.1}$$

where r is the intrinsic per capita growth rate and K is the carrying capacity of the environment. The logic behind this is very simple. As the resources (e.g., space, food, essential nutrients) are limited, every population grows into a saturated phase from which it cannot grow further; the ecological habitat of the population can carry just so much of it and no more. This suggests that the per capita growth rate is a decreasing function of the size of the population, and reaches zero as the population achieved a size K (in the saturated phase). Further, any population reaching a size that is above this value will experience a negative growth rate. The term $-rX^2/K$ may also be regarded as the loss due to intraspecies competition. Although logistic growth function became extremely popular, but, in real life situations, researchers found many evidences where the populations show a reverse trend in low population density [8,12,14,15,28,31]. This phenomenon of positive density dependence of population growth at low densities is known as the *Allee effect* [15,34].

The phenomenon of *Allee effect* is named after the US Behavioral scientist Warder Clyde Allee (although Allee never used the term 'Allee effect'). Allee described this concept in three of his papers [3–5]. Actually, the term 'Allee effect' was introduced by Odum [29]. Since the late eighties of the 20th century, the concept gained importance but there were necessity of clear-cut definitions and clarification of concepts. The necessity was fulfiled when three reviews by Stephens et al. [34], Courchamp et al. [14], Stephens and Sutherland [33]. There are many reasons for Allee effect, such as difficulty in mate finding, reduced antipredator vigilance, problem of environmental conditioning, reduced defense against predators, and many others (for thorough reviews, see references [8,15]).

The Allee effect can be divided into two main types, depending on how strong the per capita growth rate is depleted at low population densities. These two types are called the strong Allee effect [35,39,40] or critical depensation [10,11,22], and the weak Allee effect [34,38] or noncritical depensation [10,11,22]. Usually, the Allee effect is modelled by a growth equation of the form

$$\frac{dX}{dT} = rX\left(1 - \frac{X}{K}\right)\left(\frac{X}{K_0} - 1\right), \tag{1.2}$$

where $X(T)$ denotes the population density at time T, r is the intrinsic per capita growth rate, and K is the carrying capacity of the environment. Here $0 < K_0 < <K$. When $K_0 > 0$ and the population size is below the threshold level K_0, then the population growth rate decreases [6,13,17,20], and the population goes to extinction. In this case, the equation describes the *strong Allee effect* [35,39,40]. On the contrary, the description of *weak Allee effect* is also available (see references [18,39]). In this paper, we are concerned with strong Allee effect. The above growth is often said to have a *multiplicative Allee effect*. There is another mathematical form of the growth function featuring the *additive Allee effect*. In this paper, we are not interested in additive Allee effect (interested readers might see the works of Aguirre et al. (2009) (a & b)) [1,2]. A comparison of the logistic growth function of (1.1) and the function representing Allee effect in Eq. (1.2) can be found in [27].

Recently predator-prey models with Allee effect have got the attention of the theoretical ecologists (see the references cited in last three paragraphs). Unfortunately, theoretical ecology has so far remained silent about the consequence of Allee effect on tritrophic food chain model. In the present work, we present the bizarre behaviour of a tritrophic food chain model, where the prey is vulnerable to strong Allee effect.

The rest of the paper is organised as follows. In Section 2, we present a brief sketch of the construction of the model and the biological relevance of it. In Section 3, positivity and boundedness of the basic deterministic model are discussed. Some theorems on extinction of the populations are presented in Section 4. Section 5 deals with the equilibrium points and their stability analysis. The effect of discrete time-delay is studied in Section 6. In Section 7, computer simulation of a variety of numerical solutions of the system is presented. Section 8 contains the general discussions on the results and biological implications of our mathematical findings.

2. The mathematical model

Before we introduce the mathematical model, let us describe the basic assumptions that we made to formulate it.

1. The biological system we consider is composed of a single prey population whose density at time T is denoted by X. There is a middle predator and a superpredator, whose population densities at time T are Y and Z respectively. The behaviour of the entire community is assumed to arise from the coupling of these three populations, where Y is the only predator for prey population X, and superpredator Z has only food resource Y.