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The impact of Allee effect on a predator–prey system with Holling type II functional response

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ABSTRACT

In this paper, the Allee effect is incorporated into a predator–prey model with Holling type II functional response. Compared with the predator–prey model without Allee effect, we find that the Allee effect of prey species increases the extinction risk of both predators and prey. When the handling time of predators is relatively short and the Allee effect of prey species becomes strong, both predators and prey may become extinct. Moreover, it is shown that the model with Allee effect undergoes the Hopf bifurcation and heteroclinic bifurcation. The Allee effect of prey species can lead to unstable periodical oscillation. It is also found that the positive equilibrium of the model could change from stable to unstable, and then to stable when the strength of Allee effect or the handling time of predators increases continuously from zero, that is, the model admits stability switches as a parameter changes. When the Allee effect of prey species becomes strong, longer handling time of predators may stabilize the coexistent steady state.

1. Introduction

Both positive and negative interactions among species are common in communities [1,2]. For example, synchronous breeding is an important mechanism by which colonial guillemots (*Uria aalge*) increase reproductive success. Many carnivore species are better able to capture large prey by cooperative hunting and group living may thus be favored in areas with abundant large prey [3]. Historically, attention has focused on negative interactions, such as competition. However, for the last decade, the importance of positive interactions such as the Allee effect [4] has recently been recognized [1,5]. The Allee effect [4], and more recently as depensation [6] or inverse density dependence [7], refers to a decrease in per capita fertility rate at low population densities. Allee effect may occur under several mechanisms, such as difficulties in finding mates when population density is low [8,9], social dysfunction at small population sizes and increased predation risk due to failing flocking or schooling behavior [10,11]. When such mechanisms operate, the per capita fertility rate of a species increases with density, that is, positive interactions among species occur. The primary consequence of the Allee effect is that it creates a threshold density below which a population cannot survive. For example, this might correspond to the density below which it is so difficult to find a mate that reproduction does not compensate mortality. Each population whose density stochastically goes below this threshold is fated to extinction and species experiencing Allee effect are therefore more extinction prone [11]. The phenomenon has received considerable attention from ecologists [12,13]. The importance of this dynamic process in ecology has been under-appreciated and recent evidence [14] now suggests that it might have an important influence on the population dynamics of many plants and animal species. Therefore, the investigation of Allee effects is important for conservation biology [15].

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Interactions among species in a food web are multiform. Among these, the interactions between predators and prey are important. Predator–prey interactions are ubiquitous in nature and the dynamical behaviors of predator–prey system are very complex. Many forces may influence the dynamical behaviors of the predator–prey system [11,12]. It has been shown that a predator–prey model can lead to oscillatory behavior because of a nonlinear functional response. Interest in the stability of predator–prey system has continued unabated since the theoretical work of Lotka [16], Volterra [17] and the experimental work of Gause [18]. Theoreticians and experimentalists have proceeded to investigate the processes that affect the stability of predator–prey system [19,20]. Among the many processes that the Lotka–Volterra model ignores, the Allee effect may be the most important [21]. The Allee effect increases the likelihood of local and global extinction. But there have been few papers discussing its stabilizing or destabilizing effects on the predator–prey system (except for [21,22,33]). Kent et al. [22] conclude that the predator–prey system is stabilized by an influx of prey in the form of a rescue effect, and destabilized by an out flux of Allee effect. By combining mathematical analysis with numerical simulation, Zhou et al. [21] have shown that the Allee effect may be a destabilizing force in predator–prey system. However, the Lotka–Volterra model they considered does not consider the density-dependent effect of prey and the functional response is linear. Functional response is a double rate: it is the average number of prey killed by per individual predator per unit of time. In general, the functional response can be classified into two types: prey-dependent and predator-dependent. Prey-dependent means that the functional response is only a function of the prey's density, while predator-dependent means that the functional response is a function of both densities of the prey and predators. Functional response that is strictly prey-dependent, such as the Holling family, is predominant in the literature. For example, since 1959, Holling's prey-dependent type II functional response has served as the basis for many literatures on predator–prey theory. Therefore, the predator–prey model with Holling type II functional response is more realistic. However, the impact of the Allee effect on the stability of a predator–prey system with Holling type II functional response is poorly understood both empirically and theoretically.

The purpose of this paper is to show that the Allee effect of prey species has significant effects on the dynamics of predator–prey model with Holling type II functional response. We will investigate how predator and prey species are threatened by extinction when the population density of prey becomes low. Moreover, we will show that the predator–prey model with Allee effect and Holling type II functional response undergoes a sequence of bifurcations including supercritical Hopf bifurcation, subcritical Hopf bifurcation and heteroclinic bifurcation. We will also present a global analysis of the model by means of numerical simulations.

The organization of this paper is as follows. In the next section, we present the formulations of mathematical model with Allee effect. In Section 3, we present a qualitative analysis of the model. In Section 4, we use numerical simulations to reveal the global bifurcation structures and the influence of Allee effect on the dynamical behaviors of the model. A brief discussion is given in Section 5.

2. Model formulations

In this section, we first introduce the Rosenzweig–MacArthur predator–prey model with Holling type II functional response. Based on this model, we will construct a predator–prey model with Allee effect on prey species.

2.1. Rosenzweig–MacArthur predator–prey model

The objective of this subsection is to introduce the predator–prey model with Holling type II functional response and summarize its dynamical behaviors.

The classical Lotka–Volterra predator–prey model did not contain saturating effect. More realistically, the functional response of predator population is nonlinear. The Rosenzweig–MacArthur predator–prey model with Holling type II functional response is as follows:

$$\begin{cases} \dfrac{dN}{dt} = N(b - d_1 - \alpha N) - \dfrac{sNP}{1 + sh_1 N}, \\ \dfrac{dP}{dt} = \dfrac{c_1 sNP}{1 + sh_1 N} - d_2 P, \end{cases} \tag{1}$$

where N and P denote the population densities of prey and predators at time t, respectively, b is the per capita maximum fertility rate of prey population, d_i $(i = 1,2)$ are the per capita death rates of prey and predators respectively, α denotes the strength of intra-competition of prey population, s denotes the effective search rate, h_1 denotes the handling time of predators, and c_1 denotes the conversion efficiency of ingested prey into new predators. The product, $sN/(1 + sh_1N)$, represents the predator's functional response, i.e. the relationship between prey density, N, and the amount ingested by an average predator. All the parameters are positive constants. Further, we assume that the growth rate of prey must exceed its death rate, i.e., $b > d_1$, otherwise, both prey and predators will become extinct. In addition, the maximum growth rate of predator population must exceed its death rate, i.e., $c_1/h_1 > d_2$. If not, prey population will never be able to sustain predators, which will go to extinction. In model (1), if the carrying capacity of prey $(b - d_1)/\alpha$ is low, i.e.,

$$0 < \frac{b - d_1}{\alpha} < \frac{d_2}{s(c_1 - h_1 d_2)}, \tag{2}$$