



# Intra-specific competition in predator can promote the coexistence of an eco-epidemiological model with strong Allee effects in prey



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## ABSTRACT

An eco-epidemiological model with Allee effects and disease in prey has been proposed and analyzed. The proposed model incorporates intra-specific competition in predator due to the limited food source, and assumes standard incidence disease transmission. We analyzed the corresponding submodels with and without the Allee effects to obtain the complete dynamics of the full model. Our results show that our full model shows multi-stability between the planner equilibriums (where the susceptible prey coexists with infected prey or predator); both the full model and its submodels exhibit the hydra effects caused by the intra-specific competition in predator. We determined the existence of multiple interior attractors and their stability. Our analysis shows that our system has at most two interior equilibria whose stability is either both saddle or one stable with another one saddle. One of the most interesting findings is that the competition in the predator can promote the coexistence of all the three populations. In addition, we discussed how the frequency-dependent transmission differs from the model with the density-dependent transmission and compare the hydra effects observed in our model to other existing models in literature.

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## 1. Introduction

An Allee effect is a natural phenomenon describing a positive correlation between the population size/density and the per-capita growth rate ( $pgr$ ) at low population densities (Allee, 1931; Odum and Allee, 1954). Component Allee effects are measurable ecological components that increase with population size. The synergy of component Allee effects and negative density factors such as competition can result in demographic Allee effects (Stephens et al., 1999; Courchamp et al., 2008). When a species experiences a demographic Allee effect, there is a critical threshold population density (known as Allee threshold) below which the  $pgr$  becomes negative and extinction becomes an almost certain event; above which the  $pgr$  is positive and the species may sustain. Due to the significant biological relevance of Allee effects, the concept of Allee effects receives substantial attention from both theoretical and applied ecologists. Allee effects have great impacts in species' establishment, persistence, invasion (Amarasekare, 1998; Wang et al., 2002,

2011b; Drake, 2004; Taylor and Hastings, 2005; Shi and Shivaji, 2006; Berezovskaya et al., 2010) and evolutionary traits (Cushing and Hudson, 2012). Empirical evidence of the Allee effect has been reported in many natural populations, including plants (Groom, 1998; Ferdy et al., 1999), insects (Kuussaari et al., 1998), marine invertebrates (Stoner and Ray-Culp, 2000), birds and mammals (Courchamp et al., 2000a). For details of the Allee effects we refer the reader to see the reviews of Courchamp et al. (2008), William (2010) and the references therein. Allee effects on population interaction have been studied by many researchers [e.g., see (Schreiber, 2003; Zhou et al., 2004; Jang, 2011; Kang and Yakubu, 2011; Wang et al., 2011a; Kang et al., 2014b)]. Disease is known as one of the basic reasons for species extinction. When disease is coupled with Allee effects then the systems are more prone to extinction (Hilker et al., 2007). The combined impact of disease and the Allee effect are observed in African wild dog *Lycaon pictus* (Courchamp et al., 2000b) and island fox *Urocyon littoralis* (Angulo et al., 2007). Recently much research has been done on Allee effects in the presence of disease (Yakubu, 2007; Hilker et al., 2009; Thieme et al., 2009; Sasmal and Chattopadhyay, 2013; Kang et al., 2014a; Sasmal et al., 2014). These studies suggest that Allee effects have important roles in population dynamics, especially when it couples with disease.

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It has long been known that increasing a predator's mortality rate can increase its population size (Rosenzweig and MacArthur, 1963). A review by Abrams (2009) discusses how the greater mortality rate increases the population size. This phenomenon is known as "hydra effects" (Abrams and Matsuda, 2005). Hydra effects have been recognized in many discrete-time ecological models (Sinha and Parthasarathy, 1996; Schreiber, 2003; Hilker and Westerhoff, 2006; Seno, 2008; Zipkin et al., 2009; Liz, 2010; Dattani et al., 2011; Sieber and Hilker, 2012) and continuous-time models (Abrams et al., 2003; Matsuda and Abrams, 2004) as well as models with delays (Terry and Gourley, 2010). For more details we refer to see the recent review by Abrams (2009) and the references therein on hydra effects. In this study, prey population is subject to strong Allee effects and disease, and there is no alternative food source for the predator population. Due to the limited food resource, predator population experiences intra-specific competition.

The prey–predator interaction model with disease is termed as the eco-epidemiological model, which was first introduced by Haderler and Freedman (1989). After that, researchers are paying more interest to the eco-epidemiological models that merge the research of ecology and epidemiology (Freedman, 1990; Beltrami and Carroll, 1994; Venturino, 1995, 2002; Beretta and Kuang, 1998; Chattopadhyay and Arino, 1999; Xiao and Chen, 2001; Chattopadhyay and Pal, 2002; Hethcote et al., 2004; Bairagi et al., 2007; Su et al., 2008). Disease transmissions are often influenced by aggregation patterns in the host population as well as its social organization. Two different types of incidence rates, i.e., density-dependent and frequency-dependent, are usually distinguished and used in epidemiology (Hethcote, 2000; McCallum et al., 2001; Begon et al., 2002; Potapov et al., 2012). Functional response is also a very important factor in the dynamical outcomes of predator–prey interaction models. Holling type I/II/III (Holling, 1959) functional responses are more common in literature.

In this article, we extend the model studied by Kang et al. (2014a) to a new model incorporating (1) the frequency-dependent disease transmission instead of the density-dependent disease transmission; and (2) the intra-specific competition in the predator population due to the limited food resource. We have performed a methodical study on the stability behavior of our proposed system to explore the interplay among the Allee effects, disease, predation and hydra effects. The rest of the paper is organized as follows: Section (2) provides the development of the model; in Section (3), we discuss the dynamics of the full model with disease free/ predation free, and compare the dynamics of submodels with and without the Allee effects. Detailed analysis of the full model and related numerical simulations are discussed in Section (4). In this section, we also provide the biological impacts of the Allee effects, disease and predation in presence of hydra effects. The paper ends with a discussion in Section (5).

## 2. Formulation of the model

Our model is an eco-epidemiological model with strong Allee effects and disease in the prey population. Our proposal model is distinct from the model studied by Kang et al. (2014a) with the following two modifications.

First, we have considered that the disease is transmitted through the frequency-dependent law (Hethcote, 2000; McCallum et al., 2001; Begon et al., 2002; Potapov et al., 2012) instead of the density-dependent disease transmission as studied in Kang et al. (2014a). Two different types of incidence rate are usually distinguished; one is density-dependent and another one is frequency-dependent (Hethcote, 2000; McCallum et al., 2001). If the disease is transmitted by the mass action law, then disease may die out as the population density decreases, but if the host's growth is subjected

to the Allee effect, then the system may be destabilized through the catastrophic population crash (Hilker et al., 2009). Thus it will be interesting to study how the frequency-dependent incidence rate may produce different dynamics in the presence of the Allee effects.

Second, we have considered that predator population experiences intra-specific competition due to the limited number of prey, since preys are suffered from the strong Allee effects and disease. We also assume that there is no alternative food source for the predator. The additional mortality of predator due to intra-specific competition may generate "hydra effect" that promotes the persistence of predator (Rosenzweig and MacArthur, 1963; Abrams and Matsuda, 2005; Abrams, 2009). It would be interesting to see how the intra-specific competition in predator affect the dynamical outcomes of prey and predator population in the presence of strong Allee effects and disease in prey.

Thus, an eco-epidemiological model with susceptible prey, infected prey and predator along with the strong Allee effects on prey and intra-specific competition on predator, is given by the following set of nonlinear differential equations (the detailed modeling approach is described in Kang et al. (2014a)).

$$\begin{aligned} \frac{dS}{dt} &= S \left[ (S - \theta)(1 - S - I) - \frac{\beta I}{S + I} - aP \right], \\ \frac{dI}{dt} &= I \left[ \frac{\beta S}{S + I} - aP - \mu \right], \\ \frac{dP}{dt} &= P [caS + \delta aI - d - fP] = P [bS + \alpha I - d - fP]. \end{aligned} \quad (2.1)$$

where all parameters except  $\delta$  are nonnegative. The parameter  $\beta$  represents the disease transmission rate of susceptible prey, whereas the parameter  $a$  represents the predation rate of both susceptible prey and infected prey by predator. Parameters  $\mu$  and  $d$  are the death rate of infected prey and predator respectively where  $\mu$  is the sum of natural death and disease induced additional death. The parameter  $c \in (0, 1]$  is the conversion rate of susceptible prey biomass into predator biomass, and  $\delta$  indicates that the effects of the consumption of infected prey on predator which could be positive or negative. We assume that  $-\infty < \delta < c$ ;  $\delta < 0$  indicates that consumption of infected prey increases the death rate of predator (Sasmal and Chattopadhyay, 2013; Kang et al., 2014a). The parameter  $f$  is the predator's crowding effect. Our modeling approach and assumptions require that the parameters of (2.1) are subject to the following conditions:

$$0 < \theta < 1, \quad 0 < b = ac \leq a \quad \text{and} \quad -\infty < \alpha < b. \quad (2.2)$$

The basic dynamical property of (2.1) can be summarized in the next lemma.

**Lemma 2.1.** [Basic dynamical features] Assume that  $b \leq a$ ,  $-\infty < \alpha < b$ ,  $\theta \in (0, 1)$ , then system (2.1) is positively invariant and bounded in  $\mathbb{R}_+^3$  with the following property

$$\limsup_{t \rightarrow \infty} \{S(t) + I(t)\} \leq 1.$$

In addition, if  $S(0) < \theta$ , then we have  $\lim_{t \rightarrow \infty} \max\{S(t), I(t), P(t)\} = 0$ .

Here we omit the proof of basic dynamical features of the model (2.1), since it is easy to proof and studied by many researchers (Kang et al., 2014a).

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