



## Original Research Article

## Dynamics of a predator–prey model with Allee effect on prey and ratio-dependent functional response

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## ABSTRACT

We analyze a ratio-dependent predator–prey model with Allee effect on the prey by making a parametric analysis of the stability properties of the dynamics of the system in which the functional response is a function of the ratio of prey to predator abundance. An important mathematical feature of these type of models is that while the functional response is undefined at the origin, the origin is singular equilibrium. We present the different types of system behaviors for different parameter values, showing the existence of separatrix curves in the phase plane determining that the long-term system's dynamic is dependent on the initial conditions. The model is studied analytically as well as numerically, including stability and bifurcation analysis. We also discuss the biological relevance of the model regarding both coexistence (conservation) and extinction (biological control) issues.

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## 1. Introduction

The traditional predator–prey model can be expressed by a bi-dimensional system of equations (or vector field) of the following form:

$$X_v : \begin{cases} \frac{dx}{dt} = xf(x) - yg(x) \\ \frac{dy}{dt} = eyg(x) - \mu y \end{cases} \quad (1)$$

with  $v = (e, \mu) \in \mathbb{R}_+^2$ , and where  $x(t)$  and  $y(t)$  represent the populations, at time  $t$ , of prey and predator respectively. The parameter  $e$  represents the predator efficiency rate and  $\mu$  the predator death rate. The function  $f(x)$  represents the average prey rate of growth in the absence of predator, and the function  $g(x)$  is known as functional response when in the prey equation and numerical response when in the predator equation.

In this paper, to the best of our knowledge, we present a new theoretical predator–prey mathematical model considering ratio-dependent functional response and double Allee effect on the growth function of the prey. We analyze a Gause type predator–prey model which is described by an autonomous bi-dimensional system of differential equations (1) considering the following aspects: (a)

the prey population is affected by Allee effect, and (b) the functional response is ratio-dependent (Arditi and Ginzburg, 1989). That is, we present a model where the average rate of growth of the prey is affected by the Allee effect by introducing an Allee term into the function  $f(x)$  and we incorporate the concept of ratio-dependence into the functional response function  $g(x)$ .

The objective of this study is to describe the dynamics of the model establishing a bifurcation analysis of relevant parameters and regions of stability.

The modified model with Allee effect on the prey equation provides an interesting dynamics, since it presents up to five equilibrium points, a separatrix curve, a Hopf bifurcation, and a Bogdanov–Takens bifurcation. We analyze stability of the model in the framework of biological control.

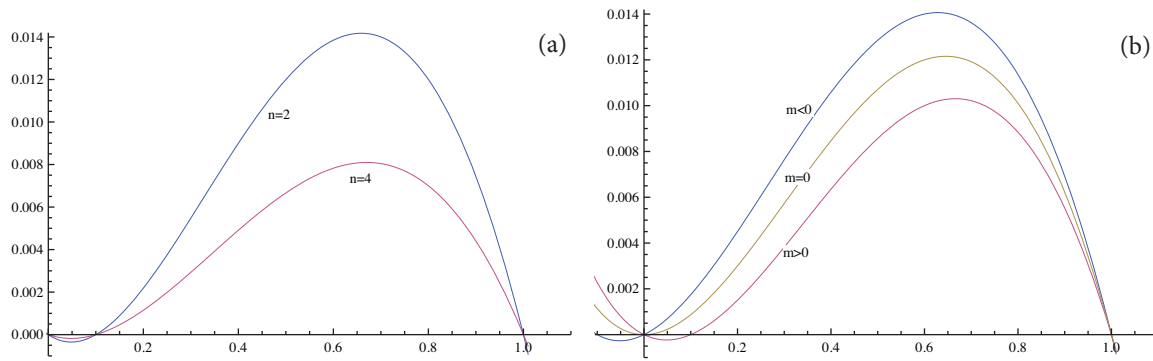
The rest of this Section 1 describes the concepts of Allee effect and ratio-dependent functional response used in the proposed model. Section 2 contains the description of the model, the main results are presented in Section 3, and a discussion in Section 4.

## 1.1. The Allee effect

The positive relationship between the population density and the reproduction and survival of individuals is known as *Allee effect* (Courchamp et al., 1999; Stephens and Sutherland, 1999; Stephens et al., 1999) or *negative competition effect* (Wang et al., 2011) in population dynamics, and as *depensation* (Clark, 1990; Liermann and Hilborn, 2001) in fisheries sciences. That is, an Allee effect is

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**Fig. 1.** The growth function of the prey in the absence of predator. (a) The effect of  $n$  ( $n = 2$  and  $4$ ) in the demographic Allee effect. (b) The weak Allee effect ( $m < 0$  and  $m = 0$ ) and strong Allee effect ( $m > 0$ ).

observed on the population growth rate if an increase in the per capita growth rate occurs over certain ranges of population density (Courchamp et al., 1999), and it can affect population persistence (Courchamp et al., 1999; Stephens and Sutherland, 1999).

Two main types of Allee effects are well known, depending how strong the per prey capita growth rate is depleted at low population size; (a) the *strong Allee effect* (Wang et al., 2011) or *critical depensation* (Clark, 1990), which is characterized by the existence of a critical threshold below which the population experiences extinction, and (b) *weak Allee effect* (Wang et al., 2011) or *pure depensation* (Clark, 1990) which is known by not having a threshold that must be surpassed by a population in order to grow. Fig. 1(b) illustrates both types of Allee effects.

A wide range of biological phenomena are invoked to produce the Allee effect dynamics, such as reduced antipredator vigilance, social thermoregulation, genetic drift, mating difficulty, social thermoregulation, reduced antipredator defense, and deficient feeding to low densities (Courchamp et al., 1999); however several other causes may generate this phenomenon (Berec et al., 2007; Courchamp et al., 2008).

Recent ecological research suggests the possibility that two or more Allee effects can generate mechanisms acting simultaneously on a single population (Table 2 in Berec et al., 2007), specially in renewable resources (Gascoigne and Lipcius, 2004). The combined influence of some of these phenomena have been named as *multiple Allee effect* (Berec et al., 2007).

In this work, we present a model considering the function proposed in Berec et al. (2007), describing double Allee effects. The formula proposed in Berec et al. (2007) is introduced into the equation of prey population and we assume that different causes might lead to an Allee effect; some of them are linked to reproduction and others to survival (Gascoigne and Lipcius, 2004).

When the Allee effect is incorporated into predator-prey models, richer and more interesting dynamics of the systems are obtained (Flores et al., 2007; Sen et al., 2012), producing new results on the interaction of both species.

The prey growth function with Allee effect formula we consider in this study is the following;

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) \left(1 - \frac{m+n}{x+n}\right). \quad (2)$$

It was proposed in Boukal and Berec (2002) and has been incorporated in predator-prey models (Boukal et al., 2007; González-Olivares et al., 2011) and in a bioeconomic model (Flores et al., 2007).

Eq. (2) can be expressed as

$$\frac{dx}{dt} = \frac{rx}{x+n} \left(1 - \frac{x}{K}\right) (x - m). \quad (3)$$

In the factor  $r(x) = rx/(x+n)$ , the parameter  $n$  indicates the population size necessary to reach  $r/2$ , the half rate saturation. The parameter  $n$  affects the overall shape of the per-capita growth curve of the prey, as  $n$  increases, the curve becomes increasingly “flatter” and reaches lower maximum values (Boukal et al., 2007) as it is illustrated in Fig. 1(a).

In this form of the Allee effect,  $n$  can be defined as a *constant Allee effect*. The bigger  $n$  is, the stronger the Allee effect will be, and the slower the per capita growth rate of the predator population, especially when  $x$  is small (Zhou et al., 2005), i.e., the per capita growth rate of the prey population is reduced from  $rx$  to  $rx/(x+n)$ .

## 1.2. Ratio-dependent functional response

Recently models studying predator-prey interaction where predation involves searching process are considering favorably the concept of ratio-dependence (Abrams, 1994; Arditi and Ginzburg, 1989, 2012). Solid arguments have been presented to justify that in some cases (Slobodkin, 1992), especially when predators have to search (share and/or compete) for food, a more suitable predator-prey model should be based on the ratio-dependent theory (Arditi and Ginzburg, 1989, 2012; Haque, 2009; Lev et al., 1992). The ratio-dependent concept, a particular case of predator dependence, can be simply stated that the per capita predator growth rate is a function of the ratio of the prey population size to predator population size. Fig. 2 illustrates the significant difference between prey-dependent and ratio-dependent functional responses as the predator density decreases approaching zero.

Since the ratio-dependent functional response is assumed to depend on the single variable  $x/y$ , system (1) takes the form

$$X_v : \begin{cases} \frac{dx}{dt} = xf(x) - yg\left(\frac{x}{y}\right) \\ \frac{dy}{dt} = eyg\left(\frac{x}{y}\right) - \mu y. \end{cases} \quad (4)$$

As in Arditi and Ginzburg (2012) the ratio-dependent functional response we are considering is the Michaelis-Menten (or Holling type II) hyperbolic type functional response,

$$g(x) = \frac{qx}{x+a}, \quad \Rightarrow \quad g\left(\frac{x}{y}\right) = \frac{qx}{x+ay} \quad (5)$$

where  $q > 0$  is the maximum consumption rate of predator and  $a > 0$  is known as the half saturation parameter.

These ratio-dependent models are of particular mathematical interest because the functional response is undefined at the origin (Arditi and Ginzburg, 1989; Berezovskaya et al., 2001; Jost et al., 1999). However, this equilibrium point (the origin) has a significant importance on the dynamics, as it has been shown in different research papers (Berezovskaya et al., 2001; Kuang and Beretta, 1998; Sen et al., 2012). The origin is a non-hyperbolic node

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