



A Predator-Prey System with Herd Behaviour and Strong Allee Effect

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Abstract: In this paper, we have studied the dynamical behaviours of a predator-prey system. The prey exhibits herd behaviour, and is also subject to strong Allee effect. Positivity and boundedness of the system are discussed. Some criteria for the extinction of prey and predator populations are derived. Stability analysis of the equilibrium points is presented. A criterion for Hopf bifurcation is derived. Numerical simulations are carried out to validate our analytical findings. Implications of our analytical and numerical findings are discussed critically.

Keywords: *Prey-predator system; Allee effect; stability; Hopf bifurcation.*

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1 Introduction

It is a fact that species does not survive alone. Individuals of one species are usually biologically associated to members of other. Their interactions take several forms, depending on whether the influences are beneficial or detrimental. Among these interactions, predator-prey relationship is considered to be an extremely important one. It is true that the preys always try to develop the methods of evasion to avoid being eaten. However, it is certainly not true that a predator-prey relationship is always harmful for the preys,

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it might be beneficial to both. Further, such a relationship often plays an important role to keep ecological balance in nature. Mathematical modelling of predator-prey interaction was started in 1920s. Interestingly, the first predator-prey model in the history of theoretical ecology was developed independently by Alfred James Lotka (a US physical chemist) and Vito Volterra (an Italian mathematician) [29,40]. Subsequently, this model has been used as a machine to introduce numerous mathematical and practical concepts in theoretical ecology. Many refinements of the Lotka-Volterra model have also been made to overcome the shortcomings of the model and to get better insights of predator-prey interactions. If we summarize the basic considerations behind such modelling, it would be evident that the most crucial elements of predator-prey models are the choices of *growth function* of the prey and *functional response* of the predator.

So far as the growth of the prey is concerned, many modellers have considered logistic growth function to be a logically acceptable function. The function was introduced in 1838 by the Belgian mathematician Pierre Francois Verhulst [39]. If $X(T)$ denotes the population density at time T , then the logistic growth equation is given by

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

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. Therefore, the per capita growth rate is a decreasing function of the size of the population, and reaches zero as the population achieves a size that can be maintained; further, any population reaching a size that is above this value will experience a negative growth rate. However, there are many evidences where the reverse holds true in low population density [9, 18–20, 31, 34]. This phenomenon of positive density dependence of population growth at low densities is known as the Allee effect [19, 37].

Warder Clyde Allee, the US behavioral scientist after whom the phenomenon is named, was the pioneer to describe this concept (although Allee never used the term ‘Allee effect’) [2–4]. The term ‘Allee effect’ was introduced by Odum [33]. Since the late eighties of the 20th century, the concept gained importance but there was a necessity of clear-cut definitions and clarification of concepts. In 1999, three important reviews gave these much needed definitions and clarifications, which are used even today [18, 36, 37]. There might be countless reasons for the 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 [9, 19]). 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 [26, 38, 42, 43] or critical depensation [14, 15, 28], and the weak Allee effect [37, 41] or noncritical depensation [14, 15, 28]. Usually, the Allee effect is modelled by a growth equation of the form

$$\frac{dX}{dT} = rX \left(1 - \frac{X}{K} \right) \left(\frac{X}{K_0} - 1 \right), \quad (2)$$

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 $0 < K_0 \ll K$. When $K_0 > 0$ and the population size is below the threshold level K_0 , then the population growth rate decreases [10, 16, 21, 26], and the population goes to extinction. In this case,

the equation describes the *strong Allee effect* [38,42,43]. On the contrary, the description of *weak Allee effect* is also available (see [22,42]). 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. [5,6]). A comparison of the logistic growth function of (1) and the function representing the Allee effect in equation (2) is depicted in Figure 1.

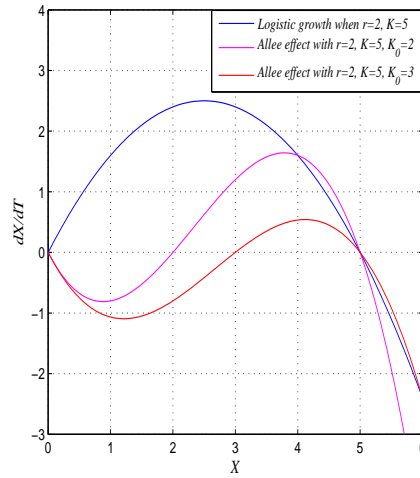


Figure 1: Comparison of the logistic growth function of (1) and the function representing the Allee effect in equation (2), when $r = 2$ and $K = 5$. The blue curve is the logistic growth curve. The magenta curve and the red curve are the graphs of the function on the right hand side of (2) when $K_0 = 2$ and $K_0 = 3$, respectively.

Let us now turn our attention from the individual growth of the prey to the interaction of the prey and its predator. The function that describes the number of prey consumed per predator per unit time for given quantities of prey and predator is known as the *functional response* or *trophic function*. Depending upon the behaviour of populations, more suitable functional responses have been developed as a quantification of the relative responsiveness of the predation rate to change in prey density at various populations of prey. In this connection, Holling family of functional responses are the most focused [24, 25]. The Holling type-I functional response (or the Lotka-Volterra functional response) is given by $F(X) = \alpha X$, where $X(T)$ is the prey density at time T and $\alpha > 0$ is a constant. In particular, the Holling type-II functional response has become extremely popular, and served as basis for a very large literature in predator-prey theory (see [30,32,35], and references therein). The type-II functional response includes the fact that a single individual can feed only until the stomach is not full, and so a saturation function would be better to describe the intake of food. This is similar to the concept of the *law of diminishing returns* borrowed from operations research, via a hyperbola rising up to an asymptotic value. In other words, the functional response would be of the following form

$$F(X) = \frac{\alpha X}{1 + T_h \alpha X}, \quad (3)$$

where $X(T)$ is the prey density at time T , α is the search efficiency of the predator for prey, T_h is the average handling time for each prey.

If a population is vulnerable to the Allee effect, there might be an important role of herd behaviour of the population. Very recently, Angulo et al. [7] have suggested that group behaviour diminishes extinction risks caused by the Allee effects. Now, when a population lives forming groups, then all members of a group do not interact at a time. There are many reasons for this herd behaviour, such as searching for food resources, defending the predators, etc. As a consequence, it is necessary to search for suitable form of functional response to describe this social behaviour. Only a few works have so far tried to enlighten this area. These works demonstrated an ingenious idea that suitable powers of the state variables can account for the social behaviour of the populations. For example, to explore the consequence of forming spatial group of fixed shape by predators, Cosner et al. [17] introduced the idea that the square root of the predator variable is to be used in the function describing the encounter rate in two-dimensional systems. Similarly, for three-dimensional systems, the two-third power of the predator in the encounter rate would better describe such group behaviour by predators. Unfortunately, such an idea has not been used by the researchers for about a decade. The work of Chattopadhyay et al. [13] may be regarded as a strong recognition of this concept. Then came the most innovative works of Ajraldi et al. [1] and Braza [12], which gave such modelling a new dimension. We recall their central ideas in the next paragraph.

Let X be the density of a population that gathers in herds, and suppose that herd occupies an area A . The number of individuals staying at outermost positions in the herd is proportional to the length of the perimeter of the patch where the herd is located. Clearly, its length is proportional to \sqrt{A} . Since X is distributed over a two-dimensional domain, \sqrt{X} would therefore count the individuals at the edge of the patch. Thus, when attack of a predator on this population is to be modelled, the functional response should be in terms of square root of prey population. This is the main idea of Ajraldi et al. [1]. Braza [12] has placed a strong emphasis on this concept, and he has introduced a new functional response, where the prey density in (3) is replaced by its square root. That is, the functional response takes the form

$$F_1(X) = \frac{\alpha\sqrt{X}}{1 + T_h\alpha\sqrt{X}}. \quad (4)$$

It is already mentioned that if a population is susceptible to the Allee effect, then living in herds might be beneficial for it [7]. Now, if there is a predator, such behaviour plays a key role so far as the vigilance and predation risk is concerned [31]. The dynamics of predator-prey systems with herd behaviour of the prey has got the attention of theoretical ecologists very recently, but in all the cases it is assumed that the prey has a logistic growth (see [11] and references therein). It would be of utmost importance to consider predator-prey systems with herd behaviour and the Allee effect. There should be no denying that such considerations would be very interesting from both theoretical and practical point of view. The dynamics of such models has so far not been studied in literature. Our endeavour might accomplish such a necessity.

The rest of the paper is organized as follows. In Section 2, we present the mathematical model with basic considerations. Boundedness and positivity of the solutions of the model are established in Section 3. Some results on the extinction of prey and predator are derived in Section 4. Section 5 deals with all the possible equilibrium points of the model and their stability analysis. A criterion for Hopf bifurcation is derived in Section

6. To illustrate our analytical findings, computer simulations of variety of solutions of the system are performed; and the results are presented in Section 7. Section 8 contains the general discussion of the paper and biological significance of our analytical findings.

2 The Mathematical Model

At time T , let $X(T)$ denote the density of the prey, and $Y(T)$ denote the density of the predator. We assume that the preys live in herds. We also consider a multiplicative Allee effect in prey population growth. These considerations motivate us to introduce the following predator-prey system within the framework of the following set of nonlinear ordinary differential equations:

$$\begin{aligned} \frac{dX}{dT} &= rX \left(1 - \frac{X}{K}\right) \left(\frac{X}{K_0} - 1\right) - \frac{\alpha\sqrt{XY}}{1 + T_h\alpha\sqrt{X}}, \quad X(0) > 0, \\ \frac{dY}{dT} &= -\delta Y + \frac{\beta\alpha\sqrt{XY}}{1 + T_h\alpha\sqrt{X}}, \quad Y(0) > 0. \end{aligned} \quad (5)$$

The parameter r is the intrinsic growth rate of the prey, K is the carrying capacity of the prey, δ represents the death rate of the predator. We assume a strong Allee effect on the prey. The parameter K_0 with $0 < K_0 \ll K$ is the prey population Allee threshold in the absence of predators. As the prey exhibits herd behaviour, here we have used the modified functional response (4) (suggested by Braza [12]) to represent the interaction between prey and predator. So α, T_h, β stand for the search efficiency of the predator for prey, the average handling time for each prey, and the biomass conversion rate, respectively. It is an obvious assumption that all the parameters are positive.

To reduce the number of parameters in the system (5), we use the following scaling

$$x = \frac{X}{K}, \quad y = \frac{Y}{K}, \quad \text{and} \quad t = r\frac{K}{K_0}T.$$

Then the system (5) takes the following form (after some simplifications)

$$\begin{aligned} \frac{dx}{dt} &= x(1-x)(x-m) - \frac{b\sqrt{xy}}{1+a\sqrt{x}}, \quad x(0) > 0, \\ \frac{dy}{dt} &= -dy + \frac{c\sqrt{xy}}{1+a\sqrt{x}}, \quad y(0) > 0, \end{aligned} \quad (6)$$

where

$$m = \frac{K_0}{K}, \quad a = T_h\alpha\sqrt{K}, \quad b = \frac{\alpha K_0}{r\sqrt{K}}, \quad c = \frac{\beta\alpha K_0}{r\sqrt{K}}, \quad d = \frac{\delta K_0}{rK}.$$

3 Positivity and Boundedness

Positivity and boundedness of a model guarantee that the model is biologically well behaved. For positivity of the system (6), we have the following theorem.

Theorem 3.1 *All solutions of the system (6) that start in \mathbb{R}_+^2 remain positive forever.*

The proof is simple and therefore it is omitted. The following theorem ensures the boundedness of the system (6).

Theorem 3.2 *All solutions of the system (6) that start in \mathbb{R}_+^2 are uniformly bounded.*

Proof. Let $(x(t), y(t))$ be any solution of the system (6). We consider two possible cases separately.

Case-I. Let $x(0) \leq 1$. We claim that $x(t) \leq 1$ for all $t \geq 0$.

If possible, assume that our claim is not true. Then it is possible to find two positive real numbers t' and t'' such that $x(t') = 1$ and $x(t) > 1$ for all $t \in (t', t'')$.

Now, for all $t \in (t', t'')$, we have from the first equation of (6)

$$x(t) = x(0) \exp \left(\int_0^t \phi(x(s), y(s)) ds \right),$$

where $\phi(x(t), y(t)) = (1 - x(t))(x(t) - m) - b \frac{y(t)}{\sqrt{x(t)(1+a\sqrt{x(t)})}$.

This implies that

$$\begin{aligned} x(t) &= x(0) \left[\exp \left(\int_0^{t'} \phi(x(s), y(s)) ds \right) \right] \left[\exp \left(\int_{t'}^t \phi(x(s), y(s)) ds \right) \right] \\ &= x(t') \exp \left(\int_{t'}^t \phi(x(s), y(s)) ds \right), \quad \text{for all } t \in (t', t''). \end{aligned}$$

Since $m < 1$, we have $\phi(x(t), y(t)) < 0$ for all $t \in (t', t'')$. Consequently, we have

$$x(t) < x(t'), \quad \text{where } x(t') = 1.$$

This is contrary to the assumption that $x(t) > 1$ for all $t \in (t', t'')$. Thus our claim is true.

Case-II. Let $x(0) > 1$. We claim that $\limsup_{t \rightarrow \infty} x(t) \leq 1$.

If possible, assume that this claim is false. Then $x(t) > 1$ for all $t > 0$. So $\phi(x(t), y(t)) < 0$ (where ϕ has the same expression as in Case-I); and consequently, we have from the first equation of (6) that

$$x(t) = x(0) \exp \left(\int_0^t \phi(x(s), y(s)) ds \right) < x(0).$$

Also from the first equation of (6), we obtain

$$\frac{dx}{dt} < (x(0) - m)x(1 - x), \quad \text{where } x(0) - m > 0.$$

This implies that $\limsup_{t \rightarrow \infty} x(t) \leq 1$, which is contradictory to our assumption. Therefore our claim is true.

From the above two cases, we have $\limsup_{t \rightarrow \infty} x(t) \leq 1$.

Let $W = cx + by$. Then, for large t , we have

$$\begin{aligned} \frac{dW}{dt} &= cx(1 - x)(x - m) - bdy \\ &= cx\{(1 + m)x - m - x^2\} - bdy \\ &\leq c(1 + m)x - bdy \\ &\leq 2c(1 + m) - \lambda W, \quad \text{where } \lambda = \min\{(1 + m), d\}. \end{aligned}$$

Therefore,

$$\frac{dW}{dt} + \lambda W \leq 2c(1+m).$$

Applying the theory of differential inequalities, we obtain

$$0 \leq W(x, y) \leq \frac{2c(1+m)}{\lambda} + \frac{W(x(0), y(0))}{e^{\lambda t}}.$$

and for $t \rightarrow \infty$,

$$0 \leq W \leq \frac{2c(1+m)}{\lambda}.$$

Thus, all the solutions of (2.2) enter into the region

$$B = \left\{ (x, y) : 0 \leq W \leq \frac{2c(1+m)}{\lambda} + \epsilon, \text{ for any } \epsilon > 0 \right\}.$$

Hence the theorem is proved. \square

4 Extinction Scenarios

In this section, we find some conditions for extinction of the prey or predator. Here we use the symbols \bar{x} and \underline{y} to represent $\limsup_{t \rightarrow \infty} x(t)$ and $\liminf_{t \rightarrow \infty} y(t)$, respectively. We frequently use the fact that $\bar{x} \leq 1$, which is proved in Theorem 3.2.

The first two theorems of this section are on the extinction of the prey species. It is quite obvious that if, after certain time, the prey population density lies below the Allee threshold (moreover there is attack of predator), then it is really impossible for the prey to survive. This fact is represented in mathematical terms in the following theorem.

Theorem 4.1 *If $\bar{x} < m$, then $\lim_{t \rightarrow \infty} x(t) = 0$.*

Proof. If possible, let $\lim_{t \rightarrow \infty} x(t) = \mu > 0$. The definition of \bar{x} implies that for any ϵ satisfying $0 < \epsilon < m - \bar{x}$, there exists $t_\epsilon > 0$ such that $x(t) < \bar{x} + \epsilon$ for $t > t_\epsilon$. Then, for $t > t_\epsilon$, we have from the first equation of (6) that

$$\begin{aligned} x(t) &= x(0) \exp \left[\int_0^t \left\{ (1-x(s))(x(s)-m) - \frac{b\sqrt{x(s)}y(s)}{x(s)(1+a\sqrt{x(s)})} \right\} ds \right] \\ &< x(0) \exp \left[\int_0^t (\bar{x} + \epsilon - m) ds \right] \\ &< x(0) \exp\{-(m - \bar{x} - \epsilon)t\} \rightarrow 0 \text{ as } t \rightarrow \infty, \end{aligned}$$

which is a contradiction. This proves the theorem. \square

If the condition of the above theorem is satisfied, then the predator has no vital role in leading the prey to extinction, because the Allee effect is enough to do this (of course, the predator might expedite the process of extinction of the prey). The following theorem shows that the predator might also play a key role to prompt the prey to die out.

Theorem 4.2 *If $\underline{y} > \frac{2\sqrt{2}}{b}(1+a\sqrt{2})(1-m)$, then $\lim_{t \rightarrow \infty} x(t) = 0$.*

Proof. If possible, let $\lim_{t \rightarrow \infty} x(t) = \mu > 0$. Since $\bar{x} \leq 1$, for any $0 < \epsilon < 1 - m$, there exists $t_\epsilon > 0$ such that $x(t) < 1 + \epsilon$ for $t > t_\epsilon$.

From the definition of \underline{y} , it follows that, for any $0 < \epsilon' < \underline{y} - \frac{2\sqrt{2}}{b}(1 + a\sqrt{2})(2 - m)$, there exists $t_{\epsilon'} > 0$ such that $y(t) > \underline{y} - \epsilon'$ for $t > t_{\epsilon'}$.

Then, for $t > \max\{t_\epsilon, t_{\epsilon'}\}$, we have from the first equation of (6) that

$$\begin{aligned} \frac{dx}{dt} &< x(1 + \epsilon - m) - \frac{b\sqrt{x}y}{1 + a\sqrt{1 + \epsilon}}, \\ &< x(1 + \epsilon - m) - \frac{bxy}{\sqrt{1 + \epsilon}(1 + a\sqrt{1 + \epsilon})}, \text{ as } x < \sqrt{1 + \epsilon}\sqrt{x}, \\ &< x \left\{ 2(1 - m) - \frac{b(\underline{y} - \epsilon')}{\sqrt{2}(1 + a\sqrt{2})} \right\}, \\ &< -\frac{bx}{\sqrt{2}(1 + a\sqrt{2})} \left\{ \underline{y} - \epsilon' - \frac{2\sqrt{2}}{b}(1 + a\sqrt{2})(1 - m) \right\} < 0, \end{aligned}$$

which implies that $\lim_{t \rightarrow \infty} x(t) = 0$, a contradiction.

Hence the theorem is established. □

A very simple criterion for the extinction of the predator is given in the following theorem.

Theorem 4.3 *If $d > c$, then $\lim_{t \rightarrow \infty} y(t) = 0$.*

Proof. Since $\bar{x} \leq 1$, for any $0 < \epsilon < \frac{d^2}{c^2} - 1$, there exists $t_\epsilon > 0$ such that $x(t) < 1 + \epsilon$ for $t > t_\epsilon$. For $t > t_\epsilon$, we have from the second equation of (6) that

$$\begin{aligned} \frac{dy}{dt} &= y \left(-d + \frac{c\sqrt{x}}{1 + a\sqrt{x}} \right) \\ &< y(-d + c\sqrt{x}) < y(-d + c\sqrt{1 + \epsilon}) \\ &< -cy \left(\frac{d}{c} - \sqrt{1 + \epsilon} \right) < 0. \end{aligned}$$

Therefore, $\lim_{t \rightarrow \infty} y(t) = 0$. □

Remark 4.1 We notice that if the predator is aggressive (characterized by the high value of b) or the Allee effect is very strong ($m \approx 1$), then the condition of Theorem 4.2 might be satisfied automatically. On the other hand, if the maximal benefit of the predator (in interaction with the prey) fails to overcome its loss due to death, then the predator will be ultimately washed out from the system.

5 Equilibria and Their Stability

In this section, we find the equilibrium points of the system (6) and study their stability. The nullclines are shown in Figure 2. The following lemma gives the equilibrium points with the conditions of their existence.

Lemma 5.1 *The trivial equilibrium $E_0(0, 0)$ of the system (6) always exists. There are two axial (predator-free) equilibrium points $E_1(1, 0)$ and $E_2(m, 0)$, each of which also exists unconditionally. The interior or coexistence equilibrium $E^*(x^*, y^*)$ exists if and*

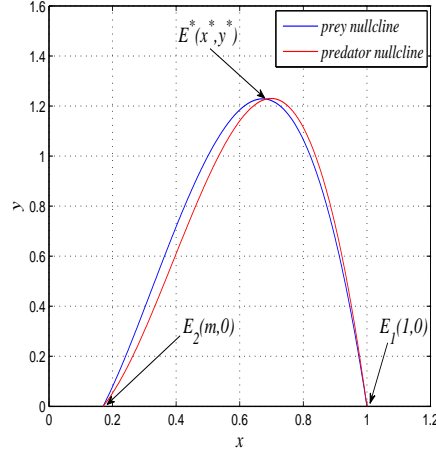


Figure 2: Nullclines of the system (6) for $a = 0.89$, $b = 0.19$, $c = 0.21$, $d = 0.1$, $m = 0.17$.

only if $(c - ad)\sqrt{m} < d < (c - ad)$. When $E^*(x^*, y^*)$ exists, the expressions for x^* and y^* are given by

$$x^* = \frac{d^2}{(c - ad)^2}, \quad y^* = \frac{cx^*(1 - x^*)(x^* - m)}{bd}.$$

It is not possible to linearize the system (6) about the trivial equilibrium. Therefore, local stability of $E_0(0, 0)$ cannot be studied. However, results of the previous section could provide some results on global stability of $E_0(0, 0)$. For example, if the conditions of Theorem 4.1 and Theorem 4.3 are satisfied simultaneously, then $E_0(0, 0)$ is globally stable. Also $E_0(0, 0)$ is globally stable if the conditions of Theorem 4.2 and Theorem 4.3 are satisfied. We are not interested to restate those results here.

The Jacobian matrix $J(E_1)$ at $E_1(1, 0)$ is given by

$$J(E_1) = \begin{bmatrix} m - 1 & -\frac{b}{1+a} \\ 0 & -d + \frac{c}{1+a} \end{bmatrix}.$$

Clearly, the eigenvalues of $J(E_1)$ are $m - 1$ and $-d + \frac{c}{1+a}$. Since $m < 1$, the first eigenvalue $m - 1$ is always negative. The second one will also be negative if and only if $c < d(1 + a)$. Thus we have the following theorem on stability of $E_1(1, 0)$.

Theorem 5.1 *The equilibrium $E_1(1, 0)$ is locally asymptotically stable if and only if $c < d(1 + a)$.*

Remark 5.1 We notice that the existence of E^* destabilizes E_1 .

The Jacobian matrix $J(E_2)$ at $E_2(m, 0)$ is given by

$$J(E_2) = \begin{bmatrix} m(1 - m) & -\frac{b\sqrt{m}}{1+a\sqrt{m}} \\ 0 & -d + \frac{c\sqrt{m}}{1+a\sqrt{m}} \end{bmatrix}.$$

The eigenvalues of $J(E_2)$ are $m(1 - m)$ and $-d + \frac{c\sqrt{m}}{1+a\sqrt{m}}$. The first eigenvalue is always positive, as $0 < m < 1$. The second one will be negative if and only if $c\sqrt{m} < d(1+a\sqrt{m})$. Therefore, we have the following theorem.

Theorem 5.2 *The equilibrium $E_2(m, 0)$ is always unstable. It is a saddle point if and only if $c\sqrt{m} < d(1 + a\sqrt{m})$.*

Finally, we consider the stability issue of the most important equilibrium $E^*(x^*, y^*)$. We have the following Jacobian matrix at $E^*(x^*, y^*)$:

$$J(E^*) = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & 0 \end{bmatrix},$$

where

$$a_{11} = (1 - 2x^*)(x^* - m) + x^*(1 - x^*) - \frac{by^*}{2\sqrt{x^*}(1 + a\sqrt{x^*})^2},$$

$$a_{12} = -\frac{b\sqrt{x^*}}{1 + a\sqrt{x^*}}, \quad a_{21} = \frac{cy^*}{2\sqrt{x^*}(1 + a\sqrt{x^*})^2}.$$

The characteristic equation of $J(E_3)$ is

$$\lambda^2 + P\lambda + Q = 0,$$

where $P = -\text{tr } J(E^*) = -a_{11}$, $Q = \det J(E^*) = -a_{12}a_{21} > 0$. A little algebraic manipulation yields

$$P = \frac{ABm - d^2\{2c(A - d^2) + B\}}{2cA^2},$$

where $A = (c - ad)^2$ and $B = (c + ad)A - (3c + ad)d^2$. Then we have the following theorem guaranteeing the stability of $E^*(x^*, y^*)$.

Theorem 5.3 *The necessary and sufficient condition for local asymptotic stability of the interior equilibrium $E^*(x^*, y^*)$ is that $\Delta = ABm - d^2\{2c(A - d^2) + B\} > 0$.*

It would be interesting if we can establish some sort of global behaviour of the interior equilibrium. Let $\Omega = \{(x, y) \in \mathbb{R}^2 : 0 < x < 1, y > 0\}$. Clearly, $E^*(x^*, y^*) \in \Omega$. Then we have the following theorem.

Theorem 5.4 *If $E^*(x^*, y^*)$ is locally asymptotically stable with $d > c + m + 2$, then E^* attracts all solutions of the system (6) lying in Ω .*

Proof. Let us write the first equation of the system (6) as $\frac{dx}{dt} = P(x, y)$, and the second equation as $\frac{dy}{dt} = Q(x, y)$. Then, for all $(x, y) \in \Omega$, we notice that

$$\begin{aligned} \frac{\partial P}{\partial x} + \frac{\partial Q}{\partial y} &= (1 - 2x)(x - m) + x(1 - x) - \frac{by}{2\sqrt{x}(1 + a\sqrt{x})^2} - d + \frac{c\sqrt{x}}{1 + a\sqrt{x}} \\ &\leq 2x + 2mx - m - d + c\sqrt{x} \\ &\leq 2 + m - d + c < 0. \end{aligned}$$

Therefore, by Bendixson’s criterion, there is no periodic orbit in Ω . Hence the theorem follows from the Poincaré-Bendixson theorem. □

6 Hopf Bifurcation

In this section, we provide conditions for the occurrence of a simple Hopf bifurcation near the interior equilibrium $E^*(x^*, y^*)$. We use the Hopf bifurcation theorem [8, 23, 32] for this purpose.

Theorem 6.1 *If the equilibrium point $E^*(x^*, y^*)$ exists, then Hopf bifurcation occurs at $m = m^* = \frac{d^2\{2c(A-d^2)+B\}}{AB}$, provided m^* is positive.*

Proof. We notice that

- (i) $[\text{tr } J(E^*)]_{m=m^*} = 0$,
- (ii) $[\det J(E^*)]_{m=m^*} > 0$,
- (iii) when $m = m^*$ the characteristic equation is $\lambda^2 + \det J(E^*) = 0$, whose roots are purely imaginary,
- (iv) $[(d/dm)(\text{tr } J(E^*))]_{m=m^*} = -\frac{B}{2cA} \neq 0$.

Hence all the conditions of the Hopf-bifurcation theorem are satisfied, and the theorem follows. \square

7 Numerical Simulation

In this section, we present computer simulations of some solutions of the system (6). These simulations are performed to validate the analytical findings of the last two sections.

First, we take the parameters of the system (6) as $m = 0.2$, $b = 0.19$, $a = 0.89$, $d = 0.1$ and $c = 0.17$. Then $c < d(1 + a)$, and consequently by Theorem 5.1, $E_1(1, 0)$ is locally asymptotically stable. Figure 3 illustrates this. Clearly, x approaches 1 and y dies out in finite time.

Next we consider the stability of the interior equilibrium. We take the parameter values as $m = 0.17$, $b = 0.19$, $a = 0.89$, $d = 0.1$ and $c = 0.21$. Then $\Delta = 0.0000016314 > 0$. Therefore, by Theorem 5.3, the interior equilibrium point $E^*(x^*, y^*) = (0.6830, 1.2276)$ is locally asymptotically stable. The corresponding phase portrait for different choices of $(x(0), y(0))$ is depicted in Figure 4. Clearly the trajectories are stable spirals converging to E^* . Figure 5 shows the behaviour of x and y with time, when $(x(0), y(0)) = (0.85, 1.2)$, and it is evident that (x, y) approaches to (x^*, y^*) in finite time.

If we gradually increase the value of m , keeping other parameters fixed, then following Theorem 6.1, we have a critical value $m^* = 0.2096$ such that E^* loses its stability as m passes through m^* . For $m = 0.22 > m^*$, we verify that $E^*(0.6830, 1.1080)$ is unstable ($\Delta = -0.0000004274 < 0$) and there is a periodic orbit near E^* (see Figure 6). The oscillations of x and y in time are shown in Figure 7.

A bifurcation diagram is shown in Figure 8. As the parameter m passes through the bifurcation value $m^* = 0.2096$, there is a change in stability behaviour.

8 Concluding Remarks

Recently it has been suggested by researchers that herd behaviour of populations could act as a buffer against population extinction due to the Allee effect (see [7]). Modelling of the Allee effect has been done by many researchers. Nowadays there has been a growing concern about modelling of herd behaviour of populations. In this paper, we

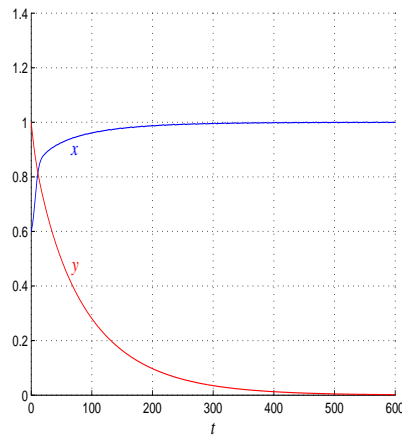


Figure 3: Behaviour of the system (6) with time when $m = 0.2$, $b = 0.19$, $a = 0.89$, $d = 0.1$ and $c = 0.17$.

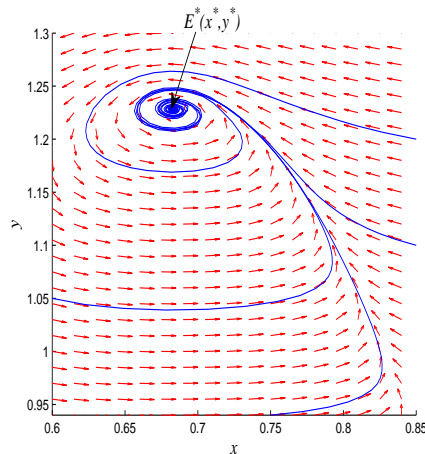


Figure 4: Here $m = 0.17$, $b = 0.19$, $a = 0.89$, $d = 0.1$ and $c = 0.21$. Phase portrait of the system (6) for different choices of $x(0)$ and $y(0)$ showing stable spirals converging to $E^*(0.6830, 1.2276)$.

have considered a predator-prey model where the prey shows herd behaviour and also susceptible to the Allee effect. The number of parameters of the model has been reduced by suitable scaling. Then the dynamical behaviours of the resulting model (6) is studied. It is shown (in Theorem 3.1 and Theorem 3.2) that the solutions of the system (6) remain non-negative forever, and they are uniformly bounded. These, in turn, imply that the system is biologically well-behaved. We have derived some results on extinction of prey and predator. It is seen that if there is a very strong the Allee effect, then it is almost impossible for the prey to survive. Also, an aggressive predator might cause extinction

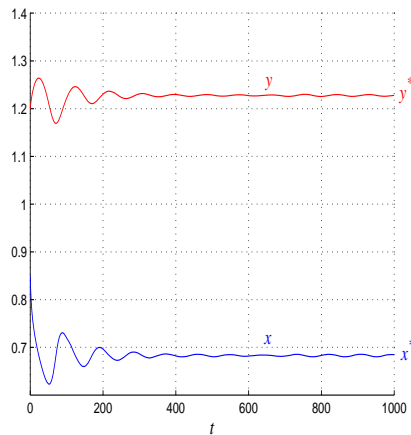


Figure 5: Here the values of the parameters are as in Figure 4. When $(x(0), y(0)) = (0.85, 1.2)$, both the populations converge to their equilibrium-state values in finite time. The blue curve represents x and the red one represents y .

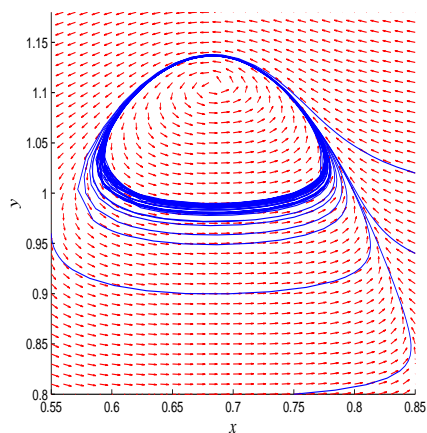


Figure 6: Here all the parameters are same as in Figure 4 except $m = 0.22 > m^*$. Phase portrait of the system (6) showing a periodic orbit near $E^*(0.6830, 1.1080)$.

of the prey, and this ultimately backfires (because the predator dies out in starvation, which is clear from the second equation of (6)). It is also established that if the maximal benefit of the predator (in interaction with the prey) fails to overcome its loss due to death, then the predator would ultimately be washed out.

It has long been recognized that most of the studies of continuous time deterministic models reveal two basic patterns: approach to an equilibrium or to a limit cycle. The basic rationale behind such type of analysis is perhaps that these two patterns are very common in many predator-prey systems we observe in nature. From this viewpoint, we

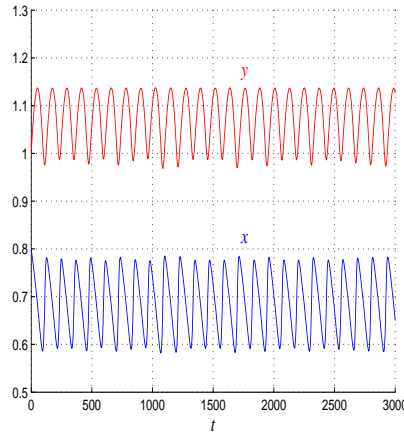


Figure 7: Here all the parameters are same as in Figure 6. It shows oscillations of the x and y in time. The blue curve represents x and the red one represents y .

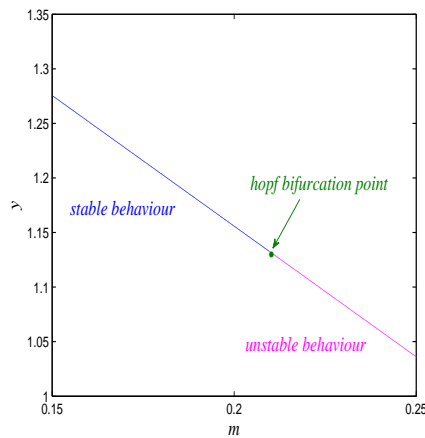


Figure 8: A bifurcation diagram with m as bifurcation parameter, when $b = 0.19$, $a = 0.89$, $d = 0.1$ and $c = 0.21$. The blue curve depicts stable behavior and the magenta curve depict unstable behavior.

have presented the stability analysis of the equilibrium points, and bifurcation analysis of the most important interior equilibrium point. The criterion for existence of the interior equilibrium suggests that an aggressive predator with moderate death rate might give a guarantee for the coexistence equilibrium to be feasible. Also, the existence of the interior equilibrium destabilizes E_1 . The Allee effect has a negative effect on the fitness of the predator (see Figure 8). Further, the bifurcation analysis presented here shows that the Allee effect could have a regulatory impact on the whole system.

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