Bifurcation analysis of the prey-predator models incorporating herd behaviours

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Abstract: In ecology, herd behaviour corresponds to the situation how a group of animals of the same species interacts in the time of danger. A herd mechanism offers more protection for preys against predators. But this mechanism can also provide defence from predators. To address this problem, we consider two ecological models of prey-predator interactions with the presence of different herd behaviours. While the first system represents a simple prey-predator model incorporating herd behaviour in prey populations only, the second one considers the herd behaviour in both prey and predator populations. We examine how different strategies of herd behaviours can determine the outcomes of species interactions. To do this, we employ stability analysis and numerical simulations to illustrate different dynamical behaviours of the two models, e.g. coexistence and extinction steady states and also limit cycles. By using bifurcation analysis, we observe the occurrences of Hopf bifurcation, transcritical bifurcation, limit point and limit point of cycles. These bifurcations can shape the overall dynamics of these two ecological systems.

1. Introduction

Herd behaviour corresponds to the situation how a group of animals of the same species interact in the time of danger. The preys will employ various defensive mechanisms to save themselves from predator [1]. For example, when animals are in herd, they will move together at the same time; one or two leaders start, then momentum builds as more and more will join until a large group are all heading in the same direction. Another example of herd behaviour mechanism employed by preys: when they are approached by predators, they will move together as close as possible to the centre of the fleeing group with a hope of reducing danger to themselves [2]. The larger the prey population is, the smaller the success of hunting by predators [3]. However, predators can also employ a herd behaviour mechanism to capture these individual preys. For example, wolves will usually live and hunt in family groups so that they can pursue larger prey. Besides that, predators live in group because they can protect their little ones from another large predator. Therefore, the main purpose of this paper is to get better understanding about the herd behaviour mechanisms in both prey-predator populations. To achieve this objective, we examine two ecological models of prey-predator interactions with herd behaviours using bifurcation analysis and techniques from dynamical systems.

In general, ecological models are developed to understand how population abundance of predators affects each individual prey. Various authors have studied the herd behaviour mechanisms in prey-
predator interactions [1,4,5,6]. Braza [6] proposed the prey-predator models in which the prey exhibits herd behaviour and the system leads to square root of prey density. The following system given by

\[
\frac{dX}{dT} = rX \left(1 - \frac{X}{K}\right) - \frac{\alpha \sqrt{XY}}{1 + T_h \alpha \sqrt{X}}
\]

\[
\frac{dY}{dT} = -\delta Y + \frac{\beta \alpha \sqrt{XY}}{1 + T_h \alpha \sqrt{X}}
\]

where \( X \) and \( Y \) denote the density of the prey and predator, respectively. It is assumed that all parameters are constant and positive where the parameter \( r \) is the growth rate of prey, \( K \) is the carrying capacity of the prey, \( \alpha \) represents the rate which predator destroys prey or attack rate, \( \delta \) represents the death rate of predator, \( T_h \) is the average handling time and \( \beta \) stand for biomass conversion rate. For ecological model (1), Braza assumed that the average handling time is zero and this leads to a simple Lotka-Volterra system.

In this paper, our intention is to establish the different effects of herd behaviours in prey-predator populations as the magnitude of some ecologically-relevant parameters change. In particular, we seek to answer the following questions: when does the herd behaviours matter in determining the dynamics of species interactions change and when does this phenomenon depends on ecological process e.g. conversion rate of prey? This paper only focuses on the parameter of the conversion rate of prey; where predators attacking and consuming preys and hence preys converts into new-born of predators. We chose to vary that parameter because we want to investigate what happen to the prey and predator population when the herd behaviour mechanisms take place in the two different ecological models; while the first model employs the herd behaviour in prey populations only and the other model employs the herd behaviour in both prey and predator populations. Since preys live in herd (as a protection against predators), then predators might hesitate to attack preys. But then, if the predators also live in herd, it might be more effective at pulling down a herd of prey. Therefore, these situations are very interested to study. From ecological hypothesis, if the conversion rate of prey increases, this can lead to the extinction of prey and survival of predators. These situations or hypothesis will be explained and discussed further in Section 4 and 5.

This paper is organized as follows. Section 2 discusses a simple prey-predator model incorporating herd behaviour in prey populations only. Section 3 highlights the prey-predator model with herd behaviour in both prey and predator populations. Both models are extended version, the first one proposed by Bera et al. [5], another one proposed by Maiti et al. [4]. Existence of equilibrium and stability is discussed in Section 2 and 3 simultaneously. Numerical simulations and bifurcation analysis are demonstrated in Section 4. Section 5 contains the general discussion and the conclusion of the paper.

2. A Model with Herd Behaviour in Preys
To model herd behaviours in prey populations, some studies [5,6] proposed a deterministic model (1) with prey-predator interactions. This model can be non-dimensionalized with the following scaling:

\[
x = \frac{X}{K}, \quad y = \frac{Y}{K}, \quad t = rT
\]
System (1) then takes the form:

\[
\frac{dx}{dt} = x(1-x) - \frac{b\sqrt{xy}}{1+a\sqrt{x}}, \quad x(0) > 0,
\]

\[
\frac{dy}{dt} = -dy + \frac{c\sqrt{xy}}{1+a\sqrt{x}}, \quad y(0) > 0,
\]

where \(a = T_a\alpha\sqrt{K}, \quad b = \frac{\alpha\sqrt{K}}{r}, \quad c = \frac{\beta\alpha\sqrt{K}}{r}, \quad d = \frac{\delta}{r} \).

Parameters \(a\) represent the time spent of predator in handling one prey, \(b\) is the attack rate at which predator captures their prey, \(c\) is the conversion rate each individual prey into new-borns of predators and \(d\) stand for death rate of predator. Positivity and boundedness of the system are discussed in [5]. The system always has the trivial equilibrium \(E_0 = (0,0)\) where both prey and predator populations can go extinct, a boundary equilibrium \(E_1 = (1,0)\) where only prey survives and the interior equilibrium \(E^* = (x^*, y^*)\) where both prey and predator populations coexist with

\[
x^* = \frac{d^2}{(c-ad)^2},
\]

\[
y^* = \frac{cd((c-ad)^2-d^2)}{b(c-ad)^4}.
\]

The stability at \(E_0 = (0,0)\) cannot be evaluated since the system (2) is not linearizable at \((0,0)\); this is due to the square root term and the Jacobian matrix becomes indeterminate, to analyse the stability of \(E_0\), one can proceed to use the method proposed in [5]. At \(E_1 = (1,0)\), the system (2) is stable if \(c < d(1+a)\). Next, we consider the stability of the interior equilibrium \(E^* = (x^*, y^*)\) by the given Jacobian matrix

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

where

\[
a_{11} = \frac{(c+ad)(c-ad)^2-(ad+3c)d^2}{2c(c-ad)^2},
\]

\[
a_{12} = \frac{bd}{c},
\]

\[
a_{21} = \frac{(c-ad)^2-d^2}{2b(c-ad)}.
\]

If \((ad+3c)d^2-(c+ad)(c-ad)^2 > 0\), then \(E^* = (x^*, y^*)\) is locally asymptotically stable. To prove this statement, we have the following characteristic equation of \(J(E^*)\)
\[ \lambda^2 + A\lambda + B = 0, \]  

(3)

where

\[ A = -\text{tr} \ J(E^*) = -a_{11} - a_{22} = \frac{(c + ad)(c - ad)^2 - (ad + 3c)d^2}{2c(c - ad)^2} \]

\[ B = -\det J(E^*) = a_{11}a_{22} - a_{12}a_{21} = \frac{d((c - ad)^2 - d^2)}{2bc(c - ad)}. \]

For existence of \( E^*(x^*, y^*) \), we have \( d < \frac{c}{1 + a} \) that confirms \( B > 0 \) and \( A > 0 \) also. Thus, the root of (3) is given by

\[ \lambda_{1,2} = -\frac{A \pm \sqrt{A^2 - 4AB}}{2}, \]

with negative real part and this guaranteed the stability of \( E^*(x^*, y^*) \).

3. A Model with Herd Behaviour in Both Preys and Predators

The prey-predator system is originally formulated by Maiti et al. [4]. The authors assumed that both prey and predator population live in herds and square root term are employed in both prey and predator density. The following system given by:

\[ \frac{dx}{dt} = x(1 - x) - \frac{b\sqrt{x}\sqrt{y}}{1 + a\sqrt{x}} \]

\[ \frac{dy}{dt} = -dy + \frac{c\sqrt{x}\sqrt{y}}{1 + a\sqrt{x}} \]

(4)

where \( a = T\alpha\sqrt{K} \), \( b = \frac{\alpha}{r} \), \( c = \frac{\beta\alpha}{r} \), \( d = \frac{\delta}{r} \).

The stability at \( E_0 = (0,0) \) and \( E_1 = (1,0) \) cannot be evaluated since the system (4) are not linearizable at (0,0) and (1,0); this is due to the square root term and the Jacobian matrix becomes indeterminate, to analyse the stability of \( E_0 \) and \( E_1 \), one can proceed to use the method proposed as in [4]. The stability of the interior or coexistence equilibrium \( E^* = (x^*, y^*) \) are determined by the given Jacobian matrix

\[ J(E^*) = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}. \]
where

\[ a_{11} = 1 - 2x^* - \frac{b\sqrt{y^*}}{2\sqrt{x^*(1 + a\sqrt{x^*})^2}} \]
\[ a_{12} = -\frac{b\sqrt{x^*}}{2\sqrt{y^*}(1 + a\sqrt{x^*})^2} \]
\[ a_{21} = \frac{c\sqrt{y^*}}{2\sqrt{x^*(1 + a\sqrt{x^*})^2}} \]
\[ a_{22} = -\frac{d}{2}. \]

The characteristics equation of \( J(E^*) \) is given by

\[ \lambda^2 + C\lambda + D = 0, \]

where

\[ C = -\text{tr} \, J(E^*) = -a_{11} - a_{22} \]
\[ D = -\det \, J(E^*) = a_{11}a_{22} - a_{12}a_{21}. \]

The stability of interior equilibrium is discussed further in [4].

4. Numerical Bifurcation Analysis

A bifurcation analysis has been carried out to demonstrate different dynamical behaviours of the models in Section 2 and 3 as conversion rate \( c \) is varied. In particular, we perform some simulation using MatCont (MATLAB continuation package) for the models (2) and (4) with parameter values as in Table 1.

| Parameter | Definition       | Value | Source |
|-----------|------------------|-------|--------|
| \( a \)  | Handling time    | 0.4   | [2]    |
| \( b \)  | Attack rate      | 0.15  | [2]    |
| \( c \)  | Conversion rate  | 0.85  | [4]    |
| \( d \)  | Death rate       | 0.5   | [4]    |
Using bifurcation analysis (figure 1), we observed different types of behaviour as bifurcation parameter $c$ changes. For $c < c_{IR}$, single-species steady state $(1,0)$ is stable: preys are free from predation and hence achieved the carrying capacity of the population since the predators go extinct in this case. At $c = c_{IR}$, we observed the occurrences of transcritical bifurcation (BP). There is an exchange of stability between single-species steady state $(1,0)$ with two-species steady state $(x^*, y^*)$. When
$c_{iT} < c < c_{iH}$, two-species steady state is stable. At $c = c_{iH}$, supercritical Hopf bifurcation (HB) occurs. For $c_{iH} < c < c_{iC}$, the two-species steady state becomes unstable with corresponding creation of stable limit cycles. As parameter $c$ increases, the stable limit cycles continue to grow in amplitude until this cycle collides with a saddle point at $c = c_{iC}$; this phenomenon is called homoclinic bifurcation and this occurs when $c = c_{iC}$. As $c > c_{iC}$, the limit cycles disappears completely. Thus, this situation causes the preys to go extinct, then followed by the exclusion of predators.

Figure 2 shows the bifurcation analysis for ecological model (4) when parameter $c$ changes. When $c_{2H} < c < c_{2S}$, two-species steady state is unstable. At $c = c_{2S}$, the limit point (LP) occurs whenever at $c = c_{2H}$, subcritical Hopf bifurcation occurs. For $c_{2H} < c < c_{2L}$, the two-species steady state becomes stable with corresponding creation of unstable limit cycles. As parameter $c$ decreases, the unstable limit cycles continue to grow in amplitude until this cycle meets the limit point of cycle (LPC) when $c = c_{2L}$. As $c < c_{2L}$, the limit cycles disappears completely and both prey and predator populations coexist since the two-species steady state is stable.

Next, three different values (see table 2 and 3) of bifurcation parameter $c$ are chosen to describe the dynamics of the prey-predator systems with herd behaviour as bifurcation parameter changes. The phase portraits and time series graphs for each values of $c$ are plotted (see figure 3-8).

**Table 2.** Stability and bifurcation analysis results of model (2).

| Bifurcation parameter $c$ | Steady states $E^* = (x^*, y^*)$ | Eigenvalues | Characteristics | Figure |
|---------------------------|----------------------------------|-------------|-----------------|--------|
| $c = 0.95$                | $(0.4444, 3.1276)$               | $\lambda_1 = -0.0541 + 0.3267i$ | Stable steady state | 3(a)   |
|                           |                                  | $\lambda_2 = -0.0541 - 0.3267i$ |                 | 3(b)   |
| $c = 1.069$               | $(0.3311, 3.1565)$               | $\lambda_1 = 0.0330 + 0.3672i$  | Stable limit cycle (unstable steady state) | 4(a)   |
|                           |                                  | $\lambda_2 = 0.0330 - 0.3672i$  |                 | 4(b)   |
| $c = 1.15$                | $(0.2770, 3.0709)$               | $\lambda_1 = 0.0737 + 0.3793i$  | Unstable steady state (stable steady state at $E_0(0,0)$ only) | 5(a)   |
|                           |                                  | $\lambda_2 = 0.0737 - 0.3793i$  |                 | 5(b)   |

**Table 3.** Stability and bifurcation analysis results of model (4).

| Bifurcation parameter $c$ | Steady states $E^* = (x^*, y^*)$ | Eigenvalues | Characteristics | Figure |
|---------------------------|----------------------------------|-------------|-----------------|--------|
| $c = 3.55$                | $(0.2700, 9.3292)$               | $\lambda_1 = -0.0461 + 0.1843i$ | Stable steady state | 6(a)   |
|                           |                                  | $\lambda_2 = -0.0541 - 0.1843i$ |                 | 6(b)   |
| $c = 3.6285$              | $(0.2378, 8.7689)$               | $\lambda_1 = -0.0222 + 0.1669i$ | Unstable limit cycle (stable steady state) | 7(a)   |
|                           |                                  | $\lambda_2 = -0.0222 - 0.1669i$ |                 | 7(b)   |
| $c = 3.75$                | $(0.173, 7.1590)$                | $\lambda_1 = 0.0246 + 0.1148i$  | Unstable steady state (stable steady state at $E_0(0,0)$ only) | 8(a)   |
|                           |                                  | $\lambda_2 = 0.0246 - 0.1148i$  |                 | 8(b)   |
Figure 3. Phase portrait (a) and time series graph (b) for system (2) with $c = 0.95$ and initial conditions $x(0) = 0.1$ and $y(0) = 3$. The equilibrium point $E^*$ is a stable focus (a). The prey $x(t)$ and predator $y(t)$ populations converge to an equilibrium value (b).

Figure 4. Phase portrait (a) and time series graph (b) for system (2) with $c = 1.069$ and initial conditions $x(0) = 0.33$ and $y(0) = 3.16$. The equilibrium point $E^*$ is an unstable focus and there is a stable periodic solution arises as time ($t$) increases.
Figure 5. Phase portrait (a) and time series graph (b) for system (2) with $c = 1.15$ and initial conditions $x(0) = 0.28$ and $y(0) = 3.07$. The equilibrium point $E^*$ is an unstable focus (a). The prey $x(t)$ and predator $y(t)$ populations diverge from an equilibrium value (b).

Figure 6. Phase portrait (a) and time series graph (b) for system (4) with $c = 3.55$ and initial conditions $x(0) = 0.4$ and $y(0) = 0.5$. The equilibrium point $E^*$ is a stable focus (a). The prey $x(t)$ and predator $y(t)$ populations converge to an equilibrium value (b).
Figure 7. Phase portrait (a) and time series graph (b) for system (4) with \( c = 3.6285 \) and initial conditions \( x(0) = 0.15 \) and \( y(0) = 6.5 \). The equilibrium point \( E^* \) is a stable focus (a).

Figure 8. Phase portrait (a) and time series graph (b) for system (4) with \( c = 3.75 \) and initial conditions \( x(0) = 0.17 \) and \( y(0) = 7.15 \). The equilibrium point \( E^* \) is an unstable focus (a). The prey \( x(t) \) and predator \( y(t) \) populations diverge from an equilibrium value (b).

5. Discussion and ecological implications

In this paper, the dynamics of the two ecological models of prey-predator is studied to understand the joint effects of herd behaviour mechanism and prey conversion rate in determining the population dynamics of species. Correspondingly, the ecological model (2) employs the herd behaviour in prey populations and the other model (4) employs the herd behaviour in both prey and predator populations. The stability and bifurcation results of each bifurcation parameter \( c \) are carried out by using mathematical continuation software i.e. in MATCONT and XPPAUT.

By using bifurcation analysis (see table 2, figure 1), we observed the occurrences of Supercritical Hopf and Homoclinic bifurcation on the model (2). Homoclinic bifurcation occurs when a periodic orbit collides with a saddle point [7]. As bifurcation parameter \( c \) increases, the limit cycle grows until it exactly intersects the saddle point, yield an orbit of infinite duration but if parameter increases further, the limit cycle disappears completely (see figure 1). We also observed the occurrences of Subcritical Hopf bifurcation on the model (4). It occurs when the stability of the equilibrium changes via a pair of purely imaginary eigenvalues and will result in unstable limit cycles [8] (see figure 2).

Ecologically, in comparison to the herd behaviour mechanisms of the two ecological models, the value of parameter \( c \) are discussed and summarized into three categories i.e. the low, moderate and high value of \( c \). The low value of \( c \) shows an extinction of predator in model (2); since the preys live in herd, therefore the predators might hesitate to attack preys. However, when the predators also live in
herd, it is very effective for them to pull down a herd of prey, and this will result the coexistence of two-species in model (4). For moderate value of $c$, both models (2) and (4) shows two-species coexistence; the prey and predator populations never goes to an extinction (see figure 3, figure 6). But then, in model (2), oscillatory solutions emerged due to Hopf bifurcation, where the prey and predators start to oscillate as the time changes (see figure 4). At this point, the preys oscillate to a very low population density will be excluded entirely and consequently, these situations can cause destabilized of coexistence of the two-species. For this reason, as the high value of $c$, there is an extinction of two-species in both models (2) and (4); the prey population first goes to extinction and then the predator population follows suit (see figure 5, figure 8).

In short, this paper illustrates the significant roles of herd behaviour mechanisms in the dynamics of prey-predator systems. By introducing herd behaviour mechanisms in predator populations, it helps the predator to survive themselves in nature and subsequently, the two-species coexist and this can increase the species diversity. For future research, it is interesting to explore more about the herd behaviour mechanisms, such as comparing the two ecological models in terms of two-parameter bifurcations analysis.

6. References
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