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Dynamics of a Predator–Prey System with Wind Effect and Prey Refuge

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Abstract

The natural environment of living organisms is not only affected by biotic factors but also by abiotic factors, including omnipresent wind. There has been less exploration on the effects of both biotic and abiotic factors on the dynamics of predator-prey interactions. In this work, we propose and study the dynamics of a predator-prey system incorporating wind effects and prey refuge. A refuge can be described as any strategy to avoid or reduce predation risks. We first prove positivity and boundedness of solutions for the system. We analyze the existence of equilibria under certain parametric restrictions. We also derive sufficient conditions for the global stability of the coexistence equilibrium using a suitable Lyapunov functional. Further dynamical analysis reveals that the system experiences local codimension one bifurcations including Hopf and transcritical bifurcations. Our findings show that when prey refuge is in use, it has a stabilizing effect on the system and also increases the equilibrium density of the prey population while the predator equilibrium density decreases. We also observe that the strength of wind flow has both stabilizing and destabilizing effects. We support our theoretical findings with numerical experiments and give their ecological implications.

1 Introduction

The study of complex dynamics displayed by predator-prey interactions using mathematical models continues to be at the forefront of recent scientific inquiries. One of the easily observed interactions is predation, which involves direct killing of prey which reduces the prey population size [1, 2]. Studies on predator-prey dynamics have evolved from the seminal work of Lotka and Volterra [3]. Later on, intensive studies in this field has progressed with collaborative efforts between biologists and mathematicians. In the ecological modeling of predator–prey dynamics, there has been a lot of attention paid to biotic factors in their modeling framework. Among these include migration [4–6], mutualism [7], cannibalism [8–10], group defense [11–14] and competition [15–17]. These factors have been shown to have complex dynamical effects on predator-prey relationships.

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In reality, population dynamics are not only affected by biotic factors. Abiotic themes also play crucial roles in the ecosystem. It is important to investigate abiotic effects on living organisms as there are widespread expected changes in the abundance, distribution and interaction of species resulting from ongoing global climatic change [18]. Limited abiotic factors have been investigated by ecologists in the pursuit to better understand predator–prey dynamics, including temperature and wind [18]. A growing body of literature has shown how abiotic factors such as wind, influence predator–prey relationships [19–25]. Wind is found everywhere in the ecosystem and blows in different patterns and speed intensity [26]. For example, increased wind intensity has an inhibitory effect on the flight control of aerial invertebrate insect predators. On the other hand, vertebrate aerial predators benefit from this intensity as their hunting timespan is increased [19]. The strength and directionality of wind flow can either cause an increase or a decrease in predation risk. Experiments conducted in [27] showed that wind can reduce predation risk in southern mule deer. This is due to the wind carrying the scent and sound of the approaching predator to the prey, as well as the wind hindering the advancement of the predator by virtue of wind noise and moving vegetation. Opposingly, the strength and direction of wind can decrease a prey's capability of detecting a predator since the wind can aid in masking the scent and sound of the approaching predator, thus increasing its predation risk. For example, at high wind speeds, lions are successful in hunting springbok and zebras [28]. In all, Cherry et al [19] concluded that wind speed can alter the dynamics of the food web and also weakening or strengthening its top-down control. In addition, wind can cause environmental disturbances such as loss of habitats and destruction of abodes which expose prey to predation [29]. The effect of wind as an abiotic factor affects behavior of mammals in forested environments. The behavior of three boreal forest mammals including free-ranging red squirrels, snowshoe hares and Canada lynx were found to have altered their behavioral response to average daily wind speeds in winter [30]. For example, the number of feeding events of lynx increased by 40% on windy days. Rothschild et al [31] suggested that the effects of wind inducing small-scale turbulence is an important component of plankton trophodynamics including larval fish. They analytically showed that the feeding rates of zooplankton may be underestimated in the assessment of the potential frequency of interactions between predators and prey when wind effects are not considered. Sundby et al [32] reported that winds impacted on the feeding rates of cod larvae. Their feeding rate was two-fold increased when winds were 6 ms^{-1} compared to times when winds were only 2 ms^{-1}. MacKenzie et al [33] also used an empirical turbulence model to estimate the contact rates between fish larvae and prey using multiple combinations of wind speed and water depth.

Therefore it is important to include the effects of abiotic factors such as wind in population dynamics modeling to understand how they affect the strength and nature of species interactions. Recently, Barman et al [22] modeled the effect of wind and herd behavior in a predator-prey system. The temporal system is given by

$$\begin{aligned}\frac{dx}{dt} &= rx(1-\frac{x}{K}) - \frac{\alpha x^{\delta} y}{(1+w)[1+b(1+w)x^{\delta}]},\\ \frac{dy}{dt} &= \frac{\beta x^{\delta} y}{(1+w)[1+b(1+w)x^{\delta}]} - my,\end{aligned} \tag{1}$$

where x and y denote the prey and predator population respectively. The parameters δ and w also respectively represent the prey herd shape and the strength of the wind flow. We refer the reader to [22] for a detailed derivation of the model and a description of the system parameters. The system (1) was shown to possess very rich dynamics. The spatial version of the system did not exhibit Turing patterns but rather irregular patchy chaotic patterns were observed. Research done by Panja in [25] also showed that the effects of wind direction and the anti-predator behavior of prey can have a stabilizing impact on the system's dynamics.

In recent times, the survival of species has emerged as a topic of concern in population dynamics, with the aim of exploring strategies to maintain ecological population balance. In predator-prey interactions, there are several defense mechanisms that prey populations exhibit in order to avoid predation. Included among these are prey defense, herd behavior, migration, prey counter attack, group defense and refuge [4–6, 14, 34–39]. Refuge can be defined as a strategy to avoid harm or lessen the predation rate of predators. For example, in a wolf-ungulate system, ungulates migrate to seek refuge at regions which are outside the core domain of wolves [40]. Other examples of refuge include spatial refuges (burrows, heavy vegetation), prey aggregation and reduced search activities by prey, all of which function to minimize contact with predators. This positively affects the growth of prey populations and reduces that of predator populations. It therefore plays an important role on the coexistence of prey and predator populations. The impact of prey refuges on population ecology can be very complex. Due to refuges being safe, they can lead to a reduction in the birth rate of the prey population since the refuges hardly offer mating and feeding opportunities [37]. Several mathematical models in literature have studied the effect of prey refuge in predator prey interactions [37, 38, 41, 42]. Sih [41] showed that, prey refuges have a stabilizing effect when the proportion of prey in refuges reduce with an increasing prey density or increase when predation pressure and predator density are both increasing. Similar results of the stabilizing effect of prey refuge can be found in [43–45]. Research done by Chen et al [38] showed that prey refuge had no impact on the persistent property of a predator prey-system with a Leslie Gower functional response incorporated into the modeling construct. Similar results were obtained in [46]. Ma et al [37] also showed that, under some parametric restrictions, prey refuge has a destabilizing effect on the dynamical system. Refuge has also been shown to be an effective tool in controlling chaotic dynamics in predator-predator systems [47]. Interestingly, prey refuge can cause even more chaotic, random-like dynamics in discrete predator-prey model with Holling type I functional response [48]. Spatially explicit predator-prey models have also been studied to explore the impacts of prey refuge. The development of spatiotemporal patterns were found to be controlled by prey refuge [39, 49]. To the best of our knowledge, very little or no studies has been done to explore the impact of prey refuge together with abiotic factors such as wind effects on predator-prey dynamics. This motivates the work done in this paper. In the real ecological system, the combined effects of wind and prey refuge can result in complex dynamics and is worth investigating. As such, we propose and study the dynamics of a predator prey model incorporating wind effects and prey refuge. In this manuscript, we report the following:

- Prey refuge has a stabilization effect on the dynamics of the system.
- The strength of wind can stabilize or destabilize the system.
- Under certain parametric restrictions, the coexistence equilibrium is globally stable via Theorem 6.
- The system experiences a Hopf bifurcation and a transcritical bifurcation via Theorem 7 and 8 respectively.

The rest of the paper is organized as follows: Section 2 deals with the formulation of the model. We perform mathematical analysis of the model including local bifurcation analysis in Section 3 and corroborate our theoretical results with numerical simulations in Section 4. We finally present a discussion and conclusion of our work in Section 5.

2 Model formulation

We revisit the model by Barman et al [22] and its derivation therein and study the model without herd behavior but with a prey refuge. We denote the prey and predator populations with the state variables

Table 1 Parameters used in Eq. (2).

Parameter	Description
b	half saturation constant when there is no wind flow
c_1	prey consumption rate by predator
c_2	food conversion rate of prey by predator
δ	natural death rate of predators
K	carrying capacity of the environment
m	prey refuge size
r	growth rate of prey
w	wind flow strength

u and v at any time instant t. The nonlinear system of ordinary differential equations modeling the impact of wind and prey refuge is given by

$$\begin{aligned}\frac{du}{dt} &= ru(1-\frac{u}{K}) - \frac{c_1 u(1-m)v}{(1+w)[1+b(1+w)u(1-m)]},\\ \frac{dv}{dt} &= \frac{c_2 u(1-m)v}{(1+w)[1+b(1+w)u(1-m)]} - \delta v,\end{aligned} \tag{2}$$

with positive initial conditions $u(0) = u_0$ and $v(0) = v_0$. All parameters used are assumed positive and their descriptions are given in Table 1. The prey is assumed to grow logistically with a growth rate r. We incorporate a refuge which protects mx of prey, where $m \in [0,1)$ is a constant. This makes $(1-m)x$ of the prey available to the predator.

3 Mathematical analysis

3.1 Positivity and boundedness

We first ensure that solutions to system (2) are positive and bounded, indicating solutions are biologically meaningful. Here, positivity of solutions implies that the population survives over some time domain. Since available resources are scarce, the population sizes of both prey and predator population cannot grow unboundedly and hence restricted. The following theorem relates to the positivity and boundedness of solutions to system (2).

Theorem 1. *All solutions to the system (2) lie in the positive octant* $\sum = \{(u,v) \in \mathbb{R}^2_+ : u(0) > 0, v(0) > 0\}$.

Proof. For $t > 0$, we can write system (2) as

$$u(t) = u(0)e^{\int_0^t [r(1-\frac{u}{K}) - \frac{c_1(1-m)v}{(1+w)[1+b(1+w)u(1-m)]}]ds} > 0,$$

$$v(t) = v(0)e^{\int_0^t (\frac{c_2 u(1-m)}{(1+w)[1+b(1+w)u(1-m)]} - \delta)ds} > 0.$$

Therefore $u(t) > 0, v(t) > 0$ whenever $u(0) > 0, v(0) > 0$. ■

Theorem 2. *All solutions of system (2) which start from* $\mathbb{R}^2_+$ *are bounded.*

Proof. Let us consider the function $W(t) = u(t) + \frac{c_1}{c_2}v(t)$. Then,

$$\begin{aligned}\frac{dW}{dt} &= \frac{du}{dt} + \frac{c_1}{c_2}\frac{dv}{dt},\\ &= ru(1-\frac{u}{K}) - \frac{c_1}{c_2}\delta v,\end{aligned}$$

Now, we let $\beta \in \mathbb{R}_+$, such that $\beta \leq \delta$. Then

$$\begin{aligned}\frac{dW}{dt}+\beta W &= ru(1-\frac{u}{K})+\beta u-\frac{c_1}{c_2}(\delta-\beta)v,\\ \frac{dW}{dt}+\beta W &\leq (r+\beta)u-\frac{ru^2}{K},\\ &\leq \frac{K(r+\beta)^2}{4r}=M \text{ say.}\end{aligned}$$

This implies that

$$W \leq \frac{M}{\beta}+(W(0)-\frac{M}{\beta})e^{-\beta t}$$

by standard theory in differential inequality. As $t\to\infty$,

$$\limsup W(t) \leq \frac{M}{\beta}. \tag{3}$$

Therefore by Theorem 1 and (3), all solutions of (2) with initial conditions $u(0)>0$ and $v(0)>0$ are bounded in the region

$$\Pi = \{(u,v)\in\ \mathbb{R}^2_+ : W(t)\leq \frac{M}{\beta}+\epsilon, \text{for any positive } \epsilon\}.$$

Hence proof. ■

3.2 Equilibria and local stability analysis

We compute for the equilibria by solving $\frac{du}{dt}=\frac{dv}{dt}=0$. The system (2) thus possesses the following non-negative equilibria:

- $E_0=(0,0)$,
- $E_1=(K,0)$ and
- $E_2=(u^*,v^*)$

where

$$u^*=\frac{\delta(w+1)}{(1-m)\,[c_2-b\delta(w+1)^2]}$$

and

$$v^*=\frac{c_2r(w+1)\,(\delta(w+1)(bK(m-1)(w+1)-1)+c_2k(1-m))}{c_1K(m-1)^2\,[c_2-b\delta(w+1)^2]^2}.$$

We note that, the interior equilibrium E_2 exists provided $c_2>b\delta(w+1)^2$.

After obtaining the steady states of system (2), we study its dynamics close to these states. A computation of the Jacobian of system (2) evaluated at an equilibrium point $E(u^*,v^*)$ is given as

$$J^*=\begin{pmatrix}J_{11} & J_{12}\\ J_{21} & J_{22}\end{pmatrix} \tag{4}$$

where

$$
\begin{aligned}
J_{11} &= \frac{c_1(m-1)v^*}{(w+1)[b(m-1)u^*(w+1)-1]^2} - \frac{2ru^*}{K} + r, \\
J_{12} &= -\frac{c_1(m-1)u^*}{(w+1)[b(m-1)u^*(w+1)-1]}, \\
J_{21} &= -\frac{c_2(m-1)v^*}{(w+1)[b(m-1)u^*(w+1)-1]^2}, \\
J_{22} &= \frac{c_2(m-1)u^*}{(w+1)[b(m-1)u^*(w+1)-1]} - \delta.
\end{aligned}
$$

We use this computation in aiding us perform local stability analysis on the equilibria of system (2). We state the following theorem.

Theorem 3. *The trivial equilibrium point E_0 is a saddle.*

Proof. An evaluation of the Jacobian at E_0 yields

$$J^*_{E_0} = \begin{pmatrix} r & 0 \\ 0 & -\delta \end{pmatrix} \tag{5}$$

and its associated eigenvalues are $\lambda_1 = r > 0$ and $\lambda_2 = -\delta < 0$. Hence E_0 is a saddle point and thus locally unstable. ■

Theorem 4. *The boundary equilibrium point E_1 is a saddle if $\frac{c_2K(1-m)}{(w+1)[1+bK(1-m)(w+1)]} > \delta$.*

Proof. A similar evaluation of the Jacobian at E_1 gives

$$J^*_{E_1} = \begin{pmatrix} -r & -\dfrac{c_1K(m-1)}{(w+1)[bK(m-1)(w+1)-1]} \\ 0 & \dfrac{c_2K(m-1)}{(w+1)[bK(m-1)(w+1)-1]} - \delta \end{pmatrix}. \tag{6}$$

The characteristic equation of J^* at E_1 is

$$(\lambda + r)(-\frac{c_2K(m-1)}{(w+1)[bK(m-1)(w+1)-1]} + \delta + \lambda) = 0.$$

Solving this yields $\lambda_1 = -r < 0$ and $\lambda_2 = -\delta + \frac{c_2K(1-m)}{(1+w)[1+bK(1-m)(1+w)]}$. If $\lambda_2 > 0$, then E_1 is a saddle point and locally unstable. ■

Theorem 5. *The coexistence equilibrium point E_2 is locally stable if $\frac{c_2(1-m)u^*}{(w+1)[b(1-m)u^*(w+1)+1]} < \delta$.*

Proof. Let $\frac{c_2(1-m)u^*}{(w+1)[b(1-m)u^*(w+1)+1]} < \delta$. It is enough to show that if the Trace$(J^*_{E_2}) < 0$ and Det$(J^*_{E_2}) > 0$, then E_2 is locally stable. It is obvious that $u(t) \leq K$ and therefore $J_{11} < 0$, $J_{12} < 0$, $J_{21} > 0$. Since $\frac{c_2(1-m)u^*}{(w+1)[b(1-m)u^*(w+1)+1]} < \delta$, we have that $J_{22} < 0$. Hence the Trace$(J^*_{E_2}) < 0$ and Det$(J^*_{E_2}) > 0$ and so E_2 is locally stable. ■

Theorem 6. *The coexistence equilibrium point E_2 is globally stable if $\frac{r}{K} \geq \frac{c_1(1-m)^2bv^*}{[1+b(1+w)u^*(1-m)]}$.*

Proof. Let us consider the Lyapunov function $F(t) = A[u(t) - u^* - u^* \ln(\frac{u(t)}{u^*})] + B[v(t) - v^* - v^* \ln(\frac{v(t)}{v^*})]$ where A and B are positive constants to be determined later. We can easily see that $F = 0$ at $(u, v) = (u^*, v^*)$ and also $F > 0$ when $(u, v) \neq (u^*, v^*)$. Taking the time derivative yields

$$\begin{aligned}\dot{F} &= A(1 - \frac{u^*}{u})\dot{u} + B(1 - \frac{v^*}{v})\dot{v},\\ &= A(u - u^*)[r(1 - \frac{u}{K}) - \frac{c_1(1-m)v}{(1+w)[1+b(1+w)u(1-m)]}] + B(v - v^*)[\frac{c_2(1-m)u}{(1+w)[1+b(1+w)u(1-m)]} - \delta].\end{aligned}$$

We use the following results:

$$\frac{c_1(1-m)v^*}{(1+w)[1+b(1+w)u^*(1-m)]} = r(1 - \frac{u^*}{K}), \quad \delta = \frac{c_2(1-m)u^*}{(1+w)[1+b(1+w)u^*(1-m)]}.$$

The time derivative of F becomes

$$\begin{aligned}\dot{F} =& A(u-u^*)[-\frac{r}{K}(u-u^*) + \frac{c_1(1-m)}{(1+w)}(\frac{-(v-v^*) + b(1+w)(1-m)[uv^* - u^*v]}{[1+b(1+w)u^*(1-m)][1+b(1+w)u(1-m)]})]\\ &+ B(v-v^*)[\frac{c_2(1-m)u}{(1+w)[1+b(1+w)u(1-m)]} - \frac{c_2(1-m)u^*}{(1+w)[1+b(1+w)u^*(1-m)]}],\\ =& A(u-u^*)[-\frac{r}{K}(u-u^*) + \frac{c_1(1-m)}{(1+w)}(\frac{-(v-v^*) + b(1+w)(1-m)[v^*(u-u^*) - u^*(v-v^*)]}{[1+b(1+w)u^*(1-m)][1+b(1+w)u(1-m)]})]\\ &+ \frac{B(v-v^*)c_2(1-m)(u-u^*)}{[1+b(1+w)u^*(1-m)][1+b(1+w)u(1-m)]},\\ =& -A(u-u^*)^2[\frac{r}{K} - \frac{c_1(1-m)^2bv^*}{[1+b(1+w)u^*(1-m)][1+b(1+w)u(1-m)]}]\\ &+ \frac{(1-m)(v-v^*)(u-u^*)}{(1+w)[1+b(1+w)u^*(1-m)][1+b(1+w)u(1-m)]}[Bc_2 - Ac_1(1 + (1-m)bu^*(1+w))].\end{aligned}$$

We can choose $B = \frac{Ac_1}{c_2}[1 + (1-m)bu^*(1+w)]$ and obtain

$$\begin{aligned}\dot{F} &= -A(u-u^*)^2[\frac{r}{K} - \frac{c_1(1-m)^2bv^*}{[1+b(1+w)u^*(1-m)][1+b(1+w)u(1-m)]}],\\ &= \frac{-A(u-u^*)^2}{1+b(1+w)u(1-m)}[\frac{r}{K}(1+b(1+w)u(1-m) - \frac{c_1(1-m)^2bv^*}{1+b(1+w)u^*(1-m)})].\end{aligned} \tag{7}$$

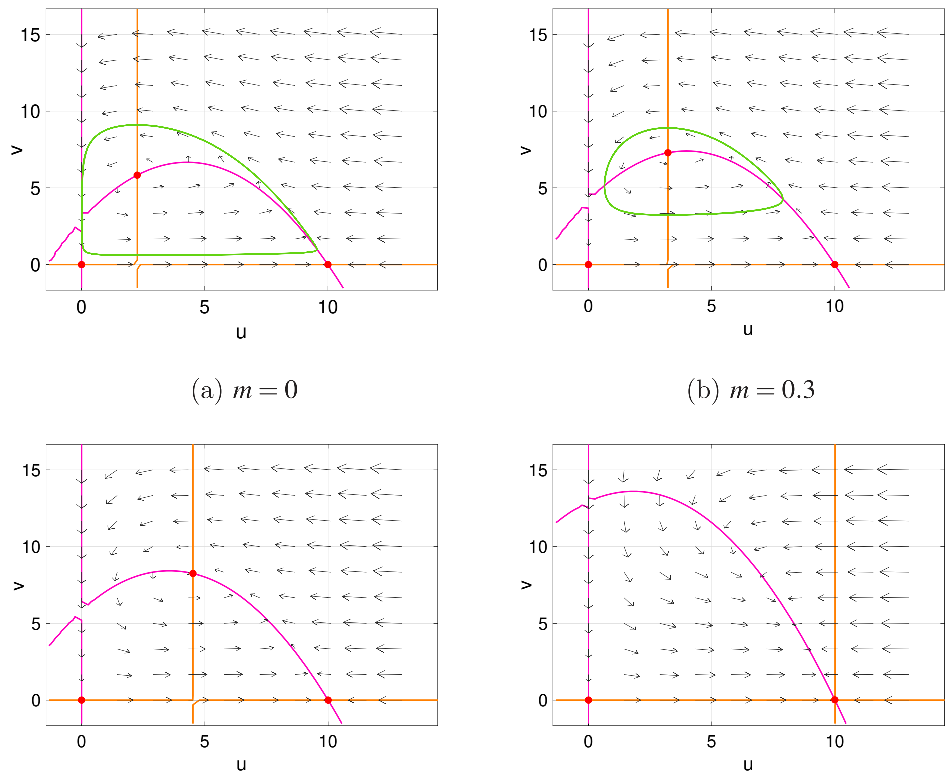
Next, if we impose the condition $\frac{r}{K} \geq \frac{c_1(1-m)^2bv^*}{[1+b(1+w)u^*(1-m)]}$ on Eq.(7) then $\dot{F} < 0$. Therefore the coexistence equilibrium E_2 is globally stable. Hence proof. ■

3.3 Bifurcation analysis

Bifurcation analysis is important in studying how systems transition in their qualitative behavior when parameters are continuously varied. Depending on a chosen set of parameteric values, equilibrium points can be created or destroyed and their stability status can change. In this section, we are concerned with the effects that wind strength and prey refuge parameters have on the dynamics of system (2) respectively. We explored local codimension-one bifurcations and obtained a Hopf and a transcritical bifurcation.

3.3.1 Hopf bifurcation

This subsection focuses on the conditions that guarantees the existence of a Hopf bifurcation around the interior equilibrium for system (2) in the preceding theorem. We choose the prey refuge parameter m as our bifurcation parameter.



(a) $m = 0$ (b) $m = 0.3$

(c) $m = 0.5$ (d) $m = 0.77419$

Fig. 1 Phase plots showing dynamics for various constant prey refuge sizes. Parameters used are $r = 0.5, K = 10, w = 2.5, b = 0.2, c_1 = 0.6, c_2 = 0.4, \delta = 0.1$. The magenta and orange colors depict the prey and predator nullcline respectively. The green closed loop is a stable limit cycle.

Theorem 7. *Consider the Jacobian of system (2). Then the system (2) undergoes a Hopf bifurcation at E_2^* with respect to the bifurcation parameter $m = m^*$ if $m^* > 1 - \frac{\delta(w+1)}{k[c_2 - b\delta(w+1)^2]}$ and $\frac{2c_2}{b\delta(1+w)^2 - c_2} < 1$ and the following hold,*

(i) $Tr(J^*)|_{E_2^*} = 0$,

(ii) $Det(J^*)|_{E_2^*} > 0$,

(iii) $\frac{d}{dm}(Tr(J^*))|_{E_2^*} \neq 0$ *at* $m = m^*$.

Proof. We begin the proof by evaluating the Jacobian of system (2) at E_2^* and obtain

$$J^*_{E_2^*} = \begin{pmatrix} \dfrac{\delta r(w+1)\left(\frac{bk(m-1)(w+1)-1}{c_2} - \frac{2}{b\delta(w+1)^2 - c_2}\right)}{k(m-1)} & -\dfrac{c_1\delta}{c_2} \\ \dfrac{c_2 k(m-1)r - \delta r(w+1)(bk(m-1)(w+1)-1)}{c_1 k(m-1)} & 0 \end{pmatrix}.$$

Let $m^* > 1 - \frac{\delta(w+1)}{k[c_2 - b\delta(w+1)^2]}$ and $\frac{2c_2}{b\delta(1+w)^2 - c_2} < 1$. The trace of $J^*_{E_2^*}$ is

$$Tr(J^*)|_{E_2^*} = \frac{\delta r(w+1)\left(\frac{bk(m-1)(w+1)-1}{c_2} - \frac{2}{b\delta(w+1)^2 - c_2}\right)}{k(m-1)}.$$

Clearly, $Tr(J^*)|_{E_2^*} = 0$ when $m^* = 1 + \frac{1}{bk(1+w)}(\frac{2c_2}{b\delta(1+w)^2 - c_2} + 1)$. We have $m^* > 0$ since $\frac{2c_2}{b\delta(1+w)^2 - c_2} < 1$. Recall that E_2^* exists provided $c_2 > b\delta(w+1)^2$. It is therefore clear that $m^* > 1 - \frac{\delta(w+1)}{k[c_2 - b\delta(w+1)^2]}$. The determinant of $J^*_{E_2^*}$ is given by

$$Det(J^*)|_{E_2^*} = \delta r(1 - \frac{\delta(w+1)(bk(m-1)(w+1)-1)}{c_2 k(m-1)}).$$

For $J^*_{E_2^*} > 0$, we require that $1 > \frac{\delta(w+1)(bk(m-1)(w+1)-1)}{c_2 k(m-1)}$. Simple calculations show that, $J^*_{E_2^*} > 0$ when $m^* > 1 - \frac{\delta(w+1)}{k[c_2 - b\delta(w+1)^2]}$. Furthermore, by the transversality condition of the Hopf bifurcation theorem [50], we have

$$\frac{d}{dm}(Tr(J^*))|_{E_2^*} = -\frac{2\delta r(w+1)}{k(1-m)^2[b\delta(w+1)^2 - c_2]} < 0.$$

Hence, the system (2) experiences a Hopf bifurcation around E_2^* with respect to the bifurcation parameter m at $m = m^*$. ■

3.3.2 Transcritical bifurcation

A transcritical bifurcation occurs when two equilibrium points collide and exchange their stability. We will investigate the possible occurrence of a transcritical bifurcation in the next theorem when the prey refuge parameter m is varied.

Theorem 8. *The system experiences a transcritical bifurcation around the predator free equilibrium state E_1^* when the prey refuge size is $m = m^* = 1 - \frac{\delta(1+w)}{k(c_2 - b\delta(1+w)^2)}$ and $c_2 \neq b\delta(1+w)^2$.*

Proof. Let $c_2 \neq b\delta(1+w)^2$. When we evaluate the Jacobian matrix of system (2) at E_1^* and $m = m^* = 1 - \frac{\delta(1+w)}{k(c_2 - b\delta(1+w)^2)}$, we obtain

$$J_{E_1^*} = \begin{pmatrix} -r & -\frac{c_1\delta}{c_2} \\ 0 & 0 \end{pmatrix}.$$

The associated eigenvalues are $\lambda_1 = 0$ and $\lambda_2 = -r$. Therefore $J_{E_1^*}$ has a zero eigenvalue at $m = m^*$. Now, we let $X(x_1, x_2)^T$ and $Y(y_1, y_2)^T$ represent the eigenvectors corresponding to the zero eigenvalues of the the matrices $J_{E_1^*}$ and $J^T_{E_1^*}$ respectively. By direct computation, we obtain $X = (-\frac{\delta c_1}{rc_2}, 1)^T$ and $Y = (0,1)^T$. Now we let $N = (N_1, N_2)^T$ where

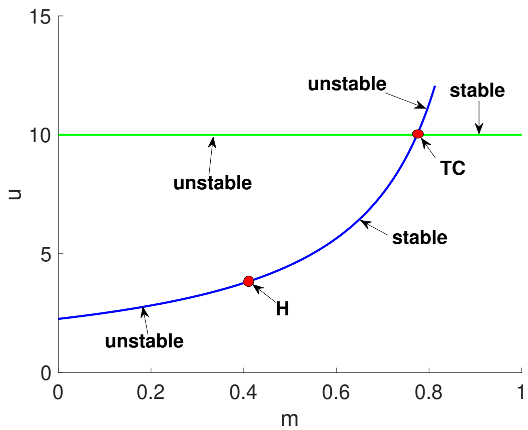
$$\begin{aligned} N_1 &= ru(1 - \frac{u}{K}) - \frac{c_1 u(1-m)v}{(1+w)[1+b(1+w)u(1-m)]}, \\ N_2 &= \frac{c_2 u(1-m)v}{(1+w)[1+b(1+w)u(1-m)]} - \delta v. \end{aligned} \tag{8}$$

We proceed to validate the transversality condition using Sotomayor's theorem [51].

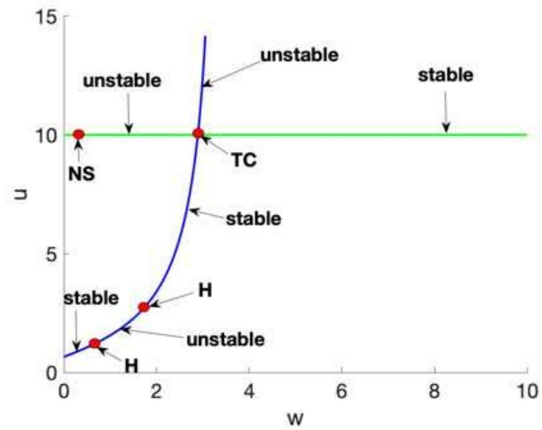
$$Y^T N_{m^*}(E_1^*, m) = (0,1)(0,0)^T = 0.$$

Also,

$$\begin{aligned} Y^T[DN_m(E_1, m^*)X] &= \begin{pmatrix} 0 & 1 \end{pmatrix} \begin{pmatrix} 0 & \frac{c_1 k\left(c_2 - b\delta(w+1)^2\right)^2}{c_2^2(w+1)} \\ 0 & -\frac{k\left(c_2 - b\delta(w+1)^2\right)^2}{c_2(w+1)} \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \\ &= -\frac{k\left(c_2 - b\delta(w+1)^2\right)^2}{c_2(w+1)} \neq 0, \end{aligned}$$



(a)



(b)

Fig. 2 Plot showing existence of a Hopf bifurcation and a transcritical bifurcation for the parameters $r = 0.5, K = 10, b = 0.2, c_1 = 0.6, c_2 = 0.4, \delta = 0.1$. In (a), $w = 2.5$ and initial condition was chosen as $(u_0, v_0) = (1,1)$. Also, $m = 0.6$ was used and an initial condition $(u_0, v_0) = (6,4)$ were chosen in plot (b). Multiple Hopf bifurcations and a transcritical bifurcation are observed therein. (Note: H=Hopf point, TC=Transcritical point, NS=Neutral Saddle (not a bifurcation point).)

and

$$Y^T \left[D^2 N\left(E_1, m^*\right)(X,X)\right] = \begin{pmatrix} 0 & 1 \end{pmatrix} \begin{pmatrix} -\frac{2bc_1^2\delta^3(w+1)^2}{c_2^3kr} \\ \frac{2c_1\delta^2\left(b\delta(w+1)^2-c_2\right)}{c_2^2kr} \end{pmatrix}$$
$$= \frac{2c_1\delta^2\left(b\delta(w+1)^2 - c_2\right)}{c_2^2kr} \neq 0.$$

Therefore by the Sotomayor's theorem system (2) experiences a transcritical bifurcation at $m = m^* = 1 - \frac{\delta(1+w)}{k(c_2 - b\delta(1+w)^2)}$ around E_1^*. ■

Theorem 9. *The system experiences a transcritical bifurcation around the predator free equilibrium state E_1^* when the wind strength crosses a critical threshold $w = w^*$.*

Proof. The proof is similar to the proof of Theorem 8 and is therefore omitted. ■

4 Numerical simulations

We perform numerical simulations with the help of PPLANE8 and MATCONT softwares [52]. The numerical simulations show various dynamics of system (2) and also corroborate our theoretical findings. From Fig.1, when there is no prey refuge in a windy environment, the system is unstable and there is an occurrence of a stable limit cycle. From Fig.2(a), a further increase in m results in system (2) experiencing a Hopf bifurcation around the coexistence equilibrium $E_2(u^*, v^*) = (3.798, 7.852)$ at $m^* = 0.40553$. With the help of Matcont software, the first Lyapunov coefficient was calculated as $\sigma = -5.25578106e^{-3}$ and hence the Hopf bifurcation is supercritical. A further increase in the constant refuge size m leads to a loss in stability of the coexistence equilibrium point and a gain in stability of the boundary equilibrium point via a transcritical bifurcation around $E_1(u^*, v^*) = (10,0)$ when $m^* = 0.77419$. In this case, the constant refuge size m has a stabilizing effect.

Remark 1. A gradual increment in the size of the prey refuge stabilizes the coexistence equilibrium and also increases the density of the prey population size. Here, the predator free equilibrium is unstable. A further increase in the refuge size leads to a loss in stability of the coexistence equilibrium, an increase in prey population density and a decrease in the density of predators leading to their extinction. At this point, the predator free equilibrium gains stability and the prey population grows to its carrying capacity. Therefore prey refuge aids in prey species conservation.

Furthermore, from the bifurcation diagram seen in Fig.2(b), we observe multiple Hopf bifurcations and a transcritical bifurcation for the strength of wind effect w. The system (2) experiences a Hopf bifurcation at $w^* = 0.63655$ and transitions from a stable coexistence to an unstable coexistence state at $E_2^* = (1.180997, 3.4717386)$. The first Lyapunov coefficient is given by $\sigma = -2.101887e^{-3}$ and thus the Hopf bifurcation is supercritical. A further increase in the wind strength leads to the system transitioning from oscillatory dynamics to stable dynamics via a Hopf bifurcation around the coexistence equilibrium $E_2^* = (2.7048593, 6.577443)$. Similar computation of the Lyapunov coefficient is given by $\sigma = -3.393e^{-3}$, thus, the obtained Hopf bifurcation is supercritical as well. This indicates that, the strength of wind has both a stabilizing and a destabilizing effect on the population dynamics. When w is further increased to $w^* = 2.890598$, the coexistence equilibrium E_2^* and the predator free equilibrium E_1^* collide and exchange their stability via a transcritical bifurcation at $E_1^* = (10, 0)$. Thus E_2^* becomes unstable and E_1^* becomes stable.

Remark 2. When the prey population is offered some level of protection through a refuge, a gradual increment in wind strength stabilizes the coexistence equilibrium. A further increase in the wind strength destabilizes the coexistence equilibrium and the populations go through self sustained periodic oscillations. An extra increase in the wind speed enables the coexistence equilibrium gain stability again. In each of these incremental stages of the wind strength, the density of the prey population increases and the predator free equilibrium remains unstable. A final additional increase in the wind strength causes the coexistence equilibrium to exchange stability with the predator free equilibrium which becomes stable. At this point, the prey population grows to carrying capacity. Therefore, the strength of wind also helps in prey species conservation in the presence of prey refuge.

5 Discussion and conclusion

In this present work, we proposed a system of ordinary differential equations which model the effect of wind strength and prey refuge in a predator prey system. Preliminary results such as positivity and boundedness results were derived. Conditions for biological meaningfulness of equilibrium points were also obtained and subsequent stability analysis of these equilibria were carried out. We established global stability results on the coexistence equilibrium point under certain parametric restrictions. See Theorem 6. Once this parametric restriction is met, it implies that the two species will continue to persist and/or coexist. Our investigations revealed that increasing the size of prey refuge had a stabilizing effect on the dynamics of the prey population, transitioning from an unstable to a stable state via a Hopf bifurcation. From Fig.1, we observed that when the prey refuge size is large enough, the prey are well protected. Since it is difficult for the predators to attack the prey, the prey population density increases while the predator population decreases to extinction via a transcritical bifurcation. See Fig.2(a). We provided rigorous proofs for both Hopf and transcritical bifurcations. See Theorem 7 and Theorem 8.

Furthermore, we observed the occurrence of multiple Hopf bifurcations for the strength of wind flow parameter w. The ecological implication of this result is that, the strength of wind flow has both a stabilizing and a destabilizing effect when some form of protection is offered to the prey. See Fig.2(b). When the strength of wind flow is increased, the coexistence equilibrium loses its stability after colliding with the predator free equilibrium via a transcritical bifurcation. In this case the ecological implication is that increased wind flow strength can provide benefits to the prey via a reduction in predation risk. This phenomenon has been shown in experiments from [27]. A key biological significance of transcritical bifurcation is that, it provides useful information to stakeholders and ecologists on optimal or threshold control rates in management strategies invested in pest eradication, invasive species control and species conservation. For example, in our case, the transcritical bifurcation provides information on the optimal refuge size to provide the prey population to enable them to persist if we wanted to completely eradicate the predator population. It will be interesting to study system (2) with competition between predators when prey are offered some level of protection in a windy environment. It will also be interesting to study system (2) with different functional responses as well.

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Competing interests

The authors declare that they have no competing interests.

Author Contributions

EMT, KC, AD and CM contributed equally to the conceptualization of the problem and writing of this manuscript. All authors read and approved the final manuscript.

Availability of data and material

Not Applicable.

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