



A predator-prey model incorporating fear effect, prey vigilance costs, and predator hunting cooperation: Analysis and simulations

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Abstract

In this study, we propose and analyze a predator-prey model that incorporates prey vigilance, fear effects, and predator cooperative hunting to capture key behavioral mechanisms influencing population dynamics. The model explicitly accounts for nonconsumptive effects of predation risk, whereby prey fear and vigilance reduce effective prey growth and modify predator-prey interactions even in the absence of direct predation. We first establish the mathematical structure of the model and identify all biologically meaningful equilibria, including the extinction equilibrium, the predator-free equilibrium, and the coexistence equilibrium. Local stability analysis reveals that fear and vigilance significantly alter classical stability thresholds by reducing prey reproductive potential and limiting predator access to prey. Using Lyapunov-based methods, we derive sufficient conditions for the global asymptotic stability of the extinction and predator-free equilibria, demonstrating that strong fear effects combined with prey vigilance or elevated predator mortality can suppress predator persistence regardless of initial population densities. For the coexistence equilibrium, we show that stable coexistence occurs under balanced levels of fear, vigilance, and predator cooperation, while excessive cooperation destabilizes the equilibrium. This destabilization is characterized analytically by a Hopf bifurcation with respect to the predator cooperation parameter, leading to the emergence of sustained population oscillations. Numerical simulations, including phase-plane portraits and

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time-series analyses, are presented to support the theoretical results and confirm the analytical stability and bifurcation findings.

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1 Introduction

Classical predator-prey models, such as the Lotka–Volterra equations, assume that predators impact prey solely through direct consumption, with prey growth unaffected by predator presence aside from mortality losses [12, 23]. In reality, however, prey species have evolved a variety of anti-predator behaviors and life-history adjustments in response to predation risk, forcing them to balance the conflicting demands of foraging and avoiding predators [11, 10]. In recent decades, ecologists have recognized that predators can influence prey not only by killing individuals but also by inducing fear and associated nonconsumptive effects on prey physiology and behavior [3, 4, 10]. The mere presence of a predator (even if no kill occurs) can trigger costly defensive responses in prey —such as reduced foraging, heightened stress, or habitat shift— which in turn may lower prey survival or reproduction [3, 4]. These so-called “fear effects” on prey populations can be powerful. For instance, field experiments have demonstrated that chronic predation risk alone (without any actual predation) can significantly depress prey reproductive success [6, 15]. In one landmark study, song sparrows exposed to predator cues (playback of predator sounds) produced about 40% fewer offspring over a breeding season compared to controls, despite suffering no direct predation [6]. Similarly, under high perceived predation risk, large herbivores like elk exhibit reduced fertility and altered physiology [4]. The cascading consequences of fear have been observed at the community level as well —for example, the mere fear of large carnivores can cause trophic cascades by altering the behavior of mesopredators and herbivores [20]. Recent empirical work is now quantifying these demographic impacts of fear in nature, confirming that risk-induced behavioral changes in prey can substantially affect prey population growth [15].

One of the most common prey anti-predator responses is vigilance: Prey invest time and energy in scanning their surroundings for predators, which improves early detection and escape chances [6]. Increased vigilance by an individual can significantly reduce its immediate risk of predation, especially when a predator is nearby [16]. However, time spent being vigilant is time not spent feeding, courting, or caring for young. Thus, heightened vigilance carries a direct cost in

lost foraging opportunities and energy intake [8, 9]. Empirical studies have quantified these costs; for example, foraging efficiency in ungulates declines with increasing vigilance, leading to lower energy gain and potentially reduced fecundity [8, 9]. In the present study, we represent these vigilance costs primarily through reduced prey reproduction rather than through an increase in baseline mortality, reflecting the dominant opportunity-cost mechanism emphasized in the ecological literature. Because vigilance is costly yet beneficial for safety, prey tend to modulate their vigilance level according to the level of predation threat [16]. In periods or areas of higher perceived risk, animals increase their vigilance, whereas they can afford to feed more and scan less under low risk. Social grouping further mediates this trade-off via the “many-eyes” effect [7]: In larger groups, individuals can collectively maintain high overall surveillance while each individual spends less time being vigilant. As a result, per-capita vigilance typically decreases as group size increases, improving the feeding rate of group members [7]. This group-size effect on vigilance has clear fitness benefits—for instance, studies on birds have shown that larger coveys or flocks suffer lower per-capita predation because each individual can devote more time to foraging while still achieving early predator detection in the group [25]. In short, prey vigilance is a dynamic trait that improves survival at the cost of reproduction, and its optimal level reflects a trade-off between safety and feeding [11, 10, 8, 9].

Predators, on the other hand, often benefit from cooperative hunting strategies. Many social predators hunt in groups to subdue prey that would be difficult or dangerous to kill alone [13, 2, 17, 19, 18, 5]. Cooperative hunting has been documented across a wide range of species—from lions and cheetahs to canids like wolves and African wild dogs, and even in some primates [13, 2, 17, 19, 18, 5]. Group hunting frequently leads to higher success rates and allows predators to tackle larger or more formidable prey. For example, the hunting success of African wild dogs increases with pack size [5], and grey wolves in larger packs achieve greater per-capita food intake than lone wolves or small packs [18]. Chimpanzees have also been observed to coordinate hunts of monkeys, increasing their success compared to individual foraging [2]. These observations underscore the evolutionary advantages of group foraging [13]: Larger groups can overwhelm prey defenses and flush out prey more effectively, yielding greater food rewards per predator. An important consequence of cooperative predation is the potential for an Allee effect in predator populations [22]. When predator numbers are very low, hunting success can be so depressed (due to lack of cooperation) that the predators struggle to obtain enough food to sustain themselves or reproduce. But as predator group size grows, hunting efficiency improves nonlinearly, leading to disproportionately higher gains for each additional hunter [5, 18]. Theoretical models of predator-prey dynamics have incorporated such cooperative effects via modified functional responses, which indeed often produce dynamics consistent with an Allee effect [22, 1]. Cooperative hunting can also introduce destabilizing feedbacks into predator-prey systems, potentially leading to

complex dynamics like multiple equilibria or oscillations when predator cooperation is strong [14, 1].

Given the growing evidence that both prey risk-avoidance behaviors and predator cooperative tactics can fundamentally alter ecological outcomes, recent research has focused on extending predator-prey models to include these effects. In particular, much attention has been paid to modeling the fear effect —the impact of predation risk on prey demographics. The incorporation of a fear factor into prey population equations was pioneered by Wang et al. [24], who added a term to represent the reduction in prey birth rate due to anti-predator stress or reduced feeding in the presence of predators. Their mathematical analysis showed that sufficiently high levels of fear can stabilize the predator-prey system by damping or eliminating oscillatory cycles. Subsequent studies have considered fear effects in various contexts and extensions of the basic model [14], consistently finding that antipredator responses tend to have a net stabilizing influence on predator-prey dynamics. On the other hand, predator hunting cooperation has been modeled by modifying the predator’s functional response to increase efficiency at higher predator densities [22, 1]. Such models predict that predator cooperation can create bistability or a threshold phenomenon [22]. More recently, Pal et al. [14] analyzed a predator-prey model that included both a fear effect on the prey and cooperative hunting among the predators. Likewise, a very recent study by Takyi et al. [21] examined a model where prey exhibit vigilance behavior and predators engage in cooperative hunting. Their results showed that intense predator cooperation can lead to Hopf bifurcations and bistability, implying oscillatory predator-prey dynamics or sudden regime shifts under high cooperation strength [21]. Overall, the existing modeling literature suggests that prey anti-predator adaptations generally have a stabilizing or buffering effect on predator-prey interactions [24, 14, 21], whereas predator cooperative hunting tends to have a destabilizing effect if cooperation is sufficiently strong [14, 22, 1]. However, to our knowledge, no single theoretical model has yet incorporated all three of these factors —fear, vigilance, and cooperation— together in one framework.

In this paper, we develop and analyze a new predator-prey model that explicitly includes (i) a fear effect in the prey, (ii) prey vigilance behavior, and (iii) predator hunting cooperation. By integrating all three mechanisms, our model provides a more comprehensive representation of predator-prey dynamics under behaviorally realistic assumptions. We derive conditions for the existence of various equilibria and investigate their stability, and we carry out bifurcation analysis to determine how fear, vigilance, and cooperation influence oscillatory dynamics or alternative stable states. Numerical simulations are also performed to illustrate the system’s behavior under different parameter regimes.

The remainder of the paper is organized as follows: Section 2 presents the formulation of the mathematical model and defines the key parameters. In Section 3, we explain the boundedness

property of the model, while in Section 4 we analyze the equilibrium points of the system and their local and global stability, and we examine possible bifurcations that arise as parameters vary. Section 5 contains numerical simulations that validate and complement the analytical results. Finally, Section 6 concludes the paper with a summary of findings and a discussion of their ecological implications.

2 Model formulation

We consider an unstructured predator-prey system in which $x(t)$ and $y(t)$ denote the prey and predator population densities, respectively, at time t . The prey is assumed to follow logistic growth in the absence of predation, and the predator population increases by consuming prey. In addition to these classical assumptions, we incorporate (i) predator-induced fear, (ii) prey vigilance behaviour, and (iii) cooperative hunting in predators.

We begin with the prey dynamics in the absence of predators, fear, and vigilance. The logistic growth of prey can be separated into three parts: A birth (production) term, a natural death term, and a density-dependent death term due to intra-species competition. Hence,

$$\frac{dx}{dt} = rx - \delta x - \frac{r}{K}x^2,$$

where r denotes the intrinsic birth (production) rate of the prey, δ is the natural death rate, and $\frac{r}{K}x^2$ represents the density-dependent death due to intra-species competition (with K being the carrying capacity).

Next, we incorporate the cost of vigilance. Let $v \in [0, 1]$ denote the level of prey vigilance, with larger values of v corresponding to stronger vigilance. Biologically, vigilance imposes an opportunity cost: Time and energy devoted to scanning for predators are diverted from feeding, mating, and parental care, thereby reducing reproductive output. In this model, we therefore assume that the principal demographic effect of vigilance acts through the prey birth term, while its direct effect on the natural mortality rate δ is negligible or secondary. This assumption is adopted both to isolate the dominant reproductive cost of vigilance and to maintain analytical tractability. It is also consistent with fear-effect models in which predation risk is commonly represented through reduced prey reproduction rather than increased background mortality [24], as well as with empirical studies documenting foraging–vigilance trade-offs and their consequences for energy intake and fecundity [8, 9]. Accordingly, we modify only the prey production term by multiplying it by $(1 - v)$, while leaving the density-dependent competition term unchanged.

We now incorporate predator-induced fear. Predator presence can suppress prey production through fear-related behavioral responses. To capture this mechanism, we introduce a fear function $f(k, y)$ that depends on predator density y and a fear level parameter $k > 0$, and we again let it act only on the prey production term. In particular, we adopt

$$f(k, y) = \frac{1}{1 + ky}, \quad k > 0,$$

which is chosen for its simplicity, analytical tractability, and its ability to capture a natural saturation of fear effects as predator density increases. Other functional forms, such as e^{-ky} , are also biologically plausible, but the reciprocal form provides a convenient normalized representation for the present analysis. The sensitivity of the system to alternative fear functions could be explored in future work. This function satisfies the following biologically reasonable properties:

$$\begin{aligned} \frac{dx}{dt} &= r(1 - v)x - \delta x - \frac{r}{K}x^2, \\ f(0, y) &= 1, \quad f(k, 0) = 1, \quad \lim_{k \rightarrow \infty} f(k, y) = 0, \quad \lim_{y \rightarrow \infty} f(k, y) = 0, \\ \frac{\partial f}{\partial k} &< 0, \quad \frac{\partial f}{\partial y} < 0. \end{aligned}$$

Accordingly, incorporating both vigilance and fear into the prey production term gives

$$\frac{dx}{dt} = r(1 - v)f(k, y)x - \delta x - \frac{r}{K}x^2.$$

We proceed by introducing predation using a Holling type II functional response. We assume that prey vigilance reduces predation success through a protective factor $(1 + \mu v)$, where $\mu > 0$ measures the effectiveness of vigilance in lowering capture probability. Moreover, we assume that predators cooperate while hunting, so that the effective encounter/attack pressure increases with predator density. Hence, we define the predation (consumption) term as

$$G(x, y, v) = \frac{(q + cy)xy}{(1 + hx)(1 + \mu v)},$$

where $q > 0$ is the baseline encounter rate, $c \geq 0$ measures the strength of predator hunting cooperation, and $h > 0$ is the Holling type II saturation (handling) parameter. Incorporating predation, the prey equation becomes

$$\frac{dx}{dt} = r(1 - v)f(k, y)x - \delta x - \frac{r}{K}x^2 - G(x, y, v).$$

Finally, the predator population increases through consumption of prey with conversion efficiency $\gamma > 0$ and decreases due to natural mortality at rate $\delta_1 > 0$. Thus,

$$\frac{dy}{dt} = \gamma G(x, y, v) - \delta_1 y.$$

Combining the above components, we obtain the following nonlinear predator-prey system with fear effect, prey vigilance, and predator hunting cooperation:

$$\begin{aligned} \frac{dx}{dt} &= \frac{r(1-v)x}{1+ky} - \delta x - \frac{r}{K}x^2 - \frac{(q+cy)xy}{(1+hx)(1+\mu v)}, \\ \frac{dy}{dt} &= \gamma \frac{(q+cy)xy}{(1+hx)(1+\mu v)} - \delta_1 y, \end{aligned} \quad (1)$$

The biological interpretations of all model variables and parameters are summarized in Table 1. We assume positive initial conditions $x(0) = x_0 > 0$ and $y(0) = y_0 > 0$. We assume all parameters are positive unless otherwise stated, and $v \in [0, 1]$.

Table 1: Parameters used in the combined predator-prey model.

Parameter	Description
x	prey population density
y	predator population density
r	prey birth/production rate
K	prey carrying capacity (controls intra-species competition via $\frac{r}{K}x^2$)
δ	prey natural death rate
δ_1	predator natural death rate
v	level of prey vigilance ($v \in [0, 1]$)
k	fear-effect strength (predator-induced suppression of prey production)
μ	effectiveness of vigilance in reducing predation
q	baseline predator encounter/attack rate
c	hunting cooperation strength in predators
h	Holling type II saturation/handling parameter
γ	conversion efficiency (prey biomass to predator biomass)

3 Boundedness of solutions

The boundedness property guarantees that neither population can grow unboundedly due to limited resources and habitat constraints.

Theorem 1. Assume that all parameters of the system are positive and that $v \in [0, 1]$. Then every solution $(x(t), y(t))$ of system (1) with initial condition $(x(0), y(0)) \in \mathbb{R}_+^2$ is bounded. In particular, there exists a constant $M > 0$ such that

$$0 \leq x(t) \leq (1 - v)K, \quad 0 \leq x(t) + \frac{1}{\gamma}y(t) \leq M \quad \text{for all sufficiently large } t.$$

Proof. First, since

$$\frac{r(1-v)x}{1+ky} \leq r(1-v)x \quad \text{and} \quad -\delta x - \frac{(q+cy)xy}{(1+hx)(1+\mu v)} \leq 0,$$

we obtain

$$\frac{dx}{dt} \leq r(1-v)x - \frac{r}{K}x^2 = rx \left((1-v) - \frac{x}{K} \right).$$

By the comparison principle for scalar differential equations, it follows that

$$\limsup_{t \rightarrow \infty} x(t) \leq (1-v)K.$$

Next, define the auxiliary function

$$W(t) = x(t) + \frac{1}{\gamma}y(t).$$

Differentiating and using the system equations yields

$$\frac{dW}{dt} = \frac{dx}{dt} + \frac{1}{\gamma} \frac{dy}{dt} = \frac{r(1-v)x}{1+ky} - \delta x - \frac{r}{K}x^2 - \frac{\delta_1}{\gamma}y.$$

Dropping the nonpositive term $-\frac{r}{K}x^2$ and using $\frac{r(1-v)x}{1+ky} \leq r(1-v)x$, we obtain

$$\frac{dW}{dt} \leq r(1-v)x - \delta x - \frac{\delta_1}{\gamma}y \leq r(1-v)x - \delta x - \frac{\delta_1}{\gamma}y.$$

Using the bound $\limsup_{t \rightarrow \infty} x(t) \leq (1-v)K$, we have for sufficiently large t ,

$$r(1-v)x(t) \leq r(1-v)^2K.$$

Hence, for large t ,

$$\frac{dW}{dt} \leq r(1-v)^2K - \delta x - \frac{\delta_1}{\gamma}y.$$

Let $\varepsilon = \min\{\delta, \delta_1\} > 0$. Then

$$-\delta x - \frac{\delta_1}{\gamma} y \leq -\varepsilon \left(x + \frac{1}{\gamma} y \right) = -\varepsilon W(t),$$

so that for large t ,

$$\frac{dW}{dt} + \varepsilon W(t) \leq r(1-v)^2 K.$$

Solving this differential inequality gives

$$\limsup_{t \rightarrow \infty} W(t) \leq \frac{r(1-v)^2 K}{\varepsilon}.$$

Therefore, both $x(t)$ and $y(t)$ are bounded for $t \geq 0$, and all solutions initiating from $\mathbb{R}_+^2$ are bounded. $\square$

4 Equilibria

To obtain the equilibria of the system, we solve $\dot{x} = 0$ and $\dot{y} = 0$ simultaneously for system (1). The system possesses the following nonnegative equilibria:

1. Extinction Equilibrium: $E_0 = (0, 0)$.
2. Predator-free equilibrium: $E_1 = (x_1, 0)$, where

$$x_1 = K \left(1 - v - \frac{\delta}{r} \right).$$

We note that E_1 is feasible whenever $x_1 > 0$, equivalently, if $r(1-v) > \delta$.

3. Coexistence equilibrium: $E_2 = (x^*, y^*)$, where (x^*, y^*) is a coexistence equilibrium with $x^* > 0$ and $y^* > 0$.

To derive the coexistence equilibrium, set $\dot{y} = 0$. If $y^* > 0$, then

$$0 = \gamma \frac{(q + cy^*)x^*y^*}{(1 + hx^*)(1 + \mu v)} - \delta_1 y^* \implies \gamma \frac{(q + cy^*)x^*}{(1 + hx^*)(1 + \mu v)} = \delta_1.$$

Define

$$A = \frac{\gamma}{1 + \mu v} > 0.$$

Then the above relation becomes

$$q + cy^* = \frac{\delta_1(1 + hx^*)}{Ax^*},$$

and hence

$$y^* = \frac{1}{c} \left(\frac{\delta_1(1 + hx^*)}{Ax^*} - q \right).$$

Therefore, E_2 is feasible only if $y^* > 0$, that is,

$$\frac{\delta_1(1 + hx^*)}{Ax^*} > q \iff 0 < x^* < \frac{\delta_1}{Aq - h\delta_1},$$

which requires $Aq - h\delta_1 > 0$.

Next, set $\dot{x} = 0$ and assume $x^* > 0$. Dividing the prey equation by x^* yields

$$0 = \frac{r(1 - v)}{1 + ky^*} - \delta - \frac{r}{K}x^* - \frac{(q + cy^*)y^*}{(1 + hx^*)(1 + \mu v)}.$$

Using $q + cy^* = \frac{\delta_1(1 + hx^*)}{Ax^*}$ and $A = \frac{\gamma}{1 + \mu v}$, we obtain

$$\frac{(q + cy^*)y^*}{(1 + hx^*)(1 + \mu v)} = \frac{\delta_1 y^*}{\gamma x^*}.$$

Hence, the coexistence equilibrium satisfies

$$\frac{r(1 - v)}{1 + ky^*} = \delta + \frac{r}{K}x^* + \frac{\delta_1 y^*}{\gamma x^*},$$

together with

$$y^* = \frac{1}{c} \left(\frac{\delta_1(1 + hx^*)}{Ax^*} - q \right), \quad A = \frac{\gamma}{1 + \mu v}.$$

Once a positive real root x^* satisfying the feasibility conditions is obtained, y^* follows uniquely from the above expression, and thus $E_2 = (x^*, y^*)$.

The stability of the equilibrium points is determined by the nature of the eigenvalues of the Jacobian matrix $J(x, y)$ of system (1).

Let

$$F(x, y) = \frac{r(1 - v)x}{1 + ky} - \delta x - \frac{r}{K}x^2 - \frac{(q + cy)xy}{(1 + hx)(1 + \mu v)},$$

$$H(x, y) = \gamma \frac{(q + cy)xy}{(1 + hx)(1 + \mu v)} - \delta_1 y.$$

Then

$$J(x, y) = \begin{pmatrix} \frac{\partial F}{\partial x} & \frac{\partial F}{\partial y} \\ \frac{\partial H}{\partial x} & \frac{\partial H}{\partial y} \end{pmatrix}.$$

A direct computation gives

$$J(x, y) = \begin{pmatrix} \frac{r(1-v)}{1+ky} - \delta - \frac{2r}{K}x - \frac{y(q+cy)}{(1+\mu v)(1+hx)^2} - \frac{rk(1-v)x}{(1+ky)^2} - \frac{x(q+2cy)}{(1+\mu v)(1+hx)} \\ \gamma \frac{y(q+cy)}{(1+\mu v)(1+hx)^2} - \gamma \frac{x(q+2cy)}{(1+\mu v)(1+hx)} - \delta_1 \end{pmatrix}.$$

Theorem 2. The extinction equilibrium point $E_0 = (0, 0)$ of system (1) is locally asymptotically stable if $r(1-v) < \delta$, and it is unstable (a saddle point) if $r(1-v) > \delta$.

Proof. Evaluating the Jacobian $J(x, y)$ at $E_0 = (0, 0)$ yields

$$J_{E_0} = J(0, 0) = \begin{pmatrix} r(1-v) - \delta & 0 \\ 0 & -\delta_1 \end{pmatrix}.$$

Therefore, the eigenvalues of $J(E_0)$ are

$$\lambda_1 = r(1-v) - \delta, \quad \lambda_2 = -\delta_1.$$

Since $\delta_1 > 0$, we have $\lambda_2 < 0$. Therefore, both eigenvalues have negative real parts if and only if $r(1-v) - \delta < 0$, that is, $r(1-v) < \delta$, and in this case E_0 is locally asymptotically stable. If $r(1-v) > \delta$, then $\lambda_1 > 0$ and $\lambda_2 < 0$, so E_0 is a saddle point and hence unstable. $\square$

Theorem 3. Assume that $r(1-v) > \delta$ so that the predator-free equilibrium point

$$E_1 = (x_1, 0), \quad x_1 = K \left(1 - v - \frac{\delta}{r} \right),$$

is feasible. Then E_1 is locally asymptotically stable if

$$\gamma \frac{qx_1}{(1+\mu v)(1+hx_1)} < \delta_1,$$

and it is unstable (a saddle point) if

$$\gamma \frac{qx_1}{(1+\mu v)(1+hx_1)} > \delta_1.$$

Proof. Evaluating the Jacobian $J(x, y)$ at $E_1 = (x_1, 0)$ yields

$$J_{E_1} = J(x_1, 0) = \begin{pmatrix} r(1-v) - \delta - \frac{2r}{K}x_1 - rk(1-v)x_1 - \frac{qx_1}{(1+\mu v)(1+hx_1)} \\ 0 \quad \gamma \frac{qx_1}{(1+\mu v)(1+hx_1)} - \delta_1 \end{pmatrix}.$$

Since $x_1 = K \left(1 - v - \frac{\delta}{r}\right)$, we obtain

$$r(1 - v) - \delta - \frac{2r}{K}x_1 = -(r(1 - v) - \delta).$$

Hence,

$$J_{E_1} = \begin{pmatrix} -(r(1 - v) - \delta) & * \\ 0 & \gamma \frac{qx_1}{(1 + \mu v)(1 + hx_1)} - \delta_1 \end{pmatrix},$$

which is an upper triangular matrix. Therefore, the eigenvalues of $J(E_1)$ are

$$\lambda_1 = -(r(1 - v) - \delta), \quad \lambda_2 = \gamma \frac{qx_1}{(1 + \mu v)(1 + hx_1)} - \delta_1.$$

Since $r(1 - v) > \delta$, we have $\lambda_1 < 0$. Thus, E_1 is locally asymptotically stable if and only if $\lambda_2 < 0$, that is,

$$\gamma \frac{qx_1}{(1 + \mu v)(1 + hx_1)} < \delta_1.$$

If $\gamma \frac{qx_1}{(1 + \mu v)(1 + hx_1)} > \delta_1$, then $\lambda_2 > 0$ while $\lambda_1 < 0$, so E_1 is a saddle point and hence unstable. $\square$

Theorem 4. The coexistence equilibrium $E_2 = (x^*, y^*)$ with $x^* > 0$ and $y^* > 0$ is locally asymptotically stable if

$$\text{tr}(J(E_2)) < 0 \quad \text{and} \quad \det(J(E_2)) > 0,$$

and it is unstable if either $\text{tr}(J(E_2)) > 0$ or $\det(J(E_2)) < 0$.

Proof. Evaluating the Jacobian matrix $J(x, y)$ at $E_2 = (x^*, y^*)$ yields

$$J(E_2) = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix},$$

where

$$a_{11} = \frac{r(1 - v)}{1 + ky^*} - \delta - \frac{2r}{K}x^* - \frac{y^*(q + cy^*)}{(1 + \mu v)(1 + hx^*)^2},$$

$$a_{12} = -\frac{rk(1 - v)x^*}{(1 + ky^*)^2} - \frac{x^*(q + 2cy^*)}{(1 + \mu v)(1 + hx^*)},$$

$$a_{21} = \gamma \frac{y^*(q + cy^*)}{(1 + \mu v)(1 + hx^*)^2},$$

$$a_{22} = \gamma \frac{x^*(q + 2cy^*)}{(1 + \mu v)(1 + hx^*)} - \delta_1.$$

The characteristic equation of $J(E_2)$ is

$$\det(\lambda I - J(E_2)) = 0 \iff \lambda^2 - \operatorname{tr}(J(E_2))\lambda + \det(J(E_2)) = 0,$$

where

$$\operatorname{tr}(J(E_2)) = a_{11} + a_{22}, \quad \det(J(E_2)) = a_{11}a_{22} - a_{12}a_{21}.$$

By the Routh-Hurwitz criterion for a second-order polynomial, both eigenvalues of $J(E_2)$ have negative real parts if and only if

$$\operatorname{tr}(J(E_2)) < 0 \quad \text{and} \quad \det(J(E_2)) > 0.$$

Therefore, E_2 is locally asymptotically stable when the above inequalities hold. If instead $\operatorname{tr}(J(E_2)) > 0$, then at least one eigenvalue has positive real part and hence E_2 is unstable. If $\det(J(E_2)) < 0$, then the eigenvalues have opposite signs, implying that E_2 is a saddle point and thus unstable. $\square$

Theorem 5. The extinction equilibrium point $E_0 = (0, 0)$ of system (1) is globally asymptotically stable in $\mathbb{R}_+^2$ if

$$r(1 - v) < \delta.$$

Proof. Consider the Lyapunov function

$$V(x, y) = x + \frac{1}{\gamma}y.$$

Clearly, $V(0, 0) = 0$ and $V(x, y) > 0$ for $(x, y) \neq (0, 0)$ in $\mathbb{R}_+^2$. Differentiating V along solutions gives

$$\dot{V} = \dot{x} + \frac{1}{\gamma}\dot{y} = \frac{r(1-v)x}{1+ky} - \delta x - \frac{r}{K}x^2 - \frac{\delta_1}{\gamma}y \leq (r(1-v) - \delta)x - \frac{r}{K}x^2 - \frac{\delta_1}{\gamma}y.$$

If $r(1 - v) < \delta$, then $(r(1 - v) - \delta)x \leq 0$ for $x \geq 0$, hence

$$\dot{V} \leq -\frac{r}{K}x^2 - \frac{\delta_1}{\gamma}y < 0 \quad \text{for all } (x, y) \neq (0, 0).$$

Therefore, V is strictly decreasing along all nontrivial solutions, and by Lyapunov's direct method, $E_0 = (0, 0)$ is globally asymptotically stable in $\mathbb{R}_+^2$. $\square$

Theorem 6. Assume that $r(1 - v) > \delta$ so that the predator-free equilibrium

$$E_1 = (x_1, 0), \quad x_1 = K \left(1 - v - \frac{\delta}{r} \right),$$

is feasible. Let

$$\varepsilon = \min\{\delta, \delta_1\}.$$

From the boundedness result (Theorem 1), we have

$$\limsup_{t \rightarrow \infty} W(t) \leq \frac{r(1-v)^2 K}{\varepsilon},$$

where $W(t) = x(t) + \frac{1}{\gamma}y(t)$. Since $y(t) \leq \gamma W(t)$ for all $t \geq 0$, it follows that

$$\limsup_{t \rightarrow \infty} y(t) \leq \chi, \quad \text{where} \quad \chi = \frac{\gamma r(1-v)^2 K}{\varepsilon}.$$

If

$$1 < \frac{(1 + \mu v)\delta_1}{\gamma x_1(q + c\chi)},$$

then the predator-free equilibrium E_1 is globally asymptotically stable in the region

$$\Omega = \{(x, y) \in \mathbb{R}_+^2 : x > 0, y \geq 0\}.$$

Proof. Consider the Lyapunov function

$$V(x, y) = A_1 \left[x - x_1 - x_1 \ln \left(\frac{x}{x_1} \right) + \frac{y}{\gamma} \right],$$

where $A_1 > 0$ is a constant to be chosen. Clearly, $V(x_1, 0) = 0$ and $V(x, y) > 0$ for all $(x, y) \neq (x_1, 0)$ with $x > 0, y \geq 0$. Differentiating V along solutions yields

$$\dot{V} = A_1 \left[\left(1 - \frac{x_1}{x} \right) \dot{x} + \frac{1}{\gamma} \dot{y} \right].$$

Substituting $\dot{x}$ and $\dot{y}$ and simplifying the predation terms gives

$$\dot{V} = A_1 \left(\left(1 - \frac{x_1}{x} \right) \left[\frac{r(1-v)x}{1+ky} - \delta x - \frac{r}{K}x^2 \right] + \frac{(q+cy)x_1 y}{(1+hx)(1+\mu v)} - \frac{\delta_1}{\gamma} y \right).$$

Since $\frac{1}{1+ky} \leq 1$, we have

$$\begin{aligned} \left(1 - \frac{x_1}{x} \right) \left[\frac{r(1-v)x}{1+ky} - \delta x - \frac{r}{K}x^2 \right] &\leq \left(1 - \frac{x_1}{x} \right) \left[r(1-v)x - \delta x - \frac{r}{K}x^2 \right] \\ &= -\frac{r}{K}(x - x_1)^2 \leq 0, \end{aligned}$$

where we used $r(1 - v) - \delta = \frac{r}{K}x_1$. Therefore,

$$\dot{V} \leq A_1 \left[-\frac{r}{K}(x - x_1)^2 + y \left(\frac{(q + cy)x_1}{(1 + hx)(1 + \mu v)} - \frac{\delta_1}{\gamma} \right) \right].$$

Using $(1 + hx) \geq 1$ and the ultimate bound $y(t) \leq \chi$ (for large t), we obtain for large t ,

$$\frac{(q + cy)x_1}{(1 + hx)(1 + \mu v)} \leq \frac{(q + c\chi)x_1}{1 + \mu v}.$$

Hence, for large t ,

$$\dot{V} \leq A_1 \left[-\frac{r}{K}(x - x_1)^2 + y \left(\frac{(q + c\chi)x_1}{1 + \mu v} - \frac{\delta_1}{\gamma} \right) \right].$$

If

$$1 < \frac{(1 + \mu v)\delta_1}{\gamma x_1(q + c\chi)} \iff \frac{(q + c\chi)x_1}{1 + \mu v} - \frac{\delta_1}{\gamma} < 0,$$

then $\dot{V} < 0$ for all $(x, y) \neq (x_1, 0)$ (for sufficiently large t). Thus, V is a Lyapunov function ensuring global asymptotic stability of E_1 in Ω by Lyapunov's asymptotic stability theorem. $\square$

Remark 1. The sufficient condition in Theorem 6 may still hold even when $\delta_1 < \delta$, although it becomes more restrictive as δ_1 decreases. Indeed, when $\delta_1 < \delta$, we have

$$\varepsilon = \min\{\delta, \delta_1\} = \delta_1, \quad \chi = \frac{\gamma r(1 - v)^2 K}{\delta_1}.$$

For example, let

$$r = 0.8, \quad K = 5, \quad v = 0.1, \quad \delta = 0.20, \quad \delta_1 = 0.15, \quad \mu = 0.5,$$

$$\gamma = 0.2, \quad q = 0.1, \quad c = 0.02.$$

Then

$$x_1 = K \left(1 - v - \frac{\delta}{r} \right) = 5(0.9 - 0.25) = 3.25,$$

and

$$\chi = \frac{\gamma r(1 - v)^2 K}{\delta_1} = \frac{0.2 \cdot 0.8 \cdot (0.9)^2 \cdot 5}{0.15} = 4.32.$$

Hence,

$$\frac{(1 + \mu v)\delta_1}{\gamma x_1(q + c\chi)} = \frac{(1 + 0.5 \cdot 0.1)(0.15)}{0.2 \cdot 3.25 \cdot (0.1 + 0.02 \cdot 4.32)} \approx 1.30 > 1.$$

Therefore, the sufficient condition in Theorem 6 is satisfied in this case even though $\delta_1 < \delta$.

From an ecological perspective, the quantity χ represents an ultimate upper bound on predator density obtained from the boundedness estimate, rather than the actual long-term predator population level. Thus, the condition in Theorem 6 is sufficient and may be conservative, but it still provides a useful criterion ensuring that predator pressure remains weak enough for the predator-free equilibrium to be globally asymptotically stable.

Theorem 7. Assume that system (1) admits a unique coexistence equilibrium $E_2 = (x^*, y^*)$ with $x^* > 0$ and $y^* > 0$. Further assume that all solutions initiating in $\mathbb{R}_+^2$ are bounded and that the positive quadrant contains a positively invariant compact set

$$\Omega^* = \{(x, y) \in \mathbb{R}_+^2 : 0 < x \leq X, 0 < y \leq \chi\},$$

for some constants $X > 0$ and $\chi > 0$.

Suppose additionally that there exists a continuously differentiable Dulac function $B(x, y) > 0$ on Ω^* such that

$$\frac{\partial}{\partial x}(B(x, y)\dot{x}) + \frac{\partial}{\partial y}(B(x, y)\dot{y}) < 0 \quad \text{for all } (x, y) \in \Omega^*.$$

If, moreover, E_2 is locally asymptotically stable (i.e., $\text{tr}(J(E_2)) < 0$ and $\det(J(E_2)) > 0$), then E_2 is globally asymptotically stable in Ω^* .

Proof. By the boundedness result, every solution $(x(t), y(t))$ with initial condition in $\mathbb{R}_+^2$ eventually enters Ω^* and remains there for all sufficiently large t . Hence, the ω -limit set of any solution is nonempty, compact, invariant, and contained in Ω^* .

Since $B(x, y) > 0$ on Ω^* and

$$\frac{\partial}{\partial x}(B(x, y)\dot{x}) + \frac{\partial}{\partial y}(B(x, y)\dot{y}) < 0 \quad \text{in } \Omega^*,$$

the Bendixson–Dulac criterion implies that system (1) admits no nontrivial periodic orbits lying in Ω^* .

Because E_2 is the unique equilibrium in the interior of Ω^* and periodic orbits are excluded, the Poincaré–Bendixson theorem implies that the ω -limit set of any interior trajectory must be an equilibrium point. Therefore, every solution in Ω^* converges to E_2 .

Finally, since E_2 is locally asymptotically stable, the convergence is to E_2 and not to any boundary equilibrium. Hence E_2 is globally asymptotically stable in Ω^* . $\square$

Theorem 8. Assume that the coexistence equilibrium $E_2 = (x^*, y^*)$ of system (1) exists with $x^* > 0$ and $y^* > 0$. Let J_{E_2} denote the Jacobian matrix of system (1) evaluated at E_2 . Then

system (1) undergoes a Hopf bifurcation at E_2 with respect to the bifurcation parameter c provided that the following properties hold:

- (i) $\text{tr}(J_{E_2}^*) = 0$,
- (ii) $\det(J_{E_2}^*) > 0$,
- (iii) $\left. \frac{d}{dc}(\text{tr}(J_{E_2})) \right|_{c=c^*} \neq 0$,

where $J_{E_2}^* = J_{E_2}|_{c=c^*}$ and c^* denote the critical value of the predator cooperation parameter c for which the coexistence equilibrium E_2 satisfies $\text{tr}(J_{E_2}) = 0$ and $\det(J_{E_2}) > 0$.

Proof. At $E_2 = (x^*, y^*)$, the equilibrium condition from $\dot{y} = 0$ gives

$$0 = \gamma \frac{(q + cy^*)x^*y^*}{(1 + hx^*)(1 + \mu v)} - \delta_1 y^* \implies \gamma \frac{(q + cy^*)x^*}{(1 + hx^*)(1 + \mu v)} = \delta_1.$$

Define

$$A = \frac{\delta_1(1 + hx^*)(1 + \mu v)}{\gamma x^*} > 0.$$

Then the above relation becomes

$$q + cy^* = A \implies y^* = \frac{A - q}{c},$$

so E_2 is feasible only if $A > q$.

Next, evaluating the Jacobian at E_2 and using $q + cy^* = A$ and $q + 2cy^* = 2A - q$ yields

$$J_{E_2} = \begin{pmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{pmatrix},$$

where

$$\begin{aligned} J_{11} &= \frac{r(1-v)}{1 + ky^*} - \delta - \frac{2r}{K}x^* - \frac{y^*A}{(1 + \mu v)(1 + hx^*)^2}, \\ J_{12} &= -\frac{rk(1-v)x^*}{(1 + ky^*)^2} - \frac{x^*(2A - q)}{(1 + \mu v)(1 + hx^*)}, \\ J_{21} &= \gamma \frac{y^*A}{(1 + \mu v)(1 + hx^*)^2}, \\ J_{22} &= \gamma \frac{x^*(2A - q)}{(1 + \mu v)(1 + hx^*)} - \delta_1 = \delta_1 - \frac{\gamma qx^*}{(1 + \mu v)(1 + hx^*)}. \end{aligned}$$

To obtain a tractable expression for the trace, we also use the prey equilibrium condition $\dot{x} = 0$, which after dividing by $x^* > 0$ and using $q + cy^* = A$ becomes

$$\frac{r(1-v)}{1+ky^*} = \delta + \frac{r}{K}x^* + \frac{Ay^*}{(1+\mu v)(1+hx^*)} = \delta + \frac{r}{K}x^* + \frac{\delta_1 y^*}{\gamma x^*}.$$

Substituting this identity into $\text{tr}(J_{E_2}) = J_{11} + J_{22}$ simplifies the trace to

$$\text{tr}(J_{E_2}) = -\frac{r}{K}x^* + \frac{\delta_1 h y^*}{\gamma(1+hx^*)} + \delta_1 - \frac{\gamma q x^*}{(1+\mu v)(1+hx^*)}.$$

Hence, $\text{tr}(J_{E_2}) = 0$ if and only if

$$\frac{\delta_1 h y^*}{\gamma(1+hx^*)} = \frac{r}{K}x^* - \delta_1 + \frac{\gamma q x^*}{(1+\mu v)(1+hx^*)}.$$

Using $y^* = \frac{A-q}{c}$, we obtain the critical value

$$c = c^* = \frac{A-q}{\frac{\gamma(1+hx^*)}{\delta_1 h} \left(\frac{r}{K}x^* - \delta_1 + \frac{\gamma q x^*}{(1+\mu v)(1+hx^*)} \right)},$$

$$A = \frac{\delta_1(1+hx^*)(1+\mu v)}{\gamma x^*}.$$

Let $J_{E_2}^* = J_{E_2}|_{c=c^*}$. Condition (ii), namely $\det(J_{E_2}^*) > 0$, guarantees that the eigenvalues of $J_{E_2}^*$ are purely imaginary, that is,

$$\lambda_{1,2} = \pm i \sqrt{\det(J_{E_2}^*)}.$$

It remains to verify the transversality condition (iii). Since $x^* = x^*(c)$ depends on c through the equilibrium equations, we have

$$\frac{d}{dc}(\text{tr}(J_{E_2})) \Big|_{c=c^*} = \omega_1 \frac{dx^*}{dc} \Big|_{c=c^*} + \omega_2,$$

where

$$\omega_2 = \frac{\partial}{\partial c}(\text{tr}(J_{E_2})) \Big|_{c=c^*} = -\frac{\delta_1 h}{\gamma(1+hx^*)} \frac{A-q}{(c^*)^2},$$

and

$$\begin{aligned} \omega_1 &= \frac{\partial}{\partial x^*}(\text{tr}(J_{E_2})) \Big|_{c=c^*} \\ &= -\frac{r}{K} - \frac{\delta_1^2 h(1+\mu v)}{\gamma^2 c^* (x^*)^2 (1+hx^*)} - \frac{\delta_1 h^2 y^*}{\gamma(1+hx^*)^2} - \frac{\gamma q}{(1+\mu v)(1+hx^*)^2}, \end{aligned}$$

using the identity

$$\frac{dA}{dx^*} = -\frac{\delta_1(1+\mu v)}{\gamma(x^*)^2}, \quad y^* = \frac{A-q}{c^*}.$$

Therefore, if

$$\omega_1 \left. \frac{dx^*}{dc} \right|_{c=c^*} + \omega_2 \neq 0,$$

then the eigenvalues cross the imaginary axis with nonzero speed as c passes through c^* , and by the Hopf bifurcation theorem the system undergoes a Hopf bifurcation at E_2 with respect to c . $\square$

5 Numerical simulations

To gain a deeper understanding of the proposed predator-prey model, we numerically solved the system using the MATLAB `ode45` solver. In the numerical simulations, we selected positive nondimensional parameter values that are illustrative rather than calibrated to any specific empirical predator-prey system. Nevertheless, the chosen values are biologically plausible and lie within ranges commonly adopted in theoretical studies of predator-prey dynamics, while also satisfying the feasibility and stability conditions derived in the analytical sections. The parameter values used for the simulations of Figure 1 are $r = 1$, $K = 10$, $\delta = 0.1766$, $\delta_1 = 0.2429$, $v = 0.2544$, $\mu = 1.3809$, $k = 0.9421$, $q = 0.3411$, $c = 0.1636$, $h = 0.2089$, $\gamma = 0.6643$. The time evolution of the prey population $x(t)$ and the predator population $y(t)$ are depicted in Figures 1a and 1b, respectively. The numerical results show that both populations converge to a positive interior equilibrium point $E_2 = (x^*, y^*) \approx (1.4660, 0.6065)$, indicating the coexistence of the prey and predator species. Moreover, the solution trajectories approach E_2 as time increases, confirming that the coexistence equilibrium is locally asymptotically stable, in agreement with the theoretical stability analysis. Figure 2 illustrates the phase-plane dynamics of the predator-prey system for different combinations of the prey vigilance level v and the predator cooperation parameter c , while all other parameters are held fixed. The parameter values used in all panels are $r = 1$, $K = 10$, $\delta = 0.1766$, $\delta_1 = 0.2429$, $\mu = 1.3809$, $k = 0.9421$, $q = 0.3411$, $h = 0.2089$, $\gamma = 0.6643$, with the values of v and c varying across panels as indicated. The black arrows represent the vector field, the red and green curves denote the prey nullcline $\dot{x} = 0$ and predator nullcline $\dot{y} = 0$, respectively, the blue curves show solution trajectories initiated from positive initial conditions, and the equilibrium points are marked in yellow.

In panel (a), where the vigilance level is relatively high and predator cooperation is weak, the predator nullcline does not intersect the prey nullcline in the interior of the positive quadrant. As a result, no coexistence equilibrium exists, and all trajectories are directed toward the predator-

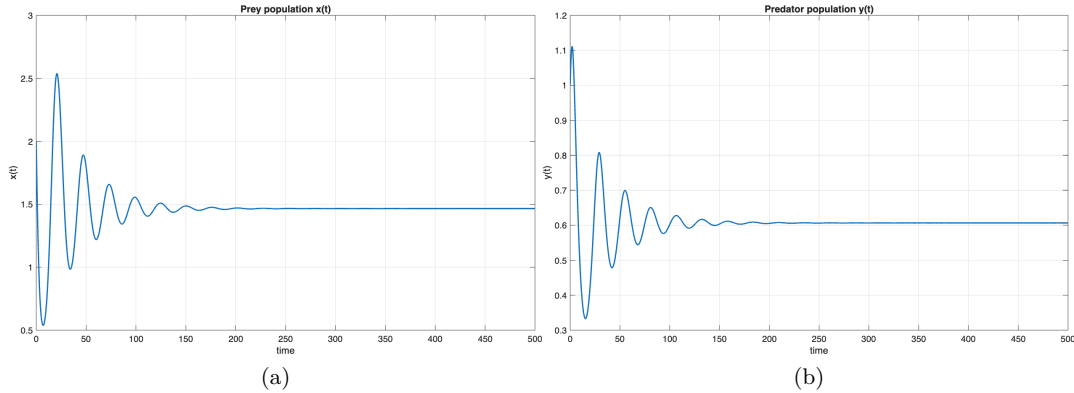


Figure 1: Time-series simulation of system (1). Panel (a) shows the prey population $x(t)$ versus time, while panel (b) shows the predator population $y(t)$ versus time.

free equilibrium E_1 . This indicates that strong prey vigilance combined with weak cooperative hunting suppresses predator persistence, ultimately leading to predator extinction.

Panels (b) and (c) show that reducing the vigilance level or increasing the cooperation parameter shifts the predator nullcline upward, leading to an intersection with the prey nullcline in the interior of the phase plane. This intersection corresponds to the coexistence equilibrium E_2 . The direction of the vector field around E_2 , together with the convergence of nearby trajectories, indicates that E_2 is locally asymptotically stable. Biologically, this reflects a balance between prey defense mechanisms and predator cooperative hunting that allows long-term coexistence of both populations.

In panel (d), which corresponds to the baseline parameter set $(v, c) = (0.2544, 0.1636)$, the coexistence equilibrium E_2 is clearly visible and acts as a stable spiral sink. All trajectories starting in the positive quadrant converge to this equilibrium, demonstrating that the system returns to steady coexistence even after moderate perturbations in population densities.

Panels (e) and (f) further emphasize the role of predator cooperation. As the cooperation parameter c increases, the predator nullcline shifts further upward, enhancing predator growth at higher population densities. Although coexistence persists, the orientation of the vector field and the shape of the trajectories indicate increasingly pronounced oscillatory transients before convergence. This behavior suggests that the system approaches the threshold of more complex dynamics, such as sustained oscillations, as cooperative hunting becomes stronger.

Overall, the phase-plane analysis in Figure 2 demonstrates that prey vigilance and predator cooperation jointly regulate the qualitative dynamics of the system. High vigilance tends to destabilize predator persistence, whereas sufficient cooperative hunting enables predators to overcome prey defenses and coexist stably with the prey population. These numerical observa-

tions are fully consistent with the analytical equilibrium and stability results established earlier.

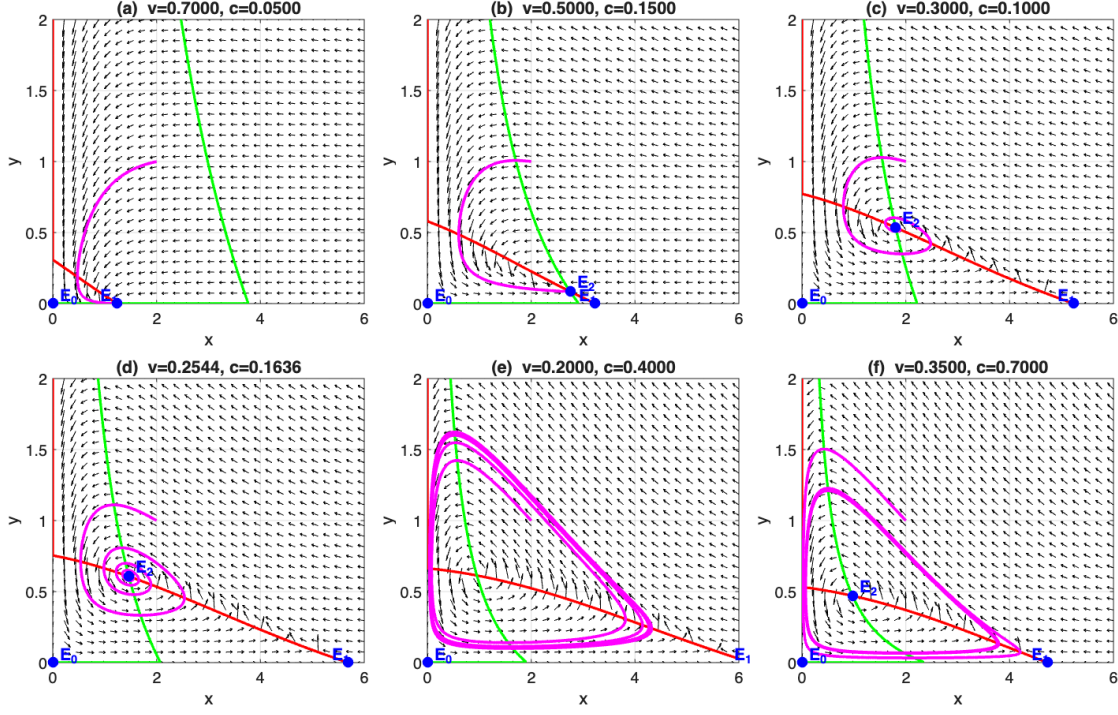


Figure 2: Phase-plane portraits of system (1) for different combinations of prey vigilance v and predator cooperation c .

Figure 3 presents the numerical phase-portrait simulations of the system using the same parameter set, $r = 1.00$, $v = 0.20$, $K = 10$, $\delta = 0.10$, $\delta_1 = 0.10$, $k = 0.50$, $\mu = 0.50$, $q = 0.50$, $c = 0.20$, $h = 0.20$, $\gamma = 0.70$. In Figure 3A, the trajectories illustrate the global behavior of the system under this parameter regime, showing convergence toward the extinction equilibrium $E_0 = (0, 0)$ when the corresponding stability condition is satisfied. Figure 3B depicts the predator-free regime, where the predator-free equilibrium $E_1 = (x_1, 0)$ exists with $x_1 > 0$ and attracts all solution trajectories initiated from positive initial conditions, indicating prey persistence in the absence of predators. Finally, Figure 3C demonstrates the coexistence regime for the same parameter values, where an interior equilibrium $E_2 = (x^*, y^*)$ exists and all trajectories starting in the positive quadrant converge to E_2 , confirming long-term coexistence of prey and predator populations. Overall, these panels numerically corroborate the analytical global stability results derived earlier.

Figures 4–6 provide numerical evidence of a Hopf bifurcation at the coexistence equilibrium $E_2 = (x^*, y^*)$ of system (1) with respect to the predator cooperation parameter c , in agreement

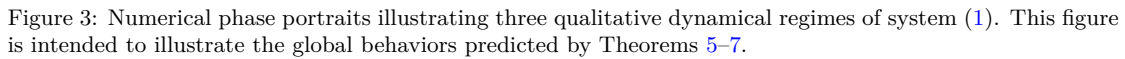


Figure 4 illustrates the numerical continuation of the predator population extrema as the cooperation parameter c varies. The maximum and minimum values of $y(t)$, computed after discarding transient dynamics, are plotted against c . For $c < c^*$, both extrema coincide, indicating convergence to the coexistence equilibrium E_2 . As c increases and crosses the critical value $c = c^*$, the extrema separate smoothly, signaling the emergence of a stable periodic orbit. This behavior confirms the birth of a limit cycle through a Hopf bifurcation at $c = c^*$.

Figure 5 presents time-series simulations for the prey and predator populations when $c < c^*$. Both $x(t)$ and $y(t)$ exhibit damped oscillations that decay toward constant values, corresponding to the locally asymptotically stable coexistence equilibrium E_2 . The associated phase portrait

shows inward spiraling trajectories converging to E_2 , further confirming its stability below the Hopf threshold.

Figure 6 displays the system dynamics for $c > c^*$. In this regime, the coexistence equilibrium E_2 becomes unstable, and the trajectories converge to a closed orbit in the phase plane. The corresponding time-series exhibit sustained oscillations with constant amplitude, which is characteristic of a stable limit cycle generated by a supercritical Hopf bifurcation. Additionally, the Jacobian trace evaluated at E_2 crosses zero at $c = c^*$ while the determinant remains positive, numerically validating conditions (i) and (ii) of Theorem 8. The smooth and nonzero slope of the trace at c^* confirms the transversality condition $\frac{d}{dc} \text{tr}(J_{E_2})|_{c=c^*} \neq 0$.

Overall, Figures 4–6 collectively demonstrate that increasing predator cooperation destabilizes the coexistence equilibrium through a Hopf bifurcation, leading to persistent oscillations in both prey and predator populations.

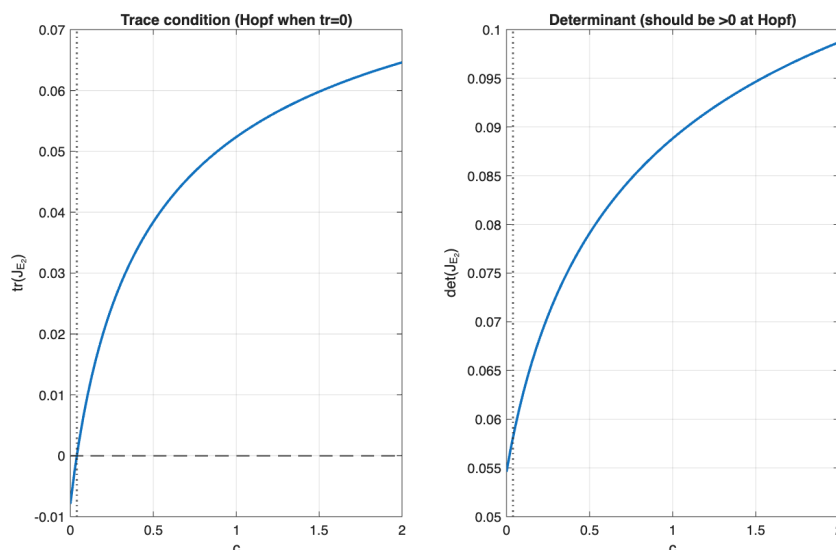


Figure 4: Numerical verification of the Hopf bifurcation conditions at the coexistence equilibrium E_2 with respect to the predator cooperation parameter c .

5.1 Sensitivity of the Hopf threshold

To assess the robustness of the Hopf bifurcation established in Theorem 8, we examined how the critical predator cooperation threshold c^* varies with several ecologically important parameters. In particular, we studied the dependence of c^* on the fear intensity k , the prey vigilance level

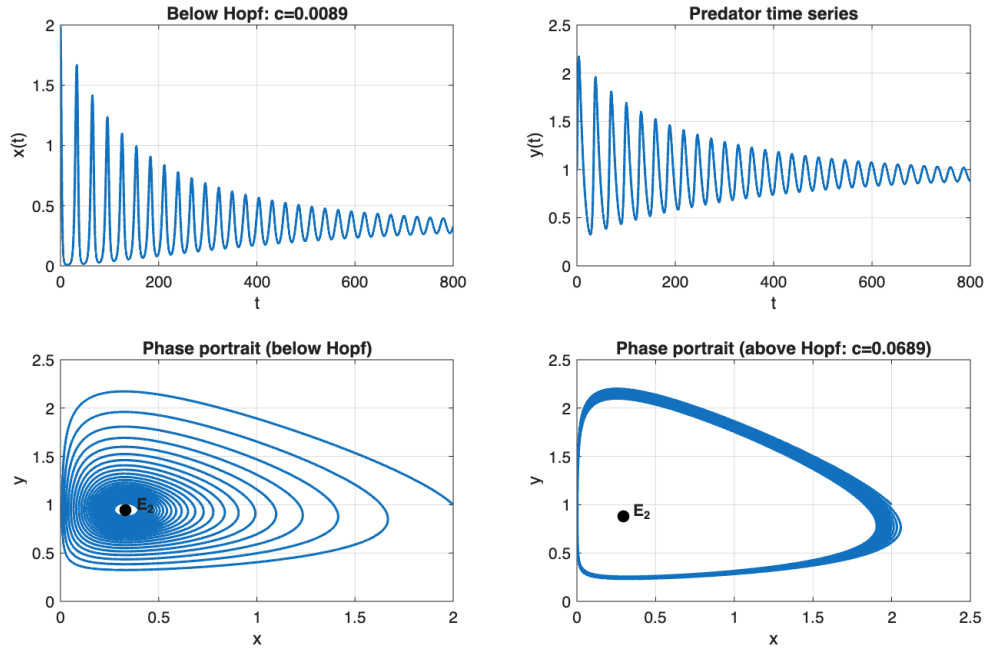


Figure 5: Numerical dynamics below and above the Hopf bifurcation threshold. Panel (a) shows the prey time series $x(t)$ for $c = 0.0089 < c^*$. Panel (b) shows the predator time series $y(t)$ for the same subcritical value $c = 0.0089 < c^*$. Panel (c) shows the corresponding phase portrait for $c = 0.0089 < c^*$, where trajectories spiral inward toward the coexistence equilibrium E_2 , indicating local asymptotic stability. Panel (d) shows the phase portrait for $c = 0.0689 > c^*$, where trajectories approach a stable closed orbit, indicating the emergence of a stable limit cycle after Hopf bifurcation.

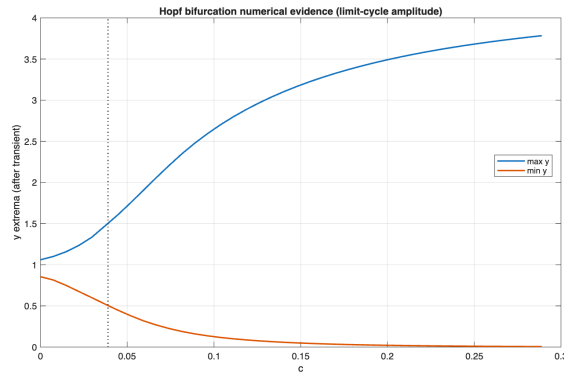


Figure 6: Numerical amplitude diagram illustrating oscillatory behavior as the predator cooperation parameter c varies.

v , the predator mortality rate δ_1 , and the predator conversion efficiency γ . In each case, all remaining parameters were fixed at the baseline values used in the Hopf-bifurcation simulations,

$$r = 1, \quad K = 10, \quad \delta = 0.10, \quad \mu = 0.50, \quad q = 0.50, \quad h = 0.20,$$

with the fixed parameters taken as

$$v = 0.20, \quad k = 0.50, \quad \delta_1 = 0.10, \quad \gamma = 0.70.$$

For each selected parameter value, the critical threshold c^* was computed numerically by solving the coexistence equilibrium conditions together with the Hopf condition

$$\dot{x} = 0, \quad \dot{y} = 0, \quad \text{tr}(J(E_2)) = 0,$$

while verifying that

$$\det(J(E_2)) > 0.$$

Figure 7 shows that the Hopf threshold varies smoothly and systematically across the tested parameter ranges, confirming that the bifurcation is not confined to a narrow parameter set. In panel (a), the threshold c^* increases with the fear parameter k . Thus, stronger fear effects require a larger degree of predator cooperation before oscillations can emerge, indicating that fear acts as a stabilizing mechanism. Panel (b) shows a similar increase of c^* with the vigilance level v , meaning that stronger prey vigilance delays the onset of destabilization by reducing predation efficiency and suppressing predator growth.

Panel (c) further shows that c^* increases with predator mortality δ_1 . Ecologically, this means that when predators experience stronger natural losses, cooperation must be sufficiently strong to offset those losses before the coexistence equilibrium can lose stability. By contrast, panel (d) shows that c^* decreases as the conversion efficiency γ increases. Hence, when predators convert consumed prey into biomass more efficiently, even relatively small increases in cooperative hunting are enough to destabilize the coexistence equilibrium and generate oscillatory dynamics.

Overall, the sensitivity analysis quantitatively supports the biological conclusions of the model: Fear, vigilance, and predator mortality act as stabilizing factors because they raise the cooperation threshold required for predator-driven oscillations, whereas stronger predator demographic efficiency lowers that threshold and promotes instability.

6 Conclusion

In this study, we proposed and rigorously analyzed a predator-prey model that integrates prey vigilance, fear effects, and predator cooperative hunting as key behavioral mechanisms governing population dynamics. Unlike classical predator-prey formulations, the present model explicitly accounts for the nonconsumptive effects of predation risk, whereby prey fear and vigilance reduce

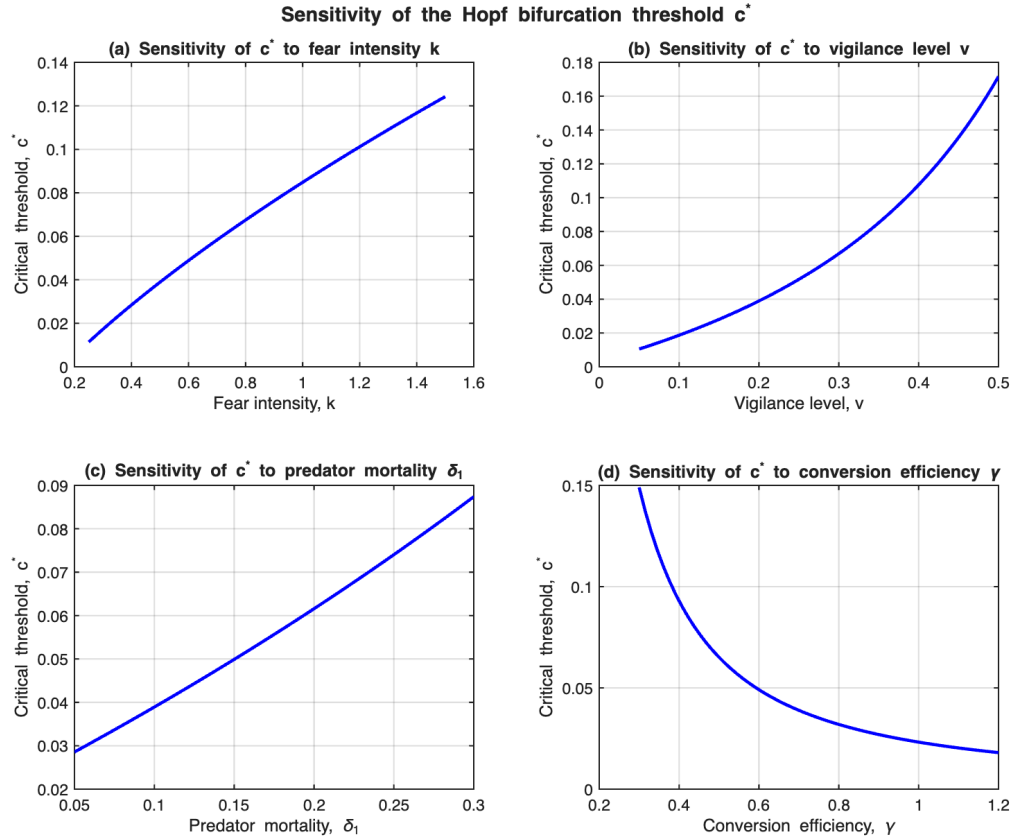


Figure 7: Sensitivity of the Hopf bifurcation threshold c^* to key parameters of system (1). Panel (a) shows c^* versus fear intensity k , panel (b) shows c^* versus vigilance level v , panel (c) shows c^* versus predator mortality δ_1 , and panel (d) shows c^* versus conversion efficiency γ . In each panel, c^* is computed numerically from the coexistence conditions together with $\text{tr}(J(E_2)) = 0$ and $\det(J(E_2)) > 0$, while all other parameters are fixed at the baseline values used in the Hopf-bifurcation simulations.

effective prey growth and alter interaction outcomes even in the absence of direct predation. This framework allows for a more realistic representation of predator-prey interactions observed in natural ecosystems.

We began by establishing the mathematical structure of the model and identifying all biologically meaningful equilibria, namely the extinction equilibrium, the predator-free equilibrium, and the coexistence equilibrium. Local stability analysis revealed that prey fear and vigilance significantly modify the stability thresholds of these equilibria by effectively reducing prey reproductive potential and limiting predator access to prey. In particular, heightened fear responses were shown to suppress predator persistence by weakening the functional response, thereby enlarging the parameter regimes in which predator extinction occurs.

Beyond local analysis, we derived sufficient conditions for global asymptotic stability of both the extinction and predator-free equilibria using Lyapunov-based arguments. These results demonstrate that strong fear effects, in combination with prey vigilance or elevated predator mortality, can globally drive the system toward predator extinction regardless of initial population sizes. From an ecological standpoint, this highlights the powerful role of fear-mediated behavioral responses in shaping long-term population outcomes, independent of direct predation pressure.

The coexistence equilibrium was shown to exist under balanced levels of fear, vigilance, and cooperative hunting. Local stability analysis indicated that moderate predator cooperation stabilizes coexistence, while excessive cooperation may destabilize the equilibrium. This destabilization mechanism was formalized through the identification of a Hopf bifurcation with respect to the predator cooperation parameter. By analytically verifying the trace, determinant, and transversality conditions of the Jacobian matrix, we established that increasing cooperative hunting can induce a transition from stable coexistence to persistent oscillatory dynamics.

Extensive numerical simulations were conducted to support the theoretical findings. Phase-plane portraits confirmed the global stability of the extinction and predator-free equilibria under the derived conditions, while time-series simulations illustrated convergence to the coexistence equilibrium when locally stable. Near the Hopf threshold, numerical evidence clearly demonstrated the emergence of stable limit cycles, confirming the analytical bifurcation results. These oscillations reflect the combined effects of predator cooperation and prey fear, producing sustained fluctuations in population densities.

Overall, the results emphasize that fear effects are not merely secondary modifiers but fundamental drivers of predator-prey dynamics. When combined with prey vigilance and predator cooperation, fear can suppress predator persistence, stabilize equilibria, or generate complex oscillatory behavior depending on the parameter regime. The proposed model therefore provides a flexible and biologically grounded framework for investigating nonlethal predator effects and cooperative behaviors in ecological systems. A sensitivity analysis of the Hopf threshold further showed that increasing fear intensity, vigilance, and predator mortality shifts the critical cooperation level upward, whereas increasing predator conversion efficiency shifts it downward, thereby confirming that antipredator responses act as stabilizing mechanisms against predator-driven oscillations.

One limitation of the present formulation is that vigilance is assumed to affect prey demography primarily through reduced reproduction rather than through a direct increase in natural mortality. In some ecological systems, however, prolonged vigilance may indirectly elevate mortality through reduced body condition, physiological stress, immunosuppression, or increased accident risk during escape. Incorporating such mortality-mediated vigilance effects, together

with extensions such as spatial diffusion, time delays, stochastic perturbations, or adaptive behavioral responses, would be a worthwhile direction for future research and could further enhance the applicability of the model to real-world ecological and conservation problems.

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Conflicts of Interest

The author declares no conflicts of interest.

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