

THE FEAR EFFECT IN PREY-PREDATOR DYNAMICS WITH PREDATOR INTRASPECIFIC COMPETITION

*(Pengaruh Ketakutan Terhadap Dinamika Mangsa-Pemangsa dengan Persaingan
Sesama Pemangsa)*

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ABSTRACT

Fear is an intrinsic factor in ecosystems and, contrary to common assumptions, exerts a measurable influence on prey-predator dynamics. This study analyses the impact of fear on the prey population in a Lotka-Volterra-type prey-predator system that incorporates intraspecific competition among predators. A system of ordinary differential equations is formulated, and stability and bifurcation analyses are then conducted. Numerical simulations and bifurcation continuation using AUTO, supported by symbolic computations in Maple and numerical integration in MATLAB, corroborate the theoretical results. Specifically, a one-parameter bifurcation with respect to the fear level reveals a transcritical bifurcation threshold that separates two regimes: below the threshold, a unique positive coexistence equilibrium is asymptotically stable, whereas above it, the interior state loses feasibility, and the dynamics converge to a predator-only equilibrium. Moreover, a two-parameter bifurcation analysis, by varying fear and predator competition, maps stability regions and shows that the bifurcation boundary shifts upward as competition strengthens, thereby enlarging the range of conditions that support coexistence. Numerical evidence further demonstrates that increasing fear consistently depresses prey abundance and may drive prey extinction, while predator density is regulated by competition. Overall, the study underscores the significant role of fear in shaping prey-predator dynamics and its potential to trigger qualitative shifts in ecosystem stability and population trajectories.

Keywords: Lotka-Volterra; fear effect; predator competition; stability; transcritical bifurcation

ABSTRAK

Ketakutan merupakan faktor intrinsik dalam ekosistem dan berlawanan dengan anggapan umum, memberikan pengaruh yang dapat diukur terhadap dinamika mangsa-pemangsa. Kajian ini meneliti kesan ketakutan terhadap populasi mangsa dalam sistem Lotka-Volterra mangsa-pemangsa yang merangkumi persaingan intraspesifik dalam kalangan pemangsa. Satu sistem persamaan pembezaan biasa telah dirumuskan, diikuti dengan analisis kestabilan dan bifurkasi. Simulasi berangka menggunakan AUTO, disokong oleh pengiraan simbolik dalam Maple serta pengamiran berangka menggunakan MATLAB, bagi mengesahkan dapatan teori. Secara khususnya, analisis bifurkasi satu parameter berhubung tahap ketakutan menunjukkan wujudnya ambang bifurkasi transkritikal yang memisahkan dua rejim: di bawah ambang tersebut, kewujudan seimbang positif yang unik adalah stabil secara asimptotik; manakala di atasnya, keadaan dalaman kehilangan kebolehlaksanaan dan dinamik beralih kepada keseimbangan hanya pemangsa. Selain itu, analisis bifurkasi dua parameter dengan memvariasikan ketakutan dan persaingan pemangsa memetakan kawasan kestabilan serta menunjukkan bahawa sempadan bifurkasi meningkat apabila persaingan semakin kuat, sekali gus memperluas julat keadaan yang menyokong kewujudan bersama. Bukti berangka selanjutnya menunjukkan bahawa peningkatan tahap ketakutan secara konsisten mengurangkan kelimpahan mangsa dan berpotensi mendorong kepupusan mangsa, sementara kepadatan pemangsa pula dikawal oleh persaingan. Secara keseluruhannya, kajian ini

menegaskan peranan penting ketakutan dalam membentuk dinamika mangsa-pemangsa serta potensinya mencetuskan perubahan kualitatif dalam kestabilan ekosistem dan trajektori populasi.

Kata kunci: Lotka-Volterra; kesan ketakutan; persaingan pemangsa; kestabilan; bifurkasi transkritikal

1. Introduction

The interaction between prey and predators has long been a central topic in ecology and mathematical biology. Classical frameworks such as the Lotka-Volterra model describe the mutual regulation between species: predators limit prey abundance through consumption, while prey availability controls predator survival and growth. Subsequent refinements incorporated more realistic mechanisms, including density dependence, prey refuge, time delay, harvesting, and disease (Freedman 1980; Murray 2007). These modifications demonstrated that prey-predator systems can exhibit a wide range of dynamic outcomes, from stable coexistence to persistent oscillations and extinction. Thus, continued development of prey-predator models are essential for understanding biodiversity maintenance and ecosystem resilience.

A major advancement in this field has been the recognition of fear effects, also termed the *ecology of fear*. In many ecosystems, predators affect prey not only through direct consumption but also by inducing behavioural and physiological changes. Prey may reduce foraging activity, alter habitat use, increase vigilance, or delay reproduction in response to perceived predation risk (Creel & Christianson 2008; Preisser & Bolnick 2008). Such non-consumptive effects have been shown experimentally to cause substantial demographic consequences. For instance, Zanette *et al.* (2011) observed a 40% reduction in song sparrow reproduction in response to predator cues, even when no predation occurred. These findings motivated the introduction of fear into mathematical models. Wang *et al.* (2016) showed that fear can stabilise prey-predator interactions by damping oscillations. In contrast, lower fear levels may allow periodic dynamics via Hopf bifurcations. Sarkar and Khajanchi (2020) further demonstrated that strong anti-predator responses can stabilise a system, while weaker responses may still generate oscillatory coexistence.

The influence of fear combined with intraspecific competition has become an important extension of this framework. Predator competition can act as a stabilising mechanism, counterbalancing the destabilising role of fear. Mukherjee (2020) analysed a prey-predator system in which fear affected both prey reproduction and mortality, alongside predator competition. The study showed that competition enlarges the persistence region and prevents predator overgrowth at high densities. Al-Momen and Naji (2023) incorporated cooperative hunting and predator competition, concluding that predator crowding moderates the risk of prey extinction and stabilises coexistence. Similarly, Ibrahim *et al.* (2025) considered predator competition with Holling type-IV dynamics and found that this mechanism raises the threshold of fear at which prey collapse occurs.

Several studies further illustrate fear effects in specific ecological systems. In a fish-zooplankton-phytoplankton model, including zooplankton fear, algal toxins, and harvesting indicated that managing risk and toxins is important for stability (Panja *et al.* 2023). In a plankton-fish system with refuge, Kaur *et al.* (2021) reported that low levels of fear can stabilise the system under certain conditions, while other parameter values simplified the dynamics. Bauman *et al.* (2021) demonstrated that on coral reefs, fear effects from predatory

fish reduced herbivory by browsing fishes, with group size modulating the strength of the response.

Understanding such trade-offs requires a bifurcation-theoretic perspective, since bifurcations signal qualitative changes in system dynamics as parameters vary. Prey-predator models with fear have been shown to admit Hopf, saddle-node, and particularly transcritical bifurcations. Hopf bifurcations correspond to the onset of oscillations, as shown by Wang *et al.* (2016), Sarkar and Khajanchi (2020), and Liu *et al.* (2021). Discrete-time models reveal more complex behaviour, including flip and Neimark-Sacker bifurcations that give rise to quasi-periodic or chaotic dynamics (Din *et al.* 2024; Lin *et al.* 2022). Majumdar *et al.* (2022) studied fear in the presence of predator harvesting and delay, showing that the non-delayed system undergoes both transcritical and Hopf bifurcations, while delays can induce richer oscillatory outcomes. Zhao and Shao (2022) investigated a prey-predator system with fear, refuge, and food subsidy, demonstrating that management interventions shift bifurcation thresholds and can stabilise or destabilise coexistence.

Among these transitions, the transcritical bifurcation is of special importance because it captures the ecological tipping point where the equilibria exchange stability (Manaf *et al.* 2021a, 2021b). By definition, a transcritical bifurcation occurs when two equilibria collide and swap stability without being created or destroyed (Strogatz 2024). Ecologically, this corresponds to a threshold at which increasing fear drives the coexistence equilibrium into extinction, transferring stability to a prey-free or predator-free state. Sahoo and Samanta (2024) confirmed this mechanism in a two-prey, one-predator system with switching predation, where fear parameters controlled transcritical bifurcations between coexistence and prey-free states. Sarkar and Khajanchi (2020) similarly identified transcritical transitions when varying prey birth rate under fear. Zhu *et al.* (2020) examined a Lotka-Volterra system with fear and additional predator food resources, showing that fear can directly lead to prey extinction via transcritical bifurcation even when predators persist on alternative food. Lin *et al.* (2022) and Li *et al.* (2025) also reported that transcritical bifurcations are the dominant mechanism organising persistence boundaries in fear-driven systems.

The contribution of Zhu *et al.* (2020) is particularly notable. Their study established that fear is one of the most influential drivers of prey extinction in prey-predator systems with additional food. However, while they identified the existence of transcritical bifurcations, the analysis did not provide an explicit threshold expression for the fear parameter. This omission limits the ecological interpretation of how small variations in fear intensity can shift population outcomes. Furthermore, their model did not fully explore the compensatory role of predator competition, which later studies have shown to be a crucial stabilising factor (Ibrahim *et al.* 2025; Mukherjee 2020). The research gap therefore lies in the absence of explicit bifurcation thresholds in Zhu *et al.* (2020) and the lack of integration of predator competition in their framework. Addressing this gap is essential for a deeper ecological understanding of how fear and predator regulation interact to determine system stability.

Accordingly, the present study formulates a model in which fear reduces the prey reproduction rate while only the predator is subject to intraspecific competition. The objective is to derive explicit threshold conditions for the fear parameter governing transcritical bifurcation, thereby formalising the precise point at which stability shifts from coexistence to predator-only persistence. In addition, the study investigates how varying the strength of predator competition influences this bifurcation threshold. Numerical validation is employed to illustrate these transitions and provide ecological interpretations relevant to the stability of prey-predator systems.

2. Methods

This section presents the formulation of the prey-predator model incorporating fear effects in the prey and intraspecific competition in the predator, followed by the analytical and numerical procedures. Symbolic computations, including derivation of Jacobian matrices and analytical conditions for equilibrium existence and stability, were performed using Maple. Numerical continuation and bifurcation analysis were carried out using AUTO, while MATLAB was employed for numerical integration, time-series simulations, and figure generation.

2.1. Formulation of prey-predator model

Zhu *et al.* (2020) introduced a prey-predator system in which the prey's effective birth rate is reduced by fear of predators and both species experience intraspecific competition. Let x and y denote the prey and predator populations, respectively. With all parameters positive, r is the baseline prey birth rate, d the natural death rate of prey, a the prey's intraspecific competition coefficient, p the predation (interspecific interaction) rate, c the conversion efficiency of consumed prey into new predators, m the intrinsic growth rate of predators, e the predators' intraspecific competition, and k the level of fear perceived by the prey. Fear acts through the term $r/(1+ky)$, which decreases the prey birth rate as predator abundance increases. The original model is:

$$\frac{dx}{dt} = \frac{rx}{1+ky} - dx - ax^2 - pxy, \quad \frac{dy}{dt} = cpxy + my - ey^2. \quad (1)$$

To isolate the role of predator self-regulation in the presence of fear, the present study adopts a simplified variant without intraspecific competition in the prey population, that is, by setting $a = 0$ in Eq. (1). This modelling choice allows the analysis to focus explicitly on the compensatory stabilising role of predator density dependence under non-consumptive fear effects, without the confounding influence of prey self-limitation. Ecologically, this assumption is appropriate for systems in which prey regulation is dominated by behavioural suppression induced by perceived predation risk, such as reduced foraging effort or delayed reproduction, rather than by density-dependent crowding effects. Under this formulation, prey persistence depends on the balance between fear-modified reproduction and predation, while predator self-regulation governs long-term stability. The modified model is:

$$\frac{dx}{dt} = \frac{rx}{1+ky} - dx - pxy, \quad \frac{dy}{dt} = cpxy + my - ey^2. \quad (2)$$

Thus, Eq. (2) serves as the basis for the subsequent positivity, equilibrium, stability, and bifurcation analyses.

2.2. Positivity

To ensure biological meaning, it is necessary to show that solutions of Eq. (2) remain non-negative. This guarantees that the state space $\mathbb{R}_{\geq 0}^2$ is forward invariant and that the population variables never take inadmissible values.

Theorem 1. For Eq. (2), every solution with non-negative initial value $(x(0), y(0)) \in \mathbb{R}_{\geq 0}^2$ remains non-negative for all t in its interval of existence. Moreover, if $x(0) > 0$ and $y(0) > 0$, then $x(t) > 0$ and $y(t) > 0$ for all such t .

Proof. Consider Eq. (2) with initial conditions $(x(0), y(0)) \in \mathbb{R}_{\geq 0}^2$. Since the right-hand sides of Eq. (2) are continuously differentiable in the non-negative quadrant, the system is locally Lipschitz, and hence a unique solution exists on its maximal interval of existence (Smith 1995).

To prove non-negativity, it is sufficient to show that the non-negative quadrant $\mathbb{R}_{\geq 0}^2$ is forward invariant. On the boundary $x=0$, the first equation gives $dx/dt=0$. Therefore, trajectories cannot cross the y -axis into the region $x<0$. Similarly, on the boundary $y=0$, the second equation gives $dy/dt=0$, so trajectories cannot cross the x -axis into the region $y<0$. By uniqueness of solutions, any trajectory starting in $\mathbb{R}_{\geq 0}^2$ remains in $\mathbb{R}_{\geq 0}^2$ for all t in its interval of existence.

Moreover, if $x(0) > 0$ and $y(0) > 0$, then continuity of solutions implies that $x(t)$ and $y(t)$ remain strictly positive for all t in the interval of existence. Therefore, every solution with non-negative initial values remains non-negative, and solutions with strictly positive initial values remain strictly positive. $\square$

2.3. Equilibrium points

Stability analysis begins by locating the steady states of Eq. (2). Solving the resulting system of algebraic equations yields three biologically relevant equilibria:

- (i) Trivial equilibrium: $E_1(0,0)$, at which both populations are extinct.
- (ii) Boundary equilibrium: $E_2\left(0, \frac{m}{e}\right)$, where the prey population is extinct and the predator persists.
- (iii) Interior equilibrium: $E_3(x^*, y^*)$ where,

$$x^* = \frac{ey^* - m}{cp} \text{ and } y^* = \frac{-(p + dk) + \sqrt{(p + dk)^2 + 4pk(r - d)}}{2pk}.$$

This equilibrium represents coexistence of both species. This interior equilibrium $E_3(x^*, y^*)$ exists and is biologically feasible only when both components are positive. In particular, positivity of the prey component requires $r > d$, ensuring that prey reproduction exceeds natural mortality in the absence of predation. If $r \leq d$, then $y^* \leq 0$, and the interior equilibrium is not biologically feasible. Therefore, throughout the analysis of E_3 , it is assumed that $r > d$ and $k < k_T$.

2.4. Local stability

Local stability is assessed by computing the Jacobian matrix and evaluating its eigenvalues at each equilibrium. For Eq. (2), the Jacobian is:

$$J(x, y) = \begin{bmatrix} \frac{r}{1+ky} - d - py & -\frac{rkx}{(1+ky)^2} - px \\ cpy & cpx + m - 2ey \end{bmatrix}. \quad (3)$$

Equilibria are then classified according to the signs of the eigenvalues.

Theorem 2. *The trivial equilibrium $E_1(0,0)$, is always unstable. More precisely, it is a saddle if $r < d$ an unstable node if $r > d$, and non-hyperbolic (and unstable) if $r = d$.*

Proof. At $E_1(0,0)$, the Jacobian Eq. (3) reduces to:

$$J(E_1) = \begin{bmatrix} r-d & 0 \\ 0 & m \end{bmatrix}.$$

The eigenvalues $\lambda_1 = r-d$ and $\lambda_2 = m$. Since $m > 0$, at least one eigenvalue is positive. If $r < d$, then $\lambda_1 < 0$, the eigenvalues have opposite signs and E_1 is a saddle. If $r > d$, both eigenvalues are positive and E_1 is an unstable node. When $r = d$, one eigenvalue is zero and the other is positive, so E_1 is non-hyperbolic. In this case, linearisation is inconclusive for determining Lyapunov stability. $\square$

The instability of the trivial equilibrium $E_1(0,0)$ when $r > d$ indicates that collapse to total extinction of both prey and predator is ecologically unlikely in systems where prey reproduction exceeds natural mortality. In such environments, even small prey introductions lead to population growth, preventing persistence at the extinction state. This result justifies the focus on non-trivial persistence states, namely the boundary equilibrium E_2 and the interior coexistence equilibrium E_3 , which represent ecologically relevant long-term outcomes.

Theorem 3. *The boundary equilibrium $E_2\left(0, \frac{m}{e}\right)$ is locally asymptotically stable for sufficiently large values of the fear parameter k , and becomes unstable for smaller values of k . More precisely, there exists a critical threshold k_T such that E_2 is locally asymptotically stable if $k > k_T$, is a saddle if $0 \leq k < k_T$, and is non-hyperbolic at $k = k_T$.*

Proof. At $E_2\left(0, \frac{m}{e}\right)$, the Jacobian Eq. (3) reduces to:

$$J(E_2) = \begin{bmatrix} \frac{r}{1+\frac{km}{e}} - d - \frac{pm}{e} & 0 \\ \frac{cpm}{e} & -m \end{bmatrix}.$$

This lower triangular matrix has eigenvalues:

$$\lambda_1 = \frac{r}{1 + \frac{km}{e}} - d - \frac{pm}{e}, \quad \lambda_2 = -m.$$

Hence stability depends on the sign of λ_1 . The inequality $\lambda_1 < 0$ is equivalent to:

$$\frac{r}{1 + \frac{km}{e}} < d + \frac{pm}{e} \Leftrightarrow r < \left(d + \frac{pm}{e}\right) \left(1 + \frac{km}{e}\right) \Leftrightarrow k > \frac{e}{m} \left(\frac{r}{d + \frac{pm}{e}} - 1\right).$$

Algebraic simplification yields the threshold:

$$k_T = \frac{re^2 - de^2 - pme}{dem + pm^2}.$$

Therefore $\lambda_1 < 0$ (and thus both eigenvalues are negative) precisely when $k > k_T$, giving local asymptotic stability. If $0 \leq k < k_T$, then $\lambda_1 > 0$ and E_2 is saddle. When $k = k_T$, $\lambda_1 = 0$ and the equilibrium is non-hyperbolic. $\square$

Theorem 4. *There exists a unique interior equilibrium $E_3(x^*, y^*)$, with $x^* > 0$ and $y^* > 0$ whenever $r > d$ and $k < k_T$. Specifically, the interior equilibrium exists and is locally asymptotically stable if $k < k_T$, where k_T is defined in the proof below.*

Proof. An interior equilibrium satisfies:

$$\frac{r}{1 + ky^*} - d - py^*, \quad cpx^* + m = ey^*.$$

The second relation gives $x^* = \frac{ey^* - m}{cp}$. Substituting this into the first yields the quadratic:

$$pk(y^*) + (dk + p)y^* + d - r = 0.$$

Since $pk > 0$ and $d - r < 0$, this equation has exactly one positive root when $r > d$, ensuring uniqueness of $y^* > 0$. Feasibility also requires $x^* > 0$, i.e. $y^* > \frac{m}{e}$. Using $r = (d + py^*)(1 + ky^*)$, and evaluating the inequality at $y^* = \frac{m}{e}$ yields the threshold:

$$y^* > \frac{m}{e} \quad \Leftrightarrow \quad k < \frac{re^2 - de^2 - pme}{dem + pm^2} = k_T.$$

For local stability, evaluating the Jacobian Eq. (3) at E_3 , reduces to:

$$J(E_3) = \begin{bmatrix} 0 & -x^* \left(\frac{rk}{(1+ky^*)^2} + p \right) \\ cpy^* & -ey^* \end{bmatrix}.$$

Hence, the trace and determinant of this Jacobian are:

$$\text{tr}(J(E_3)) = -ey^* < 0, \quad \det(J(E_3)) = x^* cpy^* \left(\frac{rk}{(1+ky^*)^2} + p \right) > 0.$$

The negative trace and positive determinant satisfy the trace-determinant stability conditions for a two-dimensional system, which follow from the Routh-Hurwitz criteria, so E_3 is locally asymptotically stable whenever $k < k_T$. $\square$

2.5. Global stability

Local stability results classify each equilibrium but do not determine the global dynamics. To characterise long-run behaviour, solutions are shown to remain bounded in the positive quadrant and closed orbits are excluded by the Bendixson-Dulac criterion. Together with positivity, these facts yield the global attractor stated in Theorem 5.

Theorem 5. *Under the standing assumptions of the model, define:*

$$k_T = \frac{re^2 - de^2 - pme}{dem + pm^2}.$$

If $k < k_T$, the unique interior equilibrium $E_3(x^, y^*)$ is globally asymptotically stable in $\Omega = \{(x, y) : x > 0, y > 0\}$. If $k > k_T$, the boundary equilibrium $E_2 = \left(0, \frac{m}{e}\right)$ is globally asymptotically stable for all initial conditions with $x(0) > 0, y(0) > 0$.*

Proof. Positivity and forward invariance of the closed first quadrant follow from Theorem 1.

A linear functional $U = (x, y) = x + ay, a \in \left(0, \frac{1}{c}\right)$, yields an absorbing rectangle, so all

trajectories are ultimately bounded. With the Dulac function $B(x, y) = \frac{1}{xy}$,

$$\frac{\partial}{\partial x}(BF_1) + \frac{\partial}{\partial y}(BF_2) = -\frac{e}{x} < 0 \text{ on } \Omega.$$

Thus, there are no periodic or homoclinic orbits in Ω . For $k < k_T$, the interior equilibrium E_3 exists and is locally asymptotically stable (Theorem 4). By Poincaré-Bendixson, every ω -limit set in Ω is an equilibrium; E_1 is unstable (Theorem 2), and the stable manifold of E_2 lies on $x=0$ (Theorem 3), so no orbit with $x(0) > 0$ can approach E_2 . Hence all interior trajectories converge to E_3 . For $k > k_T$, no interior equilibrium exists and E_2 is locally asymptotically stable (Theorem 3). The same boundedness and no-cycle argument implies every ω -limit set is an equilibrium on the boundary; since E_1 is unstable, all solutions with $y(0) > 0$ converge to E_2 . $\square$

2.6. Transcritical bifurcation

A transcritical bifurcation is a qualitative change in which two equilibria collide and then exchange stability; neither equilibrium is created or destroyed—rather, their stability properties are swapped as a parameter varies (Strogatz 2024). Having characterised global stability, the next step is to determine how stability changes as the fear parameter k varies. At a critical value k_T , the boundary equilibrium E_2 develops a simple zero eigenvalue and exchanges stability with the interior branch. The following theorem verifies, via the Sotomayor criterion, that this transition is a nondegenerate transcritical bifurcation, and records the associated eigenvectors used in the check.

Theorem 6. Assume $r, d, p, c, m, e > 0$ and $r > d + \frac{pm}{e}$ so that:

$$k_T = \frac{re^2 - de^2 - pme}{dem + pm^2} > 0.$$

At the boundary equilibrium $E_2\left(0, \frac{m}{e}\right)$ and parameter value $k = k_T$, the Jacobian has a simple zero eigenvalue. A right and a left eigenvector associated with these zero eigenvalues are:

$$V = \begin{pmatrix} 1 \\ \frac{cp}{e} \end{pmatrix}, \quad W = \begin{pmatrix} 1 \\ 0 \end{pmatrix}.$$

Moreover, the Sotomayor nondegeneracy conditions hold:

$$(i) \ W^T F_k(E_1, k_T) = 0, \quad (ii) \ W^T DF_k(E_1, k_T)V \neq 0, \quad (iii) \ W^T D^2F(E_1, k_T)(V, V) \neq 0.$$

Consequently, the system undergoes a transcritical bifurcation at $k = k_T$. In particular, for $k < k_T$ there exists a unique interior equilibrium E_3 which is locally asymptotically stable

while E_2 is a saddle; for $k > k_T$ the interior equilibrium disappears and E_2 becomes locally asymptotically stable.

Proof. The Eq. (2) is written as $\frac{dz}{dt} = F(z, k)$ with $z = (x, y)$ and:

$$F(x, y, k) = \begin{pmatrix} f(x, y, k) \\ g(x, y, k) \end{pmatrix} = \begin{pmatrix} \frac{rx}{1+ky} - dx - pxy \\ cpxy + my - ey^2 \end{pmatrix}.$$

1. Simple zero eigenvalue at (E_2, k_T) .

The Jacobian is:

$$J(x, y, k) = D_z F(x, y, k) = \begin{bmatrix} \frac{r}{1+ky} - d - py & -\frac{rkx}{(1+ky)^2} - px \\ cpy & cpx + m - 2ey \end{bmatrix}.$$

At $E_2\left(0, \frac{m}{e}\right)$ and $k = k_T$,

$$J(E_2, k_T) = \begin{bmatrix} 0 & 0 \\ \frac{cpm}{e} & -m \end{bmatrix}.$$

Since the top-left entry vanishes exactly at $k = k_T$, hence the eigenvalues are 0 and $-m < 0$.

Solving $J(E_2, k_T)V = 0$ and $J(E_2, k_T)^T W = 0$ gives the eigenvectors stated in the theorem.

2. Sotomayor nondegeneracy conditions.

The parameter derivative is:

$$F_k(x, y, k) = \frac{\partial F}{\partial k}(x, y, k) = \begin{bmatrix} -\frac{rxy}{(1+ky)^2} \\ 0 \end{bmatrix}.$$

Thus $F_k(E_2, k_T) = (0, 0)^T$, and condition (i) holds: $W^T F_k(E_1, k_T) = 0$.

The state derivative of F_k is:

$$DF_k(x, y, k) = \begin{bmatrix} -\frac{ry}{(1+ky)^2} & -\frac{rx(1+ky)^2 - rxy \cdot 2(1+ky)k}{(1+ky)^4} \\ 0 & 0 \end{bmatrix}.$$

Evaluating at (E_2, k_T) yields:

$$DF_k(E_2, k_T) = \begin{bmatrix} -\frac{r \frac{m}{e}}{\left(1 + k_T \frac{m}{e}\right)^2} & 0 \\ 0 & 0 \end{bmatrix}.$$

and hence,

$$W^T DF_k(E_1, k_T)V = -\frac{r \frac{m}{e}}{\left(1 + k_T \frac{m}{e}\right)^2} \neq 0$$

which verifies condition (ii): $W^T DF_k(E_1, k_T)V \neq 0$.

For condition (iii), only the first component of F is needed because $W = (1, 0)^T$. The Hessian of $f(x, y, k) = \frac{rx}{1+ky} - dx - pxy$ with respect to (x, y) is:

$$\nabla_z^2 f(x, y, k) = \begin{bmatrix} 0 & -\frac{rk}{(1+ky)^2} - p \\ -\frac{rk}{(1+ky)^2} - p & \frac{2rk^2x}{(1+ky)^3} \end{bmatrix}.$$

At (E_2, k_T) (where $x=0, y=\frac{m}{e}$),

$$\nabla_z^2 f(E_2, k_T) = \begin{bmatrix} 0 & -\frac{rk_T}{\left(1 + k_T \frac{m}{e}\right)^2} - p \\ -\frac{rk_T}{\left(1 + k_T \frac{m}{e}\right)^2} - p & 0 \end{bmatrix}.$$

Therefore,

$$W^T D^2 F(E_1, k_T)(V, V) = V^T (\nabla_z^2 f(E_2, k_T))V = 2 \begin{pmatrix} cp \\ e \end{pmatrix} \left[-\frac{rk_T}{\left(1 + k_T \frac{m}{e}\right)^2} - p \right] \neq 0.$$

Since all parameters are positive, condition (iii) is satisfied.

With (i)-(iii) verified, the Sotomayor criterion ensures a transcritical bifurcation at $k = k_T$.

The stated exchange of stability follows from the sign of the nonzero eigenvalue

$$\lambda_1(k) = \frac{r}{1 + \frac{km}{e}} - d - \frac{pm}{e} \text{ for } k \geq k_T, \text{ together with the existence of the interior equilibrium}$$

$$E_3(x^*, y^*) \text{ for } k < k_T. \square$$

3. Results and Discussion

The analysis of Eq. (2) uses the parameter set in Table 1. Values are taken from Zhu *et al.* (2020) where available and otherwise chosen to facilitate numerical exploration. The parameters p , c , m and e are treated as baseline values and are varied within reasonable ranges using parameter continuation in AUTO (Ermentrout 2002; Omaiye & Mohd 2019). This procedure detects bifurcation points by systematically sweeping parameters over prescribed intervals. Among all parameters, the fear level, k , is selected as the bifurcation parameter because it enters solely in the prey-recruitment term and thus directly modulates the prey's effective birth rate $r/(1+ky)$; as k increases, this rate decreases monotonically, and at the critical value k_T the system undergoes the transcritical exchange of stability between coexistence and boundary equilibria. By applying a one-parameter bifurcation analysis in k , the model reveals how changes in fear affect system stability and population persistence.

Table 1: The parameter values used

Parameter	Definition	Values	References
r	Birth rate of the prey species	2	Zhu <i>et al.</i> (2020)
d	Death rate of the prey species	1	Zhu <i>et al.</i> (2020)
p	Strength of interspecific between prey and predator	0.27	Assumed
c	Conversion efficiency of ingested prey into new predators	0.25	Assumed
m	Intrinsic grow rate of predator species	0.35	Assumed
e	Intraspecific competition of the predator species	0.8	Assumed
k	Level of fear in prey species	[1.76, 1.85]	Varied

The parameter values in Table 1 are selected to be biologically plausible and consistent with ranges commonly used in prey-predator models incorporating fear effects (e.g. Zhu *et al.* 2020). Parameters, p , c , m , and e are assigned baseline values within standard ecological ranges to ensure biological feasibility and to examine robustness of the qualitative dynamics rather than to represent a specific species system. The fear parameter k is varied over the range $1.76 < k < 1.85$, which spans the analytically determined transcritical threshold k_T and captures the transition between coexistence and predator-only persistence. The qualitative results, including the stability exchange at k_T , are robust to moderate parameter variations, with changes primarily shifting the threshold location without altering the bifurcation mechanism. Accordingly, all numerical simulations and bifurcation diagrams in Sections 3.1-3.3 are generated using the parameter values in Table 1 unless stated otherwise.

3.1. One-parameter bifurcation analysis

One-parameter bifurcation analysis tracks how steady states and their stability change as a single parameter varies. In this research, the fear level k is varied numerically in AUTO; equilibrium branches are followed while eigenvalues are monitored to detect the zero crossings that signal stability changes. This complements the local and global theory by locating parameter regions that support coexistence versus predator-only persistence.

Figure 1 (left column) shows the branches as k ranges over $1.76 < k < 1.85$. The analysis reveals a transcritical bifurcation point at $k_T \approx 1.8028$. The interior coexistence equilibrium E_3 and the boundary equilibrium E_2 collide and exchange their stability as k passes through k_T , with neither equilibrium created nor destroyed.

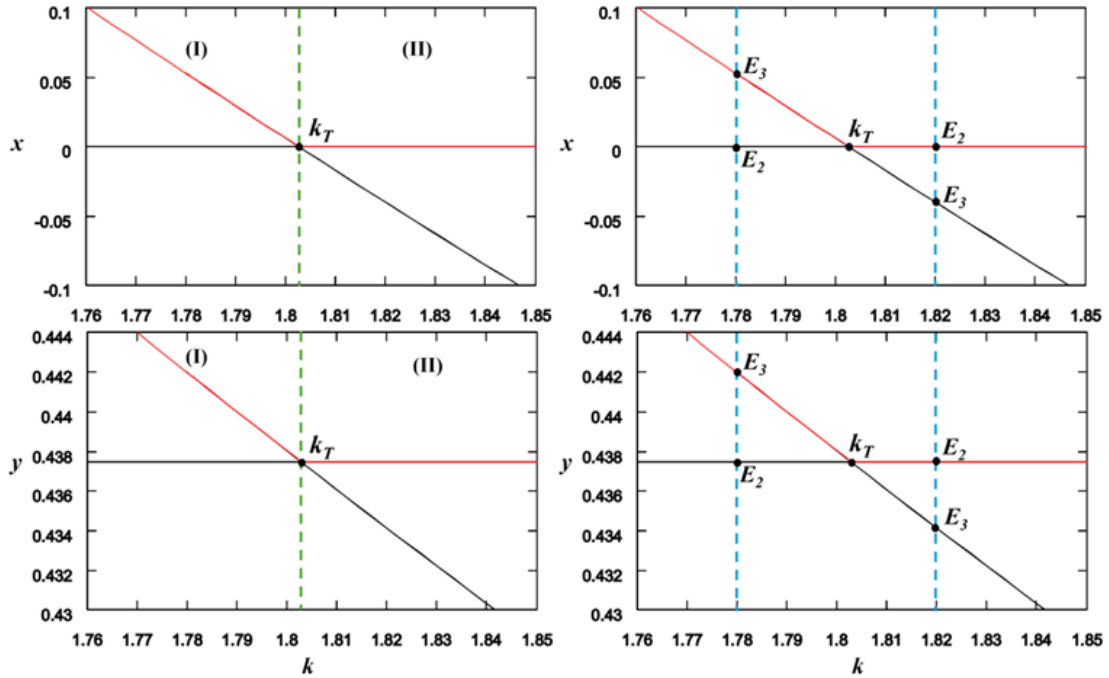


Figure 1: One-parameter bifurcation diagram for prey, x (top) and predator, y (bottom) as the fear level k varies over $1.76 < k < 1.85$ (left column), with red curves indicating stable equilibria and black curves indicating unstable equilibria; the green dashed line marks the transcritical threshold k_T . The right column shows vertical slices at $k = 1.78$ and $k = 1.82$, indicated by blue dashed lines

More precisely, for $k < k_T$, the interior equilibrium E_3 has negative eigenvalues and is locally asymptotically stable, while the boundary equilibrium E_2 is unstable. At the critical value $k = k_T$, the two equilibria intersect and a simple eigenvalue crosses zero. For $k > k_T$, stability is transferred to the boundary equilibrium E_2 , which becomes locally asymptotically stable, whereas the interior equilibrium E_3 loses stability and biological feasibility. This exchange of stability is characteristic of a transcritical bifurcation and is illustrated by the change in stable (red) and unstable (black) branches in Figure 1.

Consistently, red segments denote stable portions, and black segments denote unstable portions, which swap at the vertical green dashed line at $k = k_T$. For $k < k_T$ (Region I), $E_3(x^*, y^*)$ is stable and E_2 is unstable; for $k > k_T$ (Region II) the roles reverse. This agrees

with the local results: Theorem 3 proves that E_2 is stable if and only if $k > k_T$, and Theorem 4 shows that E_3 exists and is stable exactly when $k < k_T$.

To make the stability exchange explicit, Figure 1 (right column) presents vertical slices at $k = 1.78$ and $k = 1.82$ (blue dashed lines). At $k = 1.78 < k_T$, $E_2 = (0, 0.4375)$ is a saddle, whereas $E_3 = (0.05337, 0.44200)$ is a locally asymptotically stable node. When $k = 1.82 > k_T$, E_2 becomes a locally asymptotically stable node and the numerically continued interior branch has coordinates $E_3 = (-0.03968, 0.43415)$ with saddle type, indicating loss of biological feasibility beyond the threshold. The eigenvalues summarised in Table 2 corroborate each classification: E_2 switches from unstable at $k = 1.78$ to locally asymptotically stable at $k = 1.82$, while E_3 switches from a locally asymptotically stable at $k = 1.78$ to a saddle at $k = 1.82$. These observations precisely capture the collision and stability swap characteristic of a transcritical bifurcation and validate Theorems 3-4 together with the bifurcation verification in Theorem 6.

Ecologically, the threshold k_T represents a critical level of perceived predation risk beyond which prey reproduction is sufficiently suppressed that coexistence can no longer be maintained. Below k_T , fear-induced behavioural costs reduce prey growth but remain sufficiently compensated by predator self-regulation through intraspecific competition, allowing stable coexistence. Once k exceeds k_T , non-consumptive fear effects dominate demographic processes, driving the prey population toward extinction while predators persist at a regulated level. Such dynamics are most likely in systems where prey exhibit strong antipredator responses, such as reduced foraging or delayed reproduction, in the presence of predators whose populations are limited primarily by intraspecific competition rather than prey availability.

3.2. Phase plane and time series analysis

Phase-plane and time-series analyses give complementary views of the dynamics at fixed parameters: the phase plane visualises how trajectories from different initial conditions move through state space and which equilibria attract them, while the time series shows the corresponding transients and asymptotic levels of $x(t)$ and $y(t)$.

Figures 2-3 (left panels) display phase-plane portraits for $k = 1.78 < k_T$ and $k = 1.82 > k_T$, each started from widely separated initial conditions (coloured curves with arrows). For $k = 1.78$, every interior trajectory bends toward the coexistence point $E_3 (0.05337, 0.44200)$ and remains near it once reached; no spirals or cycles appear, and no trajectory is captured by the boundary equilibrium. For $k = 1.82$, all trajectories move leftward across the predator nullcline and converges at the boundary point $E_2 (0, 0.43750)$, again without oscillations or diversion to alternative attractors. This behaviour accords with Theorem 5 (global stability via Bendixson-Dulac): for $k < k_T$, E_3 is the global attractor for all $x(0) > 0$, $y(0) > 0$; for $k > k_T$, E_2 is globally asymptotically stable for all $x(0) > 0$, $y(0) > 0$. Positivity and boundedness keep trajectories in the biologically relevant region, and the Dulac criterion rules out closed orbits; hence the observed convergence in Figures 2-3 is independent of initial values and reflects global stability.

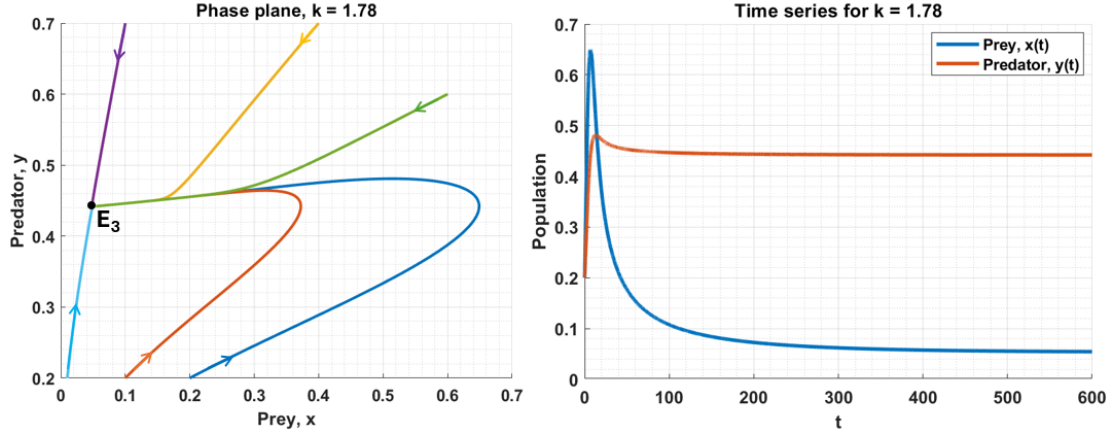


Figure 2: Phase plane (left) and time series (right) at $k = 1.78$

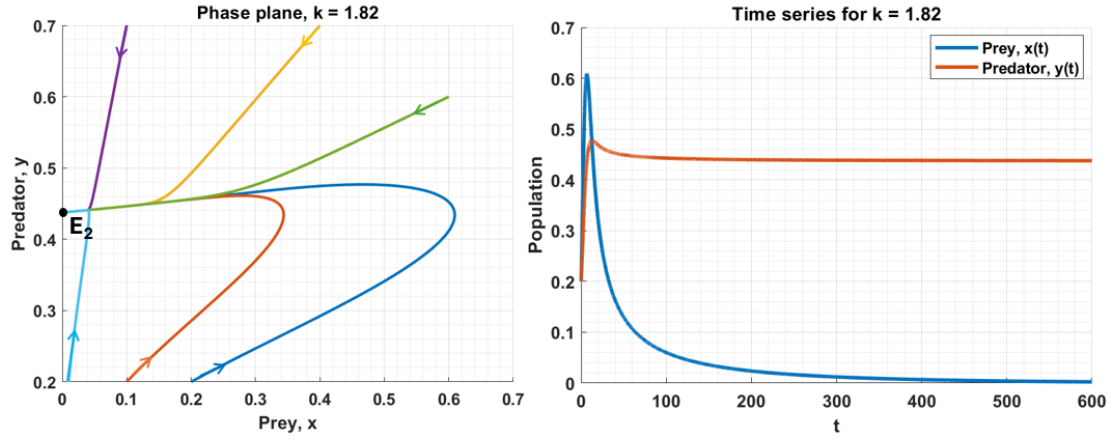


Figure 3: Phase plane (left) and time series (right) at $k = 1.82$

Table 2: Summary of stability analysis results

Fear effect, k	Equilibrium points	Eigenvalues	Stability results
$k = 1.78$	$E_1 = (0, 0)$	$\lambda_1 = 1, \lambda_2 = 0.35$	Unstable
	$E_2 = (0, 0.4375)$	$\lambda_1 = 0.00626, \lambda_2 = -0.35$	Saddle
	$E_3 = (0.05337, 0.442)$	$\lambda_1 = -0.00635, \lambda_2 = -0.34725$	Asymptotically stable
$k = 1.82$	$E_1 = (0, 0)$	$\lambda_1 = 1, \lambda_2 = 0.35$	Unstable
	$E_2 = (0, 0.4375)$	$\lambda_1 = -0.00469, \lambda_2 = -0.35$	Asymptotically stable
	$E_3 = (-0.03968, 0.43415)$	$\lambda_1 = 0.00465, \lambda_2 = -0.35196$	Saddle

The time-series traces (Figures 2-3, right panels) mirror these phase portraits and reveal a clear fast-slow relaxation without oscillation. At $k = 1.78$, the predator $y(t)$ shows a brief overshoot and then settles monotonically to $y \approx 0.442$, while the prey $x(t)$ drops rapidly before approaching $x \approx 0.053$ on a slower timescale; this two-rate approach matches the eigenvalue pattern at E_3 in Table 2 (both real and negative). At $k = 1.82$, $y(t)$ similarly

exhibits a short overshoot and relaxes to $y \approx 0.438$, whereas $x(t)$ decays monotonically to zero; the comparable fast transient followed by a very slow drift is consistent with the eigenvalues at E_2 (again, two real negatives of different magnitude).

Ecologically, the threshold at k_T captures how non-consumptive risk alters demographic rates and long-term outcomes. When fear is low ($k < k_T$), the prey's effective birth rate $r/(1+ky)$ remains high enough to offset predation losses, while predator competition prevents unchecked predator growth; the system therefore stabilises at coexistence. When fear is high ($k > k_T$), prey recruitment is suppressed to the point where the interior equilibrium is no longer feasible, forcing convergence to the predator-only equilibrium E_2 .

More generally, the interplay of risk, behaviour, and predator competition documented here mirrors findings across aquatic and terrestrial systems. In coral reef ecosystems, Bauman *et al.* (2021) showed that predator cues alone significantly reduced browsing herbivory, altering ecosystem functioning. In freshwater planktonic systems, Panja *et al.* (2023) demonstrated that fear in zooplankton, combined with algal toxins and harvesting, reorganises stability domains, while Kaur *et al.* (2021) found that low fear levels can stabilise coexistence, although stronger fear simplified dynamics. These results agree with the present model's outcomes that fear reshapes attractor landscapes depending on ecological context. In terrestrial ecosystems, Gaynor *et al.* (2019) emphasised that fear creates "landscapes of fear" where prey alter space use and reproduction, cascading into community-level effects. Together, these findings demonstrate that the threshold k_T represents a general tipping point where risk, refuge, toxins, and crowding jointly determine whether coexistence or collapse occurs.

From a management perspective, the results suggest that interventions lowering perceived risk for prey (e.g., habitat enrichment, refuge provision, or reduction of predator cues) would effectively lower the fear parameter k and maintain coexistence at E_3 . Conversely, conditions that heighten predation risk cues push k beyond k_T , making prey extinction and predator-only persistence more likely. These insights parallel management recommendations from empirical studies: increasing habitat complexity to reduce effective risk (Pal *et al.* 2019), providing refuge availability in aquatic systems (Kaur *et al.* 2021), reducing predator cue exposure (Bauman *et al.* 2021), and understanding risk landscapes for conservation planning (Gaynor *et al.* 2019). Thus, the model's predictions are not purely theoretical; they correspond closely with observed ecological phenomena and provide guidance for managing coexistence in natural and harvested systems.

In conclusion, the phase-plane and time-series analyses confirm that fear intensity governs the long-term outcomes of the system through a clear stability threshold at k_T . Below this threshold, trajectories converge globally to coexistence, whereas above it, prey extinction and predator-only persistence dominate. These findings align with both theoretical predictions and empirical observations across ecological systems, reinforcing the ecological validity of the model. The sharp switch in stability between equilibria illustrates the central role of a transcritical bifurcation as the organising mechanism. This sets the stage for the two-parameter analysis in the section, where the joint effects of prey fear and predator intraspecific competition are examined, and the precise conditions under which coexistence can be maintained are explored in greater ecological and mathematical detail.

3.3. The joint effect of prey fear and intraspecific predator competition

A two-parameter (codimension-2) continuation was conducted to examine how stability changes jointly with the fear level k and predator intraspecific competition e . Continuing the one-parameter threshold identified earlier produces a diagonal curve in the (k, e) -plane,

labelled k_T in Figure 6, depicts a transcritical bifurcation border. Along this line, the interior and boundary equilibria collide and exchange stability. Theorem 6 verifies (via the Sotomayor criterion) that this transition is a nondegenerate transcritical bifurcation, and Theorem 5 ensures global convergence to the unique stable equilibrium on either side of the border.

Choosing e as the companion to k is motivated by both analysis and ecology. Analytically, the stability threshold depends explicitly on both parameters and increases monotonically with e ; hence e directly modulates the critical fear level at which stability changes. Ecologically, k and e act on distinct mechanisms—risk-induced suppression of prey reproduction versus crowding-induced regulation of predator growth—forming a natural, antagonistic pair that shapes the transcritical boundary. Similar antagonistic roles of behavioural risk versus density-dependent predator regulation have been emphasised in (Al-Momen & Naji 2023; Ibrahim *et al.* 2025; Mukherjee 2020), who each demonstrated that stronger predator crowding enlarges persistence domains under elevated prey fear. Dynamically, e controls the asymptotic predator density at the boundary state and thus has a clear fingerprint on long-term outcomes. From a management standpoint, it is an actionable quantity influenced by territoriality, interference, habitat structure, and anthropogenic aggregation, consistent with applied frameworks describing how predator competition buffers stability (Gaynor *et al.* 2019; Zanette & Clinchy 2019). Studying the (k, e) plane therefore links the bifurcation geometry to practical levers that can enhance or erode coexistence.

The bifurcation diagram in Figure 6 partitions the parameter space into two domains. Below the k_T border (yellow region), trajectories converge to the predator-only equilibrium, whereas above the k_T (blue region), the interior coexistence equilibrium is globally attracting. The boundary rises monotonically with e , indicating that stronger predator competition permits coexistence under higher levels of prey fear. This pattern is consistent with earlier findings where intraspecific competition stabilised prey-predator systems under risk (Al-Momen & Naji 2023; Ibrahim *et al.* 2025; Mukherjee 2020). Conversely, increasing k at fixed e pushes the system toward predator-only persistence, and at sufficiently high fear the coexistence state becomes infeasible. Similar results were obtained by Zhu *et al.* (2020) and Wang *et al.* (2016), where strong non-consumptive effects drove the extinction of prey despite predators persisting on alternative resources.

Slicing the diagram clarifies these trends. Along vertical slices (fixed k), increasing e shifts outcomes from predator-only to coexistence once the slice crosses the diagonal k_T border. At a low fear level (e.g., $k = 0.4$), this transition occurs near $e \approx 0.2815$: below this value, weak predator competition allows predators to suppress prey recruitment, whereas above it, stronger interference and territoriality reduce predator pressure and permit coexistence. Comparable stabilising effects of predator self-limitation have been reported in both mathematical models (Maghool & Naji 2022; Mukherjee 2020) and empirical studies on coral reef and terrestrial systems, where interference, group size, or territoriality regulate predator density (Bauman *et al.* 2021). At higher fear $k = 1.8$ coexistence is recovered only for much larger e (about 0.799), reflecting the ecological fact that intense fear depresses prey reproduction so strongly that only pronounced predator crowding can restore balance. Similar dynamics have been described in planktonic models where fear and toxins interact to push systems toward collapse unless predator interference compensates (Kaur *et al.* 2021; Panja *et al.* 2023).

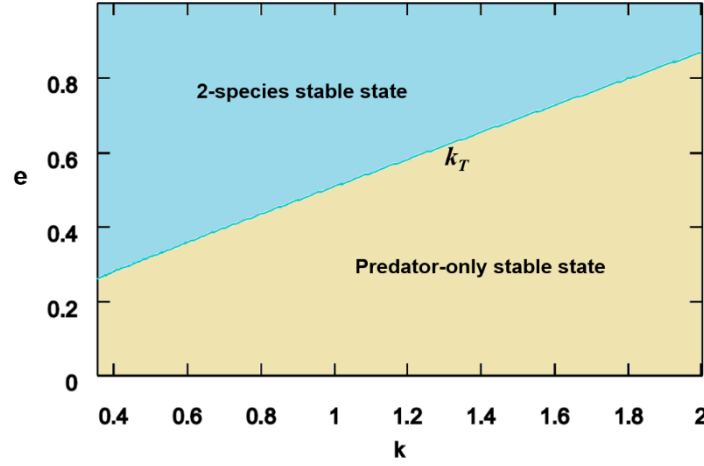


Figure 4: Two-parameter bifurcation map in (k, e) : the blue region denotes the two-species (coexistence) stable state, the yellow region denotes the predator-only stable state, and the diagonal line k_T marks the transcritical bifurcation border

Complementary horizontal slices (fixed e) show how the tolerable fear level expands with predator competition. For $e = 0.4$, coexistence persists up to $k \approx 0.706$; beyond this, prey collapse and the system converge at the predator-only state. For $e = 0.7$, the threshold rises to $k \approx 1.525$, demonstrating that stronger density dependence in predators broadens the range of fear levels compatible with coexistence. In ecological terms, the diagonal k_T line acts as a transcritical bifurcation border that is shifted upward by increasing e : predator competition systematically buffers the system against higher fear, whereas higher fear at fixed e pushes the community toward predator-only persistence. This interpretation agrees with eco-evolutionary arguments that prey scarcity induces density dependence in predators and with cross-system findings that predator interference, refuge use, and behavioural responses together restructure stability domains (Gaynor *et al.* 2019; Zanette & Clinchy 2019).

From a management perspective, the finding suggests two complementary levers to maintain coexistence. First, reduce the effective fear level (e.g., by increasing habitat complexity, enhancing refuges, or dampening predator cues) to move leftward across k_T . Empirical work has shown that habitat enrichment or predator cue reduction can reduce perceived predation risk and sustain prey reproduction (Bauman *et al.* 2021; Zanette *et al.* 2011). Second, strengthen effective predator competition, (e.g., by avoiding aggregation and subsidies and maintaining territorial structure) to move upward across k_T . This aligns with studies showing that predator competition prevents overexploitation of prey and enlarges persistence domains (Al-Momen & Naji 2023; Ibrahim *et al.* 2025; Mukherjee 2020). Both actions shift conditions away from the transcritical border and enlarge the parameter region that supports two-species persistence, reinforcing that ecological management and bifurcation structure are closely intertwined.

In conclusion, the two-parameter continuation reveals that the joint effects of prey fear and predator self-limitation organise system dynamics through a transcritical bifurcation line that cleanly separates coexistence from predator-only persistence. Ecologically, this means that risk-driven reductions in prey reproduction and density-dependent regulation in predators function as opposing forces that determine whether populations persist together or collapse into single-species dominance. The upward shift of the bifurcation border with increasing predator competition highlights how behavioural avoidance in prey and crowding in predators form a coupled stability mechanism, consistent with both theoretical predictions (Ibrahim *et*

al. 2025; Mukherjee 2020). and empirical studies across aquatic and terrestrial systems (Bauman *et al.* 2021; Panja *et al.* 2023). Together with the one-parameter analyses in Section 3.2, these results demonstrate that transcritical bifurcations serve as the canonical tipping mechanism in fear-based prey-predator systems, while ecological modifiers such as refuge, toxins, and crowding determine the precise location of the threshold. This synthesis underscores that management strategies targeting either reduced prey risk or enhanced predator competition can shift populations away from collapse and promote stable coexistence.

4. Conclusion

This research shows that non-consumptive fear effects can fundamentally alter prey–predator dynamics through their interaction with predator self-regulation. The analytical and numerical results identify a transcritical threshold k_T that separates regimes of stable coexistence from predator-only persistence. From an ecological perspective, this threshold represents a behavioural tipping point at which fear-induced suppression of prey reproduction outweighs compensatory regulation by predators, leading to loss of prey persistence even in the absence of excessive predation pressure.

The primary contribution of this study lies in providing an explicit analytical characterisation of the threshold k_T and its associated stability exchange. While related fear-based prey-predator models, including that of Zhu *et al.* (2020), have identified transcritical bifurcations through numerical continuation and simulation, the present analysis establishes closed-form existence and stability conditions under which this bifurcation occurs. In particular, the results formally link prey extinction to the interaction between fear intensity and predator intraspecific competition, thereby clarifying the ecological mechanism underlying the observed bifurcation structure.

The model involves deliberate simplifications that define its scope. In particular, prey intraspecific competition is excluded, so prey persistence depends entirely on the balance between fear-modified reproduction and predation. This formulation allows isolation of the stabilising role of predator intraspecific competition and facilitates explicit analytical verification of the transcritical threshold. At the same time, it limits applicability to ecological systems in which prey self-regulation is weak or secondary. Future research could extend this framework by incorporating prey self-limitation, spatial processes, or stochastic effects, and by examining how multiple behavioural mechanisms jointly influence system resilience under perceived predation risk.

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