CAUCHY – Jurnal Matematika Murni dan Aplikasi
Volume 11 (2) (2026), Pages 1489–1505
p-ISSN: 2086-0382; e-ISSN: 2477-3344

Dynamical Analysis of Modified Leslie-Gower Beddington-DeAngelis Model with Prey Refuge and Intraspecific Competition

Salsabil Faridah Saputri Kusbianti, Riska Wahyu Romadhonia*, and Dian Savitri

Department of Mathematics, Faculty of Mathematics and Natural Sciences, Universitas Negeri Surabaya, Surabaya, Indonesia.

Abstract

This study examines the dynamical behavior of a predator–prey model depicting the interaction between *Perca fluviatilis* (predator) and its natural prey, *Rutilus rutilus*. The model is formulated within a modified Leslie-Gower framework and employs the Beddington–DeAngelis functional response to capture mutual interference among predators during foraging. It further incorporates key ecological elements: prey refuge and nonlinear intraspecific competition arising from prey density dependence. Equilibrium points and their local stability are investigated using the Jacobian matrix and the Routh–Hurwitz criteria. The analysis identifies four equilibria: the trivial equilibrium, the predator-extinction equilibrium, the prey–extinction equilibrium, and the coexistence equilibrium. Numerical simulations corroborate these analytical results. The simulations reveal that under appropriate parameters, the stability of the system is significantly driven by both the availability of prey refuges and the degree of intraspecific competition, which ultimately determine the survival conditions for both populations.

Keywords: Beddington-DeAngelis; Intraspecific Competition; Modified Leslie-Gower; Predator-Prey Model; Prey Refuge.

1. Introduction

Freshwater environments, such as rivers and lakes, are complex systems that rely heavily on interactions between species to maintain ecological stability. Within the realm of population ecology, predator-prey dynamics are particularly crucial, as they significantly shape population sizes, the long-term survival of species, and the overall organization of food webs. In European freshwater systems, a well–documented predator-prey dynamic involves the roach (*Rutilus rutilus*) as the principal prey and the Eurasian perch (*Perca fluviatilis*) as the primary predator. The biological characteristics and ecological adaptability of *Perca fluviatilis* have attracted extensive research worldwide, owing to its broad distribution, high foraging efficiency, and sensitivity to environmental perturbations such as browning [1–4]. Ultimately, the persistence of both species depends critically on food availability, environmental conditions, and the effectiveness of prey defense mechanisms.

*Corresponding author. E-mail: riskaromadhonia@unesa.ac.id

Received: April 16, 2026 Revised: May 22, 2026 Accepted: June 22, 2026
DOI: https://doi.org/10.18860/cauchy.v11i2.41945

To elucidate these intricate dynamics, mathematical modeling has proven to be a powerful approach for forecasting population trajectories. Traditional predator–prey models are often criticized for oversimplifying dynamics by assuming that predator growth depends solely on prey abundance. To address this limitation, researchers frequently employ the modified Leslie–Gower formulation. This approach posits that the predator's carrying capacity varies proportionally with prey density, an assumption that aligns well with biological realities in aquatic environments. [5–7].

Beyond the core model structure, the functional response–which measures prey consumption per predator–is crucial for evaluating system stability. The Beddington–DeAngelis functional response is widely applied in ecological models because it accounts for prey handling time and predator interference at high densities [8–13]. In perch populations, high densities lead individuals to devote more time to social interactions and rivalry over optimal foraging sites, diverting effort from roach predation. As a result, this interference reduces overall foraging efficiency.

Moreover, intrinsic regulatory mechanisms and habitat variability exert a substantial influence on the stability of predator–prey interactions. Specifically, roach leverage aquatic vegetation and shallow littoral zones as refuges to escape predation, functioning as a safeguard against total extinction [14–16]. At the same time, the prey population faces intraspecific competition for limited resources such as food and space. This rivalry generates complex dynamics–including Allee effects and nonlinear growth trajectories–that escalate with increasing competitive intensity [17–21].

A review of the existing literature indicates that refuge-based tactics together with nonlinear intraspecific competition constitute pivotal ecological mechanisms that fundamentally reshape the stability of the system. While previous studies have independently explored the Beddington–DeAngelis functional response within Leslie–Gower frameworks [5, 7] or incorporated nonlinear intraspecific competition in simpler predator-prey settings [17, 20], the explicit mathematical amalgamation of these non-linearities remains methodologically underexplored. The principal novelty and specific contribution of the present study lie in providing a rigorous characterization of the intricate algebraic structures generated by this direct coupled interaction. Contrary to typical models in which coexistence equilibria can be derived analytically with little effort, the coupling of the density-dependent prey term—originating from nonlinear competition—with the multivariate Beddington–DeAngelis functional response imposes substantial analytical challenges. This investigation addresses those challenges by constructing a higher-order polynomial formulation that demonstrates the explicit biological admissibility of the coexistence equilibrium and rigorously derives its local stability conditions.

Unlike standard Leslie–Gower models that assume a constant predator carrying capacity, or traditional Beddington–DeAngelis formulations that overlook prey anti-predator behaviors, the proposed model uniquely integrates all these mechanisms simultaneously. By coupling a modified Leslie–Gower structure with a Beddington–DeAngelis functional response, and further incorporating both a prey refuge parameter and nonlinear intraspecific competition, this study provides a more comprehensive mathematical framework to analyze complex predator-prey dynamics that previous isolated models may fail to capture.

Although motivated by the ecological dynamics of the *Rutilus rutilus* and *Perca fluviatilis* interaction, this study serves primarily as a theoretical mathematical exploration designed to uncover how these coupled non-linear mechanisms act as regulatory drivers to prevent species depletion. These analytical efforts are expected to enrich mathematical ecology theory and enhance the dynamical understanding of freshwater habitats.

This article is organized as follows. Section 2 outlines the mathematical model. Section 3 examines the existence and local stability of equilibria and presents numerical simulations with their ecological implications. Section 4 presents the conclusions.

2. Methods

This section outlines the systematic approach and mathematical framework utilized to analyze the predator-prey interactions. First, the overarching research methodology is presented to map the procedural steps of the study. Subsequently, the precise mathematical formulation of the modified model is derived, incorporating the relevant biological complexities.

2.1. Research Methodology

This investigation employs a systematic methodology to enable comprehensive analysis of the predator–prey model representing interactions between *Perca fluviatilis* (predator) and *Rutilus rutilus* (prey). The procedural framework is depicted schematically in Fig. 1.

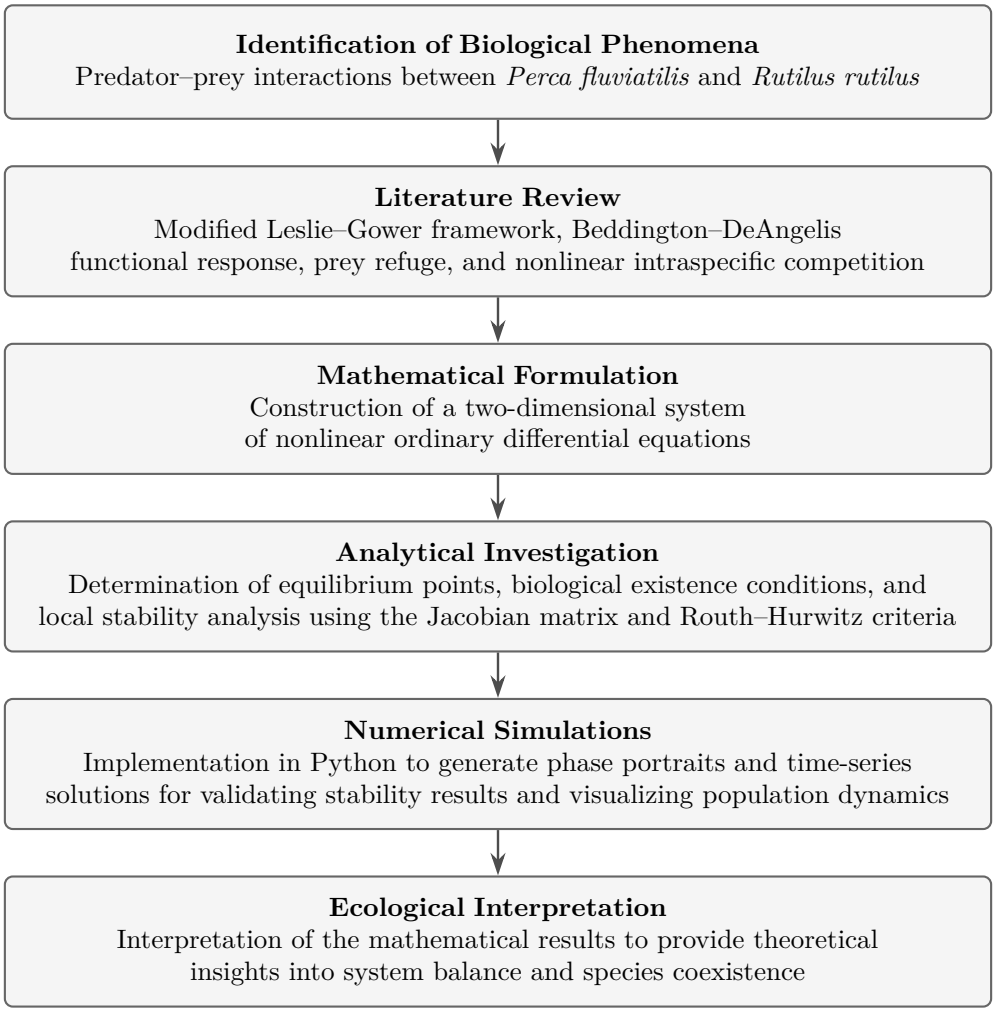

Fig. 1: Research methodology of the study.

As shown, the study commences with the identification of key biological phenomena. In particular, it investigates the impacts of prey refuge, nonlinear intraspecific competition in the prey population, and predator mutual interference via the Beddington–DeAngelis functional response. Next, a continuous mathematical model is formulated as a system of differential equations, grounded in the modified Leslie–Gower scheme. Thereafter, analytical techniques are applied to identify equilibrium points and assess their local stability, employing the Jacobian matrix and the Routh–Hurwitz criteria. Finally, numerical simulations are performed to corroborate the analytical results and illustrate the system's dynamic behaviors.

2.2. Mathematical Model Formulation

To clearly delineate the theoretical contributions of this study, it is essential to first outline the foundational paradigms upon which our model is constructed. The classical Leslie–Gower predator–prey formulation assumes that the carrying capacity of the predator population is dynamically proportional to the abundance of its prey. Concurrently, the standard Beddington–DeAngelis functional response was introduced to address the limitations of purely prey-dependent models by incorporating mutual interference among predators during foraging.

By synthesizing these foundational ecological frameworks and introducing additional realistic biological complexities, we propose a novel modification to model the interactions between the prey (*Rutilus rutilus*, roach; x) and the predator (*Perca fluviatilis*, perch; y). Specifically, we incorporate a prey refuge proportion (m) that effectively shields a fraction of the prey from predation, alongside a nonlinear density-dependent intraspecific competition term.

The modified model is rendered as the following system of nonlinear ordinary differential equations:

$$\begin{aligned} \frac{dx}{dt} &= x(r_1 - b_1 x + c_1) - \frac{a_1(1-m)xy}{k_1 + e_1(1-m)x + e_2 y} - \frac{cx^2}{x+d}, \\ \frac{dy}{dt} &= y\left(r_2 - \frac{a_2 y}{(1-m)x + k_2}\right). \end{aligned} \tag{1}$$

In this system, $x(t)$ and $y(t)$ represent prey and predator population densities at time t. Parameters r_1 and r_2 denote the intrinsic growth rates of prey and predator, respectively. The term b_1 accounts for density-dependent mortality in the prey. Predator-prey coupling occurs via the Beddington–DeAngelis functional response, governed by a_1, e_1, and e_2, where a_1 is the maximum predation rate, e_1 reflects prey-induced saturation, and e_2 captures foraging interference among predators. The parameter m indicates the fraction of prey accessing refuge from predation, with $m \in [0, 1)$. Additionally, the term $\frac{cx^2}{x+d}$ models extra mortality in the prey arising from nonlinear intraspecific competition, where c denotes the maximum competition-induced mortality rate, and d is the half-saturation constant for this process. To prevent any notational ambiguity, it is explicitly noted that m and d herein denote the refuge proportion and the half-saturation constant, respectively, rather than mortality or death rates, as sometimes conventionally used in general ecological literature. The coefficient c_1 reflects the supplementary growth rate of the prey from alternative food sources. In the predator equation, a_2 represents the conversion efficiency of consumed prey into predator biomass. The parameters k_1 and k_2 represent the environmental carrying capacities for the prey and predator, respectively. All parameters are presumed to be non-negative constants. It is important to emphasize that, while the interaction between roach and perch serves as the primary biological motivation for the structural design of this model, the parameters utilized in subsequent analyses are strictly hypothetical. Consequently, this mathematical model is not intended to generate direct empirical predictions for specific freshwater ecosystems, but rather to offer theoretical insights into the fundamental dynamics of roach-perch-like interactions.

3. Results and Discussion

This section presents the core analytical findings derived from the proposed mathematical model. The investigation begins by identifying all biologically admissible equilibrium points, which represent the potential steady states of the ecosystem. Following this, a rigorous local stability analysis is conducted for each state to establish the mathematical conditions under which the populations either coexist or face extinction.

3.1. Equilibrium Points

Equilibrium points correspond to the steady states of the system, identified by setting the time derivatives equal to zero:

$$\frac{dx}{dt} = 0 \quad \text{and} \quad \frac{dy}{dt} = 0.$$

The model outlined in System Eq. (1) admits four biologically relevant equilibrium points:

1. **Trivial Equilibrium Point (E_0)**
   This equilibrium corresponds to the extinction of both the prey (*Rutilus rutilus*) and predator (*Perca fluviatilis*) populations. Substituting $x = 0$ and $y = 0$ into System Eq. (1) yields:
   $$E_0 = (0, 0)$$
2. **Prey-Extinction Equilibrium Point (E_1)**
   This equilibrium depicts the extinction of the prey population ($x = 0$),with the predator persisting via alternative food sources—a hallmark of the modified Leslie–Gower framework. Substituting $x = 0$ into the second equation of System Eq. (1) yields:
   $$y\left(r_2 - \frac{a_2 y}{(1-m)(0) + k_2}\right) = 0$$
   Excluding the trivial solution $y = 0$, we solve for y:
   $$r_2 - \frac{a_2 y}{k_2} = 0 \implies y = \frac{r_2 k_2}{a_2}$$
   Thus, the prey-extinction equilibrium is $E_1 = (0, \frac{r_2 k_2}{a_2})$.
3. **Predator-Extinction Equilibrium Point (E_2)**
   This equilibrium depicts the predator population's extinction ($y = 0$), with the prey population persisting. Substituting $y = 0$ into the first equation of System Eq. (1) yields:
   $$x\left((r_1 + c_1) - b_1 x - \frac{cx}{x+d} - \frac{a_1(1-m)(0)}{k_1 + e_1(1-m)x + e_2(0)}\right) = 0$$
   Excluding the trivial solution $x = 0$, the predation term vanishes, and we solve for x:
   $$(r_1 + c_1) - b_1 x - \frac{cx}{x+d} = 0$$
   Multiplying by $(x + d)$ to clear the denominator yields a standard quadratic equation:
   $$b_1 x^2 + (b_1 d + c - (r_1 + c_1))\, x - d(r_1 + c_1) = 0 \tag{2}$$
   By applying the quadratic formula, the discriminant is strictly positive, given by $\Delta = (b_1 d + c - (r_1 + c_1))^2 + 4 b_1 d (r_1 + c_1)$. Thus, the explicit positive root is:
   $$x_2 = \frac{-(b_1 d + c - (r_1 + c_1)) + \sqrt{(b_1 d + c - (r_1 + c_1))^2 + 4 b_1 d (r_1 + c_1)}}{2 b_1}$$
   Thus, the predator-extinction equilibrium is $E_2 = (x_2, 0)$. The equilibrium E_2 exists biologically if
   $$r_1 + c_1 > 0 \quad \text{and} \quad d > 0$$
   These conditions indicate that the prey population can always survive and reach a stable steady state in the absence of predators, supported by their intrinsic growth and external recruitment.

4. **Coexistence Equilibrium Point (E_3)**
This equilibrium describes the predator-prey interaction in which both populations successfully coexist ($x^* > 0$ and $y^* > 0$). From the predator nullcline $\frac{dy}{dt} = 0$, we express y^* in terms of x^*:

$$y^* = \frac{r_2}{a_2}\left((1-m)x^* + k_2\right).$$

To simplify the substitution, let $y^* = Mx^* + N$, where $M = \frac{r_2(1-m)}{a_2}$ and $N = \frac{r_2 k_2}{a_2}$. Substituting y^* into $\frac{dx}{dt} = 0$ results in:

$$(r_1 + c_1 - b_1 x^*) - \frac{cx^*}{x^* + d} - \frac{a_1(1-m)(Mx^* + N)}{k_1 + e_1(1-m)x^* + e_2(Mx^* + N)} = 0.$$

Let $P = e_1(1-m) + e_2 M$ and $Q = k_1 + e_2 N$. Multiplying the entire equation by the common denominators $(x^* + d)$ and $(Px^* + Q)$ and arranging it by the powers of x^* yields a cubic polynomial equation:

$$A_1(x^*)^3 + A_2(x^*)^2 + A_3 x^* + A_4 = 0, \tag{3}$$

where the coefficients are defined as:

$$\begin{aligned}
A_1 &= b_1 P,\\
A_2 &= b_1(Pd + Q) + cP + a_1(1-m)M - P(r_1 + c_1),\\
A_3 &= b_1 dQ + cQ + a_1(1-m)(Md + N) - (r_1 + c_1)(Pd + Q),\\
A_4 &= a_1(1-m)Nd - dQ(r_1 + c_1).
\end{aligned}$$

Because solving the cubic polynomial in Eq. (3) analytically yields unwieldy expressions, the coexistence root x^* is determined numerically in practice. The coexistence equilibrium $E_3(x^*, y^*)$ exists biologically if and only if Eq. (3) has at least one positive real root $x^* > 0$, with the corresponding predator density y^* uniquely determined by Eq. (4). By applying Descartes' Rule of Signs, a simple sufficient condition for the existence of at least one strictly positive real root is that the coefficients of the cubic polynomial exhibit at least one sign change. For instance, if the leading coefficient $A_1 > 0$ and the constant term $A_4 < 0$, the polynomial is mathematically guaranteed to possess at least one positive root, thereby ensuring the biological admissibility of the coexistence equilibrium E_3.
These conditions indicate that both species can mutually survive and reach a dynamic balance, provided the prey population is sufficient to support the predators without being driven to extinction.

Theorem 1 (Existence of Equilibrium Points)**.** *In the predator-prey system described by Eq. (1), the trivial equilibrium E_0 and the prey-extinction equilibrium E_1 exist unconditionally. The predator-extinction equilibrium E_2 exists biologically if and only if $r_1 + c_1 > 0$ and $d > 0$. In contrast, the coexistence equilibrium E_3 exists biologically if and only if the associated cubic polynomial equation has at least one strictly positive real root $x^* > 0$.*

Proof. The existence of E_0, E_1, and E_2 follows directly from the algebraic solutions of the nullclines. It also relies on the uniqueness of the positive root in Eq. (2). By contrast, the existence of E_3 depends on a positive intersection between the prey and predator nullclines in the first quadrant. □

3.2. Local Stability Analysis

The local stability of the system is investigated by linearizing the nonlinear system around each equilibrium point. The general Jacobian matrix for the system evaluated at an arbitrary state

(x, y) is given by:

$$J(x,y) = \begin{pmatrix} F_x & F_y \\ G_x & G_y \end{pmatrix}$$

where the partial derivatives are calculated using standard differentiation rules (applying the quotient rule for the nonlinear competition term $\frac{cx^2}{x+d}$):

$$\begin{aligned}
F_x &= (r_1 + c_1) - 2b_1 x - \frac{cx(x+2d)}{(x+d)^2} - \frac{a_1(1-m)y(k_1 + e_2 y)}{(k_1 + e_1(1-m)x + e_2 y)^2}, \\
F_y &= -\frac{a_1(1-m)x\,(k_1 + e_1(1-m)x)}{(k_1 + e_1(1-m)x + e_2 y)^2}, \\
G_x &= \frac{a_2(1-m)y^2}{((1-m)x + k_2)^2}, \\
G_y &= r_2 - \frac{2a_2 y}{(1-m)x + k_2}.
\end{aligned}$$

Theorem 2. *The trivial equilibrium point $E_0(0,0)$ is always an unstable node.*

Proof. The Jacobian matrix evaluated at $E_0(0,0)$ yields a diagonal matrix:

$$J(E_0) = \begin{pmatrix} r_1 + c_1 & 0 \\ 0 & r_2 \end{pmatrix}$$

The eigenvalues are the diagonal entries:

$$\begin{aligned}
\lambda_1 &= r_1 + c_1, \\
\lambda_2 &= r_2.
\end{aligned}$$

Since $r_1, c_1, r_2 > 0$, it follows that $\lambda_1 > 0$ and $\lambda_2 > 0$. Therefore, E_0 is an unstable node. □

Theorem 3. *The prey-extinction equilibrium $E_1(0, y_1)$ is locally asymptotically stable if*

$$r_1 + c_1 < \frac{a_1(1-m)y_1}{k_1 + e_2 y_1}.$$

Proof. Evaluating the Jacobian at $E_1(0, y_1)$ yields a triangular matrix:

$$J(E_1) = \begin{pmatrix} (r_1 + c_1) - \frac{a_1(1-m)y_1}{k_1 + e_2 y_1} & 0 \\ G_x(0, y_1) & -r_2 \end{pmatrix}$$

The eigenvalues are:

$$\begin{aligned}
\lambda_1 &= (r_1 + c_1) - \frac{a_1(1-m)y_1}{k_1 + e_2 y_1}, \\
\lambda_2 &= -r_2.
\end{aligned}$$

Since $r_2 > 0$, then $\lambda_2 < 0$. Stability requires $\lambda_1 < 0$, which yields:

$$(r_1 + c_1) < \frac{a_1(1-m)y_1}{k_1 + e_2 y_1}.$$

□

Theorem 4. *The predator-extinction equilibrium $E_2(x_2, 0)$ is always an unstable saddle point.*

Proof. Evaluating the Jacobian matrix at $E_2(x_2, 0)$, we observe that the predator absence ($y = 0$) causes the term $G_x(x_2, 0)$ to vanish entirely. Thus, the Jacobian becomes an upper triangular matrix:

$$J(E_2) = \begin{pmatrix} F_x(x_2, 0) & F_y(x_2, 0) \\ 0 & r_2 \end{pmatrix}$$

Because the matrix is upper triangular, its eigenvalues correspond exactly to its diagonal elements:

$$\lambda_1 = F_x(x_2, 0),$$
$$\lambda_2 = r_2.$$

Clearly, the second eigenvalue is strictly positive ($\lambda_2 = r_2 > 0$). To determine the sign of λ_1, we substitute the equilibrium condition. Recall that x_2 satisfies

$$(r_1 + c_1) - b_1 x_2 - \frac{c x_2}{x_2 + d} = 0,$$

meaning

$$(r_1 + c_1) = b_1 x_2 + \frac{c x_2}{x_2 + d}.$$

Substituting this relationship into our corrected $F_x(x_2, 0)$ yields:

$$\begin{aligned} \lambda_1 &= \left(b_1 x_2 + \frac{c x_2}{x_2 + d} \right) - 2 b_1 x_2 - \frac{c x_2 (x_2 + 2d)}{(x_2 + d)^2} \\ &= -b_1 x_2 + \left(\frac{c x_2 (x_2 + d) - c x_2 (x_2 + 2d)}{(x_2 + d)^2} \right) \\ &= -b_1 x_2 - \frac{c x_2 d}{(x_2 + d)^2}. \end{aligned}$$

Since all biological parameters and the equilibrium density x_2 are strictly positive, it guarantees that

$$\lambda_1 = -b_1 x_2 - \frac{c x_2 d}{(x_2 + d)^2} < 0.$$

Because the eigenvalues possess opposite signs ($\lambda_1 < 0$ and $\lambda_2 > 0$), the predator-extinction equilibrium $E_2(x_2, 0)$ is therefore classified as an unstable saddle point. □

Theorem 5. *The coexistence equilibrium $E_3(x^*, y^*)$ is locally asymptotically stable if $tr(J(E_3)) < 0$ and $\det(J(E_3)) > 0$.*

Proof. Evaluating the Jacobian matrix of the system at the coexistence equilibrium point $E_3(x^*, y^*)$, we obtain:

$$J(E_3) = \begin{pmatrix} F_x^* & F_y^* \\ G_x^* & G_y^* \end{pmatrix},$$

where F_x^*, F_y^*, G_x^*, and G_y^* are the partial derivatives of the system evaluated at the equilib-

rium (x^*, y^*). By differentiating the system algebraically, we obtain:

$$\begin{aligned}
F_x^* &= (r_1 + c_1) - 2b_1x^* - \frac{cx^*(x^* + 2d)}{(x^* + d)^2} - \frac{a_1(1-m)y^*(k_1 + e_2y^*)}{(k_1 + e_1(1-m)x^* + e_2y^*)^2}, \\
F_y^* &= -\frac{a_1(1-m)x^*(k_1 + e_1(1-m)x^*)}{(k_1 + e_1(1-m)x^* + e_2y^*)^2}, \\
G_x^* &= \frac{a_2(1-m)(y^*)^2}{((1-m)x^* + k_2)^2}, \\
G_y^* &= r_2 - \frac{2a_2y^*}{(1-m)x^* + k_2}.
\end{aligned}$$

Note that at the interior coexistence point E_3, the predator nullcline strictly satisfies $r_2 - \frac{a_2y^*}{(1-m)x^*+k_2} = 0$, which mathematically implies that $\frac{y^*}{(1-m)x^*+k_2} = \frac{r_2}{a_2}$. By substituting this relationship, the predator's partial derivatives G_x^* and G_y^* can be elegantly simplified to:

$$\begin{aligned}
G_x^* &= \frac{r_2^2(1-m)}{a_2}, \\
G_y^* &= -r_2.
\end{aligned}$$

The trace and determinant of this Jacobian matrix are given by:

$$\begin{aligned}
\operatorname{tr}(J(E_3)) &= F_x^* - r_2, \\
\det(J(E_3)) &= -r_2F_x^* - F_y^* \left(\frac{r_2^2(1-m)}{a_2} \right).
\end{aligned}$$

The characteristic equation associated with $J(E_3)$ is formulated as:

$$\lambda^2 - \operatorname{tr}(J(E_3))\lambda + \det(J(E_3)) = 0. \tag{4}$$

From Eq. (4), the eigenvalues $\lambda_{1,2}$ are determined using the quadratic formula:

$$\lambda_{1,2} = \frac{\operatorname{tr}(J(E_3)) \pm \sqrt{(\operatorname{tr}(J(E_3)))^2 - 4\det(J(E_3))}}{2}.$$

According to the Routh–Hurwitz stability criterion for planar systems, the roots of the characteristic equation will have strictly negative real parts if and only if $\operatorname{tr}(J(E_3)) < 0$ and $\det(J(E_3)) > 0$. Therefore, under these conditions, the coexistence equilibrium point E_3 is locally asymptotically stable. □

3.3. Simulations

Numerical simulations are utilized to elucidate the qualitative dynamics and variations in system behavior near the equilibrium points. Phase portraits and time series provide visual representations of the interactions between the prey and predator populations, as captured by the two-dimensional model proposed herein. While analytical derivations (Jacobian computations) were assisted by Maple, all numerical simulations were performed exclusively using Python, leveraging its `solve_ivp` function with the standard Runge-Kutta (RK45) integration method to generate trajectories. For all phase portraits presented in this section, the colored curves represent the solution trajectories starting from various initial conditions. The light gray arrows indicate the direction of the background vector field, and the solid black dots denote the equilibrium points of the system.

For the simulations, a baseline set of nondimensional parameter values is adopted, as detailed

in Table 1. While the model is framed around the real species *Rutilus rutilus* and *Perca fluviatilis*, these hypothetical parameters are selected primarily to illustrate the mathematical behavior and dynamic properties of the system, rather than to calibrate a specific empirical dataset.

Unless stated otherwise, the simulations are conducted over a time interval of $t \in [0, 150]$ with an initial population density condition of $(x_0, y_0) = (2.0, 1.0)$. To comprehensively address the main claims of this study, the numerical analysis is divided into two key scenarios: investigating the effect of varying the intraspecific competition rate (c) and examining the impact of the prey refuge proportion (m).

Table 1: Baseline hypothetical parameter values for the system. All variables and parameters are assumed to be nondimensional.

Parameter	Value	Description	Source
r_1	1.0	Intrinsic growth rate of Roach	[16]
b_1	0.2	Linear intraspecific competition	[21]
r_2	0.2	Growth rate of Perch	[20]
a_1	1.0	Predation rate	[20]
a_2	0.2	Conversion rate of predator	[16]
k_1	10.0	Environmental carrying capacity	[5]
d	0.01	Half-saturation constant	[20]
c_1	0.05	External recruitment rate	Assumed
e_1, e_2	0.1	Mutual interference constants	Assumed
k_2	2.0	Alternative food source factor	Assumed
c	0.5	Nonlinear intraspecific competition rate	Assumed
m	0.2	Prey refuge	Assumed

Scenario 1: The Effect of Intraspecific Competition (c)

To evaluate the impact of intraspecific competition on the temporal dynamics of the two species, simulations are conducted by systematically varying the parameter c while maintaining the baseline prey refuge at $m = 0.2$. In the initial baseline case, $c = 0.5$ is applied. The associated time series, as illustrated in Fig. 2, exhibits initial oscillatory patterns that subsequently converge to an equilibrium state for both populations, thereby indicating stable coexistence.

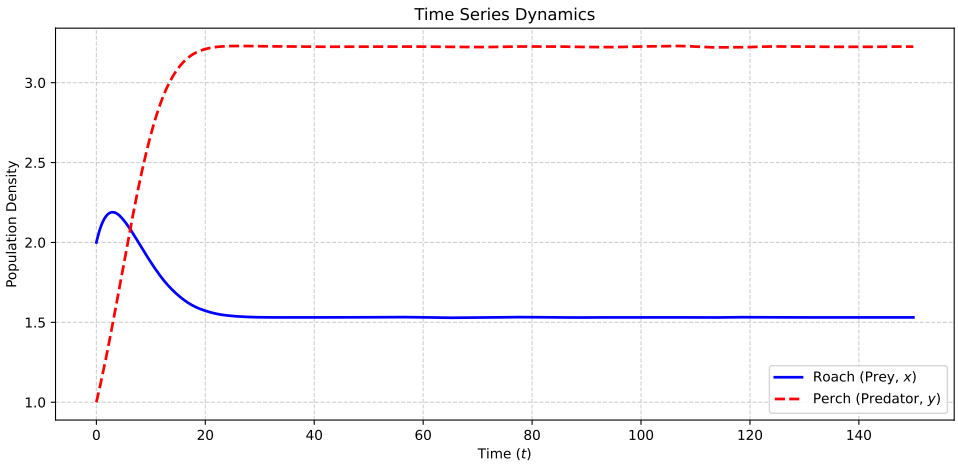

Fig. 2: Time series dynamics illustrating the baseline coexistence scenario ($c = 0.5, m = 0.2$).

Fig. 3 presents the phase portrait featuring four principal equilibrium points: E_0, E_1, E_2, and E_3, wherein E_3 is stable. Analysis of the Jacobian matrix at these points reveals that $E_0(0, 0)$ is an unstable node, characterized by two positive eigenvalues, resulting in trajectories diverging from this point. For $E_1(0, 2)$, the presence of one positive and negative eigenvalues renders it unstable, classifying it as a saddle point. Similarly, $E_2(2.75, 0)$ exhibits one positive and one

negative eigenvalue, confirming its instability as a saddle point.

The interior equilibrium $E_3(1.53, 3.22)$ is characterized by a pair of complex eigenvalues possessing negative real parts, thereby establishing it as a stable spiral. This property is evident in the distinct spiral trajectory in the figure, in which paths encircle and approach this point, signifying asymptotic convergence to the coexistence equilibrium via damped oscillations. The phase portrait further demonstrates that E_3 represents the sole biologically stable equilibrium, corresponding to a state of enduring coexistence that facilitates the long-term persistence of both species.

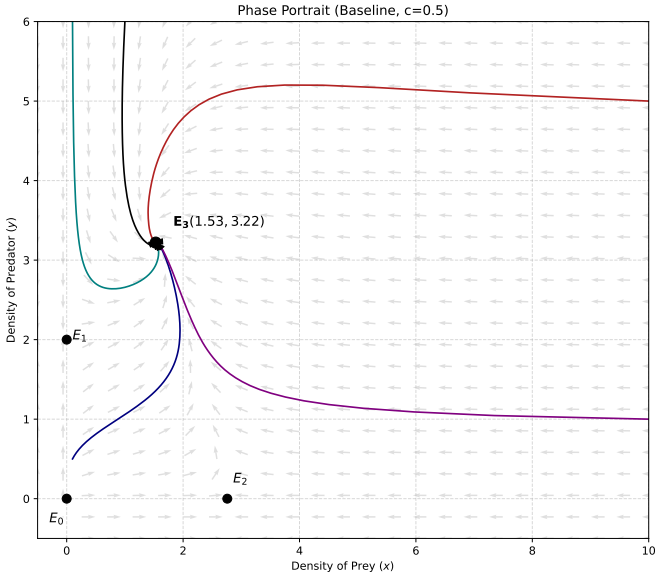

Fig. 3: Phase portrait illustrating the baseline coexistence scenario ($c = 0.5, m = 0.2$).

In order to investigate the effects of intensified intraspecific competition, a subsequent simulation is performed with $c = 0.8$, while maintaining all other parameters unchanged. Fig. 4 displays the phase portrait encompassing the four primary equilibrium points, with E_3 exhibiting stability. Consistent with the prior scenario, Jacobian matrix stability analysis at these points confirms the instability of E_0, E_1, and E_2. The interior equilibrium $E_3(0.43, 2.34)$ features a pair of complex eigenvalues with negative real parts, designating it as a stable spiral. This is manifested in the prominent spiral configuration in the figure, in which trajectories spiral inward toward this point.

An increase in c precipitates a more pronounced decline in prey density, which in turn reduces the predator population due to limited food availability. These results highlight the nonlinear competition term as a critical regulatory mechanism: heightened intraspecific competition markedly lowers the equilibrium densities of both species in the coexistence state.

Scenario 2: The Effect of Prey Refuge (m)

To directly address the significant role of prey refuge within the ecosystem, a second scenario is investigated by increasing the prey refuge parameter to $m = 0.85$, while restoring the competition rate to its baseline value of $c = 0.5$.

Fig. 5 displays the phase portrait for this elevated refuge scenario.

Consistent with the baseline stability criteria (where $m = 0.2$ in Fig. 3), the stability analysis confirms the instability of E_0, E_1, and E_2. As m increases from 0.2 to 0.85, the interior equilibrium E_3 shifts to higher prey and lower predator densities. Nevertheless, it continues to feature a pair of complex eigenvalues with negative real parts, designating it as a stable spiral. This is manifested in the prominent spiral configuration within the figure, wherein trajectories spiral inward toward the coexistence point via damped oscillations.

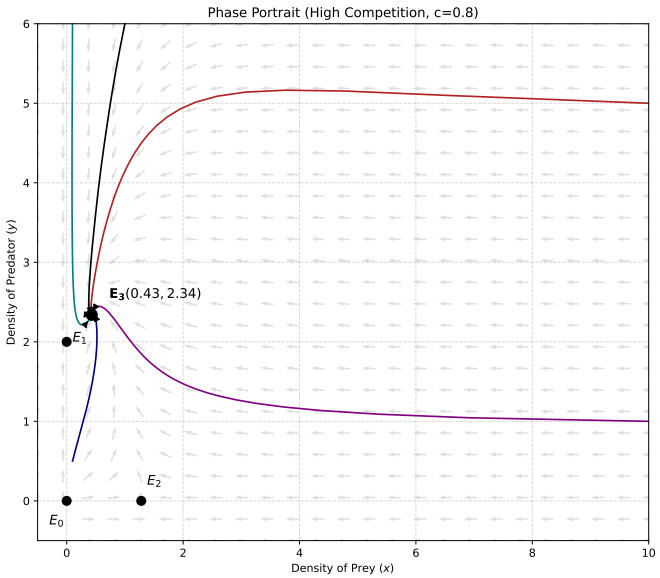

Fig. 4: Phase portrait illustrating the high intraspecific competition scenario ($c = 0.8, m = 0.2$).

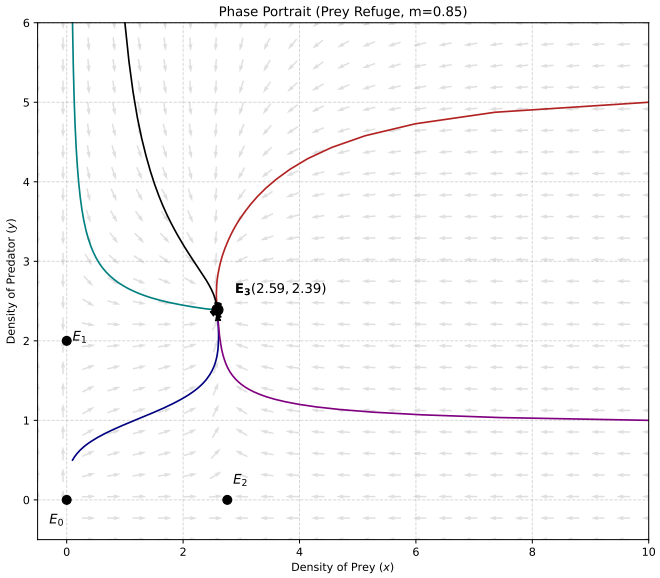

Fig. 5: Phase portrait illustrating the elevated prey refuge scenario ($c = 0.5, m = 0.85$).

An increase in the prey refuge parameter m precipitates a pronounced increase in the prey equilibrium density, as a larger fraction of the population is successfully shielded from predation. Consequently, this restricted access to the primary food source causes the predator population to decline, stabilizing at a lower density as it relies more heavily on alternative food sources.

These comprehensive numerical scenarios clearly demonstrate that both the intraspecific competition term (c) and the prey refuge parameter (m) act as critical regulatory mechanisms. Adjusting these parameters significantly alters the equilibrium densities, thereby providing theoretical support for the mathematical exploration established in the previous sections.

Scenario 3: Population Extinction Dynamics

To validate the local stability condition for the boundary equilibria, a third scenario is introduced to simulate population extinction. Based on the local stability analysis in Theorem 3, the prey-extinction equilibrium $E_1(0, y_1)$ becomes a stable attractor when the predation pressure overwhelms the prey's net growth capacity, satisfying the condition $r_1 + c_1 < \frac{a_1(1-m)y_1}{k_1+e_2y_1}$.

To numerically illustrate this phenomenon, the maximum predation rate is significantly

elevated to $a_1 = 5.0$, representing a severe top-down predation pressure, and the predator's intrinsic growth from alternative food is set to $r_2 = 0.2$. All other parameters are maintained at their baseline values.

Fig. 6 illustrates the phase plane trajectories under these specific conditions.

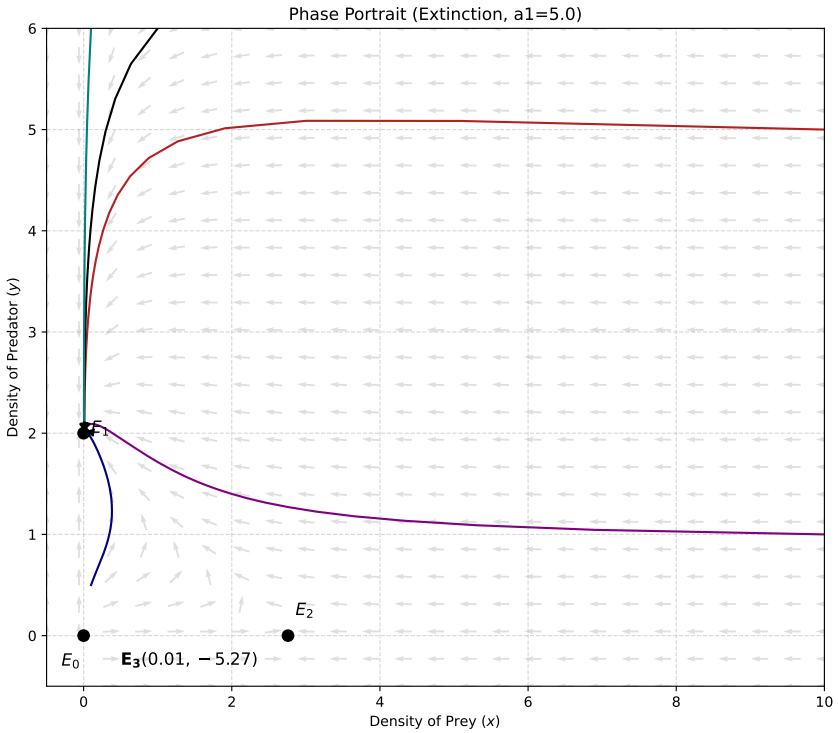

Fig. 6: Phase portrait illustrating the prey-extinction scenario with an elevated predation rate ($a_1 = 5.0$). Note that the coexistence equilibrium E_3 is non-biological in this regime because it lies outside the positive feasible region, and is therefore not displayed as a biologically admissible state.

As depicted in the phase portrait, the heightened predation rate renders the prey population unable to sustain its numbers against the rapid consumption. Consequently, regardless of the strictly positive initial population densities, all phase trajectories are asymptotically attracted to the vertical axis. The prey population is driven to extinction ($x \to 0$), while the predator population stabilizes at a positive density ($y \to y_1$), successfully surviving on it's alternative food sources due to the modified Leslie–Gower structure.

Furthermore, analytical calculations for this parameter set reveal that the theoretical interior coexistence equilibrium E_3 falls strictly outside the biologically feasible domain (featuring a negative predator density, $y \approx -5.27$). This mathematical outcome is consistent with the visual evidence that E_1 acts as the sole biological attractor in this parameter regime, numerically illustrating the proposed boundary stability theorems.

3.3.1. Ecological Implications for Roach-Perch Interactions

From a theoretical standpoint, the dynamics observed in the numerical simulations offer qualitative insights into the potential behavioral ecology of freshwater fish. While *Rutilus rutilus* (roach) are known to utilize littoral macrophytes and aquatic vegetation as structural refuges to evade predation by *Perca fluviatilis* (perch), our mathematical simulations conceptually illustrate this phenomenon: as the theoretical refuge availability (m) increases, a significant portion of the prey population is mathematically protected, promoting coexistence and leading to a more robust prey equilibrium density. Consequently, this modeled ecological shielding suggests that predators might be forced to rely on alternative food sources in the pelagic zones, which theoretically suppresses their population density and establishes a lower equilibrium.

Furthermore, the system's sensitivity to the competition parameter (c) highlights the hypothetical risks of space and resource limitations within prey communities. When the modeled refuge is abundant but competition for resources is intense (high c), the simulated prey population experiences reduced growth due to density-dependent mortality. This analytical decline in prey biomass theoretically limits the energy transfer up the food web, thereby constraining the predator population. Thus, the model suggests that maintaining spatial heterogeneity—which provides refuges—without triggering extreme intraspecific competition could be an important factor in the qualitative balance of roach-perch-like ecosystems.

Among the investigated regimes, Scenarios 1 and 2 serve as theoretical proxies for natural, undisturbed freshwater environments. Scenario 1 can be interpreted as reflecting a typical mesotrophic lake environment, where moderate habitat complexity allows for balanced mathematical coexistence. Scenario 2 provides a conceptual representation of shallow, macrophyte-rich lakes with abundant structural refuges, which hypothetically favor prey survival and force predators to adapt their foraging strategies. Conversely, Scenario 3 (prey extinction) represents an extreme mathematical boundary condition rather than a typical ecological norm. Biologically, this scenario could mimic a severely degraded habitat—such as a lake completely stripped of its aquatic vegetation—where the absence of refuges leaves the prey vulnarable to overwhelming top-down predation. While primarily vital for proving the system's boundary stability mathematically, the model's total prey collapse underscores the potential conservation value of maintaining habitat complexity (as illustrated in Scenarios 1 and 2) to prevent qualitative ecosystem collapse.

4. Conclusion

This study introduces and examines a two-dimensional predator-prey mathematical model inspired by the dynamics between *Rutilus rutilus* (roach) and *Perca fluviatilis* (perch). The model employs a modified Leslie-Gower structure coupled with a Beddington-DeAngelis functional response, while explicitly accounting for prey refuge and nonlinear intraspecific competition. Analytically, the system exhibits four biologically plausible equilibrium points: the trivial equilibrium, the prey-extinction equilibrium, the predator-extinction equilibrium, and the interior coexistence equilibrium. Local stability analysis—conducted via the Jacobian matrix and Routh-Hurwitz criteria—establishes that the coexistence equilibrium is locally asymptotically stable under specific parameter regimes.

The numerical simulations presented in this study serve strictly as qualitative illustrations rather than exact empirical forecasts. Performed under specifically selected hypothetical parameter settings, these simulations successfully support and visualize the qualitative behaviors predicted by our rigorous analytical stability theorems, highlighting the theoretical roles of prey refuge and intraspecific competition in governing long-term population dynamics. The simulation scenarios demonstrate that nonlinear intraspecific competition acts as a primary regulatory force; elevating the competition rate from $c = 0.5$ to $c = 0.8$ markedly depresses prey density, which subsequently constrains predator abundance due to diminished food resources. Conversely, adjusting the prey refuge parameter confirms its theoretical role as a protective buffer; higher refuge levels mathematically shield the prey, leading to a significantly higher prey equilibrium while reducing the predator density.

In summary, rather than providing a calibrated empirical prediction, this theoretical exploration suggests that habitat complexity—embodied by refuges—coupled with the strength of intraspecific competition, serves as a crucial regulatory mechanisms for maintaining qualitative ecological balance and stability in predator-prey systems resembling the roach-perch interaction.

CRediT Authorship Contribution Statement

Salsabil Faridah Saputri Kusbianti: Conceptualization, Methodology, Software, Formal Analysis, Writing–Original Draft, Visualization. **Riska Wahyu Romadhonia and Dian**

Savitri: Conceptualization, Validation, Writing Review & Editing, Supervision.

Declaration of Generative AI and AI-assisted technologies

Generative AI tools, including Gemini, were employed sparingly to refine language and correct grammar during manuscript preparation. All analyses, interpretations, and core scientific content were generated independently by the authors. The research findings and discussions represent the authors' original contributions.

Declaration of Competing Interest

The authors declare no competing interests.

Funding and Acknowledgments

This research received no external funding.

Data Availability

The parameter values used for the numerical simulations in this study are strictly hypothetical and assumed for the purpose of theoretical mathematical exploration. No empirical datasets or real-world biological data were generated or analyzed during this study. To facilitate full reproducibility, the Python scripts utilized to execute the numerical integrations and generate the phase portraits are provided as Supplementary Material accompanying this manuscript.

References

[1] Nathan Ning, Chris Barlow, Lee J. Baumgartner, Joachim B. Bretzel, Katherine E. Doyle, Deanna Duffy, Amina Price, and An V. Vu. "A global review of the biology and ecology of the European perch, Perca fluviatilis". In: *Reviews in Fish Biology and Fisheries* 35 (2025), pp. 587–618. DOI: 10.1007/s11160-025-09924-z.

[2] Matilda L. Andersson, Kaj Hulthén, Charlie Blake, Christer Brönmark, and P. Anders Nilsson. "Linking behavioural type with cannibalism in Eurasian perch". In: *PLOS ONE* 16.12 (2021), e0260938. DOI: 10.1371/journal.pone.0260938.

[3] Kristin Scharnweber, Ursula Strandberg, Konrad Karlsson, and Peter Eklöv. "Decrease of Population Divergence in Eurasian Perch (Perca fluviatilis) in Browning Waters: Role of Fatty Acids and Foraging Efficiency". In: *PLOS ONE* 11.9 (2016), e0162470. DOI: 10.1371/journal.pone.0162470.

[4] Viktor Nilsson-Örtman, Erik Nilsson, and Christer Brönmark. "Effects of temperature and browning on the functional response of a freshwater top predator". In: *Journal of Animal Ecology* (2026). DOI: 10.1111/1365-2656.70233.

[5] Miswanto, Windarto, and Eridani. "Dynamics of the Leslie-Gower Predator-Prey Model with the Beddington-DeAngelis Response Function, Including the Presence of Infected Prey and the Fear Factor of Susceptible Prey Toward Predators". In: *Jurnal Matematika UNAND* 13.4 (2024), pp. 373–387. DOI: 10.25077/jmua.13.4.373-387.2024.

[6] Qin Yue. "Dynamics of a modified Leslie–Gower predator–prey model with Holling-type II schemes and a prey refuge". In: *SpringerPlus* 5 (2016), p. 461. DOI: 10.1186/s40064-016-2087-7.

[7] Danang Indrajaya, Agus Suryanto, and Abdul Rouf Alghofari. "Dynamics of Modified Leslie-Gower Predator-Prey Model with Beddington-DeAngelis Functional Response and Additive Allee Effect". In: *International Journal of Ecology & Development* 31.3 (2016). http://www.ceser.in/ceserp/index.php/ijed/article/view/4525.

[8] Jai Prakash Tripathi, Syed Abbas, and Manoj Thakur. "Dynamical analysis of a prey–predator model with Beddington–DeAngelis type function response incorporating a prey refuge". In: *Nonlinear Dynamics* 80 (2015), pp. 177–196. DOI: 10.1007/s11071-014-1859-2.

[9] Raid Kamel Naji and Alla Tariq Balasim. "Dynamical behavior of a three species food chain model with Beddington-DeAngelis functional response". In: *Chaos, Solitons & Fractals* 32 (2007), pp. 1853–1866. DOI: 10.1016/j.chaos.2005.12.019.

[10] Minjuan Cui, Yuanfu Shao, Renxiu Xue, and Jinxing Zhao. "Dynamic Behavior of a Predator-Prey Model with Double Delays and Beddington-DeAngelis Functional Response". In: *Axioms* 12 (2023), p. 73. DOI: 10.3390/axioms12010073.

[11] Jinxing Zhao and Yuanfu Shao. "Stability of a delayed prey-predator model with fear, stochastic effects and Beddington-DeAngelis functional response". In: *Advances in Continuous and Discrete Models* 2025 (2025), p. 13. DOI: 10.1186/s13662-025-03875-2.

[12] Fira Fitriah, Agus Suryanto, and Noor Hidayat. "Numerical Study of Predator-Prey Model with Beddington-DeAngelis Functional Response and Prey Harvesting". In: *The Journal of Tropical Life Science* 5.2 (2015), pp. 105–109. DOI: 10.11594/jtls.05.02.08.

[13] María Carmen Vera, Marcos Marvá, Víctor José García-Garrido, and René Escalante. "The Beddington-DeAngelis Competitive Response: Intra-Species Interference Enhances Coexistence in Species Competition". In: *Mathematics* 12.4 (2024), p. 562. DOI: 10.3390/math12040562.

[14] Biswajit Saha and Md. Sabiar Rahman. "Extending the Beddington-DeAngelis Model: Stability and Bifurcation Analysis of Predator-Prey Dynamics with Fear Effects, Refuge, and Supplementary Food". In: *International Journal of Applied and Computational Mathematics* 12.9 (2026). DOI: 10.1007/s40819-025-02063-w.

[15] Abdul Rahman Mahmoud Jamil and Raid Kamel Naji. "Modeling and Analysis of the Influence of Fear on the Harvested Modified Leslie-Gower Model Involving Nonlinear Prey Refuge". In: *Mathematics* 10.16 (2022), p. 2857. DOI: 10.3390/math10162857.

[16] Maya Rayungsari, Agus Suryanto, Wuryansari Muharini Kusumawinahyu, and Isnani Darti. "Dynamical Analysis of a Predator-Prey Model Incorporating Predator Cannibalism and Refuge". In: *Axioms* 11 (2022), p. 116. DOI: 10.3390/axioms11030116.

[17] Soumyadip Pal, Fahad Al Basir, and Santanu Ray. "Impact of Cooperation and Intra-Specific Competition of Prey on the Stability of Prey-Predator Models with Refuge". In: *Mathematical and Computational Applications* 28.4 (2023), p. 88. DOI: 10.3390/mca28040088.

[18] Maruthai Selvaraj Surendar, Muniagounder Sambath, Krishnan Balachandran, and Yong-Ki Ma. "Qualitative analysis of a prey-predator model with prey refuge and intraspecific competition among predators". In: *Boundary Value Problems* 2023 (2023), p. 81. DOI: 10.1186/s13661-023-01771-w.

[19] Hafizul Molla, Sahabuddin Sarwardi, and Mohammad Sajid. "Predator-prey dynamics with Allee effect on predator species subject to intra-specific competition and nonlinear prey refuge". In: *Journal of Mathematics and Computer Science* 25 (2022), pp. 150–165. DOI: 10.22436/jmcs.025.02.04.

[20] M. Ikbal. "Dynamics of Predator-Prey Model Interaction with Intraspecific Competition". In: *Journal of Physics: Conference Series* 1940 (2021), p. 012006. DOI: 10.1088/1742-6596/1940/1/012006.

[21] Nursanti Anggriani, Hasan S. Panigoro, Emli Rahmi, Olumuyiwa James Peter, and Sayooj Aby Jose. "A predator-prey model with additive Allee effect and intraspecific competition on predator involving Atangana-Baleanu-Caputo derivative". In: *Results in Physics* 49 (2023), p. 106489. DOI: 10.1016/j.rinp.2023.106489.