



Dynamic Analysis of a Predator–Prey Model with Group Defense in Prey and Cooperative Hunting in Predators

Nabilah Meladelvia, Dian Savitri*

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

Abstract

This article discusses a single-prey and single-predator model by incorporating two behavioral mechanisms, namely group defense in prey modeled through a Holling type IV response function and cooperative hunting in predators represented by a predation rate dependent on predator density. Through system analysis, up to four equilibrium points are obtained mathematically. Among these, three equilibria are biologically feasible under typical parameter values, corresponding to total extinction, predator extinction, and coexistence states. The total extinction equilibrium is always unstable, while the stability of the predator extinction and coexistence equilibria depends on the predator attack rate. Numerical simulations in the form of phase portraits were obtained by varying the parameters related to the predator attack rate. The simulation results show various dynamic behaviors, including predator extinction, asymptotically stable coexistence between prey and predators, and bistability. Numerical continuation analysis identifies a subcritical Hopf bifurcation at $\alpha = 0.4595$, confirmed by a positive first Lyapunov coefficient, as well as a saddle-node at $\alpha = 0.0478$ and transcritical bifurcations $\alpha = 3.0505$ that alter equilibrium structure and stability. These findings demonstrate how prey group defense and predator cooperation can generate bistability and abrupt transitions between extinction and coexistence, accompanied by damped oscillatory dynamics near critical parameter values.

Keywords: Cooperative Hunting; Dynamic Analysis; Group Defense; Holling type IV; Local Stability.

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1. Introduction

Ecology studies how organisms interact with their environment, including how interspecies relationships form adaptive mechanisms in ecosystems [1]. In the context of predator–prey interactions, predation pressure acts as a powerful selective force for prey [2]. Johnson and Belk [3] explain that prey species have evolved to develop various adaptive traits to avoid predation, ranging from reducing the likelihood of detection, increasing escape ability, to developing morphology that can withstand attacks or deceive predators.

One form of adaptation in predators is cooperative hunting. Several animals exhibit cooperative hunting behavior, for example, wild dogs, lions, chimpanzees, birds, ants, spiders, crocodiles, eagles, and several other species [4]. Lions hunt in groups, dividing roles to surround, distract, and restrain the movement of zebras, thereby increasing the chances of a successful hunt. In

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

addition, male lions also use ambush strategies in dense vegetation to approach prey without being seen, while females hunt in open areas [5]. Lions are more active at night and often move to dense vegetation around water sources to ambush prey such as zebras [6]. In contrast, zebras employ a group defense strategy by forming tight formations, increasing collective vigilance, and undertaking daily migrations (diel migration) to avoid predators, thereby significantly reducing the risk of encounters with lions [7]. Zebras approach water sources during the day to feed, then move away at night, adjusting their spatiotemporal patterns to predator activity. This spatiotemporal shift significantly reduces the risk of predation, indicating that the collective strategy of prey involves not only increased vigilance, but also the regulation of space use based on predator activity patterns [7].

In ecological systems, collective responses of prey, as demonstrated by zebras, are part of a group defense strategy. This mechanism allows prey to reduce the rate of attacks by forming collective protection, which makes target selection by predators less efficient. Mathematically, this strategy is often modeled through the Holling type IV predation response function, which reduces the predator attack rate when prey density is very high. The study by Resmawan et al [8] applies the Holling type IV response in a predator-prey model with an additive Allee effect, showing how prey group defense affects population stability and bifurcation. These findings are in line with Pratama et al. [9], who modeled the effects of fear and group defense with Holling type IV response, and found that increased prey growth or predator mortality can make prey populations more likely to increase group defense. Meanwhile, Chen et al. [10] developed a stochastic model incorporating prey group defense (Holling type IV), collective predator hunting, and environmental disturbances (white noise and Lévy Jump).

On the other hand, predators also adopt a collective strategy, namely cooperative hunting. Cooperative hunting provides various advantages, including increasing the chances of a successful hunt, reducing hunting time, targeting a large number of prey, finding food more quickly, and preventing prey from being eaten by other predators [11]. In mathematical modeling, cooperative hunting is usually represented by interaction coefficients that depend on predator density, so the attack efficiency increases as the number of predators hunting together increases [12][13]. Several studies show that cooperative hunting can greatly affect ecological dynamics. Bai and Tang [12] show that the intensity of cooperative hunting can determine the global stability of a population, while Alves and Hilker [14] find that cooperative hunting can cause an Allee effect in predators, namely the dependence of predation success on the existence of a group of a certain minimum size. Furthermore, Pal et al. [4] and Du et al. [13] emphasize that cooperation in hunting can produce more complex population dynamics, including the emergence of oscillations and changes in equilibrium stability.

Recent studies show that cooperative hunting can evolve even without high cognitive abilities, suggesting broader ecological implications for predator cooperation than previously thought [15]. Furthermore, spatiotemporal models incorporating hunting cooperation and group defense reveal the formation of complex patterns and bifurcation phenomena that can affect ecosystem stability [16]. Chen and Yang [17] show that cooperative hunting combined with predator-dependent shelter use can result in Hopf bifurcation and complex dynamic behavior. The influence of the Allee effect on prey group defense and predator success has been studied by Singh et al. [18], showing a significant impact on population stability. Zhang [19] emphasizes that predator-prey models with diffusion, cooperative hunting, and predator-taxis can trigger transitions between stable and unstable conditions. Furthermore, the interaction between predator cooperative hunting and prey group defense has the potential to induce bifurcation, thereby substantially affecting ecosystem stability [20].

Although previous studies have investigated prey group defense or predator cooperative hunting as separate mechanisms, the dynamic conflict between these two adaptive strategies has not been sufficiently emphasized. Prey group defense tends to suppress predation efficiency at high prey densities, while cooperative hunting enhances predator attack success as predator

density increases. The interaction between these opposing mechanisms introduces an ecological trade-off that can fundamentally alter population stability and generate alternative dynamic outcomes. Moreover, modeling prey group defense using a Holling type IV functional response introduces a non-monotonic predation rate, which is known to promote complex dynamics such as multiple interior equilibria, bistability, and rich bifurcation structures. However, the combined effects of Holling type IV group defense and predator density dependent cooperative hunting on system stability and bifurcation behavior remain insufficiently explored. This study aims to fill this gap by developing and analyzing a predator-prey model that integrates both mechanisms within a unified framework, revealing how their interaction can produce bistability, Hopf, saddle-node, and transcritical bifurcations that are absent in classical predator-prey models. These dynamics imply that small changes in predation efficiency or initial population densities may lead to qualitatively different ecological outcomes, with important consequences for species persistence and ecosystem management.

2. Methods

The model of interaction between prey and predator studied is the Lotka-Volterra predator-prey model, incorporating two main adaptive mechanisms, namely group defense in prey through Holling type IV functional response and cooperative hunting in predators through interaction coefficients that depend on predator density [13][21]. The research methodology was developed through the following stages [22].

2.1. Biological Assumptions and Model Construction

The predator-prey model is formulated as a system of ordinary differential equations describing the temporal evolution of prey and predator populations. Prey growth follows a logistic law, reflecting intraspecific competition and environmental carrying capacity. Prey group defense is incorporated through a Holling type IV functional response, which captures the reduction in predation efficiency at high prey densities due to collective protection. Predator cooperative hunting is modeled by allowing the predation rate to depend linearly on predator density, representing increased hunting success as more predators participate. This linear form is adopted as an exploratory assumption to examine the potential impact of strong cooperation without assuming a saturation effect from the outset.

2.2. Qualitative Properties of the Model

To ensure that the model is biologically well posed, basic qualitative properties of the solutions are examined. For any positive initial conditions, the prey and predator populations remain non-negative for all future time, ensuring positivity of solutions. Moreover, boundedness of solutions is guaranteed by the logistic growth term in the prey equation and the linear mortality term in the predator equation, which prevent unbounded population growth. These properties ensure that the model dynamics are confined to a biologically meaningful region of the phase space.

2.3. Equilibrium and Stability Analysis

Equilibrium points are obtained by setting the time derivatives of the system equal to zero, leading to a set of algebraic equations. Boundary equilibria correspond to extinction or predator free states, while interior equilibria represent coexistence between prey and predators. The existence of interior equilibria is determined by analyzing a cubic polynomial equation. Local stability is analyzed by evaluating the Jacobian matrix at each equilibrium point and applying the Routh–Hurwitz criteria to determine stability conditions.

2.4. Numerical Simulation and Bifurcation Analysis

Numerical simulations are performed to illustrate the local behavior of solutions near equilibrium points and to validate the analytical results. Parameter values are selected for exploratory purposes rather than empirical calibration, allowing systematic investigation of the effects of the predator attack rate parameter α . To capture global changes in system dynamics, numerical continuation is carried out using MatCont software, enabling the detection and classification of bifurcations such as saddle-node, Hopf, and transcritical bifurcations.

3. Results and Discussion

The results presented here describe the analytical and numerical outcomes of the proposed predator-prey model. Starting with formulation of the mathematical model and identification of all the system's equilibrium points. The local stability of each equilibrium is then analyzed using the Jacobian matrix and eigenvalue criteria. Finally, numerical simulations and bifurcation analysis are provided to illustrate how variations in the predator attack rate α lead to transitions between extinction, coexistence, and bistable dynamical states.

3.1. Mathematics Model

This predator–prey interaction model was developed to describe the population dynamics of two interacting species, taking into account social behaviors commonly found in nature, namely group defense in prey and cooperative hunting in predators. When prey form groups, the chances of individuals being preyed upon decrease due to collective protection, while predators that hunt in groups can increase their success in capturing prey. To represent these two phenomena, a Holling type IV response function is used to describe the effect of group defense in prey, and $\eta + aP$ indicates an increase in hunting effectiveness due to cooperation between predators. Based on this response function, the predator-prey model with group defense in prey and cooperative hunting in predators can be written as the following system of differential equations:

$$\begin{aligned}\frac{dN}{dt} &= rN \left(1 - \frac{N}{K}\right) - (\eta + aP) \frac{\alpha NP}{b + N^2}, \\ \frac{dP}{dt} &= c(\eta + aP) \frac{\alpha NP}{b + N^2} - mP.\end{aligned}\tag{1}$$

In the model (1), N and P represent the population density of prey and predators, respectively. The parameters r , K , a , η , α , b , c , and m represent the prey growth rate, environmental carrying capacity, level of cooperation between predators in hunting, predator predation rate, predator attack rate on prey, group defense of prey, predator conversion rate, and predator mortality rate. Model (1) is given under the initial conditions $N(0) > 0$ and $P(0) > 0$, where all parameters are positive.

3.2. Equilibrium Points

The equilibrium points of model (1) is obtained by solving the equations with

$$\begin{aligned}\frac{dN}{dt} &= 0 \quad \text{and} \quad \frac{dP}{dt} = 0, \\ rN \left(1 - \frac{N}{K}\right) - (\eta + aP) \frac{\alpha NP}{b + N^2} &= 0, \\ c(\eta + aP) \frac{\alpha NP}{b + N^2} - mP &= 0.\end{aligned}$$

By solving Eq. (1), we obtain

1. $E_1 = (0, 0)$, which represents the extinction of prey and predators.

2. $E_2 = (K, 0)$, which represents the extinction of predators.
3. The interior point $E_3 = (N^*, P^*)$ represents the coexistence of prey and predator populations, where $N^* > 0$ and $P^* > 0$.

The prey density N^* at the interior equilibrium is given by the positive root of the cubic equation

$$\frac{ac^2\alpha r}{K}N^{*3} - (ac^2\alpha r - m^2)N^{*2} - m\eta c\alpha N^* + m^2b = 0$$

and the corresponding predator equilibrium is given by

$$P^* = \frac{crN^*}{m} \left(1 - \frac{N^*}{K}\right), \text{ provided that } \frac{N^*}{K} < 1$$

Since the equilibrium equation for N^* is cubic, it may admit more than one real root depending on parameter values. Consequently, in addition to the interior equilibrium point E_3 , another equilibrium point E_4 may arise. The equilibrium point E_4 is mathematically admissible and may be biologically feasible for certain parameter ranges. However, for other parameter values, E_4 yields negative predator density and thus loses biological relevance. Nevertheless, E_4 plays an important role in organizing the system dynamics, particularly in the occurrence of saddle-node and transcritical bifurcations.

3.3. Local Stability

The Jacobian matrix in the predator-prey system is obtained by calculating the partial derivatives of Eq. (1), resulting in the following Jacobian matrix.

$$J(N, P) = \begin{pmatrix} \frac{\partial f_1}{\partial N} & \frac{\partial f_1}{\partial P} \\ \frac{\partial f_2}{\partial N} & \frac{\partial f_2}{\partial P} \end{pmatrix} \quad (2)$$

with

$$\begin{aligned} \frac{\partial f_1}{\partial N} &= r \left(1 - \frac{2N}{K}\right) - (\eta + aP)\alpha P \frac{b - N^2}{(b + N^2)^2} \\ \frac{\partial f_1}{\partial P} &= -a \frac{\alpha NP}{b + N^2} - (\eta + aP) \frac{\alpha N}{b + N^2} \\ \frac{\partial f_2}{\partial N} &= c(\eta + aP)\alpha P \frac{b - N^2}{(b + N^2)^2} \\ \frac{\partial f_2}{\partial P} &= ca \frac{\alpha NP}{b + N^2} + c(\eta + aP) \frac{\alpha N}{b + N^2} - m \end{aligned}$$

Theorem 3.1. *The equilibrium point $E_1 = (0, 0)$ is unstable (saddle point)*

Proof. By substituting $E_1 = (0, 0)$ into Eq. (2), we get

$$(J_{E_1}) = \begin{pmatrix} r & 0 \\ 0 & -m \end{pmatrix}$$

than eigen values for E_1 are $\lambda_1 = r > 0$ and $\lambda_2 = -m < 0$. Therefore, equilibrium point $E_1 = (0, 0)$ is unstable (saddle point). \square

Theorem 3.2. *The equilibrium point $E_2 = (K, 0)$ is asymptotically stable if $c\eta \frac{\alpha K}{b+K^2} < m$*

Proof. By substituting $E_2 = (K, 0)$ into Eq. (2), we get

$$(J_{E_2}) = \begin{pmatrix} -r & -\eta \frac{\alpha K}{b+K^2} \\ 0 & c\eta \frac{\alpha K}{b+K^2} - m \end{pmatrix}$$

than eigen values for E_2 are $\lambda_1 = -r < 0$ and $\lambda_2 = c\eta \frac{\alpha K}{b+K^2} - m$. Hence, E_2 is locally asymptotically stable if $c\eta \frac{\alpha K}{b+K^2} < m$. \square

Theorem 3.3. *The equilibrium point $E_3 = (N^*, P^*)$ is asymptotically stable if $\text{tr } J(E_3) < 0$ and $\det J(E_3) > 0$.*

Proof. By substituting $E_3 = (N^*, P^*)$ into Eq. (2), we get

$$(J_{E_3}) = \begin{pmatrix} D_{11} & D_{12} \\ D_{21} & D_{22} \end{pmatrix}$$

where each of the components is defined as

$$\begin{aligned} D_{11} &= r \left(1 - \frac{2N^*}{K} \right) - (\eta + aP^*)\alpha P^* \frac{b - N^{*2}}{(b + N^{*2})^2} \\ D_{12} &= -a \frac{\alpha N^* P^*}{b + N^{*2}} - (\eta + aP^*) \frac{\alpha N^*}{b + N^{*2}} \\ D_{21} &= c(\eta + aP^*)\alpha P^* \frac{b - N^{*2}}{(b + N^{*2})^2} \\ D_{22} &= ca \frac{\alpha N^* P^*}{b + N^{*2}} + c(\eta + aP^*) \frac{\alpha N^*}{b + N^{*2}} - m \end{aligned}$$

Since the linearization at E_3 yields a two dimensional autonomous system, the local stability is completely determined by the trace and determinant of the Jacobian matrix. This results in the characteristic equation, namely:

$$\lambda^2 - (\text{tr } J)\lambda + \det(J) = 0 \quad (3)$$

where

$$\begin{aligned} \text{tr } J &= D_{11} + D_{22}, \\ \det(J) &= D_{11}D_{22} - D_{12}D_{21} \end{aligned}$$

From characteristic in Eq. (3), the eigen value of J_{E_3} are given by:

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

Based on the Routh-Hurwitz stability criterion for planar systems [23], the equilibrium point E_3 is asymptotically stable if and only if $\text{tr } J(E_3) < 0$ and $\det J(E_3) > 0$. \square

3.4. Numerical Simulation

To ensure reproducibility of the numerical simulations, the baseline parameter values used throughout the analysis are summarized in Table 1.

Table 1: Parameter Values

| Parameter | Description | Values | Source |
|-----------|---|--------|------------|
| r | Intrinsic growth rate of prey | 9.03 | [11] |
| K | Environmental carrying capacity of the prey | 5 | [24] |
| η | Predator predation rate | 0.5 | [14] |
| a | Level of cooperation between predators in hunting | 0.5 | [4] |
| b | Prey group defense parameter | 3.6 | Assumption |
| c | Predator conversion rate | 0.3 | [4] |
| m | Natural mortality rate of the predator | 0.08 | Assumption |

Numerical simulations are used to show changes in system dynamics around the equilibrium point. The development of the populations of both species, namely the prey and predator populations, can be visualized through phase portraits that describe the interaction between the two based on a two dimensional prey-predator model. In this study, the entire numerical simulation process was carried out using MATLAB software, because MATLAB provides stable numerical integration functions and facilitates the visualization of phase portraits.

For simulation purposes, a set of basic parameter values was used in the model, then variations were made to one main parameter, namely the predation rate α , which represents the predator's success rate in capturing prey. The simulation process was carried out in three stages, namely the first simulation using the parameter value assumption $\alpha = 0.11$, the second simulation with the assumption $\alpha = 3$, and the third simulation with the assumption $\alpha = 5$. Each change in the value of α produces a different phase portrait, allowing us to observe how an increase in the predation rate affects the stability of the equilibrium and the evolution of the populations of both species.

After that, to find out more about the changes in the system solution, a numerical continuation process was carried out using MatCont software. Numerical continuation was applied to the parameter α to track changes in the equilibrium point and detect bifurcations, such as saddle-node bifurcations or Hopf bifurcations. The results of the numerical continuation were then displayed in the form of a bifurcation diagram, so that it could be seen how the solution structure changed when the value of the parameter α was varied.

To illustrate the qualitative behavior of the predator-prey system for different values of the predator attack rate (α), several phase portraits are generated using the parameter values listed in Table 1. Numerical simulations are first conducted using the parameter values in Table 1 with $\alpha = 0.11$ to examine the baseline dynamics of the system under a low predation rate.

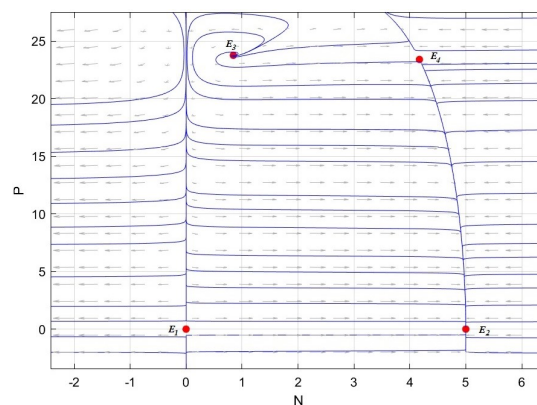


Figure 1: Phase portrait with $\alpha = 0.11$

The phase portrait in Fig. 1 shows four main equilibrium points, namely E_1 , E_2 , E_3 , and E_4 , with equilibrium point E_2 is stable. Stability analysis of the Jacobian matrix at each point shows that point E_1 is unstable (saddle point), because it has one positive and one negative eigenvalue ($\lambda_1 = 9.03 > 0$, $\lambda_2 = -0.08 < 0$), so that the trajectory moves away from that point. The point $E_2 = (5, 0)$ has two negative eigenvalues ($\lambda_1 = -9.03$, $\lambda_2 = -0.0771$), so it is asymptotically stable, and in the phase portrait, a horizontal trajectory moving towards this point is visible, depicting the extinction of the predator with a stable prey population. The interior point $E_3 = (0.8444, 23.7648)$ has a pair of complex eigenvalues with positive real parts, namely $\lambda_{1,2} = 0.5166 \pm 0.7707i$, indicating that this point is an unstable spiral. Biologically, the coexistence condition at this point is unstable, and the population will move away from this state through increasing oscillations. Meanwhile, the eigenvalues at the point $E_4 = (4.171, 23.409)$ show one positive and one negative ($\lambda_1 = -5.0834 < 0$, $\lambda_2 = 0.1065 > 0$), so this point is an unstable (saddle point).

The phase portrait shows that the biologically stable equilibrium point is dominated only by E_2 , which is the state of predator extinction with the prey population surviving at its carrying capacity. Analytically, the equilibrium point $E_2 = (K, 0)$ is asymptotically stable if $c\eta\frac{\alpha K}{b+K^2} < m$, as stated in Theorem 3.2. Based on the simulation parameters for $\alpha = 0.11$, this condition is satisfied, which is consistent with the phase portrait. The interior point E_3 , which represents prey-predator coexistence, is unstable with a spiraling away character, so that the system cannot survive in a state of coexistence in the long term. Trajectories that start around the interior point oscillate and then move away from the point towards the attraction domain E_2 .

To investigate how an increase in the predator attack rate affects the system dynamics, a second simulation is performed for $\alpha = 3$ using the same baseline parameters.

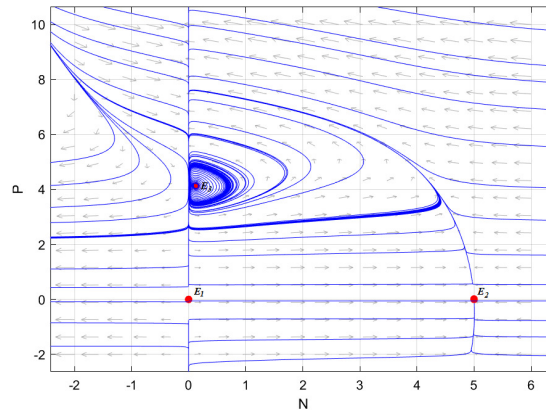


Figure 2: Phase portrait with $\alpha = 3$

The phase portrait in Fig. 2 shows three main equilibrium points, namely E_1 , E_2 , and E_3 , with equilibrium points E_2 and E_3 is stable. Stability analysis of the Jacobian matrix at each point shows that point E_1 is unstable (saddle point), because it has one positive and one negative eigenvalue ($\lambda_1 = 9.03 > 0$, $\lambda_2 = -0.08 < 0$), so that the trajectory moves away from that point. The equilibrium point $E_2 = (5, 0)$ has two negative eigenvalues ($\lambda_1 = -9.03$, $\lambda_2 = -0.0013$), so it is asymptotically stable. This stability is consistent with the analytical condition derived in Theorem 3.2. In the phase portrait, a horizontal trajectory moving towards this point is visible, depicting the extinction of the predator with a stable prey population. The interior point $E_3 = (0.1689, 5.5288)$ has a pair of complex eigenvalues with negative real parts, namely $\lambda_{1,2} = -0.0426 \pm 1.1175i$, indicating that this point is a stable spiral. This can be seen in the clear spiral pattern in the figure, where the trajectory circles toward this point, indicating asymptotic convergence to the coexistence equilibrium through damped oscillations.

The phase portrait shows two significant stable points in the biological context, namely E_2 and E_3 . Based on the simulation parameters, the calculation results show that E_2 and E_3

meet the stability requirements. The existence of these two stable points indicates a bistable phenomenon, where the direction of population development is highly dependent on the initial conditions [25]. If the initial population is in the attraction domain of E_3 , the system will move towards predator-prey coexistence. Conversely, if it is close to the attraction domain of E_2 , the system will move towards a condition where only the prey survives.

For a higher predation rate, the system behavior is further examined by considering $\alpha = 5$, which reveals a different stability structure in the phase portrait.

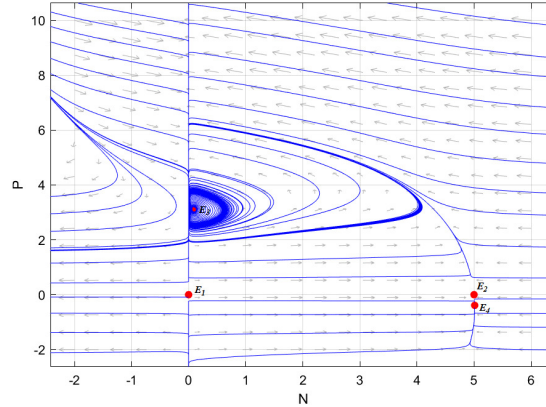


Figure 3: Phase portrait with $\alpha = 5$

The phase portrait in Fig. 3 shows four equilibrium points, namely E_1 , E_2 , E_3 , and E_4 , with the interior equilibrium point E_3 is stable. Stability analysis of the Jacobian matrix at each point shows that point E_1 is unstable (saddle point), because it has one positive and one negative eigenvalue ($\lambda_1 = 9.03 > 0$, $\lambda_2 = -0.08 < 0$), so that the trajectory moves away from that point. The point $E_2 = (5, 0)$ has one negative and one positive eigenvalue ($\lambda_1 = -9.03$, $\lambda_2 = 0.0511$), so it is unstable (saddle point), even though the streamline at the bottom of the graph appears to move horizontally towards it. For $\alpha = 5$, the stability condition $c\eta \frac{\alpha K}{b+K^2} < m$ is violated, confirming the loss of stability of, in agreement with the numerical phase portrait. Biologically, this point describes a situation where the predator becomes extinct and the prey population remains at a constant value, but this state is unstable to small disturbances in the predator variable. The interior point $E_3 = (0.0936, 3.1112)$ has a pair of complex eigenvalues with negative real parts, namely $\lambda_{1,2} = -0.03275 \pm 1.1093i$, indicating that this point is a stable spiral. This can be seen in the clear spiral pattern in the figure, where the trajectory circles toward this point, indicating asymptotic convergence to a coexistence equilibrium after transient oscillations. Meanwhile, the eigenvalues at the point $E_4 = (5.0114, -0.38882)$ show two negative values ($\lambda_1 = -9.0868 < 0$, $\lambda_2 = -0.0509 < 0$), so mathematically it is a stable point, but it is not biologically meaningful because it involves a value of $P < 0$.

The phase portrait in Fig. 3 shows that the only biologically relevant stable point is E_3 . This condition is equivalent to $\text{tr } J(E_3) < 0$ and $\det J(E_3) > 0$, so based on the Routh–Hurwitz criterion, point E_3 is asymptotically stable. The system tends to move toward predator–prey coexistence, while other points only act as saddles that form flow structures around them. The inward spiral around E_3 indicates that population dynamics will experience weakening oscillations before finally settling into that equilibrium state.

3.5. Bifurcation

The bifurcation was performed by continuing one parameter, namely in the α system, which represents the rate of predator attacks on prey. The analysis was performed using MatCont software and visualized in the form of a bifurcation diagram as shown in Fig. 4. The horizontal axis represents the parameter α , while the vertical axis represents the prey population N .



From an ecological perspective, the Hopf bifurcation marks a change in the stability of the coexistence equilibrium. The predator and prey populations exhibit transient oscillations before converging to a stable coexistence state. Such dynamics are commonly observed in ecosystems where cooperative hunting enhances predator success but does not immediately lead to prey collapse. In contrast, the transcritical bifurcation highlights a critical threshold beyond which predator extinction becomes unavoidable or unstable, emphasizing the delicate balance between predation pressure and population persistence. Compared with classical predator-prey models, such as the Lotka-Volterra and Holling type systems, the present model demonstrates richer dynamical behavior due to the combined effects of prey group defense and predator cooperation, underscoring their important roles in maintaining population sustainability and ecosystem balance.

taking the value of the parameter for the predator's attack rate on the prey (α). The numerical simulation results show that an increase in the value of α causes significant changes in the behavior of the system. For low values of the attack rate, predator extinction is observed as the only biologically stable outcome. As the attack rate increases, the system may exhibit bistable dynamics, where both predator extinction and prey–predator coexistence are locally stable, and the long-term behavior depends on initial conditions. For sufficiently high attack rates, the interior equilibrium becomes the unique biologically relevant stable state. Numerical continuation analysis reveals the presence of several bifurcation mechanisms that govern qualitative changes in system dynamics. In particular, a subcritical Hopf bifurcation when $\alpha = 0.4595$ marks a change in the stability of the interior equilibrium, with solutions exhibiting damped oscillations before converging to a stable coexistence state, while saddle-node and transcritical bifurcations when $\alpha = 3.0506$ indicate changes in the number of equilibrium points and stability exchange between coexistence and predator extinction states.

Despite these insights, several limitations should be acknowledged. The model adopts simplified functional forms, particularly the linear representation of predator cooperative hunting and the exploratory selection of parameter values, which may not fully capture saturation effects or species-specific behavioral constraints in real ecosystems. Moreover, the analysis is restricted to a deterministic and non-spatial framework, neglecting environmental variability, spatial heterogeneity, and stochastic disturbances. Future research may extend this work by incorporating nonlinear or saturated cooperative hunting functions, spatial structure, time delays, or stochastic effects, as well as by calibrating model parameters using empirical data to enhance biological realism and predictive capability.

CRediT Authorship Contribution Statement

Nabilah Meladelvia: Conceptualization, Methodology, Data Curation, Formal Analysis, Investigation, Resources, Writing–Original Draft. **Dian Savitri:** Conceptualization, Methodology, Software, Validation, Writing–Review & Editing, Visualization, Supervision.

Declaration of Generative AI and AI-assisted technologies

Generative AI tools, particularly ChatGPT, are used to a limited extent to assist with language refinement and grammar editing during the writing process. All analysis, interpretation, and key scientific substance are not generated by AI. All research findings and discussions are developed entirely by the authors themselves.

Declaration of Competing Interest

The authors declare no competing interests.

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Data Availability

The parameter values are not based on field data, and they only hypothetical parameters to illustrate the dynamics of system.

References

- [1] S. Sumarto and R. Koneri, *Ekologi Hewan*. 2016.

- [2] D. Kikuchi et al., “The evolution and ecology of multiple antipredator defences,” *Journal of Evolutionary Biology*, vol. 36, no. 7, pp. 975–991, 2023. DOI: [10.1111/jeb.14192](https://doi.org/10.1111/jeb.14192).
- [3] J. Johnson and M. Belk, “Predators as agents of selection and diversification,” *Diversity*, vol. 12, no. 11, p. 415, 2020. DOI: [10.3390/d12110415](https://doi.org/10.3390/d12110415).
- [4] S. Pal, N. Pal, S. Samanta, and J. Chattopadhyay, “Effect of hunting cooperation and fear in a predator-prey model,” *Ecological Complexity*, vol. 39, p. 100770, 2019. DOI: [10.1016/j.ecocom.2019.100770](https://doi.org/10.1016/j.ecocom.2019.100770).
- [5] S. Loarie, C. Tambling, and G. Asner, “Lion hunting behaviour and vegetation structure in an african savanna,” *Animal Behaviour*, vol. 85, no. 5, pp. 899–906, 2013. DOI: [10.1016/j.anbehav.2013.01.018](https://doi.org/10.1016/j.anbehav.2013.01.018).
- [6] S. Yiu, N. Owen-Smith, and J. Cain, “How lions move at night when they hunt?” *Journal of Mammalogy*, vol. 103, no. 4, pp. 855–864, 2022. DOI: [10.1093/jmammal/gyac025](https://doi.org/10.1093/jmammal/gyac025).
- [7] N. Courbin et al., “Zebra diel migrations reduce encounter risk with lions at night,” *Journal of Animal Ecology*, vol. 88, no. 1, pp. 92–101, 2019. DOI: [10.1111/1365-2656.12910](https://doi.org/10.1111/1365-2656.12910).
- [8] Resmawan, A. Suryanto, I. Darti, and P. H., “Dynamical analysis of a predator-prey model with additif allee effect and prey group defense,” vol. 12, no. 11, p. 415, 2024. DOI: [10.31219/osf.io/9ufkn](https://doi.org/10.31219/osf.io/9ufkn).
- [9] R. Pratama, M. Loupatty, W. Hariyanto H.and Caesarendra, and W. Rahmانيar, “Fear and group defense effect of a holling type iv predator-prey system intraspecific competition,” *Emerging Science Journal*, vol. 7, no. 2, pp. 385–395, 2023. DOI: [10.28991/ESJ-2023-07-02-06](https://doi.org/10.28991/ESJ-2023-07-02-06).
- [10] H. Chen, M. Liu, and X. Xu, “Dynamics of a prey–predator model with group defense for prey, cooperative hunting for predator, and lévy jump,” *Axioms*, vol. 12, no. 9, p. 878, 2023. DOI: [10.3390/axioms12090878](https://doi.org/10.3390/axioms12090878).
- [11] S. Salwa, L. Shakira, and D. Savitri, “Dinamika model mangsa-pemangsa lotka volterra dengan adanya kerja sama berburu pada pemangsa,” *Jurnal Riset dan Aplikasi Matematika (JRAM)*, vol. 7, no. 2, pp. 195–205, 2023.
- [12] D. Bai and J. Tang, “Global dynamics of a predator–prey system with cooperative hunting,” *Applied Sciences*, vol. 13, no. 14, p. 8178, 2023. DOI: [10.3390/app13148178](https://doi.org/10.3390/app13148178).
- [13] Y. Du, B. Niu, and W. J., “A predator-prey model with cooperative hunting in the predator and group defense in the prey,” *Discrete and Continuous Dynamical Systems-Series B*, vol. 27, no. 10, 2022. DOI: [10.3934/dcdsb.2021298](https://doi.org/10.3934/dcdsb.2021298).
- [14] M. Alves and F. Hilker, “Hunting cooperation and allee effects in predators,” *Journal of theoretical biology*, vol. 419, pp. 13–22, 2017. DOI: [10.1016/j.jtbi.2017.02.002](https://doi.org/10.1016/j.jtbi.2017.02.002).
- [15] K. Tsutsui, R. Tanaka, K. Takeda, and K. Fujii, “Collaborative hunting in artificial agents with deep reinforcement learning,” *Elife*, vol. 13, e85694, 2024. DOI: [10.7554/eLife.85694](https://doi.org/10.7554/eLife.85694).
- [16] Y. Xu, J. Zhao, and X. Wei, “Spatiotemporal dynamics in a delayed diffusive predator-prey model with cooperative hunting and group defense,” *Advances in Continuous and Discrete Models*, vol. 2025, no. 1, p. 113, 2025. DOI: [10.1186/s13662-025-03971-3](https://doi.org/10.1186/s13662-025-03971-3).
- [17] M. Chen and W. Yang, “Role of cooperative hunting among predators and predator-dependent prey refuge behavior in a predator-prey model,” *Journal of Nonlinear Modeling and Analysis*, vol. 7, no. 1, pp. 209–228, 2025. DOI: [10.12150/jnma.2025.209](https://doi.org/10.12150/jnma.2025.209).
- [18] M. Singh, A. Sharma, and L. Sánchez-Ruiz, “Impact of the allee effect on the dynamics of a predator-prey model exhibiting group defense,” *Mathematics*, vol. 13, no. 4, p. 633, 2025. DOI: [10.3390/math13040633](https://doi.org/10.3390/math13040633).

- [19] H. Zhang, “Dynamics behavior of a predator-prey diffusion model incorporating hunting cooperation and predator-taxis,” *Mathematics*, vol. 12, no. 10, p. 1474, 2024. DOI: [10.3390/math12101474](https://doi.org/10.3390/math12101474).
- [20] Y. Zhang, L. Chen, F. Chen, and Z. Li, “Interplay between preys’ anti-predator behavior and predators’ cooperative hunting: A mathematical approach,” *Chaos, Solitons & Fractals*, vol. 199, p. 116 624, 2025. DOI: [10.1016/j.chaos.2025.116624](https://doi.org/10.1016/j.chaos.2025.116624).
- [21] I. Benamara and A. El Abdllaoui, “Bifurcation in a delayed predator–prey model with holling type iv functional response incorporating hunting cooperation and fear effect,” *International Journal of Dynamics and Control*, vol. 11, no. 6, pp. 2733–2750, 2023. DOI: [10.1007/s40435-023-01123-7](https://doi.org/10.1007/s40435-023-01123-7).
- [22] D. Fitri and D. Savitri, “Prey predator model with holling type ii functional response and hunting cooperation of predators,” *MATHunesa: Jurnal Ilmiah Matematika*, vol. 12, no. 3, pp. 637–645, 2024.
- [23] A. Salsabila and D. Savitri, “Dynamical analysis of holling tanner prey predators model with add food in second level predators,” *Jambura Journal of Biomathematics (JJBm)*, vol. 5, no. 2, pp. 63–70, 2024. DOI: [10.37905/jjbms.v5i2.25753](https://doi.org/10.37905/jjbms.v5i2.25753).
- [24] Z. Ju, Y. Shao, X. Xie, X. Ma, and X. Fang, “The dynamics of an impulsive predator-prey system with stage structure and holling type iii functional response,” *Journal of Animal Ecology*, vol. 2015, no. 1, 2015. DOI: [10.1155/2015/183526](https://doi.org/10.1155/2015/183526).
- [25] A. Mufidah and D. Savitri, “Analisis kestabilan model mangsa pemangsa dengan makanan tambahan pada pemangsa menggunakan fungsi respon holling tipe iv,” *Jurnal Riset dan Aplikasi Matematika (JRAM)*, vol. 7, no. 1, pp. 80–94, 2023.
- [26] D. Das, D. Banerjee, and J. Bhattacharjee, “Super-critical and sub-critical hopf bifurcations in two and three dimensions,” *Nonlinear Dynamics*, vol. 77, no. 1, pp. 169–184, 2014. DOI: [10.1007/s11071-014-1282-8](https://doi.org/10.1007/s11071-014-1282-8).
- [27] D. Savitri and H. Panigoro, “Bifurkasi hopf pada model prey-predator-super predator dengan fungsi respon yang berbeda,” *Jambura Journal of Biomathematics (JJBm)*, vol. 1, no. 2, pp. 65–70, 2020. DOI: [10.34312/jjbms.v1i2.8399](https://doi.org/10.34312/jjbms.v1i2.8399).