AIMS Mathematics, 11(7): 21412–21440.
DOI: 10.3934/math.2026868
Received: 15 May 2026
Revised: 25 June 2026
Accepted: 02 July 2026
Published: 17 July 2026

https://www.aimspress.com/journal/Math

Research article

Persistence, extinction, and chaotic dynamics in a predator-prey system with cooperative hunting and prey refuge

Thotahewage Mihiri M. De Silva[1] **and Sophia R.-J. Jang**[2,*]

[1] Department of Mathematics, University of Kelaniya, Kelaniya, Sri Lanka
[2] Department of Mathematics & Statistics, Texas Tech University, Lubbock, TX, USA

* **Correspondence:** Email: sophia.jang@ttu.edu; Tel: +18068347006; Fax: +18067421112.

Abstract: Building on the discrete host-parasitoid model of Wu and Zhao (2018), we have proposed a discrete-time predator-prey system with Ricker-type prey growth, prey refuge, and predator hunting cooperation. Analytical results showed that when the prey growth rate is moderate and the predator reproduction number exceeds one, the system is uniformly persistent: both predator and prey populations are guaranteed to remain above a strictly positive lower bound in the long term, for all positive initial conditions, regardless of the strength of hunting cooperation. We further established global asymptotic stability of the predator-free equilibrium under a sufficient condition requiring the predator nullcline to lie entirely beyond the normalized prey carrying capacity, and we identified a related condition under which a predator-extinct 2-cycle is globally stable. Numerical simulations revealed that the influence of cooperation depends strongly on prey growth: low growth leads to sensitive, possibly chaotic oscillations; moderate growth stabilizes coexistence; and high growth allows cooperation to act as a "rescue" mechanism for predators while inducing complex, non-equilibrium behavior. These results considerably extend previous discrete predator–prey models with prey refuge by demonstrating that hunting cooperation does not alter the persistence threshold but significantly enriches global dynamics by permitting bistability, oscillatory coexistence, and chaotic attractors.

Keywords: Ricker growth; uniform persistence; prey refuge; predator hunting cooperation
Mathematics Subject Classification: 92D25, 92B05

1. Introduction

Predator-prey interactions are central to understanding population dynamics in ecological systems. Classical models, dating back to Lotka and Volterra [1], have been extended in numerous ways to incorporate biologically relevant features such as predator interference [6], refuge for prey [26], stage structure [11], and nonlinear prey growth [1, 11]. Among these, prey refuge and cooperative hunting

have received particular attention for their significant and often counterintuitive effects on species persistence and stability of population equilibria.

Hunting cooperation is a widespread and evolutionarily advantageous strategy observed across diverse ecological communities. This behavior is notably prevalent among carnivores such as wolves, African wild dogs, and lions, significantly boosting their predation success while reducing energy expenditure and enabling the capture of larger prey [12]. Cooperative hunting also appears in various other species, including spiders, birds, and ants [12]. The profound ecological and evolutionary implications of this phenomenon have inspired extensive mathematical modeling efforts. Researchers have explored hunting cooperation using discrete-time models [7], ordinary differential equations [23], and reaction-diffusion systems [16]. Each modeling approach, grounded in its unique assumptions, has illuminated different biological conclusions regarding the impact of hunting cooperation on population dynamics.

Conversely, the presence of spatial refuges, where prey are shielded from predation, is equally crucial in predator-prey systems [5]. These refuges are vital not only for the persistence of prey populations but also for shaping species composition and maintaining biodiversity [5]. In mathematical models, spatial refuges are typically incorporated by assuming that either a fixed number or a fixed proportion of prey individuals remain inaccessible to predators [18,28]. The integration of prey refuges can therefore profoundly influence predator-prey coexistence. Numerous mathematical models have been developed to investigate this impact, with comprehensive discussions on continuous-time models available in [3,21,31] and the references therein.

Many natural populations, however, exhibit seasonal reproductive patterns rather than continuous reproduction. For such populations, discrete-time models, typically based on difference equations, offer invaluable tools for studying dynamics in non-overlapping generations. For instance, discrete population models have been effectively used to examine cycles and dispersal dynamics [8,13], and to gain insights into the spread and control of infectious diseases [15,22].

The concept of spatial refuges has also been explored within this discrete-time framework. Hassell [18] pioneered the incorporation of fixed-number or fixed-proportion prey refuges into a modified Nicholson–Bailey model to assess their stabilizing or destabilizing effects on populations with non-overlapping generations. His seminal work concluded that proportionate refuges can promote stability, while a constant number of prey in refuge does not. Following this foundational study, a variety of other discrete-time models addressing prey refuges have been developed and analyzed [7,9,10].

The primary aim of this study is to investigate the complex dynamical consequences of simultaneously incorporating prey refuge and predator hunting cooperation into a discrete-time predator–prey model with Ricker-type prey growth. Under Ricker growth, prey reproduction decreases sharply once the population size exceeds carrying capacity, potentially causing dramatic prey crashes, high-amplitude oscillations, and even chaotic dynamics [27,30]. This behavior has been documented in populations of insects, plankton, and other organisms with discrete generations and strong crowding effects [18,28,29].

From a modeling perspective, the use of the Ricker function enables us to explore how prey overcompensation interacts with predator cooperation and refuge mechanisms. Unlike Beverton–Holt growth, the Ricker model allows for complex dynamics, including multi-periodic cycles and chaos, thereby highlighting scenarios where predators may go extinct not only when prey are too scarce but

also when prey are initially too abundant, as overcompensation can trigger prey crashes that deprive predators of resources.

In particular, we examine how variations in the predator cooperation intensity and the prey growth rate influence long-term population dynamics, including persistence, extinction, periodicity, and chaotic behavior. We investigate the dynamics using local stability analysis, bifurcation diagrams, and numerical simulations to characterize thresholds separating stable coexistence, oscillatory regimes, and predator extinction.

From a biological standpoint, prey refuge represents the availability of safe zones or effective anti-predator behaviors that mitigate predation risk, while hunting cooperation models the enhanced efficiency predators gain by coordinating their efforts in groups. Our results reveal that these two mechanisms, prey refuge and predator cooperation, jointly determine the ultimate fate of predator and prey populations, dictating whether they stabilize, oscillate, or collapse.

We find that low prey growth rates tend to support regular predator-prey cycles even when predator cooperation is strong. Conversely, higher prey growth rates can destabilize the system, giving rise to complex dynamics or even chaos. In scenarios with very high prey growth, predators may face extinction despite the advantages of cooperative hunting, while prey populations persist in cyclic regimes sustained by density dependence. These findings resonate with real-world ecological phenomena such as boom-and-bust cycles, the perplexing collapse of predators in highly productive environments, and the intriguing dual role of cooperation as both a stabilizing and destabilizing force within predator populations.

The main contributions of this paper are summarized as follows. First, we establish uniform persistence for all cooperation strengths whenever $0 < r < 2$ and $\beta b > 1$. Second, we derive sufficient global extinction criteria based on the minimum value of the predator nullcline. In particular, predator extinction occurs when the predator nullcline $x = g(y)$ lies entirely to the right of the normalized prey carrying capacity $x = 1$. Third, we show that strong cooperation ($2c > 1$) fundamentally changes the geometry of the predator nullcline, allowing bistability and multiple coexistence equilibria. Finally, we investigate numerically how hunting cooperation influences oscillatory and chaotic dynamics under Ricker prey growth.

The remainder of this study is organized as follows. Section 2 derives the mathematical model. Section 3 analyzes its dynamics, while Section 4 presents numerical explorations. We conclude with biological findings in Section 5.

2. Model formulation

In this section, we present the mathematical model of predator-prey interactions with prey refuge and predator hunting cooperation.

In [24], a discrete-time predator-prey model incorporating prey refuge and cooperative hunting among predators is developed and analyzed, with the growth of the prey population described by the classical Beverton–Holt function. In contrast, the present study employs the classical Ricker model to represent prey growth, which captures the effects of scramble competition among individuals within the prey population.

Let x_n and y_n denote the prey and predator populations in generation n, respectively. In the absence

of predators, the prey population evolves according to the Ricker model [30]:

$$x_{n+1} = x_n e^{r(1-x_n/K)}, \tag{2.1}$$

where r is the intrinsic growth rate of the prey and K is its carrying capacity. Initially developed to predict fish populations in fisheries [30], the Ricker model captures the phenomenon of overcompensation, in which recruitment declines at high spawner abundances. The dynamics of (2.1) are well studied; see, for example, [14, 27]. In particular, the positive equilibrium at $x = K$ is globally asymptotically stable for $r < 2$, and undergoes a period-doubling bifurcation at $r = 2$. For $2 < r < r_0$, where

$$r_0 \approx 2.526, \tag{2.2}$$

the equation exhibits a unique, globally asymptotically stable 2-cycle. At $r = r_0$, a second period-doubling bifurcation occurs, leading to a cascade of bifurcations and eventually to chaotic dynamics as r increases. Unlike the model in [24], where the prey population remains stable in the absence of predators and destabilization arises only through predation, our model incorporates Ricker-type growth, allowing the prey dynamics to become periodic or chaotic even without predator effects.

It is well–known that prey populations often seek spatial refuges to evade predators [5]. Two common modeling approaches for prey refuge are to assume that either a constant number or a constant fraction of the prey population resides in a refuge free from predation [32]. Following the approach in [9, 24], we consider a constant fraction of the prey to be in the refuge. Let b, $0 < b < 1$, denote the proportion of the prey population available to predators, so that $1 - b$ represents the fraction of prey in the refuge. Individuals in refuge are assumed to remain reproductively active and therefore contribute to recruitment in the next generation.

In the absence of cooperative hunting among predators, encounters between predators and prey are assumed to occur randomly and independently during each generation. Following the classical Nicholson–Bailey framework, the total number of predator-prey encounters in generation n is modeled by the mass-action term

$$a(bx_n)y_n,$$

where $a > 0$ denotes the predator searching efficiency, bx_n is the density of prey accessible to predators, and y_n is the predator density.

Under the assumption that encounters occur independently and are uniformly distributed among the vulnerable prey population, the number of attacks experienced by a given prey individual follows a Poisson distribution. Since there are $a(bx_n)y_n$ total encounters distributed among bx_n vulnerable prey, the expected number of attacks per vulnerable prey individual is

$$\mu = \frac{a(bx_n)y_n}{bx_n} = ay_n.$$

Therefore, the probability that a vulnerable prey individual escapes predation during generation n is

$$P(\text{no attack}) = e^{-ay_n},$$

and consequently the probability that it is attacked at least once is

$$1 - e^{-ay_n}.$$

When cooperative hunting is incorporated, predator coordination increases the effective encounter rate. Following [9, 24], we model this enhancement by replacing the encounter term $a(bx_n)y_n$ with

$$a(bx_n)y_n(1 + cy_n),$$

where $c > 0$ measures the strength of hunting cooperation. The quantity $(1 + cy_n)$ represents the increase in predation efficiency due to coordinated hunting among predators. Under the same Poisson encounter assumption, the expected number of attacks per vulnerable prey individual becomes

$$ay_n(1 + cy_n),$$

so that the probability a vulnerable prey survives predation is

$$e^{-ay_n(1+cy_n)},$$

and the probability it is attacked is

$$1 - e^{-ay_n(1+cy_n)}.$$

Let $\beta > 0$ denote the conversion efficiency of predators per prey consumed. Since only a fraction b of the prey population x_n is available to predators, and each available prey has a probability $1 - e^{-ay_n}$ of being attacked, the model without hunting cooperation is then given by

$$\begin{aligned} x_{n+1} &= \left((1 - b)x_n + bx_n e^{-ay_n}\right)e^{r(1-x_n/K)}, \\ y_{n+1} &= \beta b x_n \left(1 - e^{-ay_n}\right), \end{aligned} \tag{2.3}$$

where the predator is assumed to attack the prey prior to their reproduction.

The density-dependent growth term

$$e^{r(1-x_n/K)}$$

depends on the total prey population x_n, including both vulnerable prey and prey in refuge. This modeling choice reflects the ecological assumption that refuge protects prey from predation but does not remove them from competition for shared environmental resources such as food, habitat, or breeding sites. We emphasize that our formulation is intended for ecological systems in which refuge reduces predation risk but does not eliminate competition for shared environmental resources. In ecosystems where refuge habitats are spatially isolated or have independent resource pools, alternative formulations in which only the vulnerable prey contribute to density-dependent regulation may be more appropriate. Investigating such models is an interesting direction for future research.

Thus, although only the fraction bx_n is exposed to predators, all prey individuals contribute to intra-specific competition and crowding effects that regulate reproduction. In particular, competition occurs at the population level before recruitment into the next generation, so the strength of density dependence is determined by the total prey density present during generation n.

This assumption is consistent with standard formulations of the Ricker model and related discrete-time ecological models [18, 25, 29], where predation and density-dependent reproduction are treated as distinct biological processes occurring within the same generation.

Similar to [10], to incorporate predator hunting cooperation, the number of encounters between prey and predators at time n is modified as $a(bx_n)y_n(1 + cy_n)$, where $c > 0$ is the degree of hunting

cooperation. There is no cooperation among predators if $c = 0$ and the magnitude of cooperation is stronger if c is larger. Applying a similar approach as above, $1 - e^{-ay_n(1+cy_n)}$ becomes the probability of an individual prey being preyed upon in generation n. As a result, the interaction between predators and prey is governed by the following first-order difference equations:

$$\begin{aligned} x_{n+1} &= \left((1-b)x_n + bx_n e^{-ay_n(1+cy_n)}\right)e^{r(1-x_n/K)}, \\ y_{n+1} &= \beta b x_n \left(1 - e^{-ay_n(1+cy_n)}\right), \end{aligned} \tag{2.4}$$

with $x_0 \geq 0$ and $y_0 \geq 0$.

To simplify the analysis and reduce the number of parameters, we nondimensionalize system (2.4). Let

$$\bar{x}_n = \frac{x_n}{K}, \qquad \bar{y}_n = ay_n,$$

so that $\bar{x}_n$ represents the prey density relative to the carrying capacity and $\bar{y}_n$ rescales predator density by the searching efficiency a. Substituting

$$x_n = K\bar{x}_n, \qquad y_n = \frac{\bar{y}_n}{a}$$

into system (2.4), dividing the prey equation by K, and defining

$$\bar{c} = \frac{c}{a}, \qquad \bar{\beta} = \beta K a,$$

we obtain

$$\begin{aligned} \bar{x}_{n+1} &= \left[(1-b)\bar{x}_n + b\bar{x}_n e^{-\bar{y}_n(1+\bar{c}\bar{y}_n)}\right]e^{r(1-\bar{x}_n)}, \\ \bar{y}_{n+1} &= \bar{\beta} b \bar{x}_n \left(1 - e^{-\bar{y}_n(1+\bar{c}\bar{y}_n)}\right). \end{aligned}$$

For simplicity of notation, we subsequently drop the bars and work with the rescaled system (2.5):

$$\begin{aligned} x_{n+1} &= \left[(1-b)x_n + bx_n e^{-y_n(1+cy_n)}\right]e^{r(1-x_n)}, \\ y_{n+1} &= \beta b x_n \left(1 - e^{-y_n(1+cy_n)}\right), \\ x_0 &\geq 0,\ y_0 \geq 0. \end{aligned} \tag{2.5}$$

After introducing the dimensionless prey variable x_n/K, the carrying capacity is normalized to unity. Throughout the remainder of the paper, x_n denotes the scaled prey density, so that the carrying capacity of the dimensionless system is 1. The parameter $\bar{c} = c/a$ is a dimensionless measure of the strength of predator cooperation relative to the characteristic prey-density scale introduced by the nondimensionalization. Consequently, $\bar{c} = 0$ corresponds to no cooperative hunting, while larger values of $\bar{c}$ represent stronger cooperative effects. For simplicity, the overbars are omitted in the remainder of the paper, and c thereafter denotes the dimensionless cooperation parameter.

The model with $c = 0$ was studied by Wu and Zhao [33]. In particular, the system always possesses the equilibria $E_0 = (0, 0)$ and $E_1 = (1, 0)$, where E_0 is a saddle point. The equilibrium E_1 is globally asymptotically stable if $r < 2$ and $\beta b < 1$, and it becomes unstable if either $r > 2$ or $\beta b > 1$. A unique positive equilibrium $E_2 = (x^*, y^*)$ exists if $\beta b > 1$, and E_2 is locally asymptotically stable if

$\frac{b^2\beta}{1-b} < r < 2$ and $\beta b > 1$. The model is uniformly persistent when $r < 2$ and $\beta b > 1$. Using a result of Grove and Ladas [17], [33] also shows that, under certain parameter constraints, the unique positive equilibrium is an attractor within a specified region. In the following sections, we study system (2.5) systematically for $c > 0$.

3. Mathematical analysis

In Section 3.1, the existence and stability of equilibria, as well as the boundary 2-cycle, are investigated. In Section 3.2, we examine coexistence using the concept of uniform persistence and analyze the asymptotic dynamics.

First, it is evident that solutions of (2.5) remain nonnegative and are bounded. In fact, $x_n \le \frac{e^{r-1}}{r}$ for $n \ge 1$ and $y_n \le \frac{\beta b e^{r-1}}{r}$ for $n \ge 2$.

3.1. Equilibria, stability, and the boundary 2-cycle

There are always two boundary equilibria: the extinction equilibrium $E_0 = (0, 0)$ and the predator-free equilibrium $E_1 = (1, 0)$. The Jacobian matrix $J(x, y)$ of (2.5) is given by

$$\begin{pmatrix} \left[(1-b)(1-rx) + b(1-rx)e^{-y(1+cy)}\right] e^{r(1-x)} & -bx(1+2cy)e^{-y(1+cy)}e^{r(1-x)} \\ \beta b\left(1 - e^{-y(1+cy)}\right) & \beta bx(1+2cy)e^{-y(1+cy)} \end{pmatrix}. \tag{3.1}$$

In particular, the Jacobian matrix evaluated at E_0 is $J(E_0) = \begin{pmatrix} e^r & 0 \\ 0 & 0 \end{pmatrix}$, which implies E_0 is always a saddle point with the stable manifold lying on the nonnegative y-axis. At E_1, $J(E_1) = \begin{pmatrix} 1-r & -b \\ 0 & \beta b \end{pmatrix}$. Therefore, E_1 is locally asymptotically stable if $r < 2$ and $\beta b < 1$, and unstable if either one or both inequalities are reversed. In fact, the predator-free equilibrium is a saddle point if $r > 2$ and $\beta b < 1$, or $r < 2$ and $\beta b > 1$, and is a source if $r > 2$ and $\beta b > 1$. The above discussion is summarized as follows.

Proposition 3.1. *Solutions of* (2.5) *remain nonnegative and are bounded for* $n = 0, 1, 2, \ldots$. *There are two boundary equilibria* $E_0 = (0, 0)$ *and* $E_1 = (1, 0)$, *where* E_0 *is always a saddle point.* E_1 *is asymptotically stable if* $r < 2$ *and* $\beta b < 1$, *and unstable if either* $r > 2$ *or* $\beta b > 1$.

To discuss the existence of a positive equilibrium, we examine the nontrivial x- and y-nullclines given, respectively, as

$$x = 1 + \frac{1}{r}\ln\left[(1-b) + be^{-y(1+cy)}\right] := f(y),$$
$$x = \frac{y}{\beta b(1 - e^{-y(1+cy)})} := g(y).$$

Notice $f(0) = 1$, $f(\infty) = 1 + \frac{1}{r}\ln(1-b) < f(0)$, and

$$f'(y) = \frac{-be^{-y(1+cy)}(1+2cy)}{r(1-b) + rbe^{-y(1+cy)}} < 0 \quad \text{for all } y \ge 0.$$

The function $x = g(y)$ has been studied previously in [10] with

$$g(0^+) = \frac{1}{\beta b}, \quad g(\infty) = \infty, \quad g(y) > 0 \text{ for } y > 0,$$

and

$$g'(y) = \frac{e^{-y(1+cy)}(e^{y(1+cy)} - 1 - y(1 + 2cy))}{\beta b(1 - e^{-y(1+cy)})^2}. \tag{3.2}$$

Notice $x_n < f(y_n)$ implies $x_{n+1} > x_n$ and $x_n > f(y_n)$ is equivalent to $x_{n+1} < x_n$. Similarly, $x_n < g(y_n)$ implies $y_{n+1} < y_n$ and $x_n > g(y_n)$ is equivalent to $y_{n+1} > y_n$. Further, $g'(y) > 0$ for $y > 0$ if $0 \le 2c \le 1$. If $2c > 1$, there exists a unique critical point $\tilde{y} > 0$ such that $g'(y) < 0$ on $[0, \tilde{y})$ and $g'(y) > 0$ on $(\tilde{y}, \infty)$. We separate the discussion of the existence of positive equilibrium into two cases: $2c \le 1$ and $2c > 1$.

Let $0 < 2c \le 1$. If $\beta b > 1$, then $g(0^+) = 1/(\beta b) < 1 = f(0)$, while $g(y) \to \infty$ as $y \to \infty$. Since f is strictly decreasing and g is strictly increasing, the equation $f(y) = g(y)$ has a unique positive solution.

When $2c > 1$, it is clear that there is a unique positive equilibrium E_2 if $\beta b > 1$. The case of $\beta b < 1$ is more delicate. In this case, there is no positive equilibrium if the y-isocline $x = g(y)$ lies entirely above the prey nullcline $x = f(y)$ for all $y > 0$. A single positive equilibrium (the critical case) occurs if the two curves are tangent. Finally, there are two positive equilibria when $g(\tilde{y}) < f(\tilde{y})$, which corresponds to two positive intersections of the nullclines in system (2.5).

Proposition 3.2. *The following statements hold for system* (2.5).

(a) Let $0 < 2c \le 1$. *Then system* (2.5) *has a unique positive equilibrium* $E_2 = (x^*, y^*)$ *if* $\beta b > 1$, *and has no positive equilibrium if* $\beta b \le 1$.

(b) Let $2c > 1$. *If* $\beta b > 1$, *then system* (2.5) *has a unique positive equilibrium.*
If $\beta b < 1$, *define*

$$H(y) := f(y) - g(y), \qquad I := \{y > 0 : f(y) > 0\}.$$

Then $H(0^+) < 0$ *and* $H(y) < 0$ *for all sufficiently large* y. *Let*

$$H_{\max} := \sup_{y \in I} H(y).$$

Then:

(i) If $H_{\max} < 0$, *there is no positive equilibrium;*
(ii) if $H_{\max} = 0$, *there is one positive equilibrium, corresponding to a tangential intersection of the two nullclines;*
(iii) if $H_{\max} > 0$, *there are two positive equilibria.*

Equivalently, in the case where $\beta b < 1$, *the number of positive equilibria is determined by whether the prey nullcline* $x = f(y)$ *lies strictly below, is tangent to, or crosses the predator nullcline* $x = g(y)$.

The parameter βb may be interpreted as the predator's maximum reproduction number. When the predator reproduction number is less than one, strong cooperation may nevertheless permit multiple positive equilibria. In particular, if $H_{\max} > 0$, the system has at least two positive equilibria; the present argument does not exclude additional intersections.

When $2 < r < r_0 \approx 2.526$, the predator-extinction equilibrium E_1 is unstable, and (2.5) has a unique 2-cycle on the boundary

$$\mathcal{A} := \{(\bar{x}_1, 0), (\bar{x}_2, 0)\}, \tag{3.3}$$

where $\{\bar{x}_1, \bar{x}_2\}$ is the globally attracting 2-cycle for the Ricker equation (2.1). Since $\{\bar{x}_1, \bar{x}_2\}$ is the 2-cycle for (2.1), we have $\bar{x}_2 = \bar{x}_1 e^{r(1-\bar{x}_1)}$ and $\bar{x}_1 = \bar{x}_2 e^{r(1-\bar{x}_2)}$. Therefore, $\bar{x}_1\bar{x}_2 = \bar{x}_1\bar{x}_2 e^{r(1-\bar{x}_1)} e^{r(1-\bar{x}_2)}$ implies $1 = e^{r(2-\bar{x}_1-\bar{x}_2)}$, i.e., $\bar{x}_1 + \bar{x}_2 = 2$ and $\bar{x}_1 \neq \bar{x}_2$. As a result, one may assume $\bar{x}_1 < 1 < \bar{x}_2$. Further, by the arithmetic and geometric means, $\dfrac{\bar{x}_1 + \bar{x}_2}{2} = 1$ implies $\bar{x}_1\bar{x}_2 \leq 1$, where equality occurs if and only if $\bar{x}_1 = \bar{x}_2$. Since $\{\bar{x}_1, \bar{x}_2\}$ is a 2-cycle, the inequality is therefore strict, i.e., $\bar{x}_1\bar{x}_2 < 1$.

The stability of the boundary 2-cycle $\mathcal{A}$ is determined by the eigenvalues of the monodromy matrix

$$M = J(\bar{x}_2, 0)\, J(\bar{x}_1, 0),$$

where

$$J(\bar{x}_i, 0) = \begin{pmatrix} (1 - r\bar{x}_i)e^{r(1-\bar{x}_i)} & -b\bar{x}_i e^{r(1-\bar{x}_i)} \\ 0 & \beta b \bar{x}_i \end{pmatrix}, \qquad i = 1, 2.$$

Since M is upper triangular, its eigenvalues are

$$\lambda_1 = (1 - r\bar{x}_1)e^{r(1-\bar{x}_1)}(1 - r\bar{x}_2)e^{r(1-\bar{x}_2)}$$

and

$$\lambda_2 = \beta^2 b^2 \bar{x}_1\bar{x}_2.$$

Because $\{\bar{x}_1, \bar{x}_2\}$ is the globally attracting 2-cycle of the Ricker equation, we have

$$|\lambda_1| < 1.$$

Therefore, the stability of $\mathcal{A}$ is determined by λ_2, namely,

$$\mathcal{A} \text{ is asymptotically stable if } \beta b \sqrt{\bar{x}_1\bar{x}_2} < 1,$$

and unstable if

$$\beta b \sqrt{\bar{x}_1\bar{x}_2} > 1.$$

Proposition 3.3. *Let $2 < r < r_0$. The boundary 2-cycle $\mathcal{A} = \{(\bar{x}_1, 0), (\bar{x}_2, 0)\}$ is asymptotically stable if $\beta b \sqrt{\bar{x}_1\bar{x}_2} < 1$ and unstable if $\beta b \sqrt{\bar{x}_1\bar{x}_2} > 1$.*

3.2. Coexistence and dynamical behavior

To prove coexistence of both populations, one may adopt the concept of uniform persistence. Consider a two-dimensional discrete-time system

$$\begin{aligned} x_{n+1} &= f_1(x_n, y_n), \\ y_{n+1} &= f_2(x_n, y_n), \end{aligned} \tag{3.4}$$

defined on $\mathbb{R}^2_+ = \{(x, y) \in \mathbb{R}^2 : x \geq 0,\ y \geq 0\}$, where f_1 and f_2 are continuous and the system maps $\mathbb{R}^2_+$ into itself. System (3.4) is said to be *uniformly persistent* if there exists a constant $\eta > 0$ such that, for all initial conditions (x_0, y_0) with $x_0 > 0$ and $y_0 > 0$, it holds that

$$\liminf_{n\to\infty} x_n \geq \eta \text{ and } \liminf_{n\to\infty} y_n \geq \eta.$$

When the boundary of (2.5) admits only equilibrium dynamics, that is, when $0 < r < 2$, uniform persistence occurs provided the predator reproductive number satisfies $\beta b > 1$. Interestingly, this persistence threshold is independent of the cooperation strength c, although c may substantially affect the interior dynamics and the form of coexistence.

Theorem 3.1. *Let* $0 < r < 2$ *and* $\beta b > 1$. *System* (2.5) *is uniformly persistent.*

Proof. Let Y be the boundary of $\mathbb{R}^2_+$. Then $\mathbb{R}^2_+ \setminus Y$ is positively invariant for system (2.5). Since $r < 2$, solutions (x_n, y_n) of (2.5) satisfy $\limsup_{n\to\infty} x_n \leq 1$ and $\limsup_{n\to\infty} y_n \leq \beta b$, and hence, system (2.5) has a global attractor X. The only invariant set in Y is $\{E_0, E_1\}$, where $E_i \in X$ for $i = 0, 1$. Applying [19, Theorem 4.1], we need to verify that each $\{E_i\}$ is isolated in X and that the stable set of E_i is contained in Y. Since X is closed in $\mathbb{R}^2_+$, it is sufficient to show that $\{E_i\}$ is isolated in $\mathbb{R}^2_+$ for $i = 0, 1$.

If $\{E_0\}$ is not isolated in $\mathbb{R}^2_+$, then for any $\epsilon > 0$, there exists a compact invariant set M_0 such that $\{E_0\} \subsetneq M_0 \subset \overline{B(E_0, \epsilon)} \cap \mathbb{R}^2_+$, where $\overline{B(E_0, \epsilon)}$ denotes the closed ϵ-ball centered at E_0. We write $f_1(x, y)$ as $f_1(x, y) = x\tilde{f}_1(x, y)$, where $\tilde{f}_1(0, 0) = e^r > 1$. By continuity, $\epsilon > 0$ may be chosen sufficiently small that there exists $\delta > 0$ satisfying

$$\widetilde{f_1}(x, y) \geq 1 + \delta \qquad \text{for } (x, y) \in B(E_0, \epsilon) \cap \mathbb{R}^2_+.$$

It follows that $x_n \geq (1 + \delta)^n x_0$ for $n \geq 1$ and hence $\lim_{n\to\infty} x_n = \infty$ if $x_0 > 0$. We obtain a contradiction and conclude that $\{E_0\}$ is isolated in $\mathbb{R}^2_+$.

Similarly, suppose $\{E_1\}$ is not isolated in $\mathbb{R}^2_+$. Then for any $\epsilon > 0$, there exists a compact invariant set $M_1 \subset \overline{B(E_1, \epsilon)} \cap \mathbb{R}^2_+$ with $\{E_1\} \subsetneq M_1$. Since $\beta b > 1$, there exists $\varepsilon > 0$ sufficiently small such that

$$\beta b(1 - \varepsilon)\left(1 - \frac{\varepsilon(1 + c\varepsilon)}{2}\right) > 1.$$

Using the elementary inequality

$$e^{-u} < 1 - u + \frac{u^2}{2}, \qquad u > 0,$$

we obtain

$$1 - e^{-u} > u - \frac{u^2}{2}.$$

Setting $u = \varepsilon(1 + c\varepsilon)$ yields

$$1 - e^{-\varepsilon(1+c\varepsilon)} > \varepsilon(1 + c\varepsilon)\left(1 - \frac{\varepsilon(1 + c\varepsilon)}{2}\right).$$

Hence

$$\beta b(1 - \varepsilon)\left(1 - e^{-\varepsilon(1+c\varepsilon)}\right) > \varepsilon\beta b(1 - \varepsilon)(1 + c\varepsilon)\left(1 - \frac{\varepsilon(1 + c\varepsilon)}{2}\right).$$

For sufficiently small $\varepsilon > 0$, the right-hand side exceeds ε, and therefore

$$\beta b(1-\varepsilon)\left(1-e^{-\varepsilon(1+c\varepsilon)}\right) > \varepsilon.$$

Let $(x_0, y_0) \in M_1$ with $y_0 > 0$. Then $y_n > 0$ and $(x_n, y_n) \in M_1$ for all $n \geq 0$. It follows that

$$y_{n+1} = \beta b x_n\left(1-e^{-y_n(1+cy_n)}\right) \geq \beta b(1-\epsilon)\left(1-e^{-y_n(1+cy_n)}\right),\ n = 0, 1, \ldots.$$

Consider the following difference equation:

$$z_{n+1} = \beta b(1-\epsilon)\left(1-e^{-z_n(1+cz_n)}\right), \quad z_0 = y_0 > 0.$$

Since the map induced by the above scalar equation is strictly increasing for $y \geq 0$ and $\beta b(1-\epsilon) > 1$, the scalar equation has a unique positive equilibrium $\bar{z}$ such that $\lim_{n\to\infty} z_n = \bar{z}$ if $z_0 > 0$. It follows that $\liminf_{n\to\infty} y_n \geq \bar{z}$. Since the positive equilibrium $\bar{z}$ of the scalar equation satisfies $\bar{z} > \varepsilon$, we obtain a contradiction. Therefore, we conclude that $\{E_1\}$ is isolated in $\mathbb{R}^2_+$. It is also clear that the stable sets of E_0 and E_1 lie in Y, and therefore (2.5) is uniformly persistent. □

Remark 3.1. *Theorem 3.1 shows that, when the prey growth rate is moderate ($0 < r < 2$), the threshold for uniform persistence is determined by the predator reproductive number βb and is independent of the cooperation parameter c. Thus, in this regime, hunting cooperation does not lower the basic persistence threshold: predators persist uniformly precisely when $\beta b > 1$. Although the persistence threshold coincides with that of Wu and Zhao [33], the present result establishes that this threshold remains unchanged even after incorporating nonlinear cooperative hunting. Thus cooperation is shown to be dynamically neutral with respect to persistence, while profoundly influencing the interior dynamics.*

In the following, we provide some global results and examine local stability of positive equilibrium when it exists. Observe that

$$1 - e^{-y(1+cy)} \leq y, \tag{3.5}$$

for all $y \geq 1$. By a simple calculation, it can be shown that (3.5) holds true for all $y \geq 0$ if $2c \leq 1$. However, inequality (3.5) may not be valid if $2c > 1$ and $y > 0$ is small. For example, let $c = 0.568$ and $y = 0.07$, and then $1 - e^{-0.07(1+0.568\times 0.07)} \approx 0.07019761 > 0.07$ and the inequality (3.5) is reversed.

In what follows, we investigate the model (2.5) separately for the cases $2c \leq 1$ and $2c > 1$.

3.2.1. The case of $2c \leq 1$

If $\beta b < 1$, then (2.5) has no positive equilibrium, and $E_1 = (1, 0)$ is asymptotically stable if $r < 2$. We prove that E_1 is globally asymptotically stable if $r < 2$.

Theorem 3.2. *Let $2c \leq 1$, $0 < r < 2$, and $\beta b < 1$. Then $E_1 = (1, 0)$ is globally asymptotically stable in $\{(x, y) \in \mathbb{R}^2_+ : x > 0\}$.*

Proof. Since $r < 2$, solutions (x_n, y_n) of (2.5) satisfy $x_{n+1} \leq x_n e^{r(1-x_n)}$ for $n \geq 1$ implying $\limsup_{n\to\infty} x_n \leq 1$. Thus for all $\epsilon > 0$, there exists $n_0 > 0$ so that $x_n < 1 + \epsilon$ for all $n \geq n_0$. We choose $\epsilon > 0$ so that

$$\beta b(1+\epsilon) < 1.$$

Then by (3.5),

$$y_{n+1} \le \beta b(1+\epsilon)y_n \text{ for } n \ge n_0 \text{ implies } \lim_{n\to\infty} y_n = 0.$$

As a result, E_1 is globally asymptotically stable in the given region since E_1 is locally asymptotically stable and globally attracting. □

Suppose $r > 2$ and $\beta b < 1$. Then (2.5) has no positive equilibrium and E_1 is unstable. Using the same argument as in the proof of Theorem 3.2, we have $\lim_{n\to\infty} y_n = 0$ since $2c \le 1$ and $\beta b < 1$. Therefore, solutions converge to the x-axis, where the prey population has a globally attracting 2-cycle $\{\bar{x}_1, \bar{x}_2\}$ when $2 < r < r_0 \approx 2.526$ [14]. In fact, solutions of (2.5) will eventually oscillate between $(\bar{x}_1, 0)$ and $(\bar{x}_2, 0)$ as $n \to \infty$ using the asymptotic autonomous theory for difference equations in [11]. Indeed, since $\sqrt{\bar{x}_1\bar{x}_2} < 1, \beta b < 1$ implies $\beta b\sqrt{\bar{x}_1\bar{x}_2} < 1$, the 2-cycle $\mathcal{A}$ is asymptotically stable if $\beta b < 1$.

Theorem 3.3. *Let $2c \le 1$, $2 < r < r_0$, and $\beta b < 1$. Then the 2-cycle $\mathcal{A} = \{(\bar{x}_1, 0), (\bar{x}_2, 0)\}$ is globally asymptotically stable in $\{(x, y) \in \mathbb{R}^2_+ : x > 0\}$ for* (2.5)*, where $\{\bar{x}_1, \bar{x}_2\}$ is the 2-cycle global attractor of* (2.1)*.*

Now assume $\beta b > 1$. Then (2.5) has a unique positive equilibrium $E_2 = (x^*, y^*)$, where $\dfrac{1}{\beta b} < x^* < 1$, and the predator-free equilibrium $E_1 = (1, 0)$ is unstable. By (3.1), the stability of E_2 depends on the eigenvalues of the following Jacobian matrix:

$$J(E_2) = \begin{pmatrix} 1 - rx^* & -bx^*(1+2cy^*)e^{-y^*(1+cy^*)}e^{r(1-x^*)} \\ y^*/x^* & \beta bx^*(1+2cy^*)e^{-y^*(1+cy^*)} \end{pmatrix}. \tag{3.6}$$

Suppressing the superscript *, let

$$S = e^{-y(1+cy)}, \qquad A = \beta bxS(1+2cy), \qquad B = bye^{r(1-x)}S(1+2cy).$$

At the positive equilibrium, the trace and determinant of $J(E_2)$ are

$$\operatorname{tr} J = 1 - rx + A$$

and

$$\det J = (1 - rx)A + B.$$

We verify the Jury conditions.

First, since $0 < 2c \le 1$, the function g is strictly increasing, and hence

$$\frac{1 - e^{-y(1+cy)}}{y} > (1+2cy)e^{-y(1+cy)}.$$

Using the equilibrium relation

$$y = \beta bx(1 - e^{-y(1+cy)}),$$

we obtain

$$A = \beta bxS(1+2cy) < \beta bx\frac{1 - e^{-y(1+cy)}}{y} = 1.$$

Consequently,

$$1 - \operatorname{tr} J + \det J = rx - rxA + B = rx(1 - A) + B > 0.$$

Second,

$$1 + \operatorname{tr} J + \det J = 2 - rx + (2 - rx)A + B.$$

Therefore, if $rx \leq 2$, then

$$1 + \operatorname{tr} J + \det J > 0.$$

Finally, suppose $rx \geq 1$. Since $A > 0$, we have

$$(1 - rx)A \leq 0.$$

Moreover, from the prey equilibrium equation,

$$1 = ((1 - b) + bS)e^{r(1-x)},$$

and hence

$$bS\, e^{r(1-x)} < 1.$$

It follows that

$$B = y(1 + 2cy)\, bS\, e^{r(1-x)} < y(1 + 2cy).$$

Thus, if

$$y(1 + 2cy) < 1,$$

then

$$\det J = (1 - rx)A + B < 1.$$

Therefore all three Jury conditions hold whenever

$$1 \leq rx \leq 2 \quad \text{and} \quad y(1 + 2cy) < 1.$$

We present the above derived sufficient conditions for which E_2 is locally asymptotically stable.

Proposition 3.4. *Let* $2c \leq 1$ *and* $\beta b > 1$. *Then* (2.5) *has a unique positive equilibrium* $E_2 = (x^*, y^*)$, *where* E_2 *is asymptotically stable if* $1 \leq rx^* \leq 2$ *and* $y^*(1 + 2cy^*) < 1$.

The conditions $1 \leq rx^* \leq 2$ and $y^* < \dfrac{-1 + \sqrt{1 + 8c}}{4c}$ provide biologically meaningful criteria for the local stability of the positive equilibrium. The first condition, $1 \leq rx^* \leq 2$, bounds the strength of prey density dependence. Biologically, this condition implies moderate crowding among prey, contributing to system stability.

The second condition, $y^*(1 + 2cy^*) < 1$, constrains the strength of cooperative interactions among predators. The expression $y^*(1+2cy^*)$ arises from the nonlinearity in the functional response, capturing the enhanced predation efficiency due to cooperation. If this term becomes too large, the predators may overexploit the prey, leading to instability. Hence, this condition ensures that predator cooperation remains moderate and that predator density does not become excessively large. It reflects a balance that allows both prey and predators to coexist stably.

Together, these conditions balance prey self-limitation and predator effectiveness, stabilizing the interaction and ensuring that the Jury criteria for local asymptotic stability are satisfied.

3.2.2. The case of $2c > 1$

The scenario of large cooperation $2c > 1$ is more complicated as the nontrivial y-nullcline is no longer monotone.

For the case $2c > 1$ and $\beta b > 1$, system (2.5) admits a unique positive equilibrium $E_2 = (x^*, y^*)$. Since $2c > 1$, the predator nullcline $x = g(y)$ is non-monotone: it decreases on $(0, \tilde{y})$ and increases on $(\tilde{y}, \infty)$, where $\tilde{y} > 0$ is the unique critical point satisfying $g'(\tilde{y}) = 0$. However, when $\beta b > 1$, the unique positive equilibrium E_2 is determined by the intersection of the prey isocline $x = f(y)$ with the increasing branch of $x = g(y)$. To see this, recall that $g(0^+) = 1/(\beta b) < 1 = f(0)$ when $\beta b > 1$, and $g(y) \to \infty$ as $y \to \infty$, while f is strictly decreasing with $f(y) \to 1 + \frac{1}{r}\ln(1-b)$, as $y \to \infty$. Since g first decreases and then increases, and $g(0^+) < f(0)$, the first intersection of f and g must occur on the increasing branch of g, where $g'(y^*) > 0$. Therefore we have

$$g'(y^*) > 0 \quad \text{at the unique positive equilibrium } E_2.$$

The significance of the condition $g'(y^*) > 0$ for the Jury analysis is the following. Recall from Section 3.2.1 that the key inequality used to bound the trace and determinant of $J(E_2)$ was

$$\frac{1 - e^{-y(1+cy)}}{y} > (1 + 2cy)e^{-y(1+cy)}, \tag{3.7}$$

which was established under the assumption that $g'(y) > 0$, i.e., that the equilibrium lies on the increasing branch of the predator isocline. Specifically, differentiating the expression for $g'(y)$ given in (3.2) and evaluating at $y = y^*$, one finds that $g'(y^*) > 0$ is equivalent to

$$e^{y^*(1+cy^*)} - 1 - y^*(1 + 2cy^*) > 0,$$

which after rearrangement is precisely inequality (3.7) evaluated at $y = y^*$. Therefore, the condition $g'(y^*) > 0$ is not merely a geometric observation but is the exact algebraic condition needed to validate the Jury condition. Since we have established that $g'(y^*) > 0$ holds at the unique positive equilibrium when $\beta b > 1$ and $2c > 1$, all three Jury-condition calculations from Section 3.2.1 carry over without modification, and Proposition 3.5 follows.

In contrast, when $\beta b < 1$ and two positive equilibria exist, the lower equilibrium E_{21} lies on the decreasing branch of g where $g'(y_1^*) < 0$, which reverses inequality (3.7) at $y = y_1^*$. This is why the Jury argument cannot be applied to E_{21}.

Proposition 3.5. *Let $2c > 1$ and $\beta b > 1$. Then system (2.5) admits a unique positive equilibrium $E_2 = (x^*, y^*)$. Moreover, E_2 is locally asymptotically stable if $1 \le rx^* \le 2$ and $y^*(1 + 2cy^*) < 1$.*

When $\beta b < 1$, we provide a sufficient condition for which the predator extinction equilibrium is globally asymptotically stable. Define

$$m_g := \inf_{y>0} g(y). \tag{3.8}$$

Theorem 3.4. *Assume $0 < r < 2$ and $m_g > 1$. Then the predator-free equilibrium $E_1 = (1, 0)$ is globally asymptotically stable in $\{(x, y) \in \mathbb{R}^2_+ : x > 0\}$.*

Proof. Let (x_n, y_n) be a solution of (2.5) with $x_0, y_0 > 0$. Since

$$x_{n+1} = x_n\left[(1-b) + be^{-y_n(1+cy_n)}\right]e^{r(1-x_n)} \leq x_n e^{r(1-x_n)},$$

and $0 < r < 2$, an established result gives

$$\limsup_{n\to\infty} x_n \leq 1.$$

Choose $\varepsilon > 0$ sufficiently small such that

$$1 + \varepsilon < m_g.$$

There exists $N > 0$ such that

$$x_n \leq 1 + \varepsilon, \qquad n \geq N.$$

By the definition of the predator nullcline, we have

$$\frac{y_{n+1}}{y_n} = \frac{x_n}{g(y_n)}.$$

Therefore, for $n \geq N$,

$$\frac{y_{n+1}}{y_n} \leq \frac{1+\varepsilon}{m_g} =: q < 1.$$

It follows that

$$y_n \leq q^{n-N} y_N, \qquad n \geq N,$$

and consequently

$$\lim_{n\to\infty} y_n = 0.$$

Since

$$(1-b) + be^{-y_n(1+cy_n)} \longrightarrow 1 \text{ as } n \to \infty,$$

the prey equation is asymptotically autonomous to the Ricker equation $u_{n+1} = u_n e^{r(1-u_n)}$. For $0 < r < 2$, its positive equilibrium $u = 1$ is globally asymptotically stable. Hence

$$\lim_{n\to\infty} x_n = 1.$$

Therefore,

$$\lim_{n\to\infty}(x_n, y_n) = (1, 0),$$

which proves that E_1 is globally asymptotically stable. □

Remark 3.2. *The condition $m_g := \inf_{y>0} g(y) > 1$ means that the predator nullcline $x = g(y)$ lies entirely in the region $x > 1$. Since*

$$\lim_{y\to 0^+} g(y) = \frac{1}{\beta b},$$

the condition $m_g > 1$ necessarily implies $\beta b < 1$. Moreover, since $f(y) < 1$ for every $y > 0$,

$$m_g > 1 \quad \Longrightarrow \quad f(y) < g(y) \quad \text{for all } y > 0.$$

Thus, Theorem 3.4 provides a sufficient condition under which the predator population decreases geometrically to zero and the prey population converges to its carrying capacity.

Similar to Theorem 3.3, since $x_n \leq \dfrac{e^{r-1}}{r}$ for $n \geq 1$ when $2 < r < r_0$, the dynamics of (2.5) are asymptotically autonomous to the prey equation, which leads to the following result.

Theorem 3.5. *If* $2 < r < r_0$ *and* $m_g > \dfrac{e^{r-1}}{r}$, *then the 2-cycle* $\mathcal{A} = \{(\bar{x}_1, 0), (\bar{x}_2, 0)\}$ *is globally asymptotically stable in* $\{(x, y) \in \mathbb{R}^2_+ : x > 0\}$.

When the minimum value of the predator isocline $x = g(y)$ lies below the prey isocline $x = f(y)$, system (2.5) admits two positive equilibria

$$E_{21} = (x_1^*, y_1^*), \qquad E_{22} = (x_2^*, y_2^*),$$

with

$$y_1^* < y_2^*.$$

As in Section 3.2.1, the stability analysis is based on the Jury conditions applied to the Jacobian matrix evaluated at the equilibrium.

Proposition 3.6. *Let* $2c > 1$ *and* $\beta b < 1$. *Suppose* (2.5) *has two positive equilibria* $E_{21} = (x_1^*, y_1^*)$ *and* $E_{22} = (x_2^*, y_2^*)$ *with* $y_1^* < y_2^*$, *where* E_{21} *lies on the decreasing branch and* E_{22} *lies on the increasing branch of the predator nullcline* $x = g(y)$. *Then* E_{22} *is asymptotically stable if* $1 \leq rx_2^* \leq 2$ *and* $y_2^*(1 + 2cy_2^*) < 1$.

The conditions in Proposition 3.6 for E_{22} should be interpreted as sufficient conditions. In particular, the inequalities

$$1 \leq rx_2^* \leq 2 \quad \text{and} \quad y_2^*(1 + 2cy_2^*) < 1$$

must be verified for the specific equilibrium under consideration. Although $x_2^* < 1$ in the two-equilibrium case, the lower bound $rx_2^* \geq 1$ is not automatic and depends on the parameter values. Numerical simulations suggest that the lower equilibrium E_{21} is unstable. In the examples considered in Section 4, E_{21} appears either as a saddle or a repelling equilibrium. Although numerical evidence consistently indicates that E_{21} is unstable, we have not been able to establish a complete analytical proof. Because the Jacobian entries depend nonlinearly on the equilibrium coordinates, the Jury inequalities do not appear to admit a simple characterization. We therefore leave a rigorous classification of E_{21} as an open problem.

Remark 3.3. *When strong hunting cooperation is present* ($2c > 1$), *the predator nullcline becomes non-monotone, creating the possibility of two positive equilibria. This phenomenon does not occur in the model of Wu and Zhao [33] or in the weak cooperation case. Consequently, cooperation introduces bistability and dependence on initial conditions, substantially enriching the qualitative dynamics.*

The bifurcation diagrams suggest transitions from equilibrium behavior to oscillatory or more complicated dynamics as the cooperation parameter varies. To avoid overclaiming, we do not identify these transitions rigorously as Neimark–Sacker bifurcations. A complete bifurcation analysis would require numerical continuation of the relevant invariant sets and, in the case of a Neimark–Sacker bifurcation, verification that a complex conjugate pair of eigenvalues of the appropriate fixed point crosses the unit circle together with the corresponding nonresonance and normal-form conditions. Such

an analysis is beyond the scope of the present work. Here, the bifurcation diagrams and maximal Lyapunov exponents are used only to illustrate the range of dynamical behavior, including stable coexistence, periodic oscillations, and chaotic dynamics.

When the predator cooperation coefficient is sufficiently large ($2c > 1$), the predator-prey interaction is qualitatively altered compared to the moderate or weak cooperation regime. In this case, the predator nullcline becomes non-monotone, creating the possibility of two coexistence equilibria. When predator recruitment is sufficiently strong, $\beta b > 1$, the system admits a single coexistence equilibrium. This equilibrium is stable provided that prey growth is not too fast ($1 \leq rx^* \leq 2$) and predator self-limitation remains moderate ($y^*(1 + 2cy^*) < 1$).

In the regime of $\beta b < 1$, the system may admit two positive equilibria: A high-prey/low-predator state E_{21} and a low-prey/high-predator state E_{22}. The larger equilibrium E_{22} may be asymptotically stable under conditions similar to the weak cooperation case. The coexistence of two equilibria introduces bistability. The long-term outcome depends sensitively on the initial densities of prey and predators. This phenomenon corresponds to a predator Allee effect, where predator survival requires sufficient numbers to benefit from cooperative hunting. This highlights a threshold phenomenon in which strong cooperation increases predator efficiency but also raises the risk of extinction if populations start below critical levels.

In summary, strong hunting cooperation ($2c > 1$) introduces nonlinear feedback that makes predator persistence more fragile. While cooperation can stabilize predator success under favorable conditions, it also sharpens extinction thresholds, rendering the system more sensitive to initial conditions and parameter values.

4. Numerical investigations

The parameter values used in this section are chosen to illustrate the different dynamical behaviors predicted by the model, including predator extinction, stable coexistence, bistability, periodic oscillations, and chaotic dynamics. While the present work is theoretical rather than data-driven, the qualitative parameter regimes explored here are broadly consistent with biological observations from discrete-generation predator–prey systems.

The prey growth parameter r in the Ricker model has been estimated empirically across a range of taxa. Values in the range $0 < r < 2$, corresponding to stable or damped prey dynamics, are representative of many insect host–parasitoid systems, including species of *Plodia interpunctella* (Indian meal moth) and its associated parasitoids, for which r has been estimated in the range 0.5–1.5 [18, 29]. Values of $r > 2$, which produce overcompensatory oscillations and chaos in the Ricker map, are consistent with strongly density-dependent populations such as certain blowfly (*Lucilia cuprina*) populations studied by Nicholson [27] and subsequently modeled with Ricker-type growth [27, 29].

The predator conversion efficiency parameter β and the non-refuge fraction b jointly determine the predator reproduction number βb. In host–parasitoid systems, conversion efficiencies vary widely depending on clutch size and host suitability; values of β in the range 2–10 are not unusual for parasitoids with multiple offspring per host [18]. The refuge fraction $1 - b$ reflects the proportion of prey inaccessible to predators due to spatial hiding, behavioral avoidance, or structural refuge. Values of b ranging from 0.4 to 0.9 have been used in discrete-time refuge models [10, 18], and our choices

of $b = 0.825$ and $b = 0.49$ fall within this range.

The bifurcation diagrams and maximal Lyapunov exponents suggest transitions among stable coexistence, periodic oscillations, predator extinction, and chaotic dynamics as parameters vary. We do not rigorously identify these transitions as Neimark–Sacker or period-doubling bifurcations. Such a classification would require numerical continuation of the relevant equilibrium or periodic orbit, together with verification of the appropriate eigenvalue-crossing, nonresonance, and normal-form conditions. Here, the bifurcation diagrams and maximal Lyapunov exponents are used to illustrate the range of possible long-term dynamics rather than to provide a complete bifurcation classification.

The hunting cooperation parameter c is more difficult to estimate directly, as it is a phenomenological parameter capturing the net increase in predation efficiency due to group coordination. In continuous-time models of cooperative hunters such as wolves (*Canis lupus*) and African wild dogs (*Lycaon pictus*), cooperation has been shown to substantially increase kill rates, with effective attack rates increasing nonlinearly with group size [2, 12]. In our discrete-time formulation, $c = 0$ corresponds to no cooperation and larger c reflects stronger coordination. The range $0 \le c \le 5$ explored in Figures 1 and 2 spans from no cooperation to strong cooperation, and the bistability regime $2c > 1$ examined in Section 4.2 is consistent with cooperation levels at which qualitative changes in predator persistence have been documented in cooperative hunting models [2, 10].

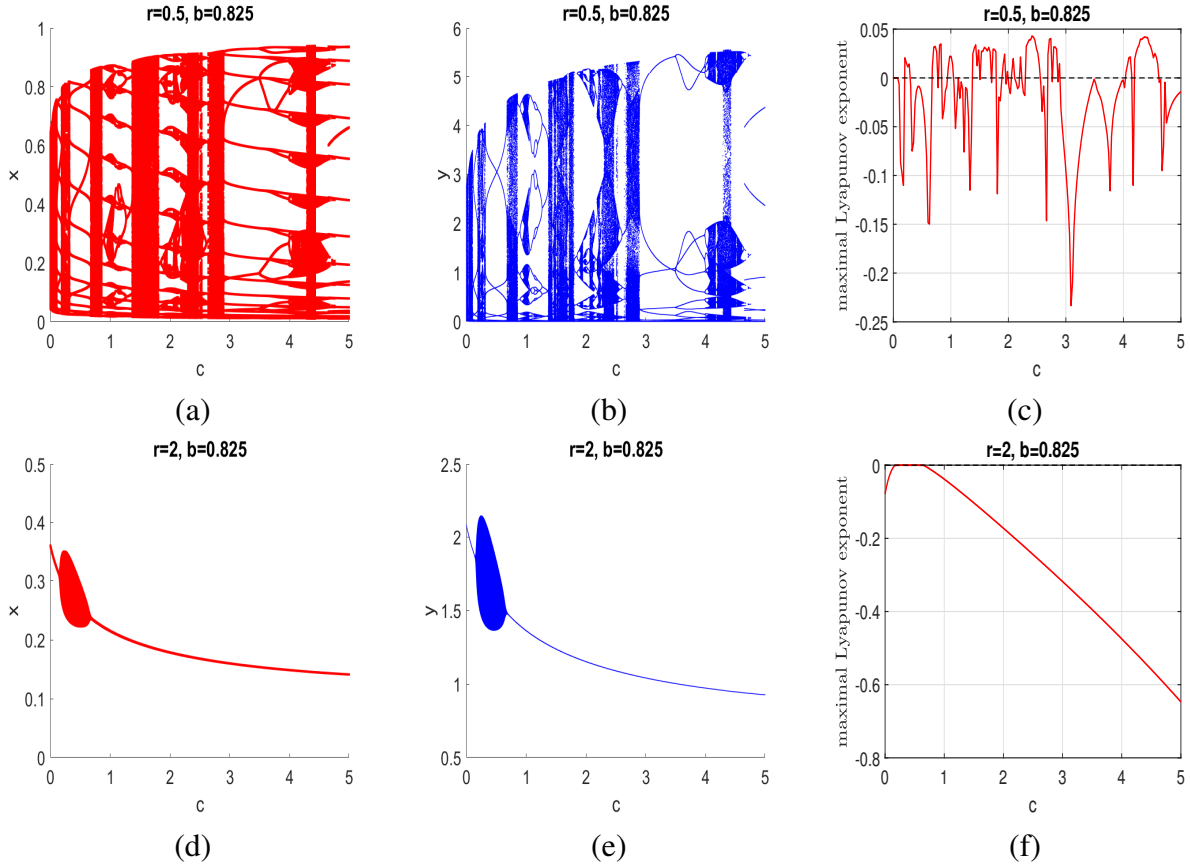


Figure 1. Bifurcation diagrams and maximal Lyapunov exponents with respect to c for $0 \le c \le 5$, with fixed parameter values $\beta = 8$ and $b = 0.825$. The prey growth rate is $r = 0.5$ in panels (a)–(c) and $r = 2$ in panels (d)–(f).

In particular, the regime of high prey growth ($r = 3.5$ and $r = 4.5$) combined with strong cooperation is motivated by systems such as the interaction between blowfly-type prey populations exhibiting strong overcompensation and generalist predators or parasitoids with group-coordinated attack behavior. The rescue effect observed in Figures 2(d)–(f), whereby sufficiently strong cooperation prevents predator extinction that would otherwise occur at intermediate cooperation levels, has a biological analog in empirical studies showing that cooperative predators can persist in prey populations undergoing boom-and-bust cycles that would eliminate solitary predators [12]. These parameter regimes are therefore not arbitrary but reflect qualitatively distinct ecological scenarios whose dynamical consequences the model is designed to illuminate.

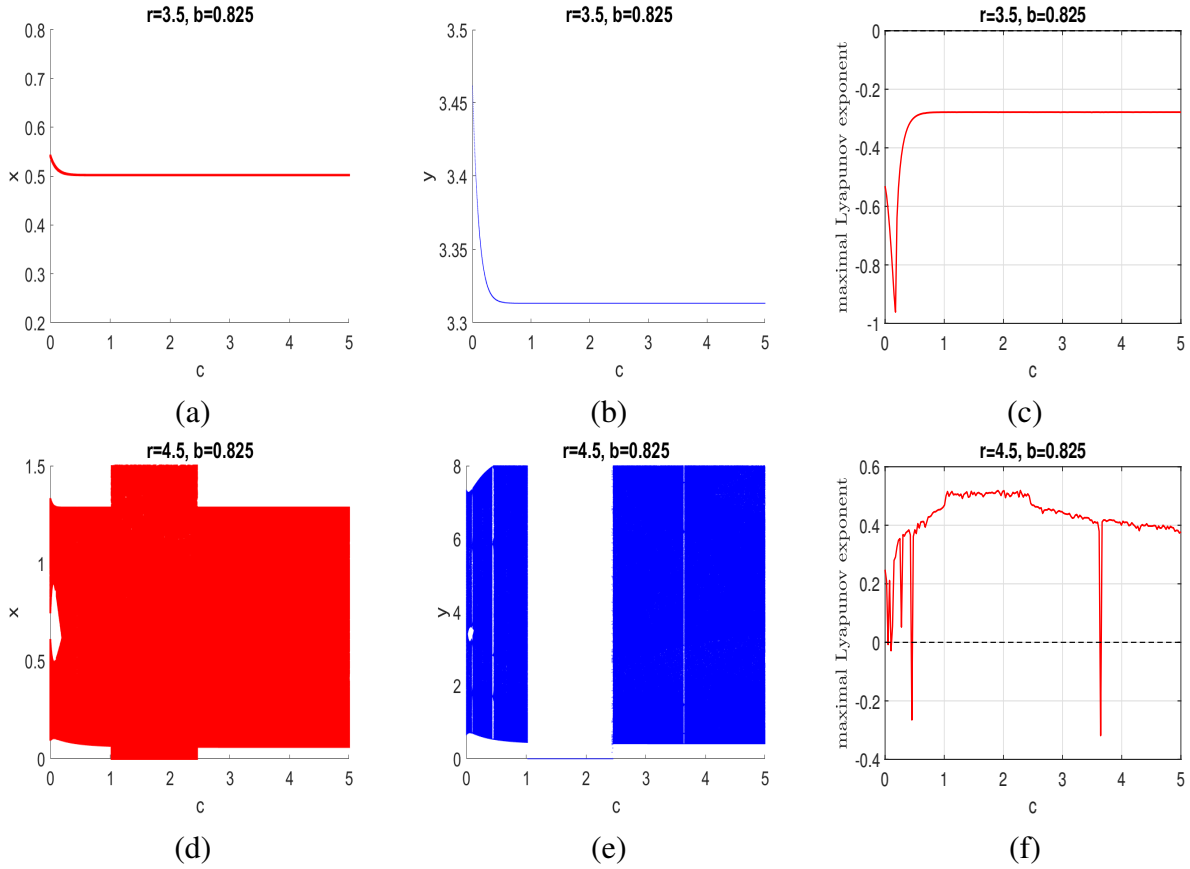


Figure 2. Bifurcation diagrams and maximal Lyapunov exponents with respect to c for $0 \le c \le 5$, with fixed parameter values $\beta = 8$ and $b = 0.825$. The prey growth rate is $r = 3.5$ in panels (a)–(c) and $r = 4.5$ in panels (d)–(f).

4.1. Bifurcation diagrams and maximal Lyapunov exponents

The maximal Lyapunov exponent was computed using the standard Benettin algorithm [4]. For each parameter value, the system was iterated for 3000 transient iterations, followed by 10,000 iterations used in the Lyapunov exponent calculation. Bifurcation diagrams were generated from the final 500 iterates after discarding the transient. The parameter step size was 0.002.

We first investigate the case for which $\beta b > 1$ with fixed $\beta = 8$ and $b = 0.825$, ensuring the existence of a unique positive equilibrium for all $c \ge 0$. Figures 1 and 2 provide bifurcation diagrams

and maximal Lyapunov exponents with c as the varying parameter for different values of r. Specifically, $r = 0.5$ and $r = 2.0$ in Figure 1 while $r = 3.5$ and $r = 4.5$ in Figure 2.

For the small prey growth case ($r = 0.5$), Figures 1(a)–(c) show that varying the cooperation strength can produce alternating windows of regular and irregular dynamics. Thus, cooperation does not act monotonically as a stabilizing mechanism; rather, changes in c can shift the system among stable, periodic, and chaotic coexistence regimes. For $r = 2$, Figures 1(d)–(f) indicate that increasing cooperation is associated with convergence toward a stable coexistence equilibrium. In this parameter regime, cooperation appears to dampen oscillations and simplify the long-term dynamics.

For $r = 3.5$, Figures 2(a)–(c) indicate convergence to a stable positive equilibrium throughout the plotted range of c. Thus, in this parameter regime, varying cooperation changes the equilibrium population levels but does not appear to change the qualitative attractor type. For $r = 4.5$, Figures 2(d)–(f) show a nonmonotone effect of cooperation: some intermediate values of c are associated with predator extinction, whereas larger values of c can restore predator-prey coexistence. However, the recovered coexistence is generally non-equilibrium and may involve large-amplitude oscillations or chaotic dynamics. Therefore, cooperation can enhance predator persistence in some regimes, but it can also intensify nonlinear feedback and reduce predictability.

The parameter b represents the fraction of prey vulnerable to predation. By varying b, the model reflects how environmental conditions or prey behavior that alter refuge availability can tip the balance between extinction, coexistence, and chaotic dynamics. Analyzing the role of b therefore provides insight into how predator–prey communities respond to changes in prey protection and availability in natural systems.

When the prey growth rate is small ($r = 0.5$), Figures 3(a)–(c), predators coexist with prey for most values of b, but there is a narrow window of small b in which predators go extinct and the system converges to prey-only dynamics. The maximal Lyapunov exponent confirms this behavior. It is negative in the extinction regime, indicating attraction to a prey-only equilibrium since $r = 0.5$, while it varies near zero or positive values within coexistence regions, reflecting transitions through periodic and chaotic predator–prey dynamics. When the prey growth rate is moderate ($r = 2.5$), Figures 3(d)–(f), coexistence dominates a wide range of b, and extinction is restricted to small intervals. In these cases, the Lyapunov exponent curve displays period-doubling bifurcations and chaotic windows, showing that richer dynamics arise within the coexistence regime. Therefore, increasing the vulnerable prey fraction generally promotes predator persistence, though narrow bands of prey refuge can still lead to predator extinction, and complex oscillations may occur due to overcompensatory prey growth.

When the prey growth rate is high ($r = 3.5$), Figures 4(a)–(c), predators persist across large values of b, but extinction can occur in an interval with small b where trajectories converge to prey-only dynamics. In these extinction regions, the maximal Lyapunov exponent is positive, reflecting the chaotic behavior of the prey on the boundary. Outside this interval, coexistence is sustained and the Lyapunov exponents indicate alternating regimes of stability, period-doubling, and chaos. For very high prey growth ($r = 4.5$), Figures 4(d)–(f), the system shows predator extinction in most of the b window where the prey follow chaotic dynamics alone. The Lyapunov exponents highlight these transitions clearly, with sign changes marking the switch between stable coexistence and chaotic prey-only regimes. These results show that when prey reproduce rapidly, predators can persist provided a sufficient fraction of prey are vulnerable.

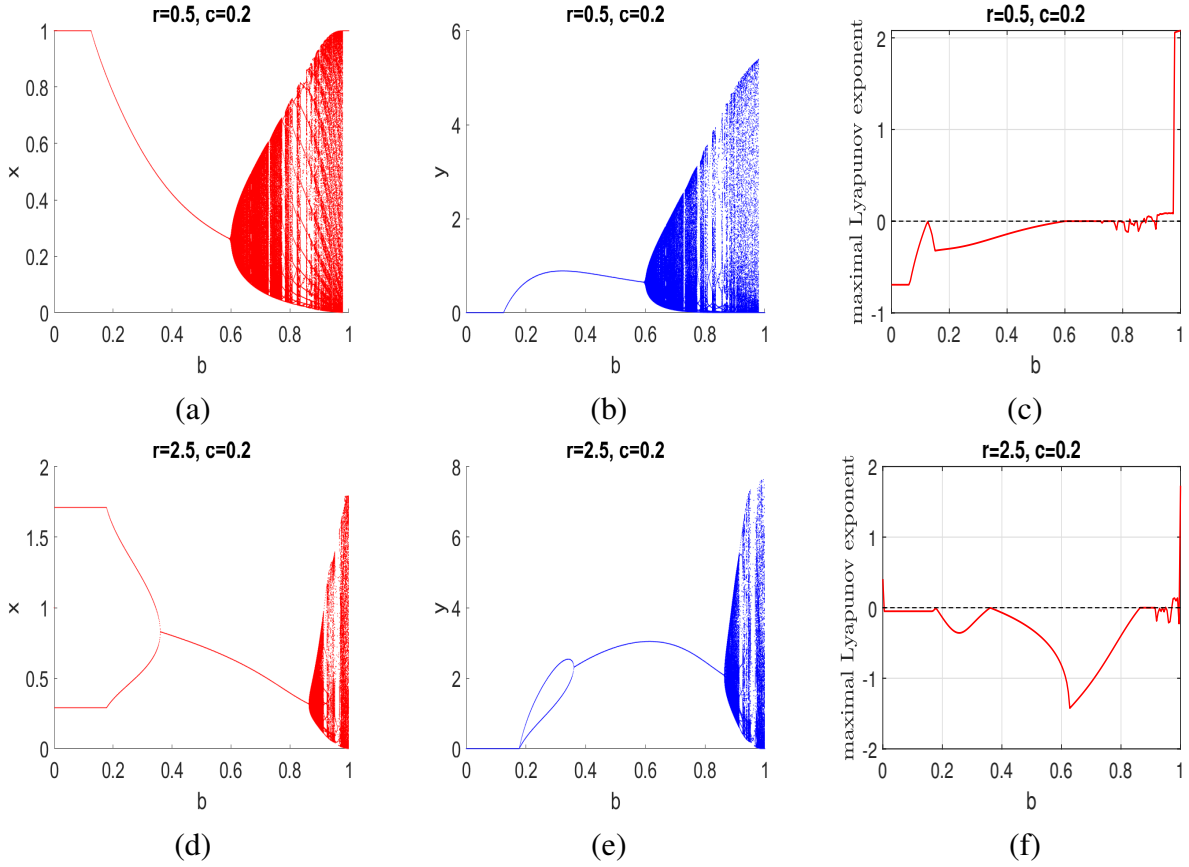


Figure 3. Bifurcation diagrams and maximal Lyapunov exponents with respect to b for $0 \leq b \leq 1$, with fixed parameter values $\beta = 8$ and $c = 0.2$. The prey growth rate is $r = 0.5$ in panels (a)–(c) and $r = 2.5$ in panels (d)–(f).

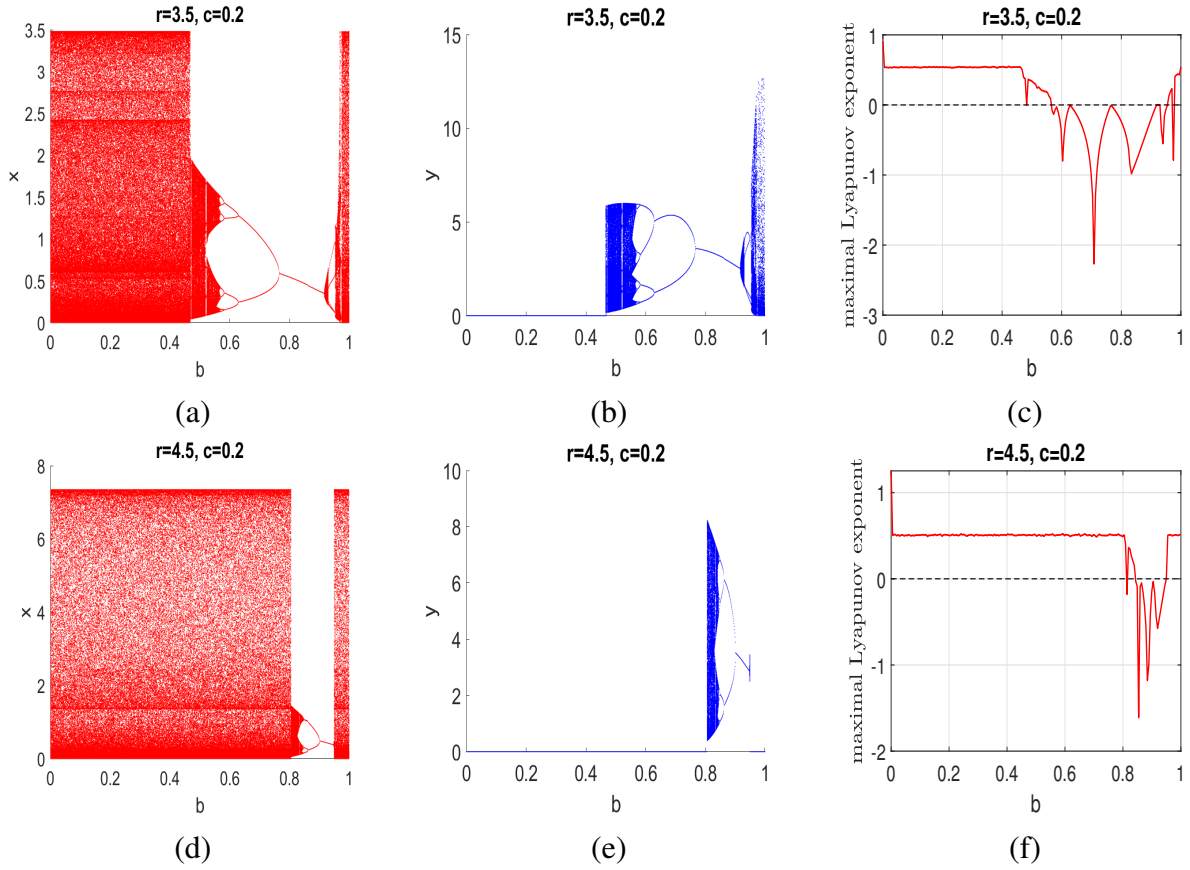


Figure 4. Bifurcation diagrams and maximal Lyapunov exponents with respect to b for $0 \leq b \leq 1$, with fixed parameter values $\beta = 8$ and $c = 0.2$. The prey growth rate is $r = 3.5$ in (a)–(c) and $r = 4.5$ in (d)–(f).

4.2. Basins of attraction

In this subsection, we examine the scenario where $\beta b < 1$ and $2c > 1$, in which the system admits two positive equilibria, by studying the corresponding basins of attraction.

Let $\beta = 2$, $b = 0.49$, $c = 3$, and $r = 1$ ($2c > 1$, $\beta b < 1$). The predator-prey interaction exhibits two positive equilibria, $E_{21} = (0.9947, 0.0104)$ (a saddle) and $E_{22} = (0.6968, 0.3645)$ (asymptotically stable), as presented in Figure 5(a). Figure 5(b) shows that the basin of attraction for $E_1 = (1, 0)$ is substantially larger than that for E_{22}. Predator persistence depends jointly on predator and prey initial densities. Very low predator densities can still lead to coexistence, as seen in the lower-left blue region of Figure 5(b). In other regimes, predators may go extinct even with very high initial prey due to Ricker overcompensation causing a prey crash and subsequent food shortage. The coexistence of the predator-free attractor and the stable coexistence equilibrium E_{22} creates a bistable coexistence-extinction scenario. Unlike a strong predator Allee effect, where persistence is impossible if the initial predator density is below a fixed threshold regardless of prey abundance, this system exhibits a weaker, prey-mediated threshold. Predators can persist from very low initial densities if the prey population begins small.

As the degree of hunting cooperation increases to $c = 24$ in Figure 5(c), the system's dynamics

change. While two positive equilibria still exist with the same stability properties, the coexistence basin shrinks noticeably. This intensified predation, combined with the Ricker overcompensation of the prey, creates a much narrower corridor of initial conditions that allow for coexistence. If predators start with a very low population, the cooperation effect does not turn on quickly enough for them to build up their numbers. Conversely, if the prey population is initially very high, the heightened predation and overcompensation can trigger a severe prey crash, starving the predators and leading to their extinction. Thus, increasing cooperative hunting strengthens the nonlinear predator impacts but ultimately makes coexistence less robust, as persistence becomes highly sensitive to the initial densities of both predator and prey.

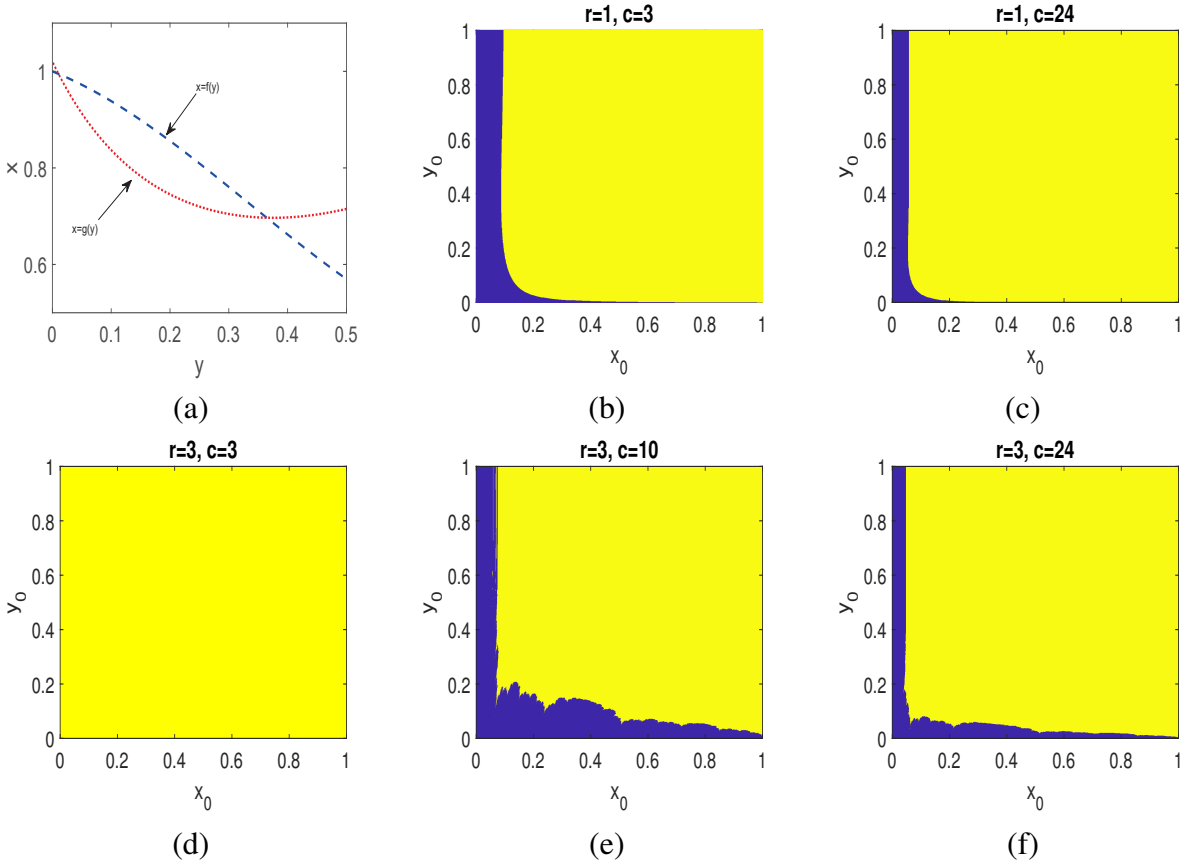


Figure 5. Basins of attraction for $\beta = 2$ and $b = 0.49$. Panel (a) shows the nontrivial nullclines for $r = 1$ and $c = 3$, illustrating two positive equilibria. Panels (b)–(c) show basins of attraction for $r = 1$, where yellow denotes initial conditions converging to $E_1 = (1, 0)$ and blue denotes initial conditions converging to E_{22}. Panels (d)–(f) show basins for $r = 3$, where yellow denotes initial conditions whose iterations approach the predator-free boundary attractor generated by the prey-only Ricker dynamics and blue denotes initial conditions leading to predator-prey coexistence. For $r = 3$, the coexistence attractor is generally not an equilibrium as shown in Figure 6.

In the above example, the prey population is stabilized at the population level 1 in the absence of predators and coexistence is in the form of a positive equilibrium. We now increase the prey

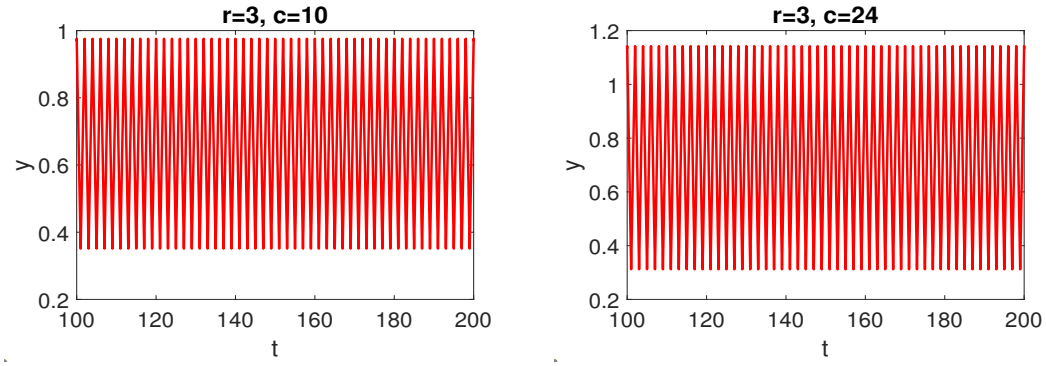
growth rate to $r = 3$ in which the prey population is chaotic in the absence of predators. In this parameter regime with $c = 3$, the two positive equilibria are $E_{21} = (0.9985, 0.0089)$ (a source) and $E_{22} = (0.8094, 0.7050)$ (a saddle point). Figures 5(d)–(f) present the basin of attraction for which the predator is extinct in yellow and there is coexistence in blue.

In Figure 5(d) ($c = 3$), the predator always goes extinct regardless of the initial condition; trajectories converge to the predator-free chaotic attractor on the prey axis. When cooperation increases to $c = 10$ (Figure 5(e)), the dynamics change qualitatively: a portion of initial conditions (blue region) lead to predator–prey coexistence, but the attractor is no longer an equilibrium point. Instead, the populations fluctuate persistently, reflecting complex predator–prey oscillations generated by the interaction of cooperative hunting and chaotic prey growth. The yellow region corresponds to predator extinction, with prey alone being chaotic.

At stronger cooperation, $c = 24$ (Figure 5(f)), the coexistence region remains but becomes smaller and more constrained. Here, the system still exhibits non-equilibrium coexistence attractors (fluctuating dynamics), but extinction is the dominant outcome for many initial conditions. This indicates that although cooperation can rescue predators from certain initial states, the chaotic growth of prey and overexploitation effects limit the robustness of coexistence.

In Figure 5, the color coding distinguishes the long-term fate of trajectories rather than only equilibrium convergence. For $r = 1$, the prey-only boundary dynamics converge to $E_1 = (1, 0)$, and the coexistence basin corresponds to convergence to the stable positive equilibrium E_{22}. In contrast, when $r = 3$, the prey-only Ricker dynamics are non-equilibrium, and trajectories in the yellow region approach a predator-free boundary attractor. The blue region corresponds to persistent predator-prey coexistence, but the attractor need not be an equilibrium; numerical trajectories indicate periodic or chaotic coexistence depending on c.

Figure 6 provides time series for Figures 5(e),(f), illustrating the periodic dynamics when $r = 3$ and c is increased to 10 and 24, respectively.



(a) (b)

Figure 6. Plots (a) and (b) provide time series for the predator population when $r = 3$, with $c = 10$ in (a) and $c = 24$ in (b).

From an ecological perspective, the bistability observed in Figure 5 indicates that long-term population outcomes depend strongly on the initial densities of both predator and prey populations. In particular, the system may converge either to predator extinction or to predator-prey coexistence under the same parameter values, depending solely on initial conditions.

This phenomenon reflects a threshold-type effect associated with cooperative hunting. When predator density is too low, cooperative benefits are insufficient to maintain predator growth, especially if prey dynamics simultaneously undergo large Ricker-type oscillations. Conversely, sufficiently favorable initial prey and predator densities may allow predators to establish and persist.

The basin structures also demonstrate that very high initial prey densities do not necessarily promote predator persistence. Due to overcompensatory prey growth, large prey populations may collapse rapidly, causing subsequent predator decline through resource limitation. Ecologically, this suggests that strong cooperation can both enhance predator persistence and increase vulnerability to prey crashes, leading to highly sensitive dependence on initial population distributions.

The numerical simulations indicate that cooperation has a dual ecological role. Moderate cooperation improves hunting efficiency and enlarges the parameter region where predators can coexist with prey. However, stronger cooperation also intensifies predator–prey feedback, producing oscillatory and eventually chaotic dynamics. Consequently, cooperation does not simply stabilize predator populations; instead, it increases the complexity of the coexistence dynamics. Under sufficiently strong refuge effects or unfavorable demographic conditions, predators may still become extinct despite cooperative hunting.

5. Conclusions

Building upon the discrete host-parasitoid framework of Wu and Zhao [33], we incorporated predator hunting cooperation into the discrete-time predator-prey system with Ricker-type prey growth and prey refuge. This addition introduces nonlinear feedback in the predation term, capturing the synergistic effects of group hunting.

Analytically, we proved that when the prey growth rate is moderate ($0 < r < 2$) and the predator reproduction number satisfies $\beta b > 1$, both populations are uniformly persistent regardless of the level of cooperation. We also established that the predator-free equilibrium is globally asymptotically stable when $m_g := \inf_{y>0} g(y) > 1$. This condition means that the predator nullcline lies entirely in the region $x > 1$. For $2 < r < r_0$, we obtained global stability of the predator-extinct boundary 2-cycle under the stronger condition $m_g > \dfrac{e^{r-1}}{r}$. Thus, hunting cooperation does not alter the uniform-persistence threshold $\beta b = 1$, although it changes the geometry of the predator nullcline and therefore affects the sufficient conditions for predator extinction and the interior dynamics.

Numerical simulations reveal that the effect of predator cooperation depends strongly on the prey growth rate and the refuge fraction. For small prey growth, changes in cooperation can move the system among regular and irregular coexistence dynamics. For moderate prey growth, cooperation may promote convergence to a stable coexistence equilibrium. For large prey growth, cooperation can have a nonmonotone effect: intermediate cooperation may be associated with predator extinction, whereas stronger cooperation can restore coexistence, often in an oscillatory or chaotic form. Thus, cooperation should not be interpreted as uniformly stabilizing or uniformly beneficial; its effect depends on the ecological regime.

Moreover, bistability emerges in certain parameter regimes, where predator persistence depends not on predator density alone but on a joint prey-predator threshold. Unexpectedly, very high initial prey densities may drive the predator to extinction through overcompensatory prey dynamics that trigger

a rapid prey collapse. This highlights the model's sensitivity to initial conditions and the complex, nonlinear interplay between cooperation, refuge, and growth.

Overall, our findings demonstrate that predator hunting cooperation, when coupled with prey refuge, can both stabilize and destabilize population dynamics depending on the ecological context. The model captures a continuum of outcomes, from extinction to stable coexistence to chaos, emphasizing that cooperation, while beneficial to predator persistence under favorable conditions, can also contribute to population collapse under specific circumstances.

Two distinct collapse mechanisms are identified in our analysis. The first operates through prey overexploitation: When cooperation is strong and prey growth is high ($r = 4.5$, Figures 2(d)–(f)), cooperative predation depresses the prey population to levels insufficient to sustain predator recruitment, triggering predator extinction even though prey persist. This is not a simultaneous collapse of both populations but rather a sequential process in which predator overexploitation of prey leads to predator loss while prey recover on the boundary attractor. The second mechanism operates through initial-condition sensitivity in the bistable regime ($2c > 1$, $\beta b < 1$, Figure 5). Here, if initial prey density is very high, Ricker overcompensation causes a rapid prey crash; the cooperative predators, having depleted prey faster than a solitary predator would, are left without sufficient resources and go extinct. In this scenario, both populations experience a sharp decline in quick succession, constituting a form of coupled collapse driven jointly by cooperation-enhanced predation and prey overcompensation.

These two mechanisms have distinct ecological implications. The first suggests that intermediate levels of cooperation may be more destabilizing than either no cooperation or very strong cooperation, consistent with the nonmonotone effect of c on predator persistence observed in Figures 2(d)–(f). The second highlights that the robustness of coexistence depends critically on the initial population state, and that conservation or management interventions targeting initial predator reintroduction density must account for prey population size at the time of introduction. Introducing predators when prey are at peak abundance may, counterintuitively, increase the risk of predator extinction through the coupled overexploitation-crash mechanism described above.

The numerical simulations presented in Section 4 indicate the existence of stable periodic coexistence solutions for certain parameter regimes. These oscillatory dynamics appear to arise through the loss of stability of the positive equilibrium and through the intrinsic period-doubling structure of the Ricker prey dynamics. Depending on the parameter values, the system may exhibit periodic, quasiperiodic, or chaotic coexistence behavior.

A rigorous theoretical analysis of the existence and stability of higher-period solutions for system (2.5) is mathematically challenging because of the nonlinear cooperative predation term and the nonmonotone geometry of the nullclines when $2c > 1$. Such an analysis is beyond the scope of the present paper and will be investigated in future work.

An interesting future direction is to extend the present deterministic model to stochastic environments incorporating environmental or demographic noise [20]. Extending the present model to stochastic environments would also permit investigation of how environmental fluctuations interact with cooperative hunting and prey refuge to alter persistence thresholds and extinction probabilities.

Author contributions

Sophia R.-J. Jang: Conceptualization, methodology, supervision, writing–original draft, formal analysis, funding acquisition, writing–review and editing; Thotahewage Mihiri M. De Silva: Conceptualization, formal analysis, numerical investigation, writing–review and editing. All authors have read and approved the final version of the manuscript for publication.

Use of Generative-AI tools declaration

The authors declare they have not used Artificial Intelligence (AI) tools in the creation of this article.

Acknowledgments

The research of S. R.-J. Jang was partially supported through Travel Support for Mathematicians from the Simons Foundation under MPS-TSM-00002532.

Conflict of interest

Sophia R.-J. Jang is a Guest Editor of special issue "Recent Advances in Mathematical Biology and Dynamical Systems" for AIMS Mathematics. Sophia R.-J. Jang was not involved in the editorial review and the decision to publish this article.

References

1. L. J. S. Allen, *Introduction to mathematical biology*, Prentice-Hall, Englewood Cliffs, NJ, 2006.
2. M. T. Alves, F. M. Hilker, Hunting cooperation and Allee effects in predators, *J. Theor. Biol.*, **419** (2017), 13–22. http://dx.doi.org/10.1016/j.jtbi.2017.02.002
3. F. S. Berezovskaya, B. Song, C. Castillo-Chavez, Role of prey dispersal and refuges on predator–prey dynamics, *SIAM J. Appl. Math.*, **70** (2010), 1821–1839. https://doi.org/10.1137/080730603
4. G. Benettin, L. Galgani, A. Giorgilli, J. M. Strelcyn, Lyapunov characteristic exponents for smooth dynamical systems; a method for computing all of them. Part 1: Theory, *Meccanica*, **15** (1980), 9–20. https://doi.org/10.1007/BF02128236
5. A. A. Berryman, B. A. Hawkins, The refuge as an integrating concept in ecology and evolution, *Oikos*, **115** (2006), 192–196. https://doi.org/10.1111/j.0030-1299.2006.15188.x
6. S. Chakraborty, B. W. Kooi, B. Biswas, J. Chattopadhyay, Revealing the role of predator interference in a predator–prey system with disease in prey population, *Ecol. Complex.*, **21** (2015), 100–111. https://doi.org/10.1016/j.ecocom.2014.11.005
7. Y. H. Chou, Y. Chow, X. Hu, S. R.-J. Jang, A Ricker-type predator–prey system with hunting cooperation in discrete time, *Math. Comput. Simulat.*, **190** (2021), 570–586. https://doi.org/10.1016/j.matcom.2021.06.003
8. Y. Chow, S. R.-J. Jang, N. Yeh, Dynamics of a population in two patches with dispersal, *J. Differ. Equ. Appl.*, **24** (2018), 543–563. https://doi.org/10.1080/10236198.2018.1428962

9. Y. Chow, S. R.-J. Jang, Neimark–Sacker bifurcations in a host–parasitoid system with a host refuge, *Discrete Cont. Dyn.-B*, **21** (2018), 1713–1728. https://doi.org/10.3934/dcdsb.2016019
10. Y. Chow, S. R.-J. Jang, H. M. Wang, Cooperative hunting in a discrete predator–prey system, *Int. J. Biomath.*, **13** (2020), 2050063. https://doi.org/10.48550/arXiv.1808.00182
11. J. M. Cushing, *An introduction to structured population dynamics*, SIAM, Philadelphia, 1998.
12. L. A. Dugatkin, *Cooperation among animals: An evolutionary perspective*, Oxford: Oxford University Press, 1997.
13. S. Elaydi, A. A. Yakubu, Basins of attraction of stable cycles, *J. Differ. Equ. Appl.*, **8** (2002), 755–760. https://doi.org/10.1080/10236190290027666
14. S. Elaydi, *An introduction to difference equations*, 3 Eds., New York: Springer, 2005.
15. J. E. Franke, A. A. Yakubu, SIS epidemic attractors in periodic environments, *J. Biol. Dynam.*, **1** (2007), 394–412. https://doi.org/10.1080/17513750701605630
16. S. Ghimire, X. S. Wang, Competition and cooperation on predation: Bifurcation theory of mutualism, *J. Biol. Syst.*, **29** (2021), 49–73. https://doi.org/10.1142/S0218339021500030
17. E. A. Grove, G. Ladas, *Periodicities in nonlinear difference equations*, Boca Raton: Chapman and Hall/CRC Press, 2004. https://doi.org/10.1201/9781420037722
18. M. P. Hassell, *The dynamics of Arthropod predator–prey systems*, Princeton: Princeton University Press, 1978.
19. J. Hofbauer, J. So, Uniform persistence and repellors for maps, *P. Am. Math. Soc.*, **107** (1989), 1137–1142.
20. H. Hu, Distributed constrained optimization for nonlinear stochastic multi-agent systems: Application to resource allocation, *Complex Syst. Stabil. Control*, **1** (2025), 5. https://doi.org/10.53941/cssc.2025.100005
21. Y. Huang, F. Chen, L. Zhong, Stability analysis of a prey–predator model with Holling type III response function incorporating a prey refuge, *Appl. Math. Comput.*, **182** (2006), 672–683. https://doi.org/10.1016/j.amc.2006.04.030
22. S. R.-J. Jang, Backward bifurcation in a discrete SIS model with vaccination, *J. Biol. Syst.*, **16** (2008), 479–494. https://doi.org/10.1142/S0218339008002630
23. S. R.-J. Jang, W. Zhang, V. Larriva, Cooperative hunting in a predator–prey system with Allee effects in the prey, *Nat. Resour. Model.*, **31** (2018), e12194. https://doi.org/10.1111/nrm.12194
24. S. R.-J. Jang, A. M. Yousef, Effects of prey refuge and predator cooperation on a predator–prey system, *J. Biol. Dynam.*, **17** (2023), 2242372. https://doi.org/10.1080/17513758.2023.2242372
25. M. Kot, *Elements of mathematical ecology*, Cambridge: Cambridge University Press, 2001.
26. G. Mandal, L. N. Guin, S. Chakravarty, R. Han, Dynamic complexities in a predator–prey model with prey refuge influenced by double Allee effects, *Math. Comput. Simulat.*, **227** (2025), 527–552. https://doi.org/10.1016/j.matcom.2024.08.015
27. R. M. May, Biological populations with nonoverlapping generations: Stable points, stable cycles, and chaos, *Science*, **186** (1974), 645–647.

28. J. Maynard-Smith, *Models in ecology*, Cambridge: Cambridge University Press, 1974.

29. W. W. Murdoch, C. J. Briggs, R. M. Nisbet, *Consumer–resource dynamics*, Princeton: Princeton University Press, 2003.

30. W. E. Ricker, Stock and recruitment, *J. Fish. Res. Board Can.*, **11** (1954), 559–623.

31. S. Saha, G. Samanta, Analysis of a predator–prey model with herd behavior and disease in prey incorporating prey refuge, *Int. J. Biomath.*, **12** (2019), 1950007. https://doi.org/10.1142/S1793524519500074

32. A. Sih, Prey refuges and predator–prey stability, *Theor. Popul. Biol.*, **31** (1987), 1–12.

33. D. Wu, H. Zhao, Global qualitative analysis of a discrete host–parasitoid model with refuge and strong Allee effects, *Math. Method. Appl. Sci.*, **41** (2018), 2039–2062. https://doi.org/10.1002/mma.4731

AIMS Press