In this study, we propose and investigate a two-stage population model with cannibalism. It is shown that cannibalism can destabilize and lower the magnitude of the interior steady state. However, it is proved that cannibalism has no effect on the persistence of the population. Based on this model, we study two systems of predator–prey interactions where the prey population is cannibalistic. A sufficient condition based on the nontrivial boundary steady state for which both populations can coexist is derived. It is found via numerical simulations that introduction of the predator population may either stabilize or destabilize the prey dynamics, depending on cannibalism coefficients and other vital parameters.

Keywords: stage structure; cannibalism; inherent net reproductive number; uniform persistence

AMS Subject Classification: 92D25, 39A30

1. Introduction

Cannibalism has been a common practice in natural populations and is frequently observed in fish species [8]. For example, adult Atlantic cod usually feed on large numbers of their young [2]. The Atlantic cod, *Gadus morhua*, is a species found on both sides of the North Atlantic. In the Northwest Atlantic, cod occur from Greenland to North Carolina. Cod may attain lengths of up to 130 cm and weights of 25–35 kg. Maximum age is in excess of 20 years. Sexual maturity is attained between the ages of two and four with spawning occurring during winter and early spring. The cod goes through several life stages: eggs, larvae and pelagic juveniles, juveniles, and adults. The adult size averages 2.3–3.6 kg. Recent studies suggest the importance of habitat segregation of age one cod from older year classes in order to avoid cannibalism by the older cod (http://www.nefsc.noaa.gov/publications/tm/tm124/tm124.pdf).

On the other hand, the cod is also preyed upon by some other species of larger fish. This population interaction results in a predator–prey system with the prey population being cannibalistic. There are many existing mathematical models in the literature including partial/ordinary differential equations and difference equations with different modeling assumptions exploring cannibalism [3,5–7,9,10,13–15,25]. It has been concluded in these mathematical models that...
cannibalism can have important effects on population dynamics. Whether cannibalism can stabilize or destabilize the systems depends on individual models and how cannibalism is incorporated into the systems.

In this study, we consider a population in which individuals can be classified as either juveniles or adults, where juveniles may become adults or remain in the juvenile stage after one unit of time if they survive. It is assumed that only adults can reproduce and adults may live for more than one unit of time and reproduce more than once. Moreover, adults may feed on their juveniles so that the population may be cannibalistic. For this two-stage model, it is proved that the system exhibits only equilibrium dynamics if the population is not cannibalistic. If the adult prey population practices cannibalism, then the model cannot undergo a discrete Hopf (Neimark-Sacker) bifurcation when the interior steady state loses its stability. The only possible bifurcation is a period-doubling bifurcation. As a result, cannibalism is an intrinsic destabilizing mechanism for this single-species population. However, it is shown that the population remains persistent even if the mechanisms of cannibalism are large. Motivated by the earlier biological example, we then consider a system of predator–prey interactions in which the prey population may be cannibalistic. A sufficient condition based on the nontrivial boundary steady state for which both populations can coexist indefinitely is derived. Moreover, numerical simulations indicate that cannibalism may stabilize or destabilize the interactions depending on the magnitudes of cannibalism and other vital parameters.

In the following section, we present a two-stage prey population model and its analysis. In Section 3, we study two systems of predator–prey interactions in which the prey population may be cannibalistic. Numerical simulations with specific functions are provided in Section 4. The final section summarizes these results.

2. A single-species model with cannibalism

In this section, we shall construct a single-species two-stage population model with cannibalism and discuss the effect of cannibalism on population dynamics. The population under this investigation has two distinct stages: juvenile and adult. Let \( x_1(t) \) and \( x_2(t) \) denote the juvenile and adult populations at time \( t = 0, 1, \ldots \), respectively. The adults may survive for more than one unit of time with a constant mortality rate \( \mu_2 \), \( 0 < \mu_2 < 1 \). We assume only adults can reproduce and adults may reproduce more than once with a per capita fertility rate \( g \) depending only on the adult population size and satisfying (H1). The juvenile survival probability per unit time interval is denoted by \( s_1 \), \( 0 < s_1 < 1 \). The surviving juveniles may become adults with a constant probability \( p_1 \), where \( 0 < p_1 < 1 \). The unit time in the model may be a day, a month, a year, a longer or a shorter time span depending on the characteristic of the species and also on the available data. Since adults are defined to be the individuals that are reproductive, a surviving juvenile may either remain in the same juvenile stage with probability \( p_1 \) or move to the adult class with probability \( 1 - p_1 \), depending on the species, the unit time, and also on the structure variable. If the structure variable is the age, and the species can reproduce say when they are more than three years old and the time unit is a year, then a newborn will remain in the juvenile stage for a few time steps if it survives. On the other hand, if the structure variable is the size, say the total length (in terms of inches) of a fish, then the newborn are eggs. The eggs will go through larval and juvenile stages. If, for example, the females mature at 11–13 inches in total length and the unit time is a year, then an egg may take 2–3 years for it to mature if the egg survives, depending on the annual growth rate of the fish species. Furthermore, the structure variable may be the weight of an individual instead of the length, depending on the population and its important characteristic. However, since it is
usually very difficult to determine an individual’s age, size (length, biomass, weight, etc.) may be a more realistic measurement and is more suitable to be used as the structure variable. In what follows, we implicitly assume that size is the stage variable, which can be either length, weight, or biomass, etc.

Motivated by the biological example of Atlantic cod and also by many other species that practicing cannibalism [8], we assume in this population that adults may feed on the juveniles. It is found in the study by Otter and Folkvord [21] on Atlantic cod that larger conspecifics would easily cannibalize a prey that is 75% of the body depth of its mouth gape. Therefore, as the juvenile increases its size, it becomes harder for the adult to prey upon it. Since surviving juveniles can either remain in the juvenile stage or move to the adult class after one unit of time depending on their sizes, the cannibalism coefficients may be different for these juveniles and are denoted by \( c_1 \) and \( c_2 \), respectively, where \( c_i \geq 0 \) for \( i = 1, 2 \). One may see from the above discussion [21] that \( c_1 \) is generally greater than \( c_2 \). However, we do not assume this relation of \( c_1 \geq c_2 \) in the model presented below. If \( c_1 = c_2 = 0 \), then the population is not cannibalistic. The dynamics of this single two-stage population are described by the following system of difference equations:

\[
\begin{align*}
x_1(t+1) &= x_2(t)g(x_2(t)) + s_1(1-p_1)x_1(t)e^{-c_1x_2(t)} \\
x_2(t+1) &= sp_1x_1(t)e^{-c_2x_2(t)} + (1-\mu_2)x_2(t),
\end{align*}
\]

where \( 0 < s_1, \mu_2 < 1, c_i \geq 0, i = 1, 2, \) and \( 0 < p_1 < 1 \). We may rewrite Equation (1) as

\[
\begin{align*}
x_1(t+1) &= x_2(t)g(x_2(t)) + ax_1(t)e^{-c_1x_2(t)} \\
x_2(t+1) &= bx_1(t)e^{-c_2x_2(t)} + (1-\mu_2)x_2(t) \\
x_1(0), x_2(0) &\geq 0,
\end{align*}
\]

where \( a > 0, b > 0, a + b < 1, 0 < \mu_2 < 1, \) and \( c_i \geq 0, i = 1, 2 \). The per capita fertility rate \( g \) is assumed to satisfy the following conditions

\begin{itemize}
  \item (H1) \( g \in C^2[0, \infty), \ g(0) = a > 0, \ g'(x) < 0, \ g(x) > 0, \ (xg(x))' > 0 \) for \( x \geq 0 \) and \( \lim_{x \to \infty} xg(x) = l < \infty \).
\end{itemize}

The assumption \( g'(x) < 0 \) for \( x \geq 0 \) models intra-specific competition of the population. Adults within the population have to compete for resources to reproduce when population size or density is larger. Since \( x_2g(x_2) \) is the number of new births produced by all the adults, it is reasonable to assume that the total number of births \( x_2g(x_2) \) increases with increasing adult population size \( x_2 \). However, the total number of newborns \( x_2g(x_2) \) remains bounded when the adult population size \( x_2 \) is large due to limited resources. These biological considerations motivate our assumptions imposed for the per capita fertility rate \( g \) in (H1). The classical Beverton–Holt fertility rate \( g(x) = l\alpha/(l + \alpha x) \) frequently used in the study of fishery models satisfies all the conditions given in (H1).

We shall study the dynamical behaviour of system (2) and the effects of cannibalism on population dynamics. To this end, we define the usual partial ordering ‘\( \leq \)’ on \( \mathbb{R}_+^2 \) by \( (x_1, x_2) \leq (y_1, y_2) \) if and only if \( x_i \leq y_i \) for \( i = 1, 2 \), \( x_1, x_2 < (y_1, y_2) \) if \( (x_1, x_2) \leq (y_1, y_2) \) and \( (x_1, x_2) \neq (y_1, y_2) \), and \( (x_1, x_2) \ll (y_1, y_2) \) if and only if \( x_i < y_i \) for \( i = 1, 2 \). A continuous map \( G : \mathbb{R}_+^2 \to \mathbb{R}_+^2 \) is said to be monotone on \( \mathbb{R}_+^2 \) if \( G(x_1, x_2) \leq G(y_1, y_2) \) whenever \( (x_1, x_2) \leq (y_1, y_2) \), and strongly monotone if \( G(x_1, x_2) \ll G(y_1, y_2) \) whenever \( (x_1, x_2) \ll (y_1, y_2) \).

Let

\[
A = \begin{pmatrix} a & 0 \\ b & 1 - \mu_2 \end{pmatrix} \quad \text{and} \quad L = \begin{pmatrix} l \\ 0 \end{pmatrix}.
\]

Using \( A \) and \( L \), we first show that the solutions of Equation (2) remain non-negative and are bounded.
Proposition 2.1  Solutions of Equation (2) remain non-negative and are bounded for \( t > 0 \).

Proof  The proof of non-negativity of solutions is trivial. To prove the boundedness, we let \( X(t) = (x_1(t), x_2(t)) \) be a solution of Equation (2). Then for \( t \geq 0 \),

\[
X^T(t + 1) \leq AX^T(t) + L,
\]

where \( T \) denotes the matrix transpose. Inductively, one has for \( t \geq 0 \)

\[
X^T(t + 1) \leq A^{t+1}X^T(0) + \sum_{i=0}^{t} A^i L = A^{t+1}X^T(0) + (I - A)^{-1}(I - A^{t+1})L.
\]

Since \( \lim_{r \to \infty} A^r \) is the zero matrix, we have

\[
\limsup_{t \to \infty} X(t) \leq X_M,
\]

where

\[
X_M = (I - A)^{-1}L.
\]

This completes the proof. ■

A simple computation yields \( X_M = (l/(1 - a)\mu_2)(\mu_2, b) \), and we rewrite \( X_M \) componentwise as \((x_{M1}, x_{M2})\). The extinction steady state \( E_0 = (0, 0) \) always exists. Its stability can be determined from the Jacobian matrix of Equation (2) evaluated at \( E_0 \) given by

\[
J(E_0) = \begin{pmatrix} a & \alpha \\ b & 1 - \mu_2 \end{pmatrix}.
\]

Applying Jury conditions [1] to \( J(E_0) \), we see that \( E_0 \) is locally asymptotically stable if

\[
\text{tr} \, J(E_0) = a + 1 - \mu_2 < 1 + \det J(E_0) = 1 + a(1 - \mu_2) - ba < 2.
\]

The second inequality is clearly true and the first inequality is equivalent to \( ba/\mu_2 + a < 1 \). Therefore, \( E_0 \) is locally asymptotically stable if \( ba/\mu_2 + a < 1 \) and unstable if \( ba/\mu_2 + a > 1 \). Furthermore, the \( x_2 \) component of an interior steady state can be shown to satisfy the following equation

\[
\frac{b}{\mu_2} g(x_2)e^{-c_2x_2} + ae^{-c_1x_2} = 1.
\]

Since \( g(0) = \alpha \) and \( g'(x) < 0 \) for \( x \geq 0 \), it follows that Equation (7) has a positive solution if and only if

\[
\frac{ba}{\mu_2} + a > 1.
\]

Notice that the above inequality is equivalent to

\[
\frac{ab}{(1 - a)\mu_2} > 1.
\]

Define the threshold

\[
\mathcal{R}_0 = \frac{ab}{(1 - a)\mu_2}.
\]

Then

\[
\mathcal{R}_0 = \frac{ab}{\mu_2} + \frac{aab}{\mu_2} + \frac{a^2ab}{\mu_2} + \cdots.
\]

\( \mathcal{R}_0 \) can be interpreted as the inherent net reproductive number of the population. It is the average number of offspring that an individual juvenile can reproduce over its lifetime when the population
size is very small. Observe that Equation (2) has an interior steady state \( E_1 = (\bar{x}_1, \bar{x}_2) \) if and only if \( R_0 > 1 \). The interior steady state \( E_1 = (\bar{x}_1, \bar{x}_2) \) is unique whenever it exists, where \( \bar{x}_2 \) satisfies Equation (7) and

\[
\bar{x}_1 = \frac{\mu_2 \bar{x}_2}{\mu_1} e^{c_2 \bar{x}_2}.
\]

(The proof of the following theorem is trivial and is omitted.)

**Theorem 2.2** If \( R_0 < 1 \), then \( E_0 = (0, 0) \) is globally asymptotically stable for system (2) in \( \mathbb{R}^2_+ \).

Suppose the inherent net reproductive number of the population is larger than one, i.e. \( R_0 > 1 \). Then \( E_0 \) is unstable and Equation (2) has a unique interior steady state \( E_1 = (\bar{x}_1, \bar{x}_2) \). One can easily verify that \( \{E_0\} \) is isolated and the stable manifold \( W^s_0 \) of \( E_0 \),

\[
W^s_0 = \left\{ (x_1, x_2) \in \mathbb{R}^2_+ : \lim_{t \to \infty} (x_1(t), x_2(t)) = E_0 \right\},
\]

consists only of \( E_0 \) when \( R_0 > 1 \). Recall that an invariant set \( B \) is called isolated if there exists a closed neighbourhood \( M \) of \( B \) such that \( B \) is the maximal invariant set in \( M \).

Let \( X(t) = (x_1(t), x_2(t)) \) be a solution of Equation (2). We rewrite Equation (2) as

\[
X^T(t + 1) = A(X(t))X^T(t),
\]

where

\[
A(X) = \begin{pmatrix} ae^{-c_1 x_2} & g(x_2) \\ be^{-c_2 x_2} & 1 - \mu_2 \end{pmatrix}.
\]

**Lemma 2.3** Let \( R_0 > 1 \). Then \( \{E_0\} \) is isolated in \( \mathbb{R}^2_+ \) and \( W^s_0 = \{E_0\} \).

**Proof** Let \( X(t) = (x_1(t), x_2(t)) \) be a solution of Equation (2) and let 0 denote the zero number and also of the zero vector simultaneously depending on the context. Observe that \( A(0) = J(E_0) \) is primitive. Let \( \lambda_0 \) be the Perron eigenvalue of \( A(0) \) and \( v \) and \( w^T \) be strictly positive right and left eigenvectors of \( A(0) \) belonging to \( \lambda_0 \), respectively. Notice \( \lambda_0 > 1 \) since \( R_0 > 1 \). Fix any \( \lambda \in (1, \lambda_0) \), we have \( w^T A(0) > \lambda w^T \). By the continuity of \( A(X) \), there exists a closed neighbourhood \( U \) of \( E_0 \) such that

\[
w^T A(X) > \lambda w^T \quad \text{for all} \quad X \in U.
\]

If \( \{E_0\} \) is not isolated, then \( U \) contains a compact invariant set \( K \) with \( \{E_0\} \subsetneq K \). Let \( X(0) \in K \) and \( X(0) \neq E_0 \). Then \( X(t) \in K \) and

\[
w^T X(t + 1) = w^T A(X(t))X(t) > \lambda^{t+1} w^T X(0) \quad \text{for} \quad t \geq 0.
\]

Since \( \lambda > 1 \) and \( w^T X(t) > 0 \), we have \( \lim_{t \to \infty} w^T X(t) = \infty \) and obtain a contradiction. Therefore, \( \{E_0\} \) is isolated in \( \mathbb{R}^2_+ \).

To prove \( W^s_0 = \{E_0\} \), suppose on the contrary there exists \( Z(0) \neq E_0 \) in \( W^s_0 \). Recall that \( \{E_0\} \) is isolated in \( \mathbb{R}^2_+ \) and there exists a closed neighbourhood \( U \) of \( E_0 \) such that \( w^T A(X) > \lambda w^T \) for all \( X \in U \), where \( \lambda > 1 \). It follows that there exists \( t_0 > 0 \) such that \( Z(t) \in U \) for \( t \geq t_0 \). By a similar proof as that of \( \{E_0\} \) being isolated, one can show that \( \lim_{t \to \infty} w^T Z(t) = \infty \) and obtain a contradiction. Therefore, we conclude that \( W^s_0 = \{E_0\} \).
Let $\mathcal{R}_0 > 1$. The Jacobian matrix of Equation (2) evaluated at $E_1 = (\bar{x}_1, \bar{x}_2)$, written in terms of $\bar{x}_2$, has the following form

$$
J(E_1) = \begin{pmatrix}
    a e^{-c_1 \bar{x}_2} & g(\bar{x}_2) + \bar{x}_2 g'(\bar{x}_2) - \frac{ac_1 \mu_2}{b} \bar{x}_2 e^{(c_2-c_1)\bar{x}_2} \\
    b e^{-c_2 \bar{x}_2} & -c_2 \mu_2 \bar{x}_2 + 1 - \mu_2
\end{pmatrix}.
$$

(11)

Based on the Jury conditions [1], $E_1$ is locally asymptotically stable if

$$
|\text{tr } J(E_1)| < 1 + \det J(E_1) < 2,
$$

(12)

where $\text{tr } J(E_1) < 1 + \det J(E_1)$ is equivalent to

$$
(a e^{-c_1 \bar{x}_2} - 1)c_2 \mu_2 \bar{x}_2 < -b \bar{x}_2 e^{-c_2 \bar{x}_2} g'(\bar{x}_2) + ac_1 \mu_2 \bar{x}_2 e^{-c_1 \bar{x}_2}.
$$

(13)

Since $0 < a < 1$ and $g'(\bar{x}_2) < 0$, $\text{tr } J(E_1) < 1 + \det J(E_1)$ always holds by Equation (13).

Let $E_1^0 = (\bar{x}_1^0, \bar{x}_2^0)$ denote the corresponding interior steady state when $c_1 = c_2 = 0$. Then

$$
J(E_1^0) = \begin{pmatrix}
    a & g(\bar{x}_2^0) + \bar{x}_2^0 g'(\bar{x}_2^0) \\
    b & 1 - \mu_2
\end{pmatrix},
$$

where

$$
\text{tr } J(E_1^0) = a + 1 - \mu_2 > 0,
$$

and by (H1)

$$
\det J(E_1^0) = a(1 - \mu_2) - b(g(\bar{x}_2^0) + \bar{x}_2^0 g'(\bar{x}_2^0)) < a(1 - \mu_2) < 1.
$$

Therefore, $E_1^0$ is locally asymptotically stable by Equations (12) and (13).

In the following, we show that $E_1^0$ is globally asymptotically stable for Equation (2) if $\mathcal{R}_0 > 1$. Since the second iteration of Equation (2) cannot be decoupled, the technique used in [13] cannot be applied to system (2). Consider a two-dimensional first-order system

$$
x_1(t+1) = g_1(x_1(t), x_2(t))
$$

$$
x_2(t+1) = g_2(x_1(t), x_2(t)),
$$

where $g_i \in C^2(\mathbb{R}_+^2, \mathbb{R}_+)$ for $i = 1, 2$. If $(\partial g_i/\partial x_j)(x_1, x_2) \geq 0$ on $\mathbb{R}_+^2$ for $i, j = 1, 2$, then it can be easily shown that the map $G = (g_1, g_2)$ induced by the system is monotone on $\mathbb{R}_+^2$. Indeed, let $X(0) = (x_1(0), x_2(0)) \leq Y(0) = (y_1(0), y_2(0))$ in $\mathbb{R}_+^2$. Then $x_i(t) \leq y_i(t)$ for $i = 1, 2$, i.e., $X(1) \leq Y(1)$ and the map $G$ is monotone on $\mathbb{R}_+^2$. Using this observation, one can see that system (2) is monotone when $c_1 = c_2 = 0$. There are several techniques (cf. [23]) available to prove global asymptotic stability of an interior steady state for two-dimensional monotone systems.

Let

$$
F(x_1, x_2) = (f_1(x_1, x_2), f_2(x_1, x_2))
$$

be the map induced by Equation (2), where

$$
f_1(x_1, x_2) = x_2 g(x_2) + a x_1 e^{-c_1 x_2} \quad \text{and} \quad f_2(x_1, x_2) = b x_1 e^{-c_2 x_2} + (1 - \mu_2) x_2.
$$

Fix any $X(0) \in \mathbb{R}_+^2$ and let $X \in \omega(X(0))$, where $\omega(X(0))$ denotes $\omega$-limit set of $X(0)$. Using $E_0$ is a repeller, we shall construct two particular vectors such that $X$ lies inside the order interval
formed by them and one of the vectors is monotone increasing while the other is monotone decreasing under forward iterations and concludes our global stability result (cf. [23]).

**Theorem 2.4** Let \( \mathcal{R}_0 > 1 \) and \( c_1 = c_2 = 0 \). Then the interior steady state \( E_1^0 = (\bar{x}_1^0, \bar{x}_2^0) \) is globally asymptotically stable in \( \mathbb{R}_+^2 \setminus \{E_0\} \).

**Proof** It is sufficient to prove that \( E_1^0 \) is globally attracting in \( \mathbb{R}_+^2 \setminus \{E_0\} \). Observe that \( F \) is monotone (indeed strongly monotone) on \( \mathbb{R}_+^2 \) since \( c_1 = c_2 = 0 \), and by Equation (5)

\[
F^T(X_M) \leq A X_M^T + L = X_M^T. \tag{14}
\]

Since solutions distinct from \( E_0 \) and starting on the coordinate axes will be mapped into the interior of \( \mathbb{R}_+^2 \) in at most two forward time steps, it is sufficient to consider \( X(0) \in \text{int}(\mathbb{R}_+^2) \), the interior of \( \mathbb{R}_+^2 \). We shall show that \( \lim_{t \to \infty} X(t) = E_1^0 \). Observe that \( E_0 \not\in \omega(X(0)) \). For otherwise, \( \{E_0\} \not\subset \omega(X(0)) \) since \( W_0^c = \{E_0\} \) by Lemma 2.3. It then follows from the discrete Butler–McGhee lemma [12, Corollary 2.4] that \( \omega(X(0)) \) would contain a point of \( W_0^c \) distinct from \( E_0 \). This is impossible since \( W_0^c = \{E_0\} \). Therefore, \( E_0 \not\in \omega(X(0)) \). Let \( X \in \omega(X(0)) \) be arbitrary but fixed. Then \( X \gg 0 \). If we can find \( Y \gg 0 \) such that

\[
Y \leq X \leq X_M \quad \text{and} \quad F(Y) \geq Y, \tag{15}
\]

then \( F^t(Y) \leq F^t(X) \leq F^t(X_M) \) for \( t \geq 0 \) by the monotonicity of \( F \). Moreover, \( \{F^t(X_M)\} \) and \( \{F^t(Y)\} \) are decreasing and increasing sequences, respectively, by Equations (14) and (15). Therefore, \( \lim_{t \to \infty} F^t(Y) \) and \( \lim_{t \to \infty} F^t(X_M) \) exist and are positive fixed points of \( F \) by the continuity of \( F \). It follows that the fixed point is \( E_1^0 \), and as a result, \( \lim_{t \to \infty} F^t(X) = E_1^0 \). We conclude that \( \omega(X(0)) = \{E_1^0\} \) since \( E_1^0 \) is locally asymptotically stable. Therefore, \( E_1^0 \) is globally attracting in \( \mathbb{R}_+^2 \setminus \{E_0\} \) as \( X(0) \in \text{int}(\mathbb{R}_+^2) \) was arbitrary. Notice \( X \leq X_M \) is trivial since \( X \in \omega(X(0)) \) and Equation (4) holds. It remains to prove the existence of \( Y = (y_1, y_2) \) satisfying Equation (15).

Toward this end, we let \( Y = \epsilon v \), where \( v \) is a strictly positive right eigenvector of \( A(0) = J(E_0) \) belonging to the Perron eigenvalue \( \lambda_0 \) and \( \epsilon > 0 \) is sufficiently small so that \( Y \leq X \) and \( Y \) is close to \( E_0 \). In addition, we need to choose an appropriate \( \epsilon > 0 \) such that \( F(Y) \geq Y \). Notice \( Y \gg 0 \), and \( Y \) is a right eigenvector of \( J(E_0) \) with respect to \( \lambda_0 > 1 \). By the Taylor series expansion around \( E_0 \), there exist vectors \( \zeta_i \), \( i = 1, 2 \), between \( E_0 \) and \( Y \), such that \( f_i(Y) = (\partial f_i / \partial x_1)(\zeta_1) y_1 + (\partial f_i / \partial x_2)(\zeta_2) y_2 \), \( i = 1, 2 \). Notice that \( \zeta_i \) depends on \( Y \) and thus \( \zeta_i \) depends on \( \epsilon \) for \( i = 1, 2 \). Since \( (\partial f_i / \partial x_j) \) is continuous and \( \lambda_0 > 1 \), we can choose \( \epsilon, \delta > 0 \) such that

\[
(\lambda_0 - 1) y_i > \delta (y_1 + y_2) \quad \text{for} \quad i = 1, 2, \tag{16}
\]

and

\[
\frac{\partial f_i}{\partial x_j}(\zeta_i) > \delta \frac{\partial f_i}{\partial x_j}(E_0) \quad \text{for} \quad i, j = 1, 2, 3. \tag{17}
\]

Therefore, by Equations (16) and (17), we have

\[
F^T(Y) = \begin{pmatrix}
\frac{\partial f_1}{\partial x_1}(\zeta_1) & \frac{\partial f_1}{\partial x_2}(\zeta_1) \\
\frac{\partial f_2}{\partial x_1}(\zeta_2) & \frac{\partial f_2}{\partial x_2}(\zeta_2)
\end{pmatrix}
\begin{pmatrix}
y_1 \\
y_2
\end{pmatrix}
\]

\[
> J(E_0)Y^T - \begin{pmatrix}
\delta & \delta \\
\delta & \delta
\end{pmatrix} Y^T
\]

\[
= \lambda_0 Y^T - \begin{pmatrix}
\delta & \delta \\
\delta & \delta
\end{pmatrix} Y^T
\]

\[
> Y^T.
\]
Consequently, the existence of $Y$ is shown and this completes the proof of global attractability of $E^0_1$. \[\square\]

We conclude from Theorem 2.4 that the population will stabilize at the equilibrium level $E^0_1$ when the population is not cannibalistic and the inherent net reproductive number $R_0$ is greater than one. From perturbation theory, it is expected that $E_1$ remains globally asymptotically stable when $c_i > 0$, $i = 1, 2$, are sufficiently small. However, how small $c_1$ and $c_2$ should be in order for $E_1$ to be globally asymptotically stable is unknown. We next derive a sufficient condition based on the magnitude of $c_1$ and $c_2$ for which $E_1$ is globally asymptotically stable. We shall restrict $c_1$ and $c_2$ so that the map $F$ induced by Equation (2) is monotone on $[0, x_{M1}] \times [0, x_{M2}]$. Then by a similar argument as in the proof of Theorem 2.4, one can show that $E_1$ is globally attracting in $(0, x_{M1}] \times (0, x_{M2}]$.

To this end, we make the following assumption:

$$
\frac{d^2(xg(x))}{dx^2} \leq 0 \text{ for } x \geq 0. \tag{18}
$$

Notice that Equation (18) is satisfied by a Beverton–Holt function $g(x) = a/(1 + \gamma x)$, where $\gamma, \alpha > 0$. Therefore, the assumption imposed in Equation (18) is biologically reasonable. We shall find $c_1$ and $c_2$ such that $(\partial f_i/\partial x_j)(x_1, x_2) \geq 0$ on $[0, x_{M1}] \times [0, x_{M2}]$ for $i, j = 1, 2$. Clearly,

$$
\frac{\partial f_1}{\partial x_1} = ae^{-c_1 x_2} > 0 \text{ and } \frac{\partial f_2}{\partial x_1} = be^{-c_2 x_2} > 0 \text{ for all } x_1, x_2 \geq 0.
$$

Furthermore, by Equation (18),

$$
\frac{\partial f_1}{\partial x_2} = -ac_1 x_1 e^{-c_1 x_2} + g(x_2) + x_2 g'(x_2) \geq -ac_1 x_1 M_1 + g(x_{M2}) + x_{M2} g'(x_{M2}).
$$

Setting the right-hand side of the above inequality greater than or equal to 0 and solving for $c_1$, we obtain

$$
c_1 \leq c_{10} := \frac{g(x_{M2}) + x_{M2} g'(x_{M2})}{a x_{M1}}. \tag{19}
$$

i.e. if $c_1 \leq c_{10}$, then $\partial f_1/\partial x_2 \geq 0$ for $(x_1, x_2) \in [0, x_{M1}] \times [0, x_{M2}]$. Similarly,

$$
\frac{\partial f_2}{\partial x_2} = -bc_2 x_1 e^{-c_2 x_2} + 1 - \mu_2 \geq -bc_2 x_{M1} + 1 - \mu_2.
$$

Setting the right-hand side of the above inequality greater than or equal to 0 and solving for $c_2$ yield

$$
c_2 \leq c_{20} := \frac{1 - \mu_2}{b x_{M1}}. \tag{20}
$$

That is, if $c_2 \leq c_{20}$, then $\partial f_2/\partial x_2 \geq 0$ for $(x_1, x_2) \in [0, x_{M1}] \times [0, x_{M2}]$. Assume Equations (19) and (20) hold. Then $\partial f_i/\partial x_j(x_1, x_2) \geq 0$ for $i, j = 1, 2$ and $(x_1, x_2) \in [0, x_{M1}] \times [0, x_{M2}]$, and therefore $F$ is monotone on $[0, x_{M1}] \times [0, x_{M2}]$.

Moreover, by applying Jury conditions, it can be verified that $E_1$ is locally asymptotically stable when $c_i \leq c_{i0}$ for $i = 1, 2$. Indeed, $\text{tr } J(E_1) > 0$ and Equation (13) holds. It remains to verify that $\det J(E_1) < 1$. But this is trivial since

$$
\det J(E_1) \leq ae^{-c_1 x_2}(-bc_2 x_1 + 1 - \mu_2) < a(1 - \mu_2) < 1
$$

by our choice of $c_i$ for which $\partial f_i/\partial x_2 \geq 0$ and $\partial f_2/\partial x_1 \geq 0$. Therefore, $E_1$ is locally asymptotically stable and hence $E_1$ globally asymptotically stable in $(0, x_{M1}] \times (0, x_{M2}]$. Since $\omega$-limit set
of any solution of Equation (2) lies in \([0, x_{M1}] \times [0, x_{M2}]\) by Equation (4), we have the following result.

**Theorem 2.5** Let \(R_0 > 1\) and assume Equations (18 – 20) hold. Then the interior steady state \(E_1\) is globally asymptotically stable in \(\mathbb{R}_+^2 \setminus \{E_0\}\).

Although \(E_1\) is globally asymptotically stable when \(c_i \leq c_{i0}\) for \(i = 1, 2\), \(E_1\) may lose its stability as either \(c_1\) or \(c_2\) increases further beyond \(c_{i0}\) or \(c_{20}\), respectively. On the other hand, it can be shown that the population can persist indefinitely if \(R_0 > 1\). That is, there exists \(\eta > 0\) such that the population distribution satisfies \(\lim \inf_{t \to \infty} x_i(t) > \eta, i = 1, 2\), whenever \(x_i(0) > 0\) for \(i = 1, 2\).

**Theorem 2.6** If \(R_0 > 1\), then system (2) is uniformly persistent.

**Proof** We apply Theorem 4.1 of [12] to show that Equation (2) is uniformly persistent with respect to \(H = \partial \mathbb{R}_+^2\), the boundary of \(\mathbb{R}_+^2\). Since system (2) is point dissipative and completely continuous, Equation (2) has a global attractor \(\mathcal{X}\) by Theorem 2.12 of [11]. Moreover, \(\mathbb{R}_+^2 \setminus H\) is positively invariant and the maximal compact invariant set in \(H\) is \(\mathcal{M} = \{E_0\} \subset \mathcal{X}\). We need to verify that \(\{E_0\}\) is isolated in \(\mathcal{X}\) and the stable set of \(E_0\) is contained in \(H\). Since \(\mathcal{X}\) is closed and \(\{E_0\}\) is isolated in \(\mathbb{R}_+^2\) by Lemma 2.3, \(\{E_0\}\) is isolated in \(\mathcal{X}\). Moreover, in Lemma 2.3, we showed that \(W_0^s = \{E_0\} \subset H\). Therefore, Equation (2) is uniformly persistent with respect to \(H\) by Theorem 4.1 of [12].

We next investigate the impact of cannibalism on the magnitude of the interior equilibrium. It is clear from Equation (7) that \(\bar{x}_2\) is a strictly decreasing function of \(c_1\) and \(c_2\). However, it is not easy to determine this for \(\bar{x}_1\). Applying implicit differentiation with respect to \(c_1\) and \(c_2\) in Equation (7) yields

\[
\frac{\partial \bar{x}_2}{\partial c_1} = \frac{\mu_2 \bar{x}_2 e^{(c_2 - c_1)\bar{x}_2}}{bg'(\bar{x}_2) - bc_2 g(\bar{x}_2) - ac_1 \mu_2 e^{(c_2 - c_1)\bar{x}_2}} < 0
\]  

(21)

and

\[
\frac{\partial \bar{x}_2}{\partial c_2} = \frac{b \bar{x}_2 g(\bar{x}_2)}{bg'(\bar{x}_2) - bc_2 g(\bar{x}_2) - ac_1 \mu_2 e^{(c_2 - c_1)\bar{x}_2}} < 0.
\]  

(22)

Using these and applying implicit differentiation to \(\bar{x}_1\) in Equation (9), we obtain

\[
\frac{\partial \bar{x}_1}{\partial c_1} = \frac{\mu_2 \bar{x}_2 e^{c_2 \bar{x}_2} (1 + c_2 \bar{x}_2)}{b} \frac{\partial \bar{x}_2}{\partial c_1} < 0
\]  

(23)

and

\[
\frac{\partial \bar{x}_1}{\partial c_2} = \frac{\mu_2 \bar{x}_2 e^{c_2 \bar{x}_2} b g(\bar{x}_2) + \bar{x}_2 g'(\bar{x}_2) - ac_1 \mu_2 \bar{x}_2 e^{(c_2 - c_1)\bar{x}_2}}{bg'(\bar{x}_2) - bc_2 g(\bar{x}_2) - ac_1 \mu_2 e^{(c_2 - c_1)\bar{x}_2}}.
\]  

(24)

Therefore, \(\bar{x}_2\) is a strictly decreasing function of \(c_1\) and \(c_2\), and \(\bar{x}_1\) is a strictly decreasing function of \(c_1\). However, it appears that \(\bar{x}_1\) may not be a decreasing function of \(c_2\) by Equation (24).

**Proposition 2.7** Let \(R_0 > 1\). Then Equation (2) has a unique interior steady state \(E_1 = (\bar{x}_1, \bar{x}_2)\), where \(\bar{x}_2\) is a strictly decreasing function of \(c_1\) and \(c_2\) and \(\bar{x}_1\) is a strictly decreasing function of \(c_1\). In addition if \(c_1 = c_2 = c\), then \(\bar{x}_1\) is also a strictly decreasing function of \(c\).
Therefore, Equation (25) is satisfied for all $c_i$.  

Proof The first statement follows from Equations (21)–(23). To prove the second statement, notice that $d\bar{x}_1/dc$ is the sum of $\partial \bar{x}_1/\partial c_1$ and $\partial \bar{x}_1/\partial c_2$ in Equations (23) and (24), respectively. Therefore, adding the two expressions in Equations (23) and (24) and simplifying yield

$$
\frac{d\bar{x}_1}{dc} = \mu_2\bar{x}_2e^{\mu_2t}\frac{a\mu_2/b + (g(\bar{x}_2) + \bar{x}_2g'(\bar{x}_2))}{bg'(\bar{x}_2) - bge(\bar{x}_2) - ac\mu_2} < 0
$$

by (H1), and hence $\bar{x}_1$ is a strictly decreasing function of $c$.  

Theorem 2.5 implies that $E_1$ is globally asymptotically stable if $c_i \leq c_{i0}$ for $i = 1, 2$ and the fertility rate $g$ satisfies Equation (18). However, $E_1$ may lose its stability and become unstable as $c_1$ or $c_2$ increases. To investigate the local bifurcation of $E_1$, we verify Jury conditions (12) on $J(E_1)$ given in Equation (11). We drop off the bars in the components of $E_1$ for simplicity. Recall that $tr\ J(E_1) < 1 + \det\ J(E_1)$ always holds by Equation (13). Therefore, Equation (2) cannot undergo a +1 bifurcation when $E_1$ loses its stability. Furthermore, $\det\ J(E_1) < 1$ if and only if

$$
a(1 - \mu_2 - c_2\mu_2x_2 + c_1\mu_2x_2)e^{-\mu_2x_2} - be^{-c_2x_2}(g(x_2) + x_2g'(x_2)) < 1. \tag{25}
$$

Since $g(x_2) + x_2g'(x_2) > 0$, $0 < a < 1$, and $c_1x_2e^{-\mu_2x_2} < 1$, the left-hand side of Equation (25) becomes

$$
a(1 - \mu_2 - c_2\mu_2x_2 + c_1\mu_2x_2)e^{-\mu_2x_2} - be^{-c_2x_2}(g(x_2) + x_2g'(x_2)) < a(1 - \mu_2) - ac_2\mu_2x_2e^{-\mu_2x_2} + a\mu_2 - be^{-c_2x_2}(g(x_2) + x_2g'(x_2)) < a - b(\mu_2) < 1.
$$

Therefore, Equation (25) is satisfied for all $c_i \geq 0$, $i = 1, 2$. Consequently, system (2) cannot undergo a discrete Hopf (a Neimark-Sacker) bifurcation [17,22,24] when $E_1$ loses its stability.

On the other hand, $-1 - \det\ J(E_1) < tr\ J(E_1)$ is equivalent to

$$-ac_1e^{-\mu_2x_2}(2 - \mu_2 + (c_1 - c_2)\mu_2x_2) + be^{-c_2x_2}(g(x_2) + x_2g'(x_2)) < 2 - \mu_2 - c_2\mu_2x_2
$$

which can be further simplified to

$$-ac_1e^{-\mu_2x_2}(2 + (c_1 - c_2)\mu_2x_2) + be^{-c_2x_2}x_2g'(x_2) < 2(1 - \mu_2) - c_2\mu_2x_2.
$$

Notice that if $c_2 = 0$, then Equation (26) is trivially true. Since Equation (25) also holds when $c_2 = 0$, $E_1$ is locally asymptotically stable if $c_2 = 0$. However, inequality (26) may not always hold. Therefore, $E_1$ may lose its stability via a period-doubling (a flip) bifurcation when $c_1$ or $c_2$ is increased [1,24].

Proposition 2.8 Let $R_0 > 1$. Steady state $E_1 = (\bar{x}_1, \bar{x}_2)$ is locally asymptotically stable if Equation (26) holds. In particular, $E_1$ is locally asymptotically stable if $c_2 = 0$, and the only possible bifurcation for Equation (2) is a period-doubling bifurcation when $E_1$ loses its stability.

If $c_2 = 0$, i.e. if adults do not cannibalize those larger juveniles that will become adults after one unit of time, then cannibalism cannot destabilize the population dynamics. The juveniles and adults can coexist as an interior steady state if their initial population sizes are close to the steady state. However, cannibalism can destabilize the population dynamics if the adults also prey on these larger juveniles. In addition, cannibalism can lower the size of the adult prey population in the interior steady state. On the other hand, since $R_0$ is independent of $c_1$ and $c_2$, the population continues to be persistent even when the magnitudes of cannibalism are large, as long as $R_0 > 1$. 
3. A predator–prey model with cannibalism in the prey

Based on the model studied in Section 2, we let \( x_1(t) \) and \( x_2(t) \) denote, respectively, the juvenile and adult prey populations at time \( t = 0, 1, \ldots \), where the adult prey population may feed on the juvenile prey population. The predator population at generation \( t \) is denoted by \( p(t), t = 0, 1, \ldots \). For simplicity, each individual predator is assumed to be identical so that there is no stage structure in the predator population. In this model, we assume that the predator only preys upon those large juveniles which will become adults after one unit of time if the juveniles survive. This is motivated by the consideration that the two types of juveniles may have different habitats and the predator is located in the habitat for which the smaller juveniles are located. Let \( f(p) \) denote the probability that an individual juvenile prey escaped from being preyed upon when the predator population is of size \( p \). As a result, \( 1 - f \) is the fraction of the juvenile prey population that is eaten during each unit time interval. Let \( \hat{\beta} > 0 \) denote the predator conversion rate and define \( \beta := \hat{\beta} p_1 \), where \( 0 < p_1 < 1 \) is the probability that a juvenile becomes an adult after one unit of time. The dynamics of the predator–prey interaction are described by the following system:

\[
\begin{align*}
    x_1(t+1) &= x_2(t)g(x_2(t)) + ax_1(t)e^{-c_1x_2(t)} \\
    x_2(t+1) &= bx_1(t)e^{-c_2x_2(t)}f(p(t)) + (1 - \mu_2)x_2(t) \\
    p(t+1) &= \beta x_1(t)(1 - f(p(t))) \\
    x_1(0), x_2(0), p(0) &\geq 0.
\end{align*}
\]

(27)

Parameters \( a, b, c_1, c_2, \) and \( \mu_2 \) have the same biological meaning as in Section 2 and \( g \) satisfies (H1). Moreover, function \( f \) satisfies the following:

(H2) \( f \in C^2[0, \infty), f(0) = 1, f'(x) < 0, f''(x) > 0 \) for \( x \geq 0 \), and \( \lim_{x \to \infty} f(x) = 0 \).

It follows from (H2) that the probability \( f \) of escaping from being preyed upon decreases with increasing predator population. Furthermore, this rate of decrease is increasing. A well-known example of \( f \) is given by Nicholson and Bailey [20], \( f(p) = e^{-dp} \), where parameter \( d > 0 \) represents the per capita searching efficiency of the parasitoids. May et al. [16] discussed the effects of timing of density dependence in host–parasitoid interactions with \( f \) given by \( f(p) = (1 + \alpha p/k)^{-k} \), where parameter \( \alpha > 0 \) is also the parasitoid’s searching efficiency and \( k > 0 \) is termed the ‘clumping’ parameter. May et al. [16] noticed that the limit of their \( f \) as \( k \) goes to infinity is the \( f \) used by Nicholson and Bailey [20], \( \lim_{k \to \infty}(1 + \alpha p/k)^{-k} = e^{-\alpha p} \). In both of these examples, \( f \) is strictly decreasing, concave up, and satisfies (H2).

Similar to the discussion of system (2), we shall study the asymptotic dynamics of model (27). Let

\[
\mathbf{B} = \begin{pmatrix} a & 0 & 0 \\ b & 1 - \mu_2 & 0 \\ \beta & \mu_2 & 0 \end{pmatrix} \quad \text{and} \quad \mathbf{Q} = \begin{pmatrix} I \\ 0 \\ 0 \end{pmatrix}.
\]

(28)

We first verify that solutions of Equation (27) remain non-negative and are bounded for forward iterations.

**Proposition 3.1** Solutions of Equation (27) remain non-negative and are bounded for \( t > 0 \).

**Proof** Non-negativity of solutions is clear. Let \( Y(t) = (x_1(t), x_2(t), p(t)) \) be a solution of Equation (27). Then for \( t \geq 0 \),

\[
Y^T(t+1) \leq \mathbf{B}^{t+1} Y^T(0) + \sum_{i=0}^{t} \mathbf{B}^i \mathbf{Q} = \mathbf{B}^{t+1} Y^T(0) + (I - \mathbf{B})^{-1}(I - \mathbf{B}^{t+1}) \mathbf{Q}.
\]
Since \(\lim_{t \to \infty} B^t\) is the zero matrix, we have
\[
\lim_{t \to \infty} \sup_{t \geq 0} Y(t) \leq Y_M, \tag{29}
\]
where
\[
y^T_M = (I - B)^{-1}Q. \tag{30}
\]
Therefore, solutions of Equation (27) are bounded.

Since \(\lim_{t \to \infty} x(t) = 0\) is locally asymptotically stable if \(\lim_{t \to \infty} x(t) = 0\) is satisfied and \(R_0 < 1\), the predator population also becomes extinct. Consequently, \(E_0 = (0, 0, 0)\) for all parameter values. The linearization of Equation (27) at \(E_0\) yields the following Jacobian matrix
\[
J(E_0) = \begin{pmatrix}
a & \alpha & 0 \\
b & 1 - \mu_2 & 0 \\
0 & 0 & 0
\end{pmatrix}. \tag{31}
\]
Since the upper left 2 \times 2 submatrix is the Jacobian matrix of Equation (2) evaluated at \((0, 0)\), \(E_0\) is locally asymptotically stable if \(R_0 < 1\), where \(R_0\) is defined as in Equation (8). It can be easily shown that \(E_0\) is globally asymptotically stable for Equation (27) in \(\mathbb{R}^3_+\) if \(R_0 < 1\). The proof of the following theorem is standard and is therefore omitted.

**Theorem 3.2** If \(R_0 < 1\), then \(E_0 = (0, 0, 0)\) is globally asymptotically stable in \(\mathbb{R}^3_+\) for Equation (27).

If the inherent net reproductive number \(R_0\) of the prey is less than one, then since the prey population cannot persist by Theorem 2.2, the predator population also becomes extinct. Consequently, \(E_0\) is globally asymptotically stable as shown in Theorem 3.2. Suppose now \(R_0 > 1\). Then Equation (27) has another boundary steady state \(E_1 = (\bar{x}_1, \bar{x}_2, 0)\), where \(\bar{x}_2\) satisfies Equation (7) and \(\bar{x}_1\) is given by Equation (9). The Jacobian matrix of Equation (27) evaluated at \(E_1\) is given by
\[
J(E_1) = \begin{pmatrix}
ae^{-c_1\bar{x}_2} & \frac{J_{11}}{\bar{x}_2} & 0 \\
b e^{-c_2\bar{x}_2} & -c_2\mu_2\bar{x}_2 + 1 - \mu_2 & b\bar{x}_1 e^{-c_2\bar{x}_2} f'(0) \\
0 & 0 & -\beta\bar{x}_1 f'(0)
\end{pmatrix}, \tag{32}
\]
where
\[
J_{11} = g(\bar{x}_2) + \bar{x}_2 g'(\bar{x}_2) - \frac{ac\mu_2}{b} \bar{x}_2 e^{(c_2-c_1)\bar{x}_2}.
\]
Notice the upper left 2 \times 2 submatrix of \(J(E_1)\) is the Jacobian matrix of Equation (2) evaluated at \((\bar{x}_1, \bar{x}_2)\). As a result, \(E_1\) is locally asymptotically stable for Equation (27) if inequality (26) is satisfied and \(-\beta\bar{x}_1 f'(0) < 1\). We let \(E^0_1 = (\bar{x}_1^0, \bar{x}_2^0, 0)\) denote the corresponding steady state when \(c_1 = c_2 = 0\). Since in this case \(E^0_1\) is globally asymptotically stable in the non-negative \(x_1, x_2\)-coordinate plane by Theorem 2.4, it can be shown that \(E^0_1\) is globally asymptotically stable in \(\mathbb{R}^3_+\), if \(-\beta\bar{x}_1^0 f'(0) < 1\) as presented in Theorem 3.3.

To this end, let \((x_1(t), x_2(t), p(t))\) be a solution of Equation (27). Then the \(x_1\) and \(x_2\) components satisfy
\[
x_1(t + 1) \leq x_2(t) g(x_2(t)) + ax_1(t)
\]
\[
x_2(t + 1) \leq bx_1(t) + (1 - \mu_2)x_2(t)
\]
for \(t \geq 0\). Since the map induced by the right-hand side of Equation (33) is strongly monotone on \(\mathbb{R}^2_+\), it follows from Theorem 2.4 that the \(x_1\) and \(x_2\) components of solutions of system (27) satisfy
\[
\lim_{t \to \infty} \sup_{t \geq 0} x_i(t) \leq \bar{x}_i^0, \quad i = 1, 2. \tag{34}
\]
Theorem 3.3. Let $\mathcal{R}_0 > 1$ and $c_1 = c_2 = 0$. Then $E_1^0 = (\bar{x}_1^0, \bar{x}_2^0, 0)$ is globally asymptotically stable for Equation (27) in $\mathbb{R}_+^3 \setminus \{(x_1, x_2, p) \in \mathbb{R}_+^3 : x_1 = x_2 = 0\}$ if $-\beta\bar{x}_1^0 f'(0) < 1$.

Proof. Let $Y(t) = (x_1(t), x_2(t), p(t))$ be a solution of Equation (27) with $x_1(0) + x_2(0) > 0$. We may assume $p(0) > 0$. Then $p(t) > 0$ for $t > 0$. By Equation (34) and the assumption $-\beta\bar{x}_1^0 f'(0) < 1$, there exist $\epsilon > 0$ and $t_0 > 0$ such that $x_1(t) < \bar{x}_1^0 + \epsilon$ for $t \geq t_0$ and

$$-\beta(\bar{x}_1^0 + \epsilon) f'(0) < 1. \tag{35}$$

By (H2), there exists $\theta \in (0, p(t))$ such that the third equation of Equation (27) satisfies

$$p(t + 1) < -\beta(\bar{x}_1^0 + \epsilon) f'(\theta) p(t) < -\beta(\bar{x}_1^0 + \epsilon) f'(0) p(t) \quad \text{for } t \geq t_0.$$

It follows from Equation (35) that $\lim_{t \to \infty} p(t) = 0$. Therefore, Equation (27) is asymptotically autonomous to system (2). Consequently, all solutions of Equation (27) that do not start on the $p$-axis converge to $E_1^0$ by Theorem 2.4.

Similarly, since $(\bar{x}_1, \bar{x}_2)$ is globally asymptotically stable for Equation (2) when $c_i \leq c_{i0}$ for $i = 1, 2$ by Theorem 2.5, one can show that $E_1$ is globally asymptotically stable for Equation (27) if in addition $-\beta\bar{x}_1 f'(0) < 1$. This result is presented in Theorem 3.4 and its proof is omitted.

Theorem 3.4. Let $\mathcal{R}_0 > 1$ and assume $c_i \leq c_{i0}$ for $i = 1, 2$. Then $E_1 = (\bar{x}_1, \bar{x}_2, 0)$ is globally asymptotically stable in $\mathbb{R}_+^3 \setminus \{E_0\}$ if $-\beta\bar{x}_1 f'(0) < 1$.

Recall that Equation (34) holds and therefore the maximal juvenile prey population size is $\bar{x}_1^0$. Consequently, $-\beta\bar{x}_1^0 f'(0)$ can be interpreted as the maximal inherent net reproductive number of the predator population. It is the average number of offspring that an individual predator can reproduce when the juvenile prey population is stabilized at $\bar{x}_1^0$ and the predator population is very small. As shown below, the predator population will become extinct if this reproductive number is less than one.

Proposition 3.5. Let $\mathcal{R}_0 > 1$. If $-\beta\bar{x}_1^0 f'(0) < 1$, then $\lim_{t \to \infty} p(t) = 0$ for any solution $(x_1(t), x_2(t), p(t))$ of Equations (27) and (27) has no interior steady state.

Proof. Let $(x_1(t), x_2(t), p(t))$ be a solution of Equation (27). Since Equation (34) holds and $-\beta\bar{x}_1^0 f'(0) < 1$, using a similar proof as that of Theorem 3.3, one can show that $\lim_{t \to \infty} p(t) = 0$. To prove that Equation (27) has no interior steady state, suppose there is one, labelled as $E^* = (x_1^*, x_2^*, p^*)$. Then there exists $\theta \in (0, p^*)$ such that

$$p^* = \beta x_1^*(1 - f(p^*)) = -\beta x_1^* f'(\theta)p^* < -\beta x_1^* f'(0)p^* < -\beta\bar{x}_1^0 f'(0)p^*.$$

Therefore $-\beta\bar{x}_1^0 f'(0) > 1$ if $E^*$ exists. We conclude that Equation (27) has no interior steady state if $-\beta\bar{x}_1^0 f'(0) < 1$.

The next result provides a sufficient condition for which both populations can coexist. The concept of uniform persistence is used to prove coexistence of both populations. However, in order to apply [12, Theorem 4.2], we only consider the situation when the boundary dynamics of Equation (27) are simple.

Theorem 3.6. Let $\mathcal{R}_0 > 1$. Assume Equation (18) holds, $c_i \leq c_{i0}$ for $i = 1, 2$, and $-\beta\bar{x}_1 f'(0) > 1$. Then system (27) is uniformly persistent.
Therefore, solutions of Equation (37) converge to an interior steady state of Equation (37) by Theorem 2.12. Notice the maximal invariant set in $Y$ is $\mathcal{M} = \{E_0, E_1\}$ by the assumption, and $\mathcal{M} \subset Y$. We apply Theorem 4.2 of [12] to prove uniform persistence of Equation (27) with respect to $Y$. We need to verify that $\{E_0, E_1\}$ is a Morse decomposition of $\mathcal{M}$, $\{E_i\}$ is isolated in $Y$ and the stable set of $\{E_i\}$ lies in $Y$ for $i = 0, 1$.

Suppose there exists $Y(0) = (x_1(0), x_2(0), p(0)) \in \text{int}(\mathbb{R}_+^3)$ such that $\lim_{t \to \infty} Y(t) = E_0$. Then for any $\epsilon > 0$ there exists $t_0 > 0$ such that $x_1(t) < \epsilon$, $i = 1, 2$ and $p(t) < \epsilon$ for $t \geq t_0$. Since $\mathcal{R}_0 > 1$, we choose $\epsilon > 0$ sufficiently small such that

$$\frac{b \alpha f(\epsilon)}{\mu_2} + a > 1.$$  \hspace{1cm} (36)

It follows that $x_2(t + 1) \geq bx_1(t)e^{-c_2 x_2(t)}f(\epsilon) + (1 - \mu_2)x_2(t)$ for $t \geq t_0$. Consider the following system for $t \geq t_0$

$$z_1(t + 1) = z_2(t)g(z_2(t)) + az_1(t)e^{-c_1 z_2(t)}$$

$$z_2(t + 1) = bz_1(t)e^{-c_2 z_2(t)}f(\epsilon) + (1 - \mu_2)z_2(t)$$

$$z_i(t_0) = x_i(t_0) > 0, i = 1, 2.$$  \hspace{1cm} (37)

Since $c_i \leq c_0$ for $i = 1, 2$ and $f(\epsilon) < 1$, system (37) is monotone on $[0, x_{M1}] \times [0, x_{M2}]$. Therefore, solutions of Equation (37) converge to an interior steady state of Equation (37) by Equation (36) and Theorem 2.5. On the other hand, $x_2(t) \geq z_2(t)$ for $t \geq t_0$. It follows that $\lim \inf_{t \to \infty} x_2(t) > 0$ and we obtain a contradiction. Therefore, the stable set of $E_0$ must be contained in $Y$. Similarly, if there exists $Y(0) \in \text{int}(\mathbb{R}_+^3)$ such that $\lim_{t \to \infty} Y(t) = E_1$, then there exists $\epsilon > 0$ such that $\bar{x}_i - \epsilon < x_i(t) < \bar{x}_i + \epsilon$ and $p(t) < \epsilon$ for all $t$ large and for $i = 1, 2$. By the assumption, we can choose $\epsilon > 0$ such that $-\beta(\bar{x}_1 - \epsilon)f'(\epsilon) > 1$. But then for all $t$ large

$$p(t + 1) = -\beta x_1(t)f'(\tilde{p})p(t) > -\beta(\bar{x}_1 - \epsilon)f'(\epsilon)p(t)$$

for some $\tilde{p} \in (0, p(t)) \subset (0, \epsilon)$. As a result, $\lim_{t \to \infty} p(t) = \infty$ and we obtain another contradiction. Therefore, the stable set of $E_1$ is also contained in $Y$.

It remains to prove that $\{E_i\}$ is isolated in $\mathbb{R}_+^3$ for $i = 0, 1$. Let $B(E_0, \epsilon)$ be the part of an open ball centred at $E_0$ of radius $\epsilon$ that is contained in $\mathbb{R}_+^3$. Since $\mathcal{R}_0 > 1$, we can choose $\epsilon > 0$ such that

$$\frac{bg(\epsilon)f(\epsilon)}{\mu_2}e^{-c_1 \epsilon} > 1 - ae^{-c_1 \epsilon}.$$  \hspace{1cm} (38)

If $\{E_0\}$ is not isolated in $\mathbb{R}_+^3$, then $B(E_0, \epsilon)$ would contain an invariant set $K$ with $\{E_0\} \nsubseteq K$. Let $Y(0) = (x_1(0), x_2(0), p(0)) \in K$ and $Y(0) \neq E_0$. We may assume $x_i(0) > 0$ for $i = 1, 2$. Then for $t \geq 0$, $Y(t) \in K \subset B(E_0, \epsilon)$ and

$$x_1(t + 1) \geq ae^{-c_1 \epsilon}x_1(t) + g(\epsilon)x_2(t)$$

$$x_2(t + 1) \geq be^{-c_2 \epsilon}f(\epsilon)x_1(t) + (1 - \mu_2)x_2(t).$$

Let

$$C = \begin{pmatrix} ae^{-c_1 \epsilon} & g(\epsilon) \\ be^{-c_2 \epsilon}f(\epsilon) & 1 - \mu_2 \end{pmatrix}.$$
Notice that Equation (38) implies that the Perron eigenvalue of the primitive matrix $C$ is greater than one. Therefore, entries of $\lim_{t \to \infty} C^t$ become unboundedly large and hence $\lim_{t \to \infty} x_i(t) = \infty$ for $i = 1, 2$. We obtain a contradiction and conclude that $\{ E_0 \}$ must be isolated in $\mathbb{R}_3^+$. Similarly, using the assumption $-\beta \bar{x}_1 f'(0) > 1$, one can show that $\{ E_1 \}$ is isolated in $\mathbb{R}_3^+$. Since $\mathcal{Y}$ is closed in $\mathbb{R}^3_+$, it follows that each $\{ E_i \}$ is isolated in $\mathcal{Y}$ for $i = 1, 2$. It is clear that $\{ E_0, E_1 \}$ is a Morse decomposition of $M$ since $\{ E_0, E_1 \}$ is an acyclic covering of $M$ as the stable manifold of $E_0$ lies on the $p$-axis while the unstable manifold of $E_1$ does not lie on the $p$-axis. Therefore, Equation (27) is uniformly persistent with respect to $Y$ by Theorem 4.2 of [12].

In particular, we have the following persistence result for $c_1 = c_2 = 0$.

**Corollary 3.7** Let $\mathcal{R}_0 > 1$ and $c_1 = c_2 = 0$. Then Equation (27) is uniformly persistent if $-\beta \bar{x}_1 f'(0) > 1$.

We proceed to study the existence of interior steady states. Let $(x_1, x_2, p)$ denote an interior steady state of Equation (27). Then from the second equation of Equation (27), one obtains

\[
x_1 = \frac{\mu_2 x_2 e^{c_2 x_2}}{bf(p)}.
\]

Substituting this equality into the first equation of Equation (27) yields

\[
\mu_2 = bg(x_2) f(p) e^{-c_2 x_2} + a \mu_2 e^{-c_1 x_2}.
\]  

(39)

Now from the first equation of Equation (27), we can write $x_1$ in terms of $x_2$ via

\[
x_1 = \frac{x_2 g(x_2)}{1 - ae^{-c_1 x_2}}.
\]

It then follows from the third equation of Equation (27) that

\[
p = \frac{\beta x_2 g(x_2)}{1 - ae^{-c_1 x_2}} (1 - f(p)).
\]  

(40)

Equation (39) yields $p$ as a function of $x_2$. Let $x_2 = 0$ in Equation (39). Then Equation (39) results in

\[
f(p) = \frac{(1 - a) \mu_2}{ba}.
\]

Since $\mathcal{R}_0 > 1$, i.e. $ba > (1 - a) \mu_2$, there exists a unique $p_0^* > 0$ satisfying the above equation. Therefore, there exists a unique $p_0^* > 0$ such that $(0, p_0^*)$ satisfies Equation (39). Similarly, one can show that the only nonnegative $p$ satisfying Equation (39) when $x_2 = \bar{x}_2$ is $p = 0$. Hence, the curve of Equation (39) passes through points $(0, p_0^*)$ and $(\bar{x}_2, 0)$. Applying implicit differentiation with respect to $x_2$ in Equation (39), one has

\[
p' = \frac{bc_2 g(x_2) f(p) e^{-c_2 x_2} + ac_1 \mu_2 e^{-c_1 x_2} - bg'(x_2) f(p) e^{-c_2 x_2}}{bg(x_2) f'(p) e^{-c_2 x_2}} < 0.
\]  

(41)
We conclude that $p$, defined by Equation (39), is a strictly decreasing function of $x_2$ that goes through $(0, p_0^*)$ and $(\bar{x}_2, 0)$, where $p_0^* > 0$ and $\bar{x}_2$ is the $x_2$ component of the interior steady state for system (2).

On the other hand, since $p/(1 - f(p))$ is strictly increasing in $p$, Equation (40) also defines $p$ as a function of $x_2$. Applying implicit differentiation with respect to $x_2$, yields

$$p' = \beta(1 - f(p))^2 \frac{(g(x_2) + x_2 g'(x_2))(1 - ae^{-c_1 x_2}) - ac_1 x_2 g(x_2) e^{-c_1 x_2}}{(1 - ae^{-c_1 x_2})^2(1 - f(p) + pf'(p))},$$  \hspace{1cm} (42)$$

where by (H2)

$$1 - f(p) + pf'(p) = p(f'(p) - f'(\eta)) > 0$$

for some $\eta \in (0, p)$. It can be easily seen that $p'(0) > 0$ in Equation (42). However, it is not clear whether $p$ is strictly increasing in $[0, \bar{x}_2]$ or not.

Notice that if $c_1 = 0$, then Equations (40) and (42) become

$$p = \frac{\beta x_2 g(x_2)}{1 - a}(1 - f(p)) \hspace{1cm} (43)$$

and

$$p' = \beta(1 - f(p))^2 \frac{(g(x_2) + x_2 g'(x_2))(1 - a)}{(1 - a)^2(1 - f(p) + pf'(p))} > 0,$$  \hspace{1cm} (44)$$

respectively. Thus, Equation (43) defines $p$ as a strictly increasing function of $x_2$. Furthermore, $p = 0$ is always a solution for $x_2 \in [0, \bar{x}_2]$. At $x_2 = \bar{x}_2$, it can be shown that Equation (43) has a positive solution $p$ if and only if $-\beta \bar{x}_1 f'(0) > 1$ and $p = 0$ is the only solution if $-\beta \bar{x}_1 f'(0) \leq 1$. Consequently, if $c_1 = 0$, then Equation (27) has a unique interior steady state if and only if $-\beta \bar{x}_1 f'(0) > 1$. We summarize this result as follows.

**Theorem 3.8** Let $R_0 > 1$ and $c_1 = 0$. Then Equation (27) has a unique interior steady state if $-\beta \bar{x}_1 f'(0) > 1$ and Equation (27) has no interior steady states if $-\beta \bar{x}_1 f'(0) \leq 1$.

It follows from Equation (42) that the same conclusion of Theorem 3.8 remains valid for those $c_1 > 0$ sufficiently small such that $p'(x_2)$ in Equation (42) is positive on $[0, \bar{x}_2]$. That is, if $c_1 > 0$ is small enough so that $p'(x_2) > 0$ for $x_2 \in [0, \bar{x}_2]$, then Equation (27) has a unique interior steady state if and only if $-\beta \bar{x}_1 f'(0) > 1$.

Suppose Equation (27) has an interior steady state $E^* = (x_1^*, x_2^*, p^*)$. By ignoring the stars for simplicity, the characteristic polynomial $P(\lambda)$ of the Jacobian matrix of system (27) at $E^*$ has the form

$$P(\lambda) = \lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3,$$

where

$$a_1 = -ae^{-c_1 x_2} + \mu_2 c_2 x_2 + \mu_2 - 1 + \beta x_1 f'(p)$$

$$a_2 = ae^{-c_1 x_2}(1 - \mu_2 - \mu_2 c_2 x_2 + \mu_2 c_1 x_2) - be^{-c_2 x_2}(g(x_2) + x_2 g'(x_2)) + \beta x_1 f'(p)(\mu_2 c_2 x_2 + \mu_2 - 1 ae^{-c_1 x_2})$$

$$a_3 = -b\beta(g(x_2) + x_2 g'(x_2))x_1 e^{-c_1 x_2} f'(p) + ac_1 \beta bx_1^2 e^{(-c_1 - c_2) x_2} f'(p) - ab \beta c_2 x_1^2 e^{(-c_1 - c_2) x_2} f(p) f'(p) + a\beta (1 - \mu_2) x_1 e^{-c_1 x_2} f'(p).$$  \hspace{1cm} (45)
We assume
\[ P_1(\lambda) = \lambda^3 \quad \text{and} \quad P_2(\lambda) = a_1\lambda^2 + a_2\lambda + a_3. \]

We assume
\[ |a_1| + |a_2| + |a_3| < 1, \quad (46) \]
where \( a_i, \ i = 1, 2, 3, \) are given by Equation (45). Then, on the unit circle \( |\lambda| = 1, \) we have \( |P_2(\lambda)| \leq |a_1| + |a_2| + |a_3| < 1 = |P_1(\lambda)|. \) It follows from Rouche’s theorem [4] that \( P(\lambda) = P_1(\lambda) + P_2(\lambda) \) and \( P_1(\lambda) \) have the same number of zeros inside the unit circle \( |\lambda| = 1. \) We conclude that \( E^* \) is locally asymptotically stable if Equation (46) holds.

**Proposition 3.9** Let \( \mathcal{R}_0 > 1 \) and assume that Equation (27) has an interior steady state \( E^* = (x_1^*, x_2^*, p^*). \) Then \( E^* \) is locally asymptotically stable if Equation (46) holds.

In particular if \( c_1 = 0 \) and \(-\beta\bar{x}_1 f'(0) > 1,\) then Equation (27) has a unique interior steady state \( E^* = (x_1^*, x_2^*, p^*) \) by Theorem 3.8 and \( E^* \) is stable if Equation (46) is satisfied where \( a_i \) can be simplified further using \( c_1 = 0 \) for \( i = 1, 2, 3. \)

**Corollary 3.10** Let \( \mathcal{R}_0 > 1, \) \( c_1 = 0 \) and \(-\beta\bar{x}_1 f'(0) > 1.\) Then the unique interior steady state \( E^* \) of Equation (27) is locally asymptotically stable if Equation (46) is satisfied.

Finally, we consider the situation when the predator feeds on juvenile prey indiscriminately, independent of whether the juveniles remain in the same class or move to the next stage class after one unit of time. The model is given below, which is very similar to system (27):

\[
\begin{align*}
    x_1(t + 1) &= x_2(t)g(x_2(t)) + ax_1(t)e^{-c_1x_2(t)}f(p(t)) \\
    x_2(t + 1) &= bx_1(t)e^{-c_2x_2(t)}f(p(t)) + (1 - \mu_2)x_2(t) \\
    p(t + 1) &= \beta x_1(t) (1 - f(p(t))) \\
    x_1(0), x_2(0), p(0) &\geq 0.
\end{align*}
\]

Parameter \( \beta > 0 \) is the predator conversion rate. All other parameters have the same biological meanings as those for model (27), and moreover, \( g \) and \( f \) satisfy (H1) and (H2), respectively. Our goals are to investigate whether different strategies of predation play a role in the stabilization or destabilization of the interactions.

Since \( f'(0) = 1 \) and \( p(t) = 0 \) for \( t > 0 \) if \( p(0) = 0, \) the nonnegative \( x_1,x_2 \)-coordinate plane is forwardly invariant under system (47) and the corresponding subsystem is given by model (2). Let \( \mathcal{R}_0 \) be as defined in Equation (8). Many of the analytical results for system (27) can be carried over to Equation (47). We state these results without providing their proofs.

**Proposition 3.11** The following statements are true for system (47).

(a) Solutions of Equation (47) remain non-negative and are bounded for \( t > 0. \)
(b) If \( \mathcal{R}_0 < 1, \) then \( E_0 = (0, 0, 0) \) is globally asymptotically stable.
(c) If \( \mathcal{R}_0 > 1, \) then \( E_0 \) is unstable and Equation (47) has another boundary steady state \( E_1 = (\bar{x}_1, \bar{x}_2, 0), \) where \( \bar{x}_1 \) is given by Equation (9) and \( \bar{x}_2 \) is the unique positive solution of Equation (7). Moreover, \( E_1 \) is locally asymptotically stable if (26) and \(-\beta\bar{x}_1 f'(0) < 1 \) hold.
(d) Let \( R_0 > 1, \ c_1 \leq c_{10}, \ c_2 \leq c_{20} \) and assume that Equation (18) holds. Then \( E_1 = (\bar{x}_1, \bar{x}_2, 0) \) is globally asymptotically stable in \( \{ (x_1, x_2, p) \in \mathbb{R}^3_+ : x_1 + x_2 > 0 \} \) if \(-\beta \bar{x}_1 f'(0) < 1 \) and Equation (47) is uniformly persistent if \(-\beta \bar{x}_1 f'(0) > 1 \). In particular, if \( c_1 = c_2 = 0 \), then Equation (47) is uniformly persistent if \(-\beta \bar{x}_1^0 f'(0) > 1 \) and \( E_1 = (\bar{x}_1^0, \bar{x}_2^0, 0) \) is globally asymptotically stable if \(-\beta \bar{x}_1^0 f'(0) < 1 \).

(e) Let \( R_0 > 1 \). If \(-\beta \bar{x}_1^0 f'(0) < 1 \), then Equation (47) has no interior steady state and solutions of Equation (47) satisfy \( \lim_{t \to \infty} p(t) = 0 \).

The existence of interior steady states for system (47) is more complicated than that for Equation (27) and cannot be resolved analytically even when \( c_1 = 0 \). Indeed, the \( x_2 \) and \( p \) components of an interior steady state \((x_1, x_2, p)\) can be shown to satisfy the following equations:

\[
\mu_2 = bg(x_2) f(p) e^{-c_1 x_2} + a \mu_2 f(p) e^{-c_1 x_2}
\]

\[
p = \frac{\beta x_2 g(x_2) (1 - f(p))}{1 - af(p) e^{-c_1 x_2}} \frac{f(p)}{f'(p)}. \tag{48}
\]

The first equation of Equation (48) defines \( p \) as a function of \( x_2 \) and there exists a unique \( \bar{p}_0 > 0 \) such that the curve goes through \((0, \bar{p}_0)\) and \((\bar{x}_2, 0)\) with

\[
p' = \frac{bc g(x_2) f(p) e^{-c_2 x_2} + ac \mu_2 e^{-c_1 x_2} - bg'(x_2) f(p) e^{-c_2 x_2}}{bg(x_2) f'(p) e^{-c_2 x_2} + a \mu_2 f'(p) e^{-c_1 x_2}} < 0.
\]

However, the second equation of Equation (48) does not have these properties. A simple calculation yields

\[
p' = \frac{\beta (g(x_2) + x_2 g'(x_2))(1 - f(p)) - ac_1 pf^2(p) e^{-c_1 x_2}}{(1 - af(p) e^{-c_1 x_2})(f(p) + pf'(p)) + \beta x_2 g(x_2) f'(p)}.
\]

Therefore, the sign of \( p' \) cannot be determined even if \( c_1 = 0 \). Similar to Proposition 3.9, based on Rouche’s theorem, one can find a sufficient condition for which an interior steady state of Equation (47) is locally asymptotically stable. However, we do not pursue this further.

4. Numerical examples and simulations

In this section, we shall use numerical techniques to study systems (2), (27) and (47). We simulate system (2) with fertility rate \( g \) given by

\[
g(x) = \frac{\alpha}{1 + \gamma x}, \tag{49}
\]

where \( \alpha, \gamma > 0 \). We choose the following parameter values:

\[
a = 0.2, \quad b = 0.6, \quad \mu_2 = 0.5, \quad \alpha = 20, \quad \gamma = 1. \tag{50}
\]

Then \( R_0 = ab/(1 - a)\mu_2 = 24.199 > 1 \), which is independent of \( c_1 \) and \( c_2 \). We first consider the case when \( c_1 = c_2 = e \) and use \( e \) as a bifurcation parameter. In this case, Equation (2) may undergo a period-doubling bifurcation when the interior steady state loses its stability by Proposition 2.8. Figure 1(a) provides a bifurcation diagram for \( e \) varying from 0 to 50. A period-doubling bifurcation occurs when \( e \) is about 5, and we see that the \( x_1 \) component, or the whole juvenile prey population size, of the stable interior steady state decreases with increasing \( e \), which confirms Proposition 2.7. We next let \( c_1 = 1 \) and vary \( c_2 \) from 0 to 20. Notice \( R_0 \) remains the same and a
Figure 1. The figure provides simulation results for system (2) with \( g \) given by Equation (49). Plot (a) is a bifurcation diagram when \( c_1 = c_2 = 1 \) while plots (b) and (c) using \( c_1 = 1 \) and \( c_1 = 1.8 \), respectively, and varying \( c_2 \). Plot (d) is a bifurcation diagram for \( c_2 = 2.8 \) and varying \( c_1 \). The vertical axis is the juvenile prey population.

period-doubling bifurcation occurs when \( c_2 \) is about 3 as indicated in Figure 1(b). As we increase \( c_1 \) to 1.8 and \( \alpha \) to 60, system (2) undergoes a cascade of period-doubling bifurcations to chaos as demonstrated in Figure 1(c).

We now fix \( c_2 = 0 \) and vary \( c_1 \) from 0 to 50 with other parameter values given by Equation (50). According to Proposition 2.8, the interior steady state of system (2) is locally asymptotically stable since \( c_2 = 0 \). There are only equilibrium dynamics for these parameter values and the bifurcation diagram is not presented. This part of the numerical study validates Proposition 2.8 for \( c_2 = 0 \). Parameter \( c_2 \) is then increased gradually until \( c_2 = 2.8 \), where we see that Equation (2) has an attracting 2-cycle solution for \( c_1 \) between 0 and 1. As \( c_1 \) increases, the system has only equilibrium dynamics for \( c_1 \) between 1 and 2. However, when \( c_1 \) is increased further, the system has 2-cycle dynamics again. Its bifurcation diagram is presented in Figure 1(d). For each of the diagrams in Figure 1, the vertical axis is the whole juvenile prey population \( x_1 \). We repeat the same simulations with \( \alpha = 10 \) and obtain similar diagrams. The corresponding bifurcation diagrams
Figure 2. The figure provides simulation results for system (2) with \( g \) given by Equation (49) and the same parameter values as those given for Figure 1 in the corresponding subplots. The vertical axis labels the adult prey population.

Figure 2 provides bifurcation analysis of the adult prey population with the same parameter values as those given for Figure 1. It can be seen that the adult prey population also undergoes similar bifurcations as those for the juvenile prey population. Moreover, the adult population size decreases in the interior steady state as cannibalism increases.

We next simulate system (27) with \( g \) given by Equation (49) and \( f \) given as:

\[
    f(x) = e^{-dx},
\]

where \( d > 0 \). We let \( d = 1.0 \) and \( \beta = 1.0 \). Other parameter values are given by Equation (50).

First consider the situation when \( c_1 = c_2 = c \) and use \( c \) as a bifurcation parameter. Recall from Figure 1(a) that in the absence of the predator population, the prey has only equilibrium dynamics when \( c \) is between 0 and around 5. Figure 3(a) and (b) provides bifurcation diagrams for \( c \in [0, 2] \) with juvenile prey and predator being on the vertical axes, respectively. We see in this case that the predator population can destabilize the prey population. We then let \( c_1 = 1 \) and vary \( c_2 \) from 0 to 2. Similar diagrams as those in Figure 3(a) and (b) are obtained and these simulations are not
Figure 3. This figure provides simulation results for system (27) with \( g \) given by Equation (49) and \( f \) given by Equation (51). Plots (a) and (b) are bifurcation diagrams when \( c_1 = c_2 = c \), while plots (c) and (d) are bifurcation diagrams when \( c_1 = 1, \beta = 0.5, \) and varying \( c_2 \).

presented. Notice in the prey population model (2), the prey population also only has equilibrium dynamics when \( c_1 = 1 \) and \( c_2 \in [0, 2] \). Therefore, introduction of the predator population can destabilize the prey dynamics. However, when \( \beta \) is decreased to \( \beta = 0.5 \), Figure 3(c) and (d) provides bifurcation diagrams for \( c_1 = 1 \) and \( c_2 \) varying from 0 to 6. We see in this case that the predator population can stabilize the prey dynamics since from Figure 1(b) a period-doubling bifurcation occurs when \( c_2 \) is about 3. As we decrease \( \beta \) further to \( \beta = 0.1 \), then the predator population becomes extinct when \( c_2 \) is about 3 and the prey population has the same dynamical behaviour as the single population. We then let \( c_2 = 2.8 \) and use \( c_1 \) as a bifurcation parameter. The bifurcation diagrams are similar to Figure 3 and therefore are not presented.

Finally, in order to compare the effects of strategies of the predator population on the dynamical consequences, we simulate systems (27) and (47) subject to the same parameter values. We only provide our simulations for the predator population. Plots in Figure 4 are the simulation results
Figure 4. This figure provides simulation results for systems (27) and (47) with $g$ given by Equation (49), $f$ given by Equation (51) and $c_1 = c_2 = c$. Plots on the left column are the predator population for Equation (27) and plots on the right column are predator population for Equation (47). The $\beta$ values for the first row and the second row are 1.5 and 0.5, respectively.

when $c_1 = c_2 = c$. The plots on the right column are for Equation (47) while the plots on the left column are for system (27). The $\beta$ values for the top and bottom two plots are, respectively, 1.5 and 0.5. We repeat similar simulations with $c_1 = 1$ and varying $c_2$. Plots on the left column of Figure 5 are for Equation (27) while the plots on the right column are for system (47). The $\beta$ values on the top, middle, and bottom rows are 1.5, 0.5, and 0.1, respectively.

Although bifurcation diagrams of systems (27) and (47) in Figure 4 look alike, bifurcations may take on different values of $c$ (see (a) and (b), and (c) and (d) of Figure 4). Moreover, one also notices that the predator population sizes for system (27) seem larger those for system (47). On the other hand, bifurcation diagrams for systems (27) and (47) also look similar in Figure 5 for all different $\beta$ values. However, it can be seen from (a) and (b) of Figure 5 that different bifurcation values may occur at different values of the cannibalism rate $c_2$. This numerical study suggests that whether the predator can stabilize or destabilize the prey dynamics depends on model parameters.
Figure 5. This figure provides simulation results for systems (27) and (47) with $g$ given by Equation (49), $f$ given by Equation (51), and $c_1 = 1$. Plots on the left column are the predator population for (27) and the plots on the right column are the predator population for Equation (47). (a) and (b), (c) and (d), and (e) and (f) have $\beta$ equals 1.5, 0.5, and 0.1, respectively.

Moreover, different strategies of predation do not seem to change the dynamical behaviour of the interactions, although bifurcations may occur at different values of cannibalism rates.

5. Discussion

Cannibalism, or intra-specific predation, is an important intrinsic mechanism that regulates population dynamics [8]. Cannibalism has been practiced by a wide variety of species across many
taxa. Its effects on population dynamics are vast and complex [8]. Cannibalism on the one hand can be an effective mechanism for the regulation and equilibration of population size [10,25]. Cannibalism on the other hand has also been found to promote population oscillations [13,15].

Since cannibalism is most commonly practiced by larger animals on smaller individuals, in this manuscript, we propose a discrete-time, discrete stage-structured population model to investigate dynamical consequences of cannibalism in Section 2. The model under this investigation is different from that studied earlier in [13] where adults may consume their eggs and all surviving juveniles become adults after one unit of time. In the present population, surviving juveniles may remain in the juvenile stage and adults may feed on juveniles but do not consume their eggs. It is proved that the population is stabilized at the interior steady state when the population is not cannibalistic (i.e. $c_1 = c_2 = 0$) and its basic reproductive number $R_0$ is larger than one (cf. Theorem 2.4). If the population practices cannibalism, then the population may be oscillating via a period-doubling bifurcation when the interior steady state loses its stability (cf. Proposition 2.8). Consequently, cannibalism can be a destabilizing factor in this two-stage single-population model (cf. [13,15]). However, as illustrated in Figure 1(d) where $c_2 = 2.8$ and $c_1$ is varied, that Equation (2) has only equilibrium dynamics when $c_1$ is between 1 and 2 and the population is oscillating when $c_1$ is either less than 1 or greater than 2, cannibalism is stabilizing. Therefore, cannibalism may be either destabilizing or stabilizing depending on cannibalism rates and other vital parameters.

In addition, since components of the interior steady state of the prey model (2) are strictly decreasing functions of cannibalism rates, cannibalism can also lower the population sizes of the interior steady state (cf. Proposition 2.7). However, since the basic reproductive number $R_0$ is independent of the cannibalism coefficients, the population continues to be persistent even when the mechanisms of cannibalism are large, as long as $R_0$ is greater than one (cf. Theorem 2.6). Moreover, it is demonstrated numerically in Section 4 that this single-species prey population may be chaotic as the mechanisms of cannibalism increase.

Motivated by the biological example of cannibalistic Atlantic cod being preyed upon by larger animals [2], we also study two predator–prey models, systems (27) and (47), assuming that the prey population may be cannibalistic. It is proved that both populations become extinct if the basic reproductive number $R_0$ of the prey is smaller than one (cf. Theorem 3.2, Proposition 3.11(b)). The extinction of both populations in this case is due to unfitness of the prey population since the prey population cannot persist in the absence of the predator population. When the basic reproductive number $R_0$ of the prey exceeds one and the dynamics of the prey population are simple, we provide a sufficient condition for the coexistence of both populations (cf. Theorem 3.6, Proposition 3.11(d)).

Numerical simulations with specific functions are also explored to study the predator–prey systems in Section 4. The introduction of the predator population may make the prey population more unstable on the one hand and may stabilize the prey dynamics on the other hand. Therefore, whether the predator can simplify or destabilize the prey population dynamics depends on the cannibalism rates and other model parameters (cf. [13,18,19]). Moreover, as illustrated in Proposition 3.11 and numerical simulations, different strategies of predation by the predator population in this study do not seem to change the qualitative behaviour of the interactions. However, bifurcations may occur at different values of cannibalism rates.

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