Nonconstant Predator Harvesting on Ratio-Dependent Predator-Prey Models

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Abstract

The dynamics of a ratio-dependent predator-prey model with two different non-constant harvesting functions depending on the predator population is studied. Equilibria and periodic orbits are computed and their stability properties are analyzed. Several bifurcations are detected as well as connecting orbits. Smooth numerical continuation is performed that allows computation of branches of solutions. Conditions for the boundedness of solutions and for the existence of a bionomic equilibrium are analyzed.

Mathematics Subject Classification: 37N25, 65L99

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1 Introduction

Population dynamics has attracted interest from the commercial harvesting industry and from many scientific communities including biology, ecology, and economics. Evidence shows that a realistic model should be based on ratio-dependent theory. In such a case the so called functional response is generally expressed as \( g(x, y) = g(x/y) \). This leads e.g. to the Michaelis-Menten model

\[
\begin{align*}
\dot{x} &= rx \left(1 - \frac{x}{K}\right) - \frac{cxy}{my+x} \\
\dot{y} &= y \left(-D + \frac{fx}{my+x}\right),
\end{align*}
\] (1)
where \( x \) and \( y \) denote the prey and predator populations, respectively. The parameters \( r, K, c, m, D, \) and \( f \) are all positive constants, \( r \) represents the intrinsic rate of growth of the prey without predation, \( K \) represents the carrying capacity of the prey, \( c \) is the capture rate of the prey, \( m \) is the half-saturation constant, \( D \) is the natural death rate of the predator and \( f \) is the prey conversion rate.

Ginzburg et. al. [3], Haque [5], as well as Xiao and Ruan [11] have shown that system (1) exhibits complex dynamics, and they have shown in detail the existence or nonexistence of periodic solutions as well as several bifurcations. Profit, overexploitation and extinction of a species being harvested are primary concerns in ecology and commercial harvesting industries. Thus, current research in dynamical systems incorporates a harvesting component in mathematical models like (1) to study the effects it has on one or multiple species. Leard et. al. [7] have studied the dynamics of ratio-dependent models that include nonconstant harvesting on the prey. Stability properties of equilibria and periodic orbits were analyzed and several types of bifurcations as well as connecting orbits were detected. T. K. Kar [6] considered harvesting on both, predator and prey on a prey-dependent model with prey refuge and included a study of optimal harvesting policy. Xiao et. al. [10] have investigated the dynamics of (1) with constant harvesting on the predator, using the following nondimensionalized system:

\[
\begin{align*}
\dot{x} &= x(1 - x) - \frac{axy}{y + x} \\
\dot{y} &= y \left( -d + \frac{bx}{y + x} \right) - h,
\end{align*}
\]

where \( a = \frac{c}{mr} \), \( b = \frac{f}{r} \) and \( d = \frac{D}{r} \) are positive constants. For simplicity, the biological meaning of the parameters \( a \), \( b \) and \( d \) are the same as \( c \), \( f \) and \( D \), respectively. Among other things, they found that there exist only two equilibria in \( \mathbb{R}_+^2 \) for particular parameter values, and saddle-node and Hopf bifurcations were detected. In this work we extend the constant predator harvesting to nonconstant functions on a ratio-dependent model, following the idea in [7]. Our study includes stability properties, boundedness of solutions, bionomic equilibria, bifurcations and some special solutions. The first harvesting policy involves a linear harvesting rate in terms of the predator species. The model is

\[
\begin{align*}
\dot{x} &= x(1 - x) - \frac{axy}{y + x} \\
\dot{y} &= y \left( -d + \frac{bx}{y + x} \right) - hy,
\end{align*}
\]

where \( h \) represents a constant harvesting effort. As the abundance of the predator species increases, the number of predator harvested will increase linearly.
In a more realistic approach, we take into account the assumption of diminishing marginal returns of the harvesting organization. This gives a rational harvesting rate in terms of the predator species:

\[
\dot{x} = x(1 - x) - \frac{axy}{y + x} \\
\dot{y} = y\left(-d + \frac{h}{y + x} - \frac{hy}{c+y}\right),
\]

where \(h\) is the maximum harvesting rate of the predator species and \(c\) is the number of predator species it takes to reach one-half of the maximum harvesting rate. This model characterizes the behavior of a commercial harvesting company when their decision to harvest depends on both the revenue and cost of harvesting. As more species become available, harvesting more at a linear rate might not be profitable, due to supply and demand factors.

2 Model One - Linear Harvesting Policy

2.1 Boundedness of the Solutions of (3)

**Theorem 2.1** All the solutions of system (3) which start in \(\mathbb{R}^2_+\) are uniformly bounded.

**Proof.** Let \(w = x + \frac{a}{b}y\). Then, for any \(c > 0\),

\[
\dot{w} + cw = x(1 - x + c) - y\left(\frac{ad}{b} + \frac{ah}{b} - \frac{ac}{b}\right) \leq \frac{(c+1)^2}{4} - y\left(\frac{a}{b}(d + h - c)\right).
\]

Let \(c < d + h\). Then, there exists \(B > 0\) such that \(\dot{w} + cw \leq B\), or \(\dot{w} \leq B - cw\). Let \(\dot{r} = B - cr\), with \(r(0) = w(0) = w_0\), whose solution \(r(t) = \frac{B}{c}(1 - e^{-ct}) + w_0e^{-ct}\) is bounded for \(t \geq 0\). Using a differential inequality [4], we get

\[
w(t) \leq r(t) = \frac{B}{c}(1 - e^{-ct}) + w_0e^{-ct} \leq \frac{B}{c} \text{ as } t \to \infty.
\]

Thus, solutions starting in \(\mathbb{R}^2_+\) stay in \(S = \{(x, y) \in \mathbb{R}^2_+: x + \frac{a}{b}y = \frac{B}{c} + \gamma\}, \text{ with } \gamma > 0\}. \square

**Remark 2.2** A similar result applies to model (4), with \(c < d\).
2.2 Equilibrium Points of (3)

We are only interested in analyzing the solutions in the closed first quadrant $R^2_+$ because any solutions outside of the first quadrant are not biologically interpretable. The equilibria $P_1 = (x_1, y_1)$ and $P_2 = (x_2, y_2)$ of this system are

\[ x_1 = 1, \quad y_1 = 0, \]  
\[ x_2 = \phi, \quad y_2 = \frac{b-d-h}{d+h} \phi, \]  

where $\phi = 1 - a + \frac{ad}{b} + \frac{ah}{b}$. At $P_2$, the predator and prey coexist under certain conditions. More precisely, $(x_2, y_2)$ lies in $R^2_+$ if $1 - a + \frac{ad}{b} - \frac{ah}{b} > 0$ and $b - (d + h) > 0$.

We observe that if $(d + h) \geq b$, then coexistence of predator and prey is not possible. That is, if the death rate combined with harvesting of the predator exceeds its conversion rate, then the predator will go extinct.

The general Jacobian of (3) is

\[ J(x, y) = \begin{bmatrix} 1 - 2x - \frac{ay^2}{(x+y)^2} & -\frac{ax^2}{(x+y)^2} - d + \frac{bx^2}{(x+y)^2} - h \end{bmatrix}. \]

At equilibrium point (5), the Jacobian is given by $J(x_1, y_1) = \begin{bmatrix} -1 & -a \\ 0 & b - (d + h) \end{bmatrix}$.

**Theorem 2.3** The two eigenvalues of the Jacobian evaluated at $(x_1, y_1)$ this point are $\lambda_1 = -1$ and $\lambda_2 = b - (d + h)$. Therefore,

1. when $b > d + h$, $(x_1, y_1)$ is a saddle point.
2. when $b < d + h$, $(x_1, y_1)$ is stable.
3. when $b = d + h$, there may exist a bifurcation at $(x_1, y_1)$, depending on further conditions discussed in Section 2.2.

The Jacobian evaluated at (6) is

\[ J(x_2, y_2) = \begin{bmatrix} a - 1 - \frac{a(d+h)^2}{(b-d-h)^2} & -\frac{a(d+h)^2}{(b-d-h)^2} \\ -\frac{(d+h)^2}{b} & -\frac{(d+h)(b-d-h)}{b} \end{bmatrix}. \]  

The trace ($\tau$) and the determinant ($D$) of the Jacobian at (7), are:

\[ \tau = a - d - h - 1 + \frac{(d+h)^2(b-a)}{b^2} \]  
\[ D = \frac{(d+h)(b-d-h)(b-ab+ad+ah)}{b^2} \]

The analysis of the stability of $P_2$ can be accomplished by analyzing the trace-determinant plane [8]. This gives the following
Theorem 2.4  When \( b > d + h \) and \( \phi > 0 \), then \((x_2, y_2)\) lies in \( \mathbb{R}^2_+ \) and

1. \((x_2, y_2)\) is an unstable focus or node if \( a > b\frac{(d+h+1)b-(d+h)^2}{b^2-(d+h)^2} \); 
2. \((x_2, y_2)\) is a stable focus or node if \( a < b\frac{(d+h+1)b-(d+h)^2}{b^2-(d+h)^2} \); 
3. \((x_2, y_2)\) is a center if \( a = b\frac{(d+h+1)b-(d+h)^2}{b^2-(d+h)^2} \).

From Theorems 2.3 and 2.4, if \((x_2, y_2)\) lies in \( \mathbb{R}^2_+ \), then \((x_1, y_1)\) is a saddle point. Further, if \( b > d + h \) along with the conditions for \((x_2, y_2)\) existing in \( \mathbb{R}^2_+ \), then \((x_2, y_2)\) is a stable focus or node. In other words, the predator conversion rate must exceed the sum of the death and the harvest rate for coexistence to occur, among other necessary conditions given above.

2.3  Bifurcations of (3)

Hopf Bifurcations. We analyze the existence of Hopf bifurcations at the point of interest, that is, the coexistence equilibrium (6).

Theorem 2.5  Under certain conditions for the equilibrium (6) to be a center, the system (3) exhibits subcritical and supercritical Hopf bifurcations.

Proof. We shift our equilibrium point to the origin via the change of coordinates \( u = x - x_2, \ v = y - y_2 \) and then we expand our expressions for \( \dot{u} \) and \( \dot{v} \) in a power series to get

\[
\dot{u} = a_{10}u + a_{01}v + a_{20}u^2 + a_{11}uv + a_{02}v^2 + a_{30}u^3 + a_{21}u^2v + a_{12}uv^2 + a_{03}v^3 + O_1(|(u, v)|^4), \\
\dot{v} = b_{10}u + b_{01}v + b_{20}u^2 + b_{11}uv + b_{02}v^2 + b_{30}u^3 + b_{21}u^2v + b_{12}uv^2 + b_{03}v^3 + O_2(|(u, v)|^4) .
\]

(10)

We then find the Lyapunov number \( \sigma_1 \) [8]. If \( \sigma_1 \neq 0 \), then a Hopf bifurcation exists. The following conditions must hold in order for (6) to be a center:

1. \( b > d + h \)  
2. \( a = b\frac{(d+h+1)b-(d+h)^2}{b^2-(d+h)^2} \)  
3. \( a_{10}b_{01} - a_{01}b_{10} > 0 \).

Numerical calculations reveal that when \( a = 2, \ b = 0.78, \ d = 0.25, \ h = 0.24956, \) we get \( \sigma_1 = -88.83527 \). For \( a = 1.658385, \ b = 0.75, \ d = 0.2, \ h = 0.2, \) we get \( \sigma_1 = 16.5430 \). Therefore there exists an open set \( S_{11} \) in the parameter space \( \langle a, b, d \rangle \) such that \( \sigma_1 > 0 \) and all of our restrictions hold:

\[
S_{11} = \left\{(b, d, h) : 0 < b - (d + h), \ a = b\frac{(d+h+1)b-(d+h)^2}{b^2-(d+h)^2}, \ a_{10}b_{01} - a_{01}b_{10} > 0, \ \text{and} \ \sigma_1 > 0 \right\} .
\]
Another such set $S_{12}$ exists such that

$$S_{12} = \left\{ (b, d, h) : 0 < b - (d + h), \quad a = b \frac{(d+h+1)b-(d+h)^2}{b^2-(d+h)^2}, \right. \left. a_{10}b_{01} - a_{01}b_{10} > 0, \quad \text{and} \quad \sigma_1 < 0 \right\}.$$  

The surface $H_{b1} = \{(a, b, d, h) : (b, d, h) \in S_{11}\}$ is the subcritical Hopf bifurcation surface of system (3) and the surface $H_{p1} = \{(a, b, d, h) : (b, d, h) \in S_{12}\}$ is the supercritical Hopf bifurcation surface of system (3). □

Using Xppaut [2], we plot the corresponding bifurcation diagram in Figure 1. Filled circles represent stable periodic orbits and empty circles represent unstable ones.

**Transcritical Bifurcation.** The system (3) undergoes a transcritical bifurcation involving the two equilibria $P_1 = (x_1, y_1)$ and $P_2 = (x_2, y_2)$. As expected, when $b > d + h$, the coexistence equilibrium $(x_2, y_2)$ is a stable focus or node, while $(x_1, y_1)$ is a saddle point. When $b = d + h$, the two equilibria coincide and become $(x_1, y_1) = (x_2, y_2) = (1, 0)$. Once $b < d + h$, both equilibria exchange stability as $(x_2, y_2)$ becomes a saddle and $(x_1, y_1)$, i.e. predator extinction, becomes a stable focus or node. Figure 2 illustrates the bifurcation in the $xy$ phase plane: Note that the transcritical bifurcation occurs when the predator conversion rate $b$ matches the sum of the its death rate $d$ and the harvesting rate $h$.

### 2.4 Periodic and Connecting Orbits

System (3) exhibits periodic solutions for several sets of parameter values, and also some heteroclinic orbits connecting equilibria with periodic orbits. We have computed some of these solutions following [1] and [9]. See those references for details. We have computed some periodic orbits of system (3) by starting with one of the periodic orbits coming out from the Hopf bifurcation.
shown in Figure 1. We let $h$ vary and compute the corresponding periods and Floquet multipliers. See Table 1.

Observe in Figure 3 that as $h \to 0.248735$, both species come very close to simultaneous extinction for a certain time interval, but are still capable of recovering and going through an oscillatory behavior. Some point-to-periodic connections are shown in Figure 4. Starting at the equilibria $(x_1, y_1) = (1, 0)$, the solutions leave along the unstable manifold and enter the periodic orbits along their stable manifolds. There is an important interpretation for these heteroclinic connections: by introducing some predators in an only-prey situation, it is possible for the system to arrive to a periodic state of coexistence. The amount of predator harvesting determines the different sizes of both populations.

<table>
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<tr>
<th>$h$</th>
<th>Period</th>
<th>Floquet multiplier</th>
</tr>
</thead>
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<td>.25341</td>
<td>27.914096</td>
<td>0.999522</td>
</tr>
<tr>
<td>.25203</td>
<td>30.379435</td>
<td>0.868345</td>
</tr>
<tr>
<td>.25000</td>
<td>36.705219</td>
<td>0.579205</td>
</tr>
<tr>
<td>.24900</td>
<td>46.381796</td>
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<td>69.678009</td>
<td>0.041170</td>
</tr>
<tr>
<td>.248736</td>
<td>82.797079</td>
<td>0.013683</td>
</tr>
</tbody>
</table>

Table 1: Period and Floquet multipliers

3 Model Two - Rational Limit Harvesting Policy

The second model of our analysis involves a rational harvesting term in the prey species equation (see system (4)). Most computations, especially the
numerical ones are similar to the ones in the first model and we omit some of them.

3.1 Equilibrium Points of (4)

If we assume that the maximum harvesting equals the death rate of the predator and that its conversion rate is higher than the harvesting itself, it is possible to obtain explicit expressions for the equilibria of (4) and to study their stability properties.

**Theorem 3.1** The following points

\[(x_1, y_1) = (0, -(1 + c)), \quad (x_2, y_2) = \left( \frac{h}{b}(c + 2), \frac{b - h(c + 2)}{b} \right) \tag{11} \]

are equilibria for model(4).

**Proof.** Assume \( h = d \). If \( x = 0 \) then, the second equation of (4) gives \( y = -(1 + c) \). Now consider \( x \neq 0 \). The same second equation can be written as

\[-hy(y + x)(1 + c + y) + bxy(c + y) = 0.\]
For \( y \neq 0 \) this becomes \(-h(y + x)(1 + c + y) + bx(c + y) = 0\). After multiplying out and grouping we get

\[(bc - h(1 + c))x - h(1 + c)y + (b - h)xy - hy^2 = 0.\]

If we set \( b = h + h/c \), then we have

\[-h(1 + c) + (b - h)x - hy = 0.\]

From the first equation of (4) we have \((1 - x)(y + x) - ay = 0\). Now if we let \( a = 1 \) we get \( x = \frac{h}{b(c + 2)}, y = \frac{b - h(c + 2)}{b} \).

**Remark 3.2** The first equilibrium \((x_1, y_1)\) denotes mutual extinction, while the second one \((x_2, y_2)\) denotes coexistence, as long as \( b > h(c + 2) \). The condition \( b = h + h/c \) in the proof of the theorem simply states that the prey conversion rate (how much the predator gains from the prey) is strictly bigger than its harvesting rate.

**Theorem 3.3** The system (4) has no closed paths on the positive quadrant \( x > 0, y > 0 \) when \( 2h(c + 2) > (b + h) + ch/(c + y)^2 \).

**Proof.** We already know that the only equilibrium of coexistence is given by \((x_2, y_2)\) in (11). The general Jacobian is

\[J(x, y) = \begin{bmatrix} 1 - 2x - \frac{y^2}{(x+y)^2} & -\frac{x^2}{(x+y)^2} \\ \frac{by^2}{(x+y)^2} & -h + \frac{bx^2}{(x+y)^2} - \frac{eh}{(c+y)^2} \end{bmatrix}.\]

However, at \((x, y) = (x_2, y_2)\) we have \( x + y = 1 \), so that the Jacobian reduces to

\[J(x, y) = J(x_2, y_2) \begin{bmatrix} -\frac{x^2}{bly^2} & -\frac{x^2}{by^2} \\ -h + bx^2 - \frac{eh}{(c+y)^2} \end{bmatrix}.\]

Then, \( \det(J) = (h + \frac{eh}{(c+y)^2} + by^2)x^2 - bx^4 \), and \( \det(J) < 0 \) if \( 2bx > (b + h) + ch/(c + y)^2 \), where \( y = y_2 \) and we used again \( y = 1 - x \). This means we must have \( 2h(c + 2) > (b + h) + ch/(c + y_2)^2 \). In such a case, the coexistence equilibrium \((x_2, y_2)\) is a saddle and therefore it has index = \(-1\), and since it is the only one in the positive quadrant, it is not possible for a close path to exist in that region. \( \square \)
3.2 Bifurcations of (4)

The model (4) exhibits some pitchfork and limit point bifurcations. In particular, a pitchfork bifurcation is detected for the parameter value $h = 1/3$ and a limit point bifurcation at $h \approx 0.38$. See Figure 5

**Theorem 3.4** The system (4) exhibits a pitchfork bifurcation at the point $(x, y) = (1, 0)$ if $c = c^* = (-1 + \sqrt{5})/2$.

**Proof.** Here we use again the condition $b = h + h/c$. The Jacobian of (4) at $(1,0)$ has a simple zero eigenvalue. A corresponding eigenvector is $v = [1 -1]^T$, and a left eigenvector is $w = [0 1]^T$. In such a case we have that $w^T f_h(1,0) = 0$. With $c = c^*$ (one unit away from the golden ratio), one can verify that $c^2 = c/(c + 1)$, which implies that $h = bc^2$. Then $w^T D^2 f(1,0)(v,v) = [0 1] \begin{bmatrix} 0 & 0 \\ 2(h - bc^2)/c^2 \end{bmatrix} = 0$. We also have that

$$w^T D^3 f(1,0)(v,v,v) = [0 1] \begin{bmatrix} 6b - (6b - 6h/c^3) \end{bmatrix} = \frac{6h}{c^3} \neq 0.$$  

Then, by Sotomayor’s theorem, system (4) has a pitchfork bifurcation at $(1,0)$.

\[\square\]

4 Bionomic Equilibrium

In this section we want to find the simultaneous biological ($\dot{x} = 0$, $\dot{y} = 0$) and economic equilibrium (total revenue equals total cost) of systems (3) and (4). Let

$c =$ fishing cost per unit effort for predator species,
$p = \text{price per unit biomass of the predator.}$

Then, the net profit at any time is given by $P(y, h) = (py - c)h$.

The bionomic equilibrium $(x_0, y_0, h_0)$ for (3) is solution of by the simultaneous equations:

\begin{align*}
(1 - x) - \frac{ay}{y + x} &= 0 \quad (12) \\
-d + \frac{bx}{y + x} - h &= 0 \quad (13) \\
(py - c)h &= 0 \quad (14)
\end{align*}

**Case 1:** If $c > py$, i.e. the cost is greater than the revenue for the predator, then the harvesting will be stopped ($h = 0$).

**Case 2:** If $c < py$, i.e. the cost is less than the revenue for the predator, then the harvesting will continue. We then have $y_0 = c/p$. Now substituting $y_0$ into (12) we get $x^2 + Bx + C = 0$ where $B = c/p - 1$ and $C = c(a - 1)/p$.

Therefore, \[ x_0^\pm = \frac{-B \pm \sqrt{B^2 - 4C}}{2} \]

Now if

(i) $C < 0$, then $x_0^+$ is the only positive solution.

(ii) $B < 0$, $C > 0$, $B^2 > 4C$, then there are two solutions $x_0^\pm$. Substituting $x_0^\pm$ into (13)

\[ h_0^\pm = \frac{px_0^\pm(b-d) - dc}{px_0^\pm + c} \]

Therefore, $h_0^\pm > 0$, provided $x_0^\pm > \frac{dc}{p(b-d)}$.

The bionomic equilibrium $(x_0, y_0, h_0)$ for the second model (4) is given by the equations (12), (14) and

\begin{align*}
-d + \frac{bx}{y + x} - \frac{h}{c + y} &= 0 \quad (15)
\end{align*}

Similar to (3), $y_0 = c/p$, and $x^2 + Bx + C = 0$ where $B = c/p - 1$ and $C = c(a - 1)/p$. Substituting $x_0^\pm$ into (15) we get

\[ h_0^\pm = \frac{pe + c}{px_0^\pm + c}[(b-d)x_0^\pm - \frac{dc}{p}] \]

Therefore, $h_0^\pm > 0$, provided $x_0^\pm > \frac{dc}{p(b-d)}$. 

5 Discussion

In this work, we have extended previous research of ratio-dependent predator-prey models by investigating two Michaelis-Menten type models with different non-constant harvesting components in the predator equations. In particular, a rational harvesting function has been considered in the model, whereas previous research on ratio-dependent models include constant and linear harvesting functions only. Our results show that coexistence is possible under both harvesting policies, and that the model exhibits interesting dynamics around the coexistence equilibria, including multiple bifurcations, periodic orbits, and connecting orbits. We have also given conditions under which one cannot expect to have close paths.

We open many different avenues for future research in predator-prey modeling, including an analysis of ratio-dependent predator-prey models with other realistic harvesting policies, such as seasonal or rotational harvesting, and general continuous and discontinuous threshold policies. All of the analysis performed and techniques used in this work can be applied to modeling different situations and problems other than predator-prey.

References


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