

Continuous Threshold Prey Harvesting in Predator-Prey Models

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Abstract—The dynamics of a predator-prey model with continuous threshold policy harvesting functions on the prey is studied. Theoretical and numerical methods are used to investigate boundedness of solutions, existence of bionomic equilibria, and the stability properties of coexistence equilibrium points and periodic orbits. Several bifurcations as well as some heteroclinic orbits are computed.

Keywords—Predator-prey models, threshold harvesting, dynamical systems

I. INTRODUCTION

POPULATION dynamics of one or more species, and in particular, predator-prey models has received great attention due to its practical importance and to the rich dynamics observed in the corresponding mathematical models. Profit, overexploitation, and extinction of a species being harvested are primary concerns in ecology and commercial harvesting industries. Thus, current research incorporates a harvesting component in mathematical models to study the effects it has on one or multiple species. This has attracted interest from the commercial harvesting industry and from many scientific communities including biology, ecology, and economics.

Most predator-prey models consider either constant or linear harvesting functions ([5], [6], [7], [10]). More recently, boundedness of solutions of a general predator-prey model and stability of a model with rational harvesting on the prey and quadratic harvesting on the predator has been studied in [1]. On the other hand, assuming that harvesting starts at $t = 0$, independent of the population size, is not very realistic. In this regard, threshold policy (TP) harvesting considers starting harvesting only when a population x has reached a certain threshold value T . Classically, such a harvesting function is defined as

$$\phi(x) = \begin{cases} 0 & \text{if } x < T \\ h & \text{if } x \geq T. \end{cases} \quad (1)$$

However, as pointed out in [9], this is impractical because it would be difficult for managers to immediately harvest at a rate h once the population x has reached its threshold value T because e.g. of time delays and capital constraints. In this work we propose two continuous threshold policy (CTP) harvesting functions on the prey; the first one has the form

$$H(x) = \begin{cases} 0 & \text{if } x < T \\ \frac{h(x-T)}{h+x-T} & \text{if } x \geq T. \end{cases} \quad (2)$$

In this way, once the prey population reaches the size $x = T$, then harvesting starts and increases smoothly to a limit value

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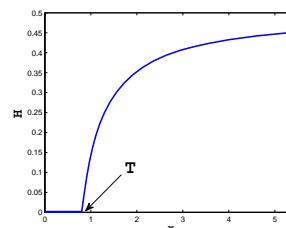


Fig. 1. Harvesting Function ($T = 0.8$, $h = 0.5$.)

h ; see Figure 1. We believe this harvesting function is more sound from a biological viewpoint.

II. MODEL ONE

We implement the harvesting function (2) on a predator-prey model with Michaelis-Menten functional response:

$$\begin{aligned} \dot{x} &= x(1-x) - \frac{axy}{1+mx} - H(x) \\ \dot{y} &= y\left(-d + \frac{bx}{1+mx}\right), \end{aligned} \quad (3)$$

where x and y denote the prey and predator populations, respectively. The parameters a, b, d, m are all positive constants: a is the capture rate of the prey, b is the prey conversion rate, d is the natural death rate of the predator. The term $\frac{ax}{1+mx}$ is known as a Holling type II functional response. For practical reasons, we are only interested in the equilibrium points of the system (3) that lie on the first quadrant, that is, $x \geq 0$ and $y \geq 0$, excluding the origin.

A. Boundedness of solutions

We start by showing that solutions of (3) that start in R_+^2 will remain there and are uniformly bounded. Indeed, we have the following

Theorem 1: Every solution of system (3) that starts in R_+^2 is uniformly bounded.

Proof: Let $x \geq T$, and let $v = x + \frac{a}{b}y$. Then for all $c > 0$,

$$\begin{aligned} \dot{v} + cv &= x(1-x+c) - \frac{h(x-T)}{h+x-T} + y\left(\frac{a}{b}(c-d)\right) \\ &\leq \frac{(c+1)^2}{4} + y\left(\frac{a}{b}(c-d)\right). \end{aligned}$$

Let $c < d$. Then there exists $A > 0$ such that $\dot{v} + cv \leq A$, or $\dot{v} \leq A - cv$. Let $\dot{r} = A - cr$, where $r(0) = v(0) =: v_0$. The solution

$$r(t) = \frac{A}{c}(1 - e^{-ct}) + v_0 e^{-ct}$$

is bounded for $t \geq 0$. Hence, by applying a differential inequality [3], we get

$$0 < v(t) \leq r(t) = \frac{A}{c}(1 - e^{-ct}) + v_0 e^{-ct} \leq \frac{A}{c} \quad \text{as } t \rightarrow \infty.$$

Therefore, every solution of (3) where $x \geq T$, starting in R_+^2 , is uniformly bounded. ■

Remark 2: The proof for the case where $x < T$ follows directly from the above proof, using the same bound on c .

B. Equilibrium Points for $x < T$

When the number of prey is less than the threshold value, the system (3) has two equilibria: $P_1 = (x_1, y_1)$ and $P_2 = (x_2, y_2)$, where

$$x_1 = \frac{d}{b - dm}, \quad y_1 = \frac{1}{a}(1 - x_1)(1 + mx_1) = \frac{b}{a} \left[\frac{b - dm - d}{(b - dm)^2} \right], \quad (4)$$

$$x_2 = 1, \quad y_2 = 0. \quad (5)$$

Thus, in order for $(x_1, y_1) \in R_+^2$, we must always have $b > (m + 1)d$. In other words, the prey conversion rate must be strictly greater than the predator death rate.

The general Jacobian of (3) for $x < T$ is:

$$J(x, y) = \begin{bmatrix} 1 - 2x - \frac{ay}{(1+mx)^2} & -\frac{ax}{1+mx} \\ \frac{by}{(1+mx)^2} & -d + \frac{bx}{1+mx} \end{bmatrix} \quad (6)$$

Thus, at P_1 it becomes

$$J(x_1, y_1) = \begin{bmatrix} \frac{bdm - bd - d^2m - d^2m^2}{b(b-dm)} & -\frac{ad}{b} \\ \frac{bd - dm - d}{a} & 0 \end{bmatrix}$$

In such a case, its trace τ_1 and determinant δ_1 are

$$\tau_1 = \frac{bdm - bd - d^2m^2 - d^2m}{b(b - dm)} = d \left[\frac{m + 1}{b} - \frac{2}{b - dm} \right].$$

and

$$\delta_1 = \frac{d}{b} [b - (m + 1)d].$$

This gives

$$\tau_1^2 - 4\delta_1 = \frac{(d^2m(m + 1) - bd(m - 1))^2}{b^2(b - dm)^2} - \frac{4(bd - d^2m - d^2)}{b}.$$

Thus, using a classical trace-determinant analysis we conclude that the equilibrium point P_1 of (3) has the following properties:

- (a) It can never be a saddle, since $\delta_1 < 0$ requires that $b < d(m + 1)$, which forces the number of predators to become negative.
- (b) If $b > (m + 1)d$ and $\tau_1^2 - 4\delta_1 \geq 0$ then P_1 is a node.
 - If $b < \frac{m(m+1)}{m-1}d$, then the node is stable.
 - If $b > \frac{m(m+1)}{m-1}d$, then the node is unstable.
- (c) If $b > (m + 1)d$ and $\tau_1^2 - 4\delta_1 < 0$, then P_1 is a focus.
 - If $b < \frac{m(m+1)}{m-1}d$, then the focus is stable.
 - If $b > \frac{m(m+1)}{m-1}d$, then the focus is unstable.

(d) P_1 is a center-type if $b = \frac{m(1+m)}{m-1}d$.

Since the Jacobian of (3) at $P_2 = (x_2, y_2)$ is

$$J(x_2, y_2) = \begin{bmatrix} -1 & -\frac{a}{m+1} \\ 0 & -d + \frac{b}{m+1} \end{bmatrix},$$

the eigenvalues are $\lambda_1 = -1$ and $\lambda_2 = \frac{b}{m+1} - d$. Therefore, we have

- If $b > (1 + m)d$, then P_2 is a saddle point.
- If $b < (1 + m)d$, then P_2 is a stable node.
- P_2 is never a focus or a center.

C. Equilibrium Points when $x \geq T$

When the number of prey is at or above the threshold value, the system (3) has the equilibria $P_3 = (x_3, y_3)$ and $P_4 = (x_4, y_4)$, where $x_3 = \frac{d}{b-dm}$,

$$y_3 = \frac{[1 + mx_3][x_3(1 - x_3)(h + x_3 - T) - h(x_3 - T)]}{a(h + x_3 - T)x_3}, \quad (7)$$

$$x_4 = x^*, \quad y_4 = 0, \quad (8)$$

where x^* is the solution of

$$x^3 + (h - T - 1)x^2 + Tx - Th = 0.$$

This cubic equation has only one positive real root for $T > 0$. For P_3 to be a coexistence equilibrium, we need

$$b > md \quad \text{and} \quad x_3(1 - x_3)(h + x_3 - T) > h(x_3 - T). \quad (9)$$

The general Jacobian of (3) for $x \geq T$ is:

$$J(x, y) = \begin{bmatrix} 1 - 2x - \frac{ay}{(1+mx)^2} - \frac{h^2}{(h+x-T)^2} & -\frac{ax}{1+mx} \\ \frac{by}{(1+mx)^2} & -d + \frac{bx}{1+mx} \end{bmatrix} \quad (10)$$

Thus, at P_4 it becomes

$$J(x_4, 0) = \begin{bmatrix} 1 - 2x_4 - \frac{h^2}{(h+x_4-T)^2} & -\frac{ax_4}{1+mx_4} \\ 0 & -d + \frac{bx_4}{1+mx_4} \end{bmatrix}.$$

The eigenvalues λ_1, λ_2 of $J(x_4, 0)$ are given by the diagonal entries (1, 1) and (2, 2) respectively. We notice that $1 - 2x_4 - \frac{h^2}{(h+x_4-T)^2} \leq 1 - 2x_4 \leq 1 - 2T$, so that $\lambda_1 < 0$ if $T > 1/2$. We also see that $\lambda_2 < 0$ if $bx_4 < d[1 + mx_4]$, or equivalently if $(b - md)x_4 < d$, that is, precisely when $x_4 < x_3$. Similarly, $\lambda_2 > 0$ when $x_4 > x_3$. Thus, we have:

- (a) P_4 is a saddle when $T > \frac{1}{2}$ and $x_4 > \frac{d}{(b-md)}$
- (b) P_4 is a stable node when $T > \frac{1}{2}$ and $x_4 < \frac{d}{(b-md)}$
- (c) P_4 is never a focus or a center

At P_3 , $J(x_3, y_3)$ becomes

$$\begin{bmatrix} 1 - 2x_3 - \frac{x_3(1-x_3)(h+x_3-T)-h(x_3-T)}{(1+mx_3)(h+x_3-T)x_3} - \frac{h^2}{(h+x_3-T)^2} & -\frac{ad}{b} \\ \frac{b[x_3(1-x_3)(h+x_3-T)-h(x_3-T)]}{a(1+mx_3)(h+x_3-T)x_3} & 0 \end{bmatrix}.$$

Theorem 3: Consider the system (3), with $x \geq T$, and let

$$A = x_3(1 - x_3)(h + x_3 - T) - h(x_3 - T),$$

$$B = (1 + mx_3)(h + x_3 - T)x_3, \quad E = \frac{A}{B} + \frac{h^2}{(h + x - T)^2}.$$

Then,

(a) P_3 is never a saddle.

(b) P_3 is a node if $\left[\frac{(1-E)(b-md)-2d}{(b-md)}\right]^2 > 4dA/B$. The node is stable if $(1-E)(b-md) < 2d$, and unstable if the inequality is reversed.

(c) P_3 is a focus if $\left[\frac{(1-E)(b-md)-2d}{(b-md)}\right]^2 < 4dA/B$. The focus is stable if $(1-E)(b-md) < 2d$, and unstable if the inequality is reversed.

(d) P_3 is a center-type if $(1-E)(b-md) = 2d$.

Proof: The Jacobian at P_3 can be written as

$$J(x_3, y_3) = \begin{bmatrix} 1 - 2x_3 - E & -\frac{ad}{b} \\ \frac{bA}{aB} & 0 \end{bmatrix},$$

where $A > 0$ because of (9), and $B > 0$ because $x_3 \geq T$. Thus, its determinant $D = \frac{dA}{B}$ is always positive, which proves (a). Observe now that we must have $x_3 < 1$, otherwise the second inequality in (9) fails, and the trace is $\tau = 1 - 2x_3 - E = \frac{(1-E)(b-md)-2d}{(b-md)}$, hence the conclusions (b), (c) and (d). ■

It is interesting to see how the stability properties of some equilibria of model (3) may change for the cases $x < T$ and $x \geq T$, that is, without and with threshold harvesting. For instance, how does harvesting affect the stability of the coexistence equilibrium $P_3 = (x_3, y_3)$, and what is its effect on possible periodic solutions?

For $a = 1, b = 0.9, d = 0.2, m = 5$, numerical calculations indicate that the stable focus $P_1 = (0.4, 1.08)$ of the system without harvesting, moves to the stable focus $P_3 = (0.4, 0.63)$ of the system with harvesting. That is, even though the number of predator decreases, the equilibrium does not lose stability; see Figure 2. Instead, for the parameter values $a = 2.5, b = 2.25, d = 0.2, m = 5$ (that is, for a much larger prey conversion rate b , but keeping the same ratio b/a), the unstable focus $P_1 = (0.16, 0.6048)$ moves to a stable node $P_3 = (0.16, 0.8298)$. Remarkably, harvesting may have a stabilizing effect on the ecosystem, and the number of predator increases. We observe that the limit cycle has disappeared. See Figure 3. (see also the Science Daily article on how “Surprisingly, Harvesting Prey Boosts Predator Fish”, www.sciencedaily.com/releases/2007/06/070624132617.htm).

Note: There are some sets of parameters (e.g. $T = 0.0217, h = 0.1323, a = 7.1607, b = 2.3368, d = 0.2428, m = 2.9566$), for which an unstable focus of the system without harvesting goes to another unstable focus of the system with harvesting. In the first case however, the prey population gets very close to extinction when approaching a stable limit cycle, but on the system with harvesting, the solution approaches a stable limit cycle far enough from prey extinction.

One can establish sufficient conditions to ensure no closed orbits of a system $\dot{x} = f(x)$ exist in the positive quadrant, by

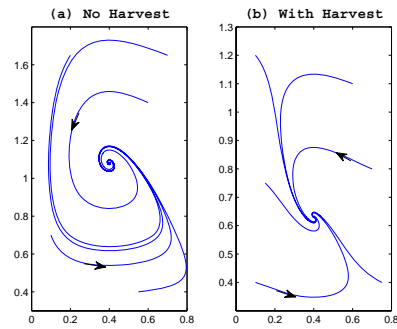


Fig. 2. Effect of harvesting: Stable to stable

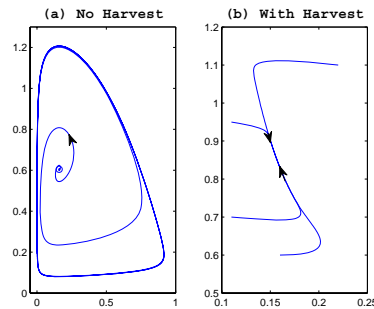


Fig. 3. Effect of harvesting: Unstable to stable

applying a generalization of Bendixson’s criterion. The idea is to use the Jacobian J of the system and define the symmetric matrix

$$S = \frac{1}{2}(J^T + J).$$

Theorem 3.3 in [8] says that if S has eigenvalues $\lambda_1 \geq \lambda_2 \geq \dots \geq \lambda_n$ such that $\lambda_1 + \lambda_2 < 0$, then no periodic solution can exist for such system. For our particular system (3) with Jacobian (10), one can readily verify that this amounts to find sufficient conditions under which

$$1 + \frac{bx}{1 + mx} < 2x + \frac{ay}{(1 + mx)^2} + \frac{h^2}{(h + x - T)^2} + d.$$

In turn, a sufficient condition to arrive to such inequality is that

$$1 + (b + m)x < d + (2 + dm)x + 2mx^2. \quad (11)$$

If $d \geq 1$, then (11) is true as long as $b < 2 + (d - 1)m$. For $d < 1$, let $p = 2 + (d - b)m$. Then one can show that (11) is true for any $x > -p + \sqrt{p^2 - 8m(d - 1)}$. We now collect the above discussion into the following

Theorem 4: Consider the system (3). Let $p = 2 + (d - b)m$, and $x \geq T$. Assume either of the following two conditions holds:

- (a) $d \geq 1$ and $b < 2 + (d + 1)m$, or
- (b) $d < 1$ and $x > \sqrt{p^2 - 8m(d - 1)} - p$.

Then the system (3) has no closed orbits.

D. Bifurcations of (3)

Next, we want to find out if there are some bifurcations present in our model. We found that the system (3) for $x \geq T$ undergoes a Hopf bifurcation. Indeed, the theorem below shows the existence of such a bifurcation. Using Xppaut[2] we have numerically detected such bifurcation for the value of the parameter $h = 0.1875$. See Figure 4.

Theorem 5: When the equilibrium point P_3 satisfies the conditions that permit it to be of center-type, the system (3) exhibits subcritical and supercritical Hopf bifurcations.

Proof: We will first shift the equilibrium point (x_3, y_3) to the origin by $u = x - x_3$ and $v = y - y_3$. We then expand the corresponding expressions \dot{u} and \dot{v} in a Taylor series. After simplifying, and noting that some coefficients vanish, the system becomes:

$$\begin{aligned} \dot{u} &= a_{10}u + a_{01}v + a_{20}u^2 + a_{11}uv + a_{30}u^3 + a_{21}u^2v \\ &\quad + O_1(|(u, v)|^4) \\ \dot{v} &= b_{10}u + b_{20}u^2 + b_{11}uv + b_{30}u^3 + b_{21}u^2v \\ &\quad + O_2(|(u, v)|^4). \end{aligned} \quad (12)$$

To determine the existence of Hopf bifurcations, we compute the Liapunov number σ , and find parameter values for which $\sigma \neq 0$. At the same time, the equilibrium (x_3, y_3) must satisfy certain conditions to be of center-type:

$$\begin{aligned} 1. \quad &b > dm & 2. \quad &a_{10} = 0 & 3. \quad &T < \frac{d}{b-dm} & 4. \\ &-a_{01}b_{10} > 0 & 5. \quad &\frac{h(b-dm)^2(T - \frac{d}{b-dm})}{h-T + \frac{d}{b-dm}} > d + b - dm, \end{aligned}$$

where a_0 is a long rational function in terms of the parameters.

Paying attention to these conditions, we find that $\sigma = 30.53189$ when $a = 58.54338$, $b = 22.78958$, $d = 1.19058$, $T = 0.00146$, $m = 0.57152$, and $h = 0.00151$. Also, with the same a, b, d, T, m , when $h = 0.56986$, $\sigma = -241.25441$. Thus, there exists an open set S_1 in the parameter space (a, b, d, m, h, T) such that $\sigma > 0$, where the stated restrictions hold:

$$\begin{aligned} S_1 = \{ &(a, b, d, m, T) \mid b > dm, a_{10} = 0, T < \frac{d}{b-dm}, \\ &-a_{01}b_{10} > 0, \text{ and } \sigma > 0\}. \end{aligned}$$

Another open set S_2 exists such that

$$\begin{aligned} S_2 = \{ &(a, b, d, m, T) \mid b > dm, a_{10} = 0, T < \frac{d}{b-dm}, \\ &-a_{01}b_{10} > 0, \text{ and } \sigma < 0\}. \end{aligned}$$

We then conclude that there exists a surface $H_1 = \{(a, b, d, h, m, T) \mid (a, b, d, m, T) \in S_1\}$ that is a supercritical Hopf bifurcation surface, and that there exists a surface $H_2 = \{(a, b, d, h, m, T) \mid (a, b, d, m, T) \in S_2\}$ that is a subcritical Hopf bifurcation surface of system (3). ■

Periodic Orbits. As indicated by the bifurcation diagram in Figure 4, the Hopf bifurcations gives out a branch of stable periodic orbits, shown as solid circles. We have explicitly computed some of these periodic orbits, as well as their corresponding Floquet multipliers, as h varies. We observe that as h approaches 0.1875, the stable multiplier approaches 1, and therefore hyperbolicity is lost. See Table I and Figure 5.

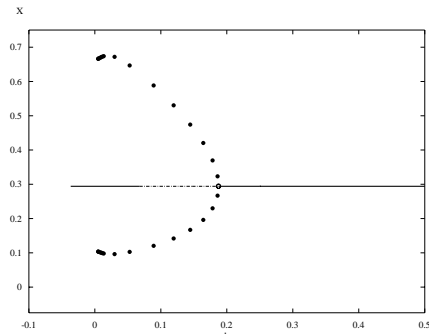


Fig. 4. Bifurcation diagram for system (3)

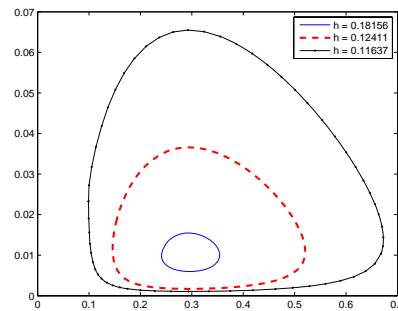


Fig. 5. Periodic orbits of (3)

Heteroclinic Orbits. Given the periodic orbits obtained from a Hopf bifurcation, it is possible to compute heteroclinic orbits connecting equilibrium points to such periodic orbits, e.g. from P_2 to the orbits around P_1 . These special solutions explicitly describe how from an equilibrium point, the populations of both species vary with respect to time until they arrive to a long-term stable periodic solution of coexistence. See Figure 6.

III. BIONOMIC EQUILIBRIUM

In this section we want to find the simultaneous biological and economic equilibrium of the system (3). Let

c = cost per unit effort for prey, ψ = price per unit biomass for the prey.

Assuming that $x \geq T$, we have a profit function:

$$P(x, h) = \psi H(x) - ch, \quad (13)$$

where $H(x)$ is given in (2). Then, the bionomic equilibria (x_i, y_i, h_i) , $i = 0, 1, 2$ are obtained by solving the system

$$x(1-x) - \frac{axy}{1+mx} - \frac{h(x-T)}{h+x-T} = 0 \quad (14)$$

$$y(-d + \frac{bx}{1+mx}) = 0 \quad (15)$$

$$\psi \left(\frac{h(x-T)}{h+x-T} \right) - ch = 0. \quad (16)$$

Disregarding the trivial case $(x_0, y_0, h_0) \equiv 0$, there are two equilibria of interest.

TABLE I
 PERIOD AND FLOQUET MULTIPLIERS

h	Period	Floquet Multiplier
0.1241173	6.71355778	0.8872880
0.151201	6.66124074	0.78218413
0.1735	6.58223366	0.91196026157
0.18156	6.54605454	0.9621362288
0.18543	6.52942041	0.98409133706
0.18735	6.49934034	0.99275482790

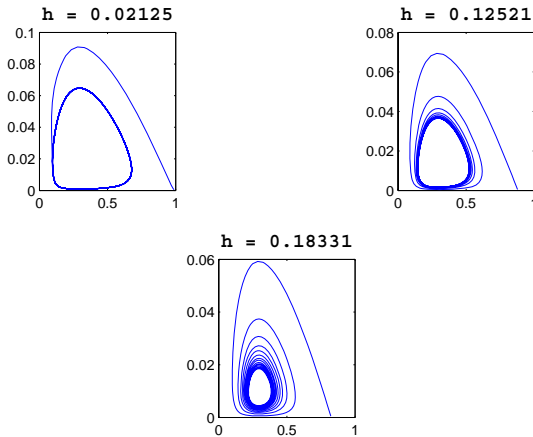


Fig. 6. Heteroclinic orbits of (3)

Case 1: Let $y = y_1 = 0$. This corresponds to the removal of predators from the system. Solving (14) for h_1 gives

$$h_1 = \frac{x_1(T - x_1)(x_1 - 1)}{x_1^2 - T}$$

Substituting into (16) gives

$$x_1^\pm = \frac{c \pm \sqrt{c^2 - 4\psi T(c - \psi)}}{2\psi}$$

Case 2: Assuming $x, y > 0$, from (15),

$$x_2 = \frac{d}{b - md}$$

Substituting for (16) produces

$$h_2 = \frac{(\psi - c)(x - T)}{c}$$

Finally, solving the last equation gives the equilibrium point

$$y_2 = \frac{b}{ad} \left[\frac{\psi d(b - dm - d) - (b - dm)(\psi - c)(d - T(b - dm))}{\psi(b - dm)^2} \right]$$

IV. MODEL TWO

We investigate our original model (3), but now with a piecewise linear threshold policy harvesting

$$H(x) = \begin{cases} 0 & \text{if } x < T_1 \\ \frac{h(x - T_1)}{T_2 - T_1} & \text{if } T_1 \leq x \leq T_2 \\ h & \text{if } x > T_2 \end{cases} \quad (17)$$

We want to study the effects that a relatively small change in the qualitative definition of the harvesting function has on the

solutions of the system itself. In the case $x < T_1$ we have the same corresponding equilibrium points as in first system.

A. Equilibrium Points when $T_1 \leq x \leq T_2$

When prey harvesting increases linearly between T_1 and T_2 , we have three equilibrium points: $P_5 = (x_5, y_5)$, $P_6 = (x_+^*, 0)$ and $P_7 = (x_-^*, 0)$, where

$$x_5 = \frac{d}{b - dm}, \quad y_5 = \frac{b}{a} \left(\frac{b - dm - d}{(b - dm)^2} - \frac{h(d - T_1(b - dm))}{d(b - dm)(T_2 - T_1)} \right),$$

$$x_\pm^* = \frac{T_2 - T_1 - h \pm \sqrt{(h - T_2 + T_1)^2 + 4hT_1(T_2 - T_1)}}{2(T_2 - T_1)}$$

We observe that for P_5 to be in the positive first quadrant we need $b > dm$ and

$$d(b - dm - d)(T_2 - T_1) > h(b - dm)(d - T_1(b - dm)). \quad (18)$$

The general Jacobian is

$$J(x, y) = \begin{bmatrix} 1 - 2x - \frac{ay}{(1+mx)^2} - \frac{h}{T_2 - T_1} & -\frac{ax}{1+mx} \\ \frac{by}{(1+mx)^2} & -d + \frac{bx}{1+mx} \end{bmatrix}. \quad (19)$$

At P_5 it becomes

$$J(x_5, y_5) = \begin{bmatrix} \frac{h(T_1(b - dm)^2 + d^2m)}{bd(T_1 - T_2)} - \frac{d(b(1 - m) + dm(m + 1))}{b(b - dm)} & -\frac{ad}{b} \\ \frac{b - dm - d}{a} - \frac{h(b - dm)(d - T_1(b - dm))}{ad(T_2 - T_1)} & 0 \end{bmatrix}$$

The corresponding determinant δ and trace τ are:

$$\delta = \frac{d(b - dm - d)(T_2 - T_1) - h(b - dm)(d - T_1(b - dm))}{b(T_2 - T_1)}$$

and

$$\tau = \frac{h(T_1(b - dm)^2 + d^2m)}{bd(T_1 - T_2)} - \frac{d(b(1 - m) + dm(m + 1))}{b(b - dm)}$$

First, notice that by (18), we always have $\delta > 0$. On the other hand, we can write:

$$J(x_5, y_5) = \begin{bmatrix} hA - B & C \\ D - hE & 0 \end{bmatrix},$$

where

$$A = \frac{T_1(b - dm)^3 + d^2m(b - dm)}{bd(T_1 - T_2)(b - dm)},$$

$$B = \frac{d(dm^2 + dm - bm + b)}{b(b - dm)}, \quad C = -\frac{ad}{b},$$

$$D = \frac{b - dm - d}{a}, \quad E = \frac{(b - dm)(d - T_1(b - dm))}{ad(T_2 - T_1)}$$

Thus, $\Delta := \tau^2 - 4\delta = (hA - B)^2 - 4C(hE - D) = A^2h^2 - (2AB + 4CE)h + (B^2 + 4CD)$. Assume that $2AB + 4CE > 0$ (we can get the conclusions for the opposite case in a similar way). Denote with $h^- < h^+$ the roots of the quadratic equation $\tau^2 - 4\delta = 0$. Thus, if we have $B^2 + 4CD > 0$, then $\Delta < 0$ for $0 < h^- < h < h^+$, and $\Delta > 0$ for $0 < h < h^-$ and $h > h^+$. Similarly, if $B^2 + 4CD < 0$, then $\Delta < 0$ if $0 < h < h^+$, and $\Delta > 0$ if $h > h^+$.

Now, by defining

$$h^* := \frac{d^2(T_1 - T_2)(b(1 - m) + dm(m + 1))}{(b - dm)(T_1(b - dm)^2 + d^2m)},$$

we see that nodes and foci are stable ($\tau < 0$) when $h > h^*$ and unstable ($\tau > 0$), when $h < h^*$. The equilibrium point P_5 is of center-type if $h = h^*$.

With the notation above, we collect this discussion into the following:

Theorem 6: Assume $2AB + 4CE > 0$. Then, the equilibrium point P_5 of (3) has the following properties

- (a) P_5 is never a saddle.
- (b) P_5 is a focus when $B^2 + 4CD > 0$ and $h^- < h < h^+$, or when $B^2 + 4CD < 0$ and $0 < h < h^+$.
 - It is stable when $h > h^*$ and unstable when $h < h^*$
- (c) P_5 is a node when $B^2 + 4CD > 0$ and $0 < h < h^-$, or when $B^2 + 4CD < 0$ and $h > h^+$.
 - It is stable when $h > h^*$ and unstable when $h < h^*$
- (d) P_5 is a center-type if $h = h^*$.

Note: To make sure that for case $B^2 + 4CD > 0$ we get only real roots, we need $E(AB + CE) - A^2D < 0$, which is satisfied, if B, D and E are positive. Thus, we need

$$m < 1 \quad \text{and} \quad d < b - md < \frac{d}{T_1}.$$

Just as we did for the threshold harvesting in Section II-C, we want to see the effects of piecewise linear threshold harvesting on the equilibrium P_5 ; we are mostly interested in the case $T_1 \leq x \leq T_2$. For the same sets of parameters as before: $a = 1, b = 0.9, d = 0.2, m = 5$, and $a = 2.5, b = 2.25, d = 0.2, m = 5$, and with $T_1 = 0.2, T_2 = 0.6$, numerical calculations indicate that the stable focus $P_1 = (0.4, 1.08)$ of the system without harvesting has moved to a stable node $P_5 = (0.4, 0.63)$; see Figure 7(a). Similarly, the unstable focus $P_1 = (0.16, 0.6048)$ has moved to a stable focus $P_5 = (0.16, 0.6948)$; see Figure 7(b). Thus, as observed before, a stable equilibrium remains to be stable when threshold harvesting is applied, and an unstable equilibrium becomes stable, that is, for some sets of parameters, harvesting has a stabilizing effect on the ecosystem.

From the above paragraph, we observe that the number of prey for such equilibrium points stays constant with or without harvesting. This is obviously true since x_5 does not depend on the harvesting. We can see instead how the predator density changes as $h > 0$ increases. It is easy to see that

$$\frac{dy_5}{dh} = \frac{b}{a(T_2 - T_1)} \left[\frac{T_1}{d} - \frac{1}{b - md} \right].$$

Therefore, the predator population density increases as h increases if the prey conversion rate b and the predator death rate d satisfy the relation $T_1 b > (mT_1 + 1)d$. The predator population decreases if the inequality is reversed.

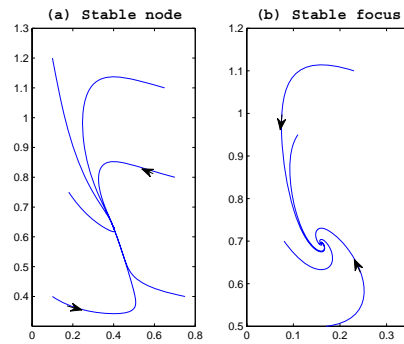


Fig. 7. Effect of harvesting (17), $T_1 \leq x \leq T_2$

The Jacobian $J_{(x_{\pm}^*, 0)}$ evaluated at the points P_6 and P_7 is

$$\begin{bmatrix} \frac{\pm\sqrt{R}}{T_1 - T_2} & -\frac{a(T_1 - T_2 + h \mp \sqrt{R})}{m(T_1 - T_2 + h \mp \sqrt{R}) + 2T_1 - 2T_2} \\ 0 & \frac{b(T_1 - T_2 + h \mp \sqrt{R})}{m(T_1 - T_2 + h \mp \sqrt{R}) + 2T_1 - 2T_2} - d \end{bmatrix},$$

where $R = (T_1 - T_2 + h)^2 - 4T_1h(T_1 - T_2)$.

Then, we have

- None of the equilibria can be foci, nor of center-type.
- P_6 is a saddle if $d < \frac{b(T_1 - T_2 + h - \phi)}{m(T_1 - T_2 + h - \phi) + 2T_1 - 2T_2}$, with $(h - T_2 + T_1)^2 + 4hT_1(T_2 - T_1) > 0$ and $m(T_1 - T_2 + h - \phi) + 2T_1 - 2T_2 \neq 0$.
- P_7 is a saddle if $d > \frac{b(T_1 - T_2 + h + \phi)}{m(T_1 - T_2 + h + \phi) + 2T_1 - 2T_2}$, with $(h - T_2 + T_1)^2 + 4hT_1(T_2 - T_1) > 0$ and $m(T_1 - T_2 + h + \phi) + 2T_1 - 2T_2 \neq 0$.
- P_6 is a node if $d > \frac{b(T_1 - T_2 + h - \phi)}{m(T_1 - T_2 + h - \phi) + 2T_1 - 2T_2} + \frac{\phi}{T_1 - T_2}$.
 - P_6 is always stable as the stability condition is the same as the node condition.
- P_7 is a node if $d < \frac{b(T_1 - T_2 + h + \phi)}{m(T_1 - T_2 + h + \phi) + 2T_1 - 2T_2} - \frac{\phi}{T_1 - T_2}$.
 - P_7 is always unstable as the stability condition is the same as the node condition.

Here, $\phi = \sqrt{(h - T_2 + T_1)^2 + 4hT_1(T_2 - T_1)}$.

B. Equilibrium Points when $x > T_2$

When the prey size is beyond the threshold value T_2 , we have constant harvesting $H(x) = h$. In this case we have three equilibrium points, $P_8 = (x_8, y_8)$, $P_9 = (\hat{x}_+, 0)$ and $P_{10} = (\hat{x}_-, 0)$, where

$$x_8 = \frac{d}{b - md}, \quad y_8 = \frac{b}{a} \left(\frac{b - md - d}{(b - md)^2} - \frac{h}{d} \right),$$

$$\hat{x}_{\pm} = \frac{1 \pm \sqrt{1 - 4h}}{2}.$$

We immediately observe that we must have $h \leq \frac{1}{4}$ for P_9, P_{10} to lie in R_+^2 , and that $P_8 \in R_+^2$ if

$$b > md \quad \text{and} \quad d[b - (m + 1)d] > h(b - md)^2. \quad (20)$$

The general Jacobian is

$$J(x, y) = \begin{bmatrix} 1 - 2x - \frac{ay}{(1+mx)^2} & -\frac{ax}{1+mx} \\ \frac{by}{(1+mx)^2} & -d + \frac{bx}{1+mx} \end{bmatrix} \quad (21)$$

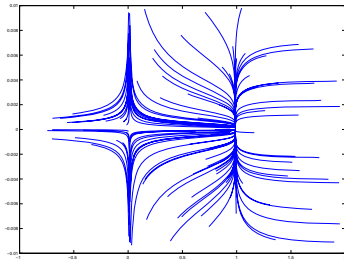


Fig. 8. Saddle point P_9 and stable node P_{10}

The Jacobian at P_8 is

$$J(x_8, y_8) = \begin{bmatrix} \frac{A-(b-md)B}{C} & -\frac{ad}{b} \\ \frac{B}{ad} & 0 \end{bmatrix},$$

where $A = bd[b - (m + 2)d]$, $B = d[b - (m + 1)d] - h(b - md)^2$, $C = bd(b - md)$.

The corresponding determinant δ and trace τ are

$$\delta = \frac{B}{b} > 0, \quad \tau = \frac{A - (b - md)B}{C}$$

Therefore, we get:

Theorem 7: The equilibrium point P_8 has the following properties

- It is never a saddle.
- It is a node when $\left[\frac{A-(b-md)B}{C}\right]^2 > 4B/b$. The node is stable if $A < (b - md)B$, and unstable if the inequality is reversed.
- It is a focus when $\left[\frac{A-(b-md)B}{C}\right]^2 < 4B/b$. The focus is stable if $A < (b - md)B$, and unstable if the inequality is reversed.
- It is a center-type if $A = (b - md)B$.

The Jacobian at P_9 and P_{10} is

$$J(\hat{x}_{\pm}, 0) = \begin{bmatrix} \pm\sqrt{1-4h} & -\frac{a(\mp 1 + \sqrt{1-4h})}{m(\mp 1 + \sqrt{1-4h}) \mp 2} \\ 0 & -d + \frac{b(\mp 1 + \sqrt{1-4h})}{m(\mp 1 + \sqrt{1-4h}) \mp 2} \end{bmatrix}$$

Therefore, for $\kappa = \sqrt{1-4h}$, we immediately have

- P_9 is a saddle when $d > \frac{b(\kappa-1)}{m(\kappa-1)-2}$.
- P_9 is a node if $d < \frac{b(\kappa-1)}{m(\kappa-1)-2}$.
- P_9 cannot be a stable node because it would require $d > \frac{b(\kappa-1)}{m(\kappa-1)-2}$.
- P_{10} is a saddle when $d < \frac{b(1+\kappa)}{m(1+\kappa)+2}$.
- P_{10} is a node if $d > \frac{b(1+\kappa)}{m(1+\kappa)+2}$.
- P_{10} cannot be an unstable node because it would require $d < \frac{b(1+\kappa)}{m(1+\kappa)+2}$.
- Neither P_9 nor P_{10} can be centers or foci.

Note: Observe that if the condition (20) is violated, then there are no coexistence equilibria, and therefore there cannot be any limit cycle on the positive first quadrant R_+^2 , because every closed orbit must contain an equilibrium point in its interior.

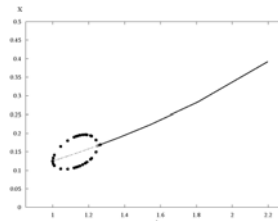


Fig. 9. Saddle point P_9 and stable node P_{10}

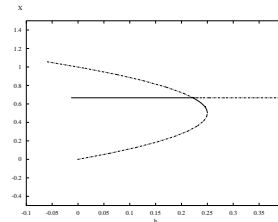


Fig. 10. Fold and transcritical bifurcations

C. Bifurcations

The system (3), with piecewise threshold harvesting (17) exhibits several bifurcations when one or more parameters are allowed to vary. Similarly as in Theorem 5, one can prove the existence of subcritical and supercritical Hopf bifurcations when conditions are given for the equilibrium point P_5 to be of center-type. Using Xppaut, a Hopf bifurcation was detected at $d = 1.25$, and a branch of periodic orbits is born out of this bifurcation. See Figure 9.

To see that there is a saddle-node (fold) bifurcation, we first observe that for $h = h^* = \frac{1}{4}$ and $b \neq (m + 2)d$, the Jacobian at P_9 has eigenvalues $\lambda_1 = 0$ and $\lambda_2 = -d + \frac{b}{m+2} \neq 0$. We shift the equilibrium $(h^*, \hat{x}_+, 0) = (\frac{1}{4}, \frac{1}{2}, 0)$ to the origin via the change of variables $\alpha = h - \frac{1}{4}$, $u = x - \frac{1}{2}$, $v = y$. Then, the new system can be written as

$$\begin{aligned} \dot{u} &= F_1(\alpha, u, v) \\ \dot{v} &= -v + F_2(\alpha, u, v). \end{aligned}$$

Then, we have $\frac{\partial F_1}{\partial \alpha}(0, 0, 0) = -1 \neq 0$, $\frac{\partial^2 F_1}{\partial u^2}(0, 0, 0) = -2 \neq 0$, which implies the existence [4, Theorem 10.9] of a saddle-node bifurcation.

There is also a transcritical bifurcation at $h = 0.22$. This tells us e.g. that as h increases, two of the equilibrium points interchange stability at $h = 0.22$; there are three equilibria for $h < \frac{1}{4}$ and only one for $h > \frac{1}{4}$. See Figure 10.

Similarly as in Section II-D, one is able to compute heteroclinic orbits connecting equilibrium points to periodic orbits coming out from the Hopf bifurcations. Finally, as in Section III, one can also explicitly compute a bionomic equilibrium for the system (3), (17). This gives

$$x = T_1 + \frac{c(T_2 - T_1)}{\psi}, \quad y = E + \frac{T_1 b h}{ad(T_2 - T_1)},$$

$$\text{where } E = \frac{b[(b-dm)(T_2-T_1-h)-d(T_2-T_1)]}{a(T_2-T_1)(b-dm)^2}.$$

Observe also in Figure 9 that below certain value of h there are no periodic orbits. As a matter of fact, one can give sufficient conditions so that the system (3) for the case $x > T_2$ has no limit cycles. More precisely, we have

Theorem 8: The system (3) has no limit cycles when $x \in (T_2, \sqrt{h})$.

Proof: Denote the system (3) by $\dot{x} = F_1(x, y)$, $\dot{y} = F_2(x, y)$, and define the function $R(x, y) = 1/xy$. Then, we get

$$\frac{\partial(RF_1)}{\partial x} + \frac{\partial(RF_2)}{\partial y} = \frac{am}{(1+mx)^2} + \frac{1}{y} \left(\frac{h-x^2}{x^2} \right),$$

which is strictly positive if $0 < x < \sqrt{h}$, but we are in the case $x > T_2 > 0$. Then, by Dulac's criterion, such system has no limit cycles if $x \in (T_2, \sqrt{h})$. ■

V. DISCUSSION

We have studied a predator-prey system with two different continuous threshold harvesting functions. The first one considers a smooth harvesting behavior after reaching the threshold value T , and the second a piecewise linear harvesting behavior after reaching the first threshold value T_1 . Both harvesting functions are biologically more realistic than the typical piecewise constant (or full constant, linear or rational harvesting) functions considered in most current literature on predator-prey models with harvesting. A theoretical and numerical analysis has revealed rich dynamics, and we have studied existence and stability of equilibria and periodic orbits, bifurcations, boundedness of solutions, heteroclinic orbits, and biomic equilibria for both models.

We have discussed how these two different harvesting functions, namely (2) and (17), affect the qualitative behavior of solutions and the stability of the equilibria. We start by comparing the equilibrium points and their properties for both models in the cases where both x and y are strictly positive. In such a case, we always have $x = \frac{d}{b-dm}$, and the corresponding y values satisfy

$$y_1 \geq y_3 \geq y_5 \geq y_8 \quad (22)$$

when

$$\frac{T(b-dm) - d}{(b-dm)(h-T) + d} \geq \frac{T_1(b-dm) - d}{(b-dm)(T_2 - T_1)},$$

but

$$y_1 \geq y_5 \geq y_3 \geq y_8 \quad (23)$$

when

$$\frac{T(b-dm) - d}{(b-dm)(h-T) + d} \leq \frac{T_1(b-dm) - d}{(b-dm)(T_2 - T_1)}.$$

In particular, inequalities (22) and (23) allow us to compare the equilibrium point $P_3 = (x_3, y_3)$ of the first model, for $x \geq T$, with the equilibria $P_5 = (x_5, y_5)$ and $P_8 = (x_8, y_8)$ of the second model, for $T_1 \leq x \leq T_2$ and $x > T_2$ respectively.

It is interesting to observe that for both models the above equilibria can be nodes, foci, and centers, but not saddles. On

the other hand, all equilibria on the x axis can be nodes or saddles but not centers nor foci.

With respect to the harvesting function on the first model for $x > T$, observe that if we allow the harvesting limit h to increase ($h \rightarrow \infty$), we get $H(x) \rightarrow x - T$, and $y_3 \rightarrow \frac{Tb}{ad} - \frac{bd}{a(b-dm)^2}$. Thus, increasing the harvesting effort on the prey, would not necessarily imply the extinction of the predator as long as the threshold value satisfies $T > \left(\frac{d}{b-dm}\right)^2$. However, the equilibrium point of interest, P_3 only exists after harvesting begins, which implies the condition that $x = \frac{d}{b-dm} > T$.

Our first model produces four equilibria, while the second model produces eight, with two equilibria, P_5 and P_8 from the second model corresponding to P_3 from the first, and four points from the second model, P_6, P_7, P_9, P_{10} , corresponding to the point P_4 from the first one. However, their stability properties do not correspond exactly, since P_3 from the first model can only be stable, while both P_5 and P_8 from the second model can be either stable or unstable. Likewise, while P_4 from the first model can be either stable or unstable, P_9 can only be unstable and P_{10} can only be stable.

We mention a few possible extensions of this work: harvesting on both the predator and the prey, a combination of threshold policy harvesting with other types of harvesting, (like seasonal harvesting), the inclusion of a infectious disease, especially when this is associated with a risk of mortality of one or both species, addition of a species refuge, addition of diffusion terms with computation of traveling waves, and the consideration of more than two species. These extensions would help realize how far our results apply to other ecosystems and population relationships.

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