



Ecology/Écologie

A focus on long-run sustainability of a harvested prey predator system in the presence of alternative prey[☆]

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ABSTRACT

Within the framework of a general equilibrium model we study the long-run dynamics of a prey-predator model in the presence of an alternative prey. Our results show that sustainability, i.e. a positive value of the population in the long run, essentially depends on individual harvesting efforts and digesting factors relative to alternative prey. A detailed bifurcation analysis evidences the richness of possible long-run dynamics. Our model clearly shows that the role of an alternative prey must be taken into consideration when studying prey-predator dynamics.

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1. Introduction

The modelling of commercial exploitations of renewable biological resources is a challenging task, as it includes the non-linear interaction of biological, economic and social components. In recent past years, many researchers have paid attention to the management of renewable resources, considering different parameters and externalities. In the management of common property renewable resources (such as fisheries, forestry and wildlife) harvested by competing individuals, societies or countries, the problem known as “The tragedy of commons” after Hardin [1]. Later on Clark [2], Masterton-Gibbons [3], Conrad [4] discussed many issues and techniques on this subject. Clark [2] discussed the problem of non-selective harvesting of two ecologically independent populations obeying logistic growth. Kar and Chaudhuri [5] discussed non-

selective harvesting of a multispecies fishery. There are also some papers on competitive fish-species and on prey-predator models (see Gordon [6]; Datta and Mirman [7]; Bischi and Kopel [8]; Dubey et al. [9]; Bischi et al. [10]). Most of the prey-predator models consider a single prey called the focal prey; however, many authors have emphasized that the presence of alternative foods can effect biological control through a variety of mechanisms. For example, the presence of one prey species can have negative effects on the population of another prey species, by allowing the population of a shared predator to increase, thus leading to higher predation rates upon both prey items. In contrast, alternative prey can also lower predation on focal prey because of predator preference for alternative prey resources (Abram and Matsuda [11]). In such instances, the alternative prey can have a positive effect on population densities of the focal prey. Many massive piscivores, including spiny dogfish in the North-West Atlantic, and Pacific hake, undertake extensive seasonal migrations on a spatial scale much larger than the habitat occupied by some of their prey, and the development of realistic models for these prey-predator systems will require consideration of alternative prey. Vence [12], Spencer and Collie [13] have considered alternative prey in their models.

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Methods used for managing predators, and associated public perception, are a crucial consideration in developing effective systems of management for predators and prey. Controlling predator populations to reduce predation on a threatened or endangered species may be difficult to achieve. Keeping wolf and cougar (wild American cat) populations in check might require reducing alternate prey. Control of mule deer populations in Sierra mountains of California might be required in addition to reductions in cougar numbers to prevent extirpation (complete destruction) of Sierra Nevada big horned sheep populations. The Alberta Government has issued additional hunting permits for moose and deer in an attempt to reduce alternate prey for wolves, hoping to reduce wolf numbers and thereby predation pressure on caribou.

In this study, we develop a simple, two species predator-prey model that incorporates the effect of alternative prey. We consider logistic production function of prey and a Holling type-II predator functional response (Holling [14]) so that there may present multiple equilibrium population levels. In our model, the growth rate of prey is formulated as

$$\frac{dN}{dT} = rN(1 - N/K) - \frac{\alpha_1 NP}{a + N} \quad (1)$$

where $N = N(T)$ = size of prey at time T , $P = P(T)$ = size of predator at time T , K = environmental carrying capacity of prey, r = intrinsic growth rate of prey, α_1 = predation coefficient, a = half-saturation constant.

The growth rate of predator population is taken as

$$\frac{dP}{dT} = \frac{\beta_1 \alpha_1 NP}{a + N} + d_1 P(1 - N/K) - \gamma_1 P \quad (2)$$

where β_1 is a conversion factor (we assume $\beta_1 < 1$, since the whole biomass of the prey is not transferred to the biomass of the predator), d_1 is the digesting factor relative to alternative prey and γ_1 is mortality rate of predator population.

Here, as the focal prey population (N) increases, the predator uses less alternative prey and when $N \rightarrow K$ the mass of alternative prey consumed tends to zero, and conversely, as the focal prey decreases, the predators increase their feeding on alternative prey. If $N \rightarrow 0$ then $dP/dT \rightarrow (d_1 - \gamma_1)P$. Thus even in case of the extinction of the focal prey the predator population maintains its growth rate, varying linearly with its density.

Now we introduce dimensionless variables by the following substitution $N = ax$, $P = ray/\alpha_1$, $T = t/r$ then our Eqs. (1) and (2) become

$$\frac{dx}{dt} = x(1 - x/K) - \frac{xy}{1 + x} \quad (3)$$

$$\frac{dy}{dt} = \frac{\beta_1 \alpha_1}{r} \frac{xy}{1 + x} + \frac{d_1}{r} y(1 - x/K) - \frac{\gamma_1}{r} y \quad (4)$$

Letting

$\frac{K}{a} = \eta$, $\frac{\beta_1 \alpha_1}{r} = \beta$, $\frac{d_1}{r} = d$, $\frac{\gamma_1}{r} = \gamma$
we can write the governing equations as

$$\frac{dx}{dt} = x(1 - x/\eta) - \frac{xy}{1 + x} \quad (5)$$

$$\frac{dy}{dt} = \frac{\beta xy}{1 + x} + dy(1 - x/\eta) - \gamma y \quad (6)$$

For considering the exploited prey-predator system, we introduce scaled harvesting efforts E_1 and E_2 for prey and predator, respectively and then the equations governing our model become

$$\frac{dx}{dt} = x(1 - x/\eta) - \frac{xy}{1 + x} - E_1 x \quad (7)$$

$$\frac{dy}{dt} = \frac{\beta xy}{1 + x} + dy(1 - x/\eta) - \gamma y - E_2 y \quad (8)$$

The Note is organized as follows. The existence of different equilibrium points are considered in section 2. Stability analysis and bifurcations are given in section 3. In section 4, detailed numerical simulations are given. The Note ends with a conclusion in section 5.

2. Equilibrium of the model

Letting $\phi_1(x) = \frac{x}{x+1}$, $\phi_2(x) = (1 - x/\eta - E_1)(x + 1)$ and $\phi_3(x) = \beta\phi_1(x) + d(1 - x/\eta) - (E_2 + \gamma)$ the governing equations (7) and (8) become

$$\frac{dx}{dt} = \phi_1(x)[\phi_2(x) - y] \quad (9)$$

$$\frac{dy}{dt} = y\phi_3(x) \quad (10)$$

The prey zero growth lines are obtained by setting $dx/dt = 0$, which gives $\phi_1(x) = 0$, $y = \phi_2(x)$ that is $x = 0$ (y -axis) and the curve $y = \phi_2(x)$. The curve $y = \phi_2(x)$ passes through the points $(0, 1 - E_1)$ and $(\eta(1 - E_1), 0)$.

We see that

$$\begin{aligned} \phi_2'(x) &= (1 - x/\eta - E_1) + (1 + x)(-1/\eta) \\ &= 1 - E_1 - 1/\eta - 2x/\eta. \end{aligned}$$

Thus, $\phi_2'(0) = 1 - E_1 - 1/\eta$, and $\phi_2'(\eta(1 - E_1)) = -(1 - E_1 + 1/\eta)$

Thus if $\eta(1 - E_1) > 1$, then $\phi_2'(0)$ and $\phi_2'(\eta(1 - E_1))$ are of opposite signs and so $\phi_2(x)$ has a local maximum between $x = 0$ and $x = \eta(1 - E_1)$. The predator zero growth lines are obtained by setting $dy/dt = 0$ i.e. $y = 0$ (x -axis) and $\phi_3(x) = 0$. Thus isoclines of predator other than x -axis are the zeros of $\phi_3(x)$.

These are given by

$$\beta\phi_1(x) + d(1 - x/\eta) - (E_2 + \gamma) = 0,$$

or,

$$-dx^2/\eta + (\beta + d - d/\eta - E_2 - \gamma)x + d - E_2 - \gamma = 0 \quad (11)$$

The zeros of $\phi_3(x)$ are given by

$$\begin{aligned} x_2, x_1 &= \frac{\eta}{2d} [(d + \beta - d/\eta - E_2 - \gamma) \\ &\pm \sqrt{(d + \beta - d/\eta - E_2 - \gamma)^2 - \frac{4d}{\eta}(E_2 + \gamma - d)}] \end{aligned} \quad (12)$$

Here we investigate the different cases for positive zeros of $\phi_3(x)$ to have interior equilibrium. From the above discussion we already have two boundary equilibria $P_0(0, 0)$, $P_1((1 - E_1)\eta, 0)$ while P_1 exists if $E_1 < 1$.

Case 1.

If $(d + \beta - \frac{d}{\eta} - E_2 - \gamma) > 0$, and $E_2 + \gamma - d < 0$, that is, if $E_2 < \text{Min}\{(\beta - \frac{d}{\eta}) + d - \gamma, d - \gamma\}$, then $\phi_3(x)$ has only one positive zero given by

$$x_2 = \frac{\eta}{2d} [(d + \beta - d/\eta - E_2 - \gamma) + \sqrt{(d + \beta - d/\eta - E_2 - \gamma)^2 - \frac{4d}{\eta}(E_2 + \gamma - d)}] \quad (13)$$

and the corresponding value of y is $y_2 = \phi_2(x_2) = (1 + x_2)(1 - \frac{x_2}{\eta} - E_1)$, which lies in R_2^+ if $E_1 < 1 - x_2/\eta$.

Thus, in this case, the trivial equilibrium $P_0(0, 0)$ always exists, the boundary equilibrium $P_1((1 - E_1)\eta, 0)$ exists if $E_1 < 1$ and the only interior equilibrium $P_2(x_2, \phi_2(x_2))$ exists if $E_1 < 1 - x_2/\eta$ and $E_2 < \text{Min}\{(\beta - \frac{d}{\eta}) + d - \gamma, d - \gamma\}$.

Here it can be observed that if P_2 exists then P_1 also exists.

Case 2.

Let $(d + \beta - \frac{d}{\eta} - E_2 - \gamma) < 0$, $E_2 + \gamma - d < 0$. In this case only one positive interior equilibrium may be obtained if $(d - \gamma) > 0$, $(\beta - d/\eta) < 0$ i.e. if $d > \max\{\gamma, \beta\eta\}$ and $(d + \beta - \frac{d}{\eta} - \gamma) < E_2 < (d - \gamma)$.

In this case $x = x_2$ is a positive zero of $\phi_3(x)$ and $P_2(x_2, \phi_2(x_2))$ is a positive interior equilibrium while $E_1 < 1 - x_2/\eta$ along with the above conditions. Therefore, in this case, the trivial equilibrium $P_0(0, 0)$ always exists, the boundary equilibrium $P_1((1 - E_1)\eta, 0)$ exists if $E_1 < 1$ and the interior equilibrium $P_2(x_2, \phi_2(x_2))$ exists if $E_1 < 1 - x_2/\eta$, $d > \max\{\gamma, \beta\eta\}$ and $(d + \beta - \frac{d}{\eta} - \gamma) < E_2 < (d - \gamma)$. Here also we see that the conditions of existence of P_2 suffice the existence of P_1 .

Case 3.

Let

$$(d + \beta - \frac{d}{\eta} - E_2 - \gamma) > 0, \quad E_2 + \gamma - d > 0$$

and

$$(d + \beta - \frac{d}{\eta} - E_2 - \gamma)^2 > \frac{4d}{\eta}(E_2 + \gamma - d)$$

More explicitly,

$$d - \gamma < E_2 < d - \gamma + \beta - \frac{d}{\eta}$$

and

$$(d + \beta - \frac{d}{\eta} - E_2 - \gamma)^2 > \frac{4d}{\eta}(E_2 + \gamma - d)$$

for $\gamma < d < \eta\beta$, or, $d < \gamma < (\beta - \frac{d}{\eta} + d)$.

Then there are two positive zeros of $\phi_3(x)$ which are x_1, x_2 given in (12) and

$$\phi_3(x) = \begin{cases} > 0 & \text{for } x_1 < x < x_2 \\ < 0 & \text{for } 0 < x < x_1, \quad x > x_2, \end{cases}$$

i.e. $\phi_3'(x_1) > 0$ and $\phi_3'(x_2) > 0$. In this case all four equilibria exist. The boundary equilibrium $P_1((1 - E_1)\eta, 0)$ exists if the condition:(H1): $E_1 < 1$ is satisfied. One interior equilibrium $P_2(x_1, \phi_2(x_1))$ exists if the following conditions are satisfied:(H2): $(d + \beta - \frac{d}{\eta} - E_2 - \gamma)^2 > \frac{4d}{\eta}(E_2 + \gamma - d)$, $E_1 < 1 - x_1/\eta$ with $\gamma < d < \eta\beta$, or $d < \gamma < (\beta - \frac{d}{\eta} + d)$, and the other interior equilibrium $P_3(x_2, \phi_2(x_2))$ exists if the conditions below are satisfied:(H3): $d - \gamma < E_2 < d - \gamma + \beta - \frac{d}{\eta}(d + \beta - \frac{d}{\eta} - E_2 - \gamma)^2 > \frac{4d}{\eta}(E_2 + \gamma - d)$, $E_1 < 1 - x_2/\eta$ with $\gamma < d < \eta\beta$ or $d < \gamma < (\beta - \frac{d}{\eta} + d)$.

It is observed that at P_2 & P_3 both the species co-exist under some conditions stated above.

3. Stability analysis

The Jacobian matrix for our model is

$$J(x, y) = \begin{bmatrix} \phi_1'(x)(\phi_2(x) - y) + \phi_1(x)\phi_2'(x) & -\phi_1(x) \\ y\phi_3'(x) & \phi_3(x) \end{bmatrix}. \quad (14)$$

Since $\phi_1(x) = \frac{x}{1+x}$, therefore $\phi_1'(x) = \frac{1}{(1+x)^2}$ and from the expressions of $\phi_2(x)$, $\phi_3(x)$ we get

$$\begin{aligned} \phi_2'(x) &= 1 - E_1 - \frac{1}{\eta} - \frac{2x}{\eta}, \\ \phi_3'(x) &= \beta\phi_1'(x) - \frac{d}{\eta} = \frac{\beta}{(1+x)^2} - \frac{d}{\eta}. \end{aligned}$$

We first investigate the stability at the trivial equilibrium $P_0(0, 0)$, the boundary equilibrium $P_1((1 - E_1)\eta, 0)$, and then the discussion of stability of interior equilibrium will be considered in different cases as they appear in terms of their existence.

At $P_0(0, 0)$ the corresponding community matrix is simplified to be

$$J(P_0) = \begin{bmatrix} 1 - E_1 & 0 \\ 0 & d - E_2 - \gamma \end{bmatrix},$$

whose eigen values are $(1 - E_1)$ and $(d - E_2 - \gamma)$. Therefore the equilibrium at P_0 is stable if

$$E_1 > 1 \text{ and } E_2 > d - \gamma \quad (15)$$

At $P_1((1 - E_1)\eta, 0)$ the matrix J is evaluated as

$$J(P_1) = \begin{bmatrix} -(1 - E_1) & \phi_1((1 - E_1)\eta) \\ 0 & \phi_3((1 - E_1)\eta) \end{bmatrix}$$

whose eigen values are $\lambda_1 = -(1 - E_1) < 0$, since $E_1 < 1$ for existence of P_1 and $\lambda_2 = \phi_3((1 - E_1)\eta)$.

Now $\lambda_2 < 0$ if

$$\frac{\beta(1 - E_1)\eta}{1 + (1 - E_1)\eta} + d(1 - \frac{(1 - E_1)\eta}{\eta}) - (E_2 + \gamma) > 0$$

i.e. if

$$E_2 > \frac{\beta(1 - E_1)\eta}{1 + (1 - E_1)\eta} + dE_1 - \gamma.$$

Thus, P_1 is a stable equilibrium if

$$E_2 > \frac{\beta(1 - E_1)\eta}{1 + (1 - E_1)\eta} + dE_1 - \gamma \tag{16}$$

and $E_1 < 1$

Now we go through the following cases for discussing the stability at interior equilibrium, taking the references of the cases of existence of equilibrium points discussed earlier.

Case 1.

Let-

$E_2 < \text{Min}\{(\beta - \frac{d}{\eta}) + d - \gamma, d - \gamma\}$ and $E_1 < 1 - x_2/\eta$, then only the positive interior equilibrium is $P_2(x_2, \phi_2(x_2))$. At this equilibrium

$$J = \begin{bmatrix} \phi_1(x_2)\phi_2'(x_2) & -\phi_1(x_2) \\ \phi_2(x_2)\phi_3'(x_2) & 0 \end{bmatrix}$$

The characteristic equation is

$$\lambda^2 - \lambda\phi_1(x_2)\phi_2'(x_2) + \phi_1(x_2)\phi_2(x_2)\phi_3'(x_2) = 0 \tag{17}$$

Since x_1, x_2 are the roots of $\phi_3(x) = 0$, therefore from Eq. (11) we have

$$\phi_3(x) = -\frac{d}{\eta}[(x - x_2)(x - x_1)]$$

where $x_2 > x_1$ and hence

$$\phi_3'(x) = -\frac{d}{\eta}[(x - x_2) + (x - x_1)]$$

so that

$$\phi_3'(x_2) = -\frac{d}{\eta}(x_2 - x_1) < 0$$

Thus $\phi_1(x_2)\phi_2(x_2)\phi_3'(x_2) < 0$ as $\phi_1(x_2), \phi_2(x_2)$ are positive and hence (17) has one positive and one negative root. Therefore in this case $P_2(x_2, \phi_2(x_2))$ is an unstable equilibrium.

Case 2.

Let

$$(d + \beta - \frac{d}{\eta} - E_2 - \gamma) < 0 \text{ and } E_2 + \gamma - d < 0.$$

In this case $P_2(x_2, \phi_2(x_2))$ is the only positive interior equilibrium. As in Case 1, $\phi_3'(x_2) < 0$ and the equilibrium is unstable at $P_2(x_2, \phi_2(x_2))$.

Case 3.

Let

$$(d + \beta - \frac{d}{\eta} - E_2 - \gamma) > 0, E_2 + \gamma - d > 0$$

and

$$(d + \beta - \frac{d}{\eta} - E_2 - \gamma)^2 > \frac{4d}{\eta}(E_2 + \gamma - d).$$

In this case two interior equilibrium points $P_2(x_1, \phi_2(x_1))$ and $P_3(x_2, \phi_2(x_2))$ exist.

Now we investigate the stability at P_2 and P_3 .

At $P_2(x_1, \phi_2(x_1))$ the community matrix is reduced to

$$J(P_2) = \begin{bmatrix} \phi_1(x_1)\phi_2'(x_1) & -\phi_1(x_1) \\ \phi_2(x_1)\phi_3'(x_1) & 0 \end{bmatrix} \tag{18}$$

whose characteristic equation is

$$\lambda^2 - \lambda\phi_1(x_1)\phi_2'(x_1) + \phi_1(x_1)\phi_2(x_1)\phi_3'(x_1) = 0 \tag{19}$$

Now $\phi_1(x_1), \phi_2(x_1), \phi_3'(x_1)$ are all positive under the conditions of existence of $P_2(x_1, \phi_2(x_1))$. Thus by Descartes' rule of signs, P_2 is a node or a focus or a centre. By Routh-Hurwitz condition, the equilibrium at $P_2(x_1, \phi_2(x_1))$ is stable if $\phi_2'(x_1) < 0$, and is unstable if $\phi_2'(x_1) > 0$. A limit cycle is expected closed to the curve $\phi_2'(x_1) = 0$. Now $\phi_2'(x_1) = 0$ implies that $1 - E_1 - \frac{1}{\eta} - \frac{2x_1}{\eta} = 0$, or $1 - E_1 = \frac{1}{\eta}(1 + 2x_1)$.

Or,

$$\begin{aligned} E_1 &= 1 - \frac{1}{\eta}(1 + 2x_1) \\ &= 1 - \frac{1}{\eta} - \frac{1}{d}[(d + \beta - \frac{d}{\eta} - E_2 - \gamma) \\ &\quad - \sqrt{(d + \beta - \frac{d}{\eta} - E_2 - \gamma)^2 - \frac{4d}{\eta}(E_2 + \gamma - d)}] \end{aligned}$$

i.e.

$$E_1 = \phi(E_2) \tag{20}$$

where

$$\begin{aligned} \phi(E_2) &= 1 - \frac{1}{\eta} - \frac{1}{d}[(d + \beta - \frac{d}{\eta} - E_2 - \gamma) \\ &\quad - \sqrt{(d + \beta - \frac{d}{\eta} - E_2 - \gamma)^2 - \frac{4d}{\eta}(E_2 + \gamma - d)}] \end{aligned} \tag{21}$$

Thus if $\phi_2'(x_1) < 0$ i.e. if $E_1 > \phi(E_2)$ then $P_2(x_1, \phi_2(x_1))$ is locally asymptotically stable and if $E_1 < \phi(E_2)$ then $P_2(x_1, \phi_2(x_1))$ is unstable in the positive quadrant of x_1x_2 - plane. For $E_1 = \phi(E_2)$ i.e., for $\phi_2'(x_1) = 0$ the roots of (19) ur discussion on stability at $P_3(x_2, \phi_2(x_2))$ we see that the characteristic equation of the community matrix at P_3 is

$$\lambda^2 - \lambda\phi_1(x_2)\phi_2'(x_2) + \phi_1(x_2)\phi_2(x_2)\phi_3'(x_2) = 0 \tag{22}$$

Since we have earlier discussed that $\phi_3'(x_2) < 0, \phi_1(x_2) > 0, \phi_2(x_2) > 0$ for the existence of P_3 ; therefore by Descartes' rule of signs, the roots of (22) are both real and of opposite sign. Thus $P_3(x_2, \phi_2(x_2))$ is an unstable saddle point whatever the sign of $\phi_2'(x_2)$ may be.

We now state the following theorem:

Theorem 1. If the conditions (H1), (H2) and (H3) are satisfied then:

- (i) $P_0(0, 0)$ is stable if $E_1 > 1, E_2 > d - \gamma$.
- (ii) $P_1((1 - E_1)\eta, 0)$ is stable if $E_2 > \frac{\beta(1 - E_1)\eta}{1 + (1 - E_1)\eta} + dE_1 - \gamma$

and is unstable when $E_2 < \frac{\beta(1 - E_1)\eta}{1 + (1 - E_1)\eta} + dE_1 - \gamma$.

(iii) $P_2(x_1, \phi_2(x_1))$ is stable if $E_1 > \phi(E_2)$ and is unstable when $E_1 < \phi(E_2)$.

(iv) $P_3(x_2, \phi_2(x_2))$ is always unstable.

We notice that

$$\begin{aligned} \frac{d}{dE_1}(\text{Trace } J)_{E_1=\phi(E_2)} &= \frac{d}{dE_1}[\phi_1(x_1)\phi_2'(x_1)]_{E_1=\phi(E_2)} \\ &= -\frac{x_1}{1+x_1} \neq 0. \end{aligned}$$

Hence by the Hopf bifurcation theorem (Hassard et al. [15]) the system (9) and (10) enters into a Hopf type small amplitude periodic oscillation at the parametric values $E_1 = \phi(E_2)$ near the positive interior equilibrium $P_2(x_1, \phi_2(x_1))$. Hence we may state the following theorem:

Theorem 2. For $E_1 = \phi(E_2)$ a super critical Hopf bifurcation takes place for the equilibrium P_2 .

Proof. Let us consider the Jacobian matrix (18). By direct calculation the eigen values are given by:

$$\lambda_{1,2} = \frac{\phi_1(x_1)\phi_2'(x_1) \pm \sqrt{\{\phi_1(x_1)\phi_2'(x_1)\}^2 - 4\phi_1(x_1)\phi_2(x_1)\phi_3'(x_1)}}{2}$$

Or, $\lambda_{1,2} = \frac{T(E_1, E_2) \pm \sqrt{T^2 - 4D(E_1, E_2)}}{2}$, where $T = \text{trace of } J$ and $D = \det J$.

Now for $T = 0, D > 0$ and in corresponding to the values of $E_1 = \phi(E_2)$ the matrix has two purely imaginary eigenvalues $\lambda_{1,2} = \pm i\sqrt{D}$. Moreover $d/dE_1(\text{Re}(\lambda_{1,2}))_{E_1=\phi(E_2)} = \phi(E_2)$. Thus, all conditions of Hopf theorem are satisfied and a stable limit cycle for $E_1 < \phi(E_2)$ may be found. All these conditions together prove the existence of a super critical Hopf bifurcation for the equilibrium P_2 .

We also have the following result on global stability in the region of local stability:

Theorem 3. If $P_2(x_1^*, \phi_2(x_1^*))$ is locally asymptotically stable, then it is globally stable in the interior of R_2^+ .

Proof. If possible, let there be a periodic orbit $\Gamma = (x(t), y(t)), 0 \leq t \leq T$ with the enclosed region Ω and consider the variational matrix J about the periodic orbit,

$$J(x, y) = \begin{bmatrix} \phi_1'(x)(\phi_2(x) - y) + \phi_1(x)\phi_2'(x) & -\phi_1(x) \\ y\phi_3'(x) & \phi_3(x) \end{bmatrix}.$$

We compute

$$\Delta = \int_0^T \phi_1'(x)[\phi_2(x) - y] + \phi_1(x)\phi_2'(x) + \phi_3(x) dt$$

For biological equilibrium in the region of local stability it can easily be seen that

$$\Delta = \int_0^T \phi_1(x)\phi_2'(x) dt < 0$$

Therefore, $\Delta < 0$ and the periodic orbit Γ is orbitally asymptotically stable (Cheng et al. [16] and Hale [17]). Since every periodic orbit is orbitally stable then there is a unique limit cycle. From the Poincare–Bendixson Theorem,

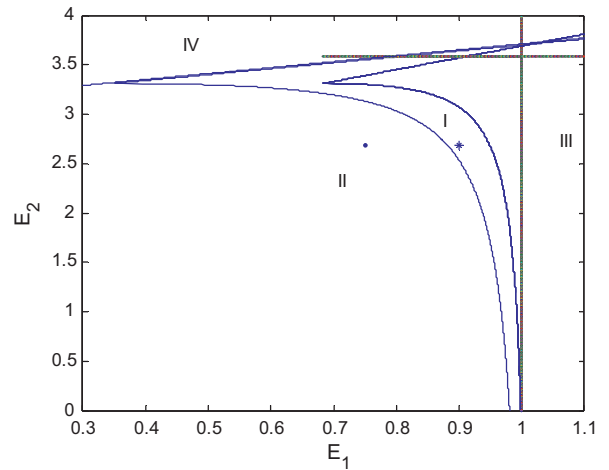


Fig. 1. Bifurcation diagram in the (E_1, E_2) plane.

it is impossible to have unique stable limit cycle enclose a stable equilibrium. This is the desired contradiction. Hence there is no limit cycle and P_2 is globally stable.

As the analytical results already indicate, the existence and stability of the interior equilibrium, as well as the stability of the trivial and boundary equilibrium will depend on the specific parameters that determine the dynamic evolution of the resource stock and the population. In the next section we present a more in-depth analysis of the complexity of the long run dynamics of population and resource stocks as they depend on the parameters of the system. The results are obtained through a detailed numerical and global bifurcation analysis.

4. Numerical simulations

We consider numerical simulations of different cases to understand the theoretical findings.

For $\eta = 60, \beta = 4, d = 0.6, \gamma = 0.9$ we have the bifurcation diagram shown in Fig. 1, and the point $(E_1, E_2) = (0.9, 2.69)$ marked by * is in stable region and the point $(E_1, E_2) = (0.75, 2.69)$ marked by • is in the region of instability.

Fig. 1 illustrates a detailed picture of the possible long run dynamics as they depend on the values of the harvesting efforts E_1 and E_2 for the benchmark case. The various dynamic behaviors are described in separate figures that show the corresponding stable and unstable equilibria in phase space together with selected time paths.

In brief, the bifurcation diagram as presented in Fig. 1 allows us to investigate the specific combination of efforts E_1 and E_2 that may cause the model to shift from sustainable long run equilibrium towards a limit cycle and finally the collapse of the system. Local bifurcation theory is the numerical tool that determines the boundaries between these regions in parameter space (Fig. 2).

We see that as d increases from 0.6 to 0.9 the area of region of stability decreases as shown in Fig. 2. If we increase d again to 1.0 the stable region of stability shrinks more, as depicted in the Fig. 3.

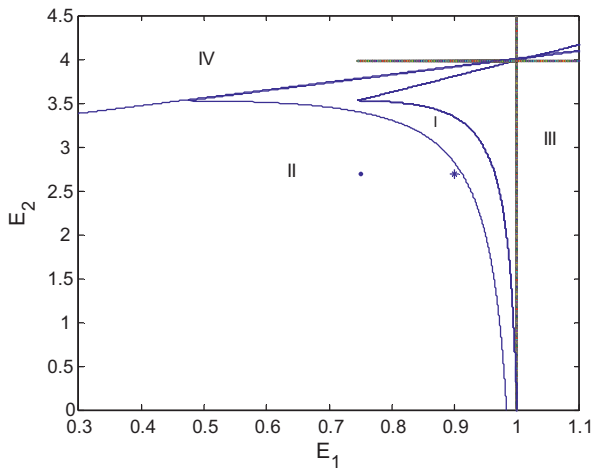


Fig. 2. Bifurcation diagram for $d = 0.9$.

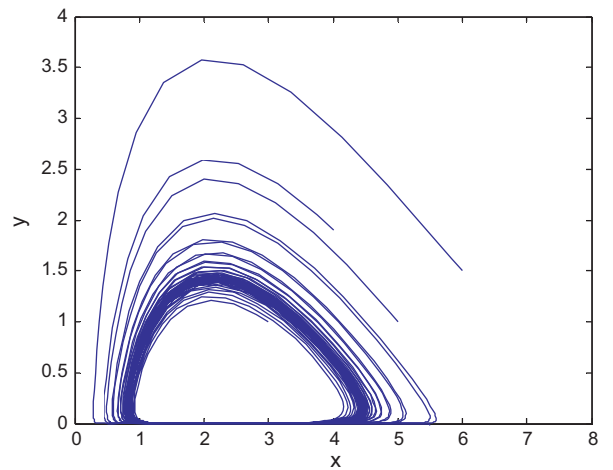


Fig. 5. The phase diagram for $(E_1, E_2) = (0.9, 2.69)$ with $d = 0.9$.

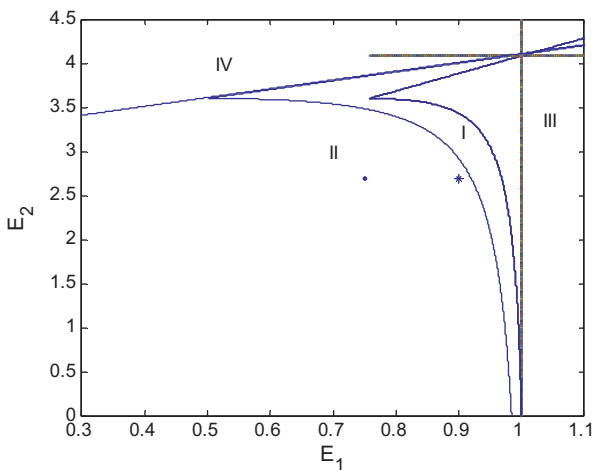


Fig. 3. Bifurcation diagram for $d = 1.0$.

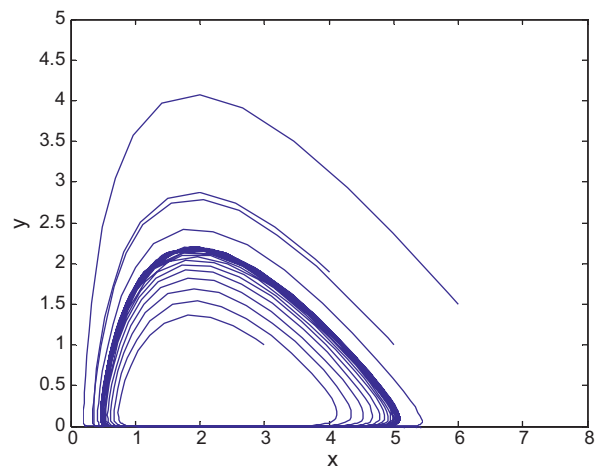


Fig. 6. The phase diagram for $(E_1, E_2) = (0.9, 2.69)$ with $d = 1.0$.

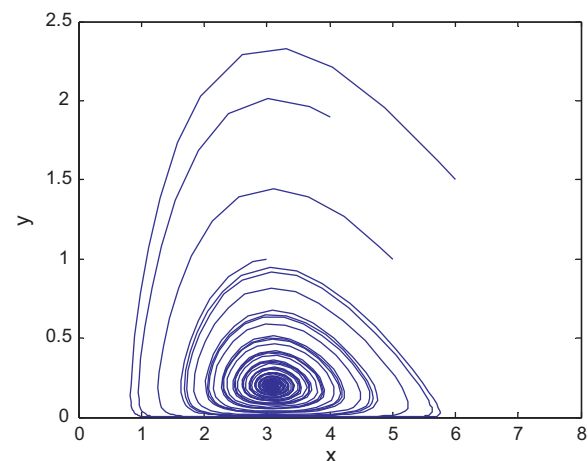


Fig. 4. The phase diagram for $(E_1, E_2) = (0.9, 2.69)$ with $d = 0.6$.

Figs. 1, 2 and 3 show bifurcation diagrams in the (E_1, E_2) -plane for $d = 0.6, 0.9$ and 1 , respectively. We see that the stability region becomes smaller as d becomes larger. We may say that d destabilizes the coexisting equilibrium P_2 . Thus for the long run sustainability of a prey-predator system, this might require reducing alternative prey (Fig. 4).

The phase diagram for $d = 0.06$ is shown in Fig. 4. When d increases to 0.9 or 1.0 then the point $(E_1, E_2) = (0.9, 2.69)$ marked by * lies outside the stable region and the interior equilibrium becomes unstable. The corresponding phase diagrams are shown in the Figs. 5 and 6.

Figs. 7 and 8 shows the phase diagram of prey and predator with a fixed value of $E_2 = 2.69$ and different values of E_1 . Fig. 9 has $E_1 = 0.39$, and $E_2 = 3.60$

Figs. 10 and 11 shows the isoclines of prey and predator with a fixed value of $E_2 = 2.69$ and different values of E_1 . It is observed that the equilibrium point for the prey population gradually decreases when the respective fishing effort used to harvest prey population is simultaneously

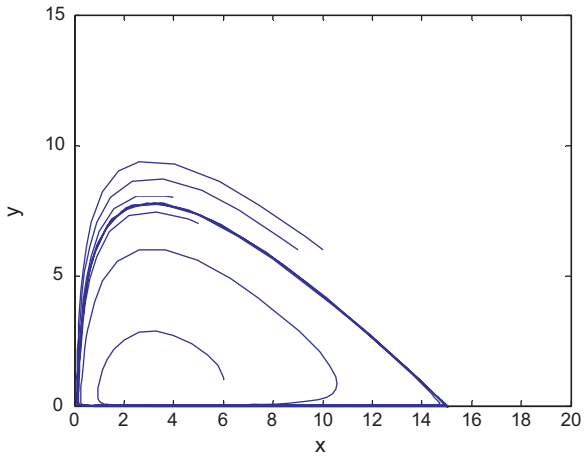


Fig. 7. The phase diagram for $(E_1, E_2) = (0.75, 2.69)$ from region-II of Fig. 1.

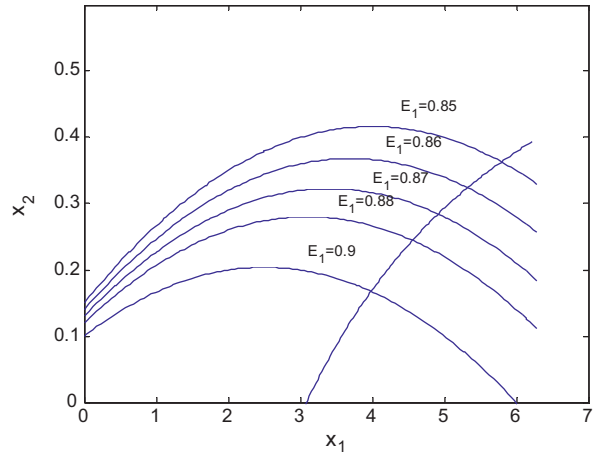


Fig. 10. For $d = 0.6$.

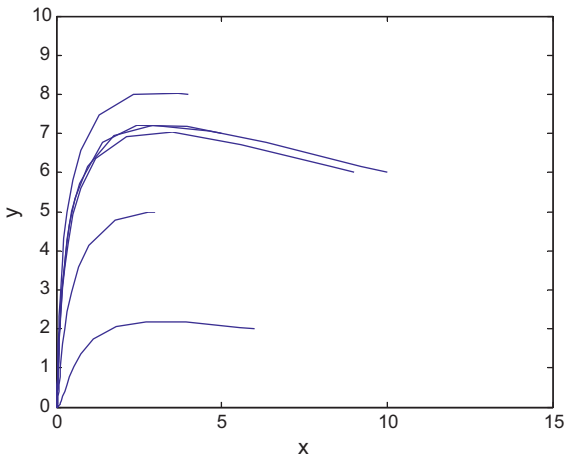


Fig. 8. The phase diagram for $(E_1, E_2) = (2, 2.69)$ in region-III of Fig. 1.

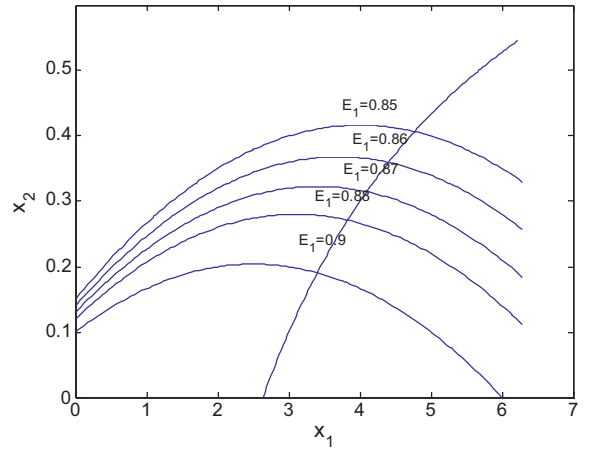


Fig. 11. For $d = 0$.

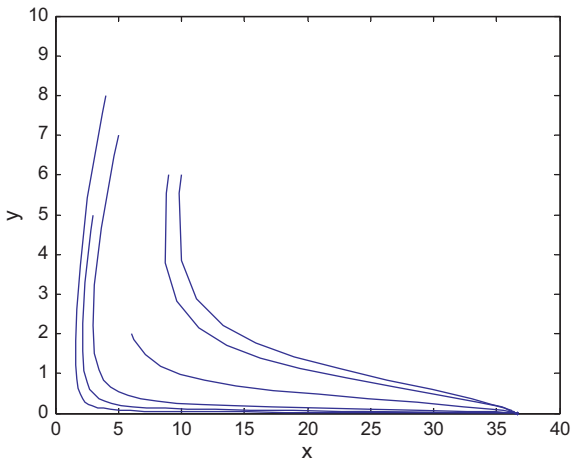


Fig. 9. The phase diagram for $(E_1, E_2) = (0.39, 3.60)$ in the Region IV of Fig. 1.

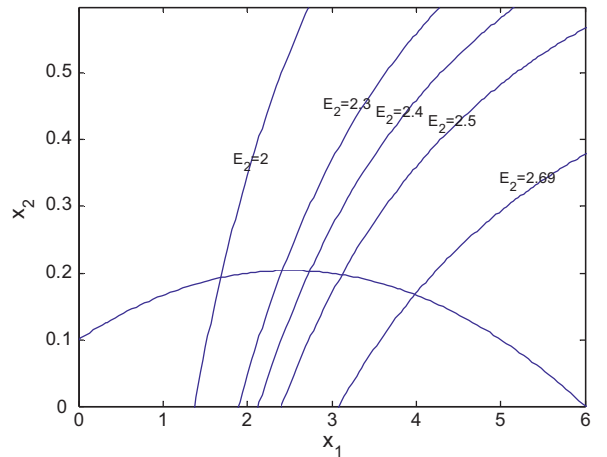


Fig. 12. For $d = 0.6$.

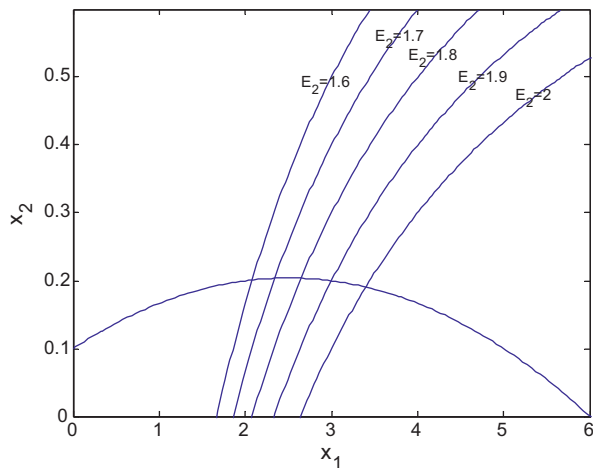


Fig. 13. For $d = 0$.

increased. In Fig 10, $d = 0.6$ and in Fig. 11 $d = 0$ (Figs. 12 and 13).

Figs. 12 and 13 show the isoclines of prey and predator population with a fixed value of $E_1 = 0.6$ and different values of E_2 . It is observed that the equilibrium point for the prey population gradually increases as the effort E_2 increases. It is natural as an increase in E_2 decreases the predator population and hence enhancing the survival rate of the prey.

5. Conclusion

Managing predator-prey systems involves complex challenges for resource managers. Many studies have demonstrated populations consequences of predators on prey population, but how managers should use this information are not easy to decide. Predator control can be effective at enhancing survival and recruitment in populations of prey, but the potential role of predators in structuring ecological communities has been recognized for sometime. For example, overexploitation of sea otter populations resulted in increase in sea urchins that subsequently destroyed kelp beds that provided habitats for fish and other marine organisms. Because of such complexity of food webs in ecological communities it is difficult to anticipate the full ramifications of eliminating or restoring predators. For example, reducing predator numbers to increase abundance of prey can have counterproductive results such as increasing disease and parasite infection in prey.

We believe that prey-predator management requires ecosystem management and this must include careful consideration of habitats as well as the particular predator prey populations. Management actions include adjusting season length and bag limits for hunter and trappers, but must also include other activities such as management of habitats that provide secure areas for prey. Ecosystem management acknowledges the value of predators in the environment.

Thus unregulated exploitation and extinction of many natural and biological resources is a major problem of

present day. This work pays attention to the exploitation or harvesting of such resources. It describes some strategies on harvesting efforts of a prey-predator model incorporating an alternative prey for the predators. It gives a study of a prey-predator model with an alternative prey, which shows some methods to control the system and how the state can be driven into equilibrium. We have considered all possible cases for the variation of parameters for the equilibrium and stability analysis of the model. It has also been discussed, how the system bifurcates from equilibrium. We have seen that the interior equilibrium in Case 3 is stable for $E_1 > \phi(E_2)$ and is unstable for $E_1 < \phi(E_2)$ and another interior equilibrium is always unstable. Some numerical examples also show how the system becomes stable at an interior equilibrium and how it bifurcates from the equilibrium and also some other features of the model.

Managing prey-predator populations for hunter harvest becomes more complex when predators are competing with humans for the same prey. Adjustments to harvest regimes may be necessary, but certainly we can have sustainable harvest of populations under predation. Elk on the northern range of Yellowstone National Park are harvested by hunters when they move into Montana during winter. The sustainability of this harvest is ensured because the Montana Department of Fish, Wildlife and Parks has density dependent harvest guidelines so that the number of tags issued for the late-Gardiner elk hunt increases with the number of elk censused on the northern range. This helps to balance the hunter harvest with wolf predation ensuring that the elk population is not driven to low levels by excessive hunter harvest.

Model that has been developed permit harvest guidelines while accommodating predators and these can be used to achieve sustainable yields. However application of this model will require data to manage a prey-predator systems.

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