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Modeling of a predator prey dynamic system with harvesting using the lattice gas approach

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This paper uses the lattice gas model to incorporate spatial and stochastic elements in a prey-predator dynamic system. In this system, the habitat is partitioned in two adjacent patches, one of them being a prey reserve. The habitat is populated by two competing prey and a common predator. In the reserve, prey harvesting is prohibited. In the other patch, harvesting of one of the prey is allowed at a constant quota rate. The evolution of the system is investigated using local species interactions. The effect of different levels of constant quota harvesting are investigated using the lattice gas approach, first by the mean field approximation method and then by simulation. The system attains a stable equilibrium below a threshold constant harvest value on condition that the survival rate of the non-harvested prey exceeds that of the harvested prey. Furthermore, the predator biomass conversion rate for the non-harvested prey should be more than that for the harvested prey. If the aforementioned conditions are not met, the population of the harvested prey outside the reserve declines to extinction in finite time. This paper concludes that the maximum constant harvest level for stable species populations can be significantly increased by introducing harvesting for the non harvested prey.

Key words: Prey, predator, constant quota harvest, lattice gas model.

INTRODUCTION

Prey-predator dynamics have been extensively investigated over the years using various approaches. The lattice gas model is one of the stochastic approaches that take into account localization of species individuals and their interactions. This is an individual based model, in which stochastic rules representing processes like death, giving birth and motion, are formulated at the level of the individual organism. Models of ecosystems using this approach are specially suited for numerical computations.

The lattice gas model was used by Satulovsky and Tome (1993) to investigate prey-predator dynamics. Their model investigates a system containing one prey and one predator with no harvesting. It exhibits oscillatory

behaviour of population densities of the prey and predator populations in both local and global levels.

Qu et al. (2008) investigates the statistical stabilities of different harvesting strategies using a stochastic cellular automata based prey-predator model. The study uses a habitat with one prey and one predator species. It concludes that for a constant quota harvest, the system is unstable. Chen et al. (2006) investigates, among other things, the effect of constant harvesting on a prey-predator model using the lattice gas model. The study imposes limits of population densities below which specified harvest rates should not be performed. It claims that constant effort harvesting leads to statistical more stable behaviours than constant quota harvesting. The study also confirms that space plays a significant role in stability properties of the predation and harvesting system, which indicates the importance of using spatially explicit models in conservation ecology.

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The aforementioned studies assume one prey species and one predator species in the models. This paper introduces a second competing prey which is not harvested. The aim is to investigate the effect of the existence of non-harvested prey on the prey-predator dynamics. This scenario better reflects the situation in real life, where not all prey are harvested. Only preys that have economic interest are usually harvested.

The model used in this paper is based on the one discussed by Rodrigues and Tome (2007) who used a lattice gas model to study the effect of mobility of the prey and predator. A second competing and non harvested prey is introduced in the system. We also introduce a prey reserve. Harvesting is done at a constant quota rate. Species interactions are localized and probabilistic. Analysis is done by the mean field approximation method and by simulation.

FORMULATION OF MATHEMATICAL MODEL

Model description

A lattice gas model is identified by several components: the lattice is a large finite set of discrete points called sites. The sites represent both species individuals and their location. Each site has a state, represented by a number, from a finite set of states. There also is a neighbourhood of a site, which is a rule that identifies the location of sites that influence that particular site. Finally, there are transition rules. These are functions of states of sites in a neighbourhood of a particular site that determine how the state of the site evolves.

In this paper, the lattice consists of a vector X of N elements called sites. These sites are arranged in a two dimensional grid. Each site has a value called state from the set $I=\{0, 1, 2, 3\}$. The vector X evolves in discrete time steps, such that the value X_t represents the value of $X=(X_1, \dots, X_N)$ at time t . The time evolution of vector X is governed by a set of rules which are both Markovian and local.

The habitat is partitioned into two patches, patch 1 and patch 2, separated by a porous boundary, which allows unimpeded migrations of individuals between them. There are three types of species: prey 1, prey 2 and the predator. In patch 1 prey harvesting is prohibited. In patch 2, harvesting is allowed, but only on prey 1. Prey 2 is never harvested. The state of a site is, respectively 0, 1, 2 and 3 depending on whether a site is empty, occupied by prey 1, occupied by prey 2 or occupied by predator. An "empty" site should be regarded as containing a resource that is the diet of the prey species.

This paper uses the Moore neighbourhood with unit radius (Tyler, 2010). The neighbourhood of a particular site is hence defined as the eight squares at distance of one unit from the site. The next state of the central site is a function of the states of the sites in its neighbourhood.

Initially, the species are assumed to be randomly distributed in the habitat. The time evolution of X is determined by a set of rules that represent birth, death, predation and harvesting of species.

Model parameters and assumptions

In this paper, N denotes the size of the lattice. The intrinsic growth rates of prey 1 and prey 2 are denoted by r and s respectively. The predator death rate is denoted by k . The per capita predation rates on prey 1 and prey 2, respectively are β_{13} and β_{23} . The constant harvesting rate is represented by v . The predator mass conversion rates for prey 1 and prey 2 are ϕ_{13} and ϕ_{23} , respectively. The proportion of habitat under reserve is denoted by α and m_i denotes the prey i migration rate. All parameters are non negative real numbers.

In the formulation of the model, we make several assumptions. We assume that the habitat is ecologically homogeneous. The two patches are connected by a porous boundary. We also assume that there is both intraspecific and interspecific competition in the prey populations. Both prey consume the same type of resources in the habitat and at the same rate per individual. The predator has no prey preference. Species interactions are local. Prey birth takes place only when the local carrying capacity is not full. In the absence of predation, growth rates in the prey populations are logistic. We ignore age structure and time lag in order to simplify the model.

The master equation

We now construct the master equation that will describe the probabilities involved in formulation of the model. There are two kinds of transitions. The first one is due to the reaction, where interactions between individual species result in changes in total species numbers. These interactions include prey birth, predation, spontaneous death of predators and harvesting. The second type is due to migration, where an individual of the prey population migrates to an adjacent empty site. At each time step, a transition will be a reaction with a specified probability; otherwise, it will be a migration. Let the probability for a stochastically evolving system to be in state θ at time t be $P(\theta, t)$. When the transition rates $W_{\theta \rightarrow \phi}(t)$ from state θ to state ϕ are known, a master equation in effect balances the transitions into and out of each state so that:

$$\frac{\partial P(\theta; t)}{\partial t} = \sum_{(\phi \neq \theta)} [W_{\phi \rightarrow \theta}(t)P(\phi; t) - W_{\theta \rightarrow \phi}(t)P(\theta; t)]$$

where $W_{\theta \rightarrow \phi}(t)$ is the conditional transitional rate from state ϕ to state θ defined by the expression:

$$W_{\phi \rightarrow \theta} = c, w_{react:\phi \rightarrow \theta}(t) + (1 - c)w_{migr:\phi \rightarrow \theta}(t)$$

with c being the probability of reaction, $W_{\phi \rightarrow \theta} = c, w_{react:\phi \rightarrow \theta}(t) + (1 - c)w_{migr:\phi \rightarrow \theta}(t)$ denoting the conditional probability associated with the migration process and $W_{\phi \rightarrow \theta} = c, w_{react:\phi \rightarrow \theta}(t) + (1 - c)w_{migr:\phi \rightarrow \theta}(t)$ denoting the conditional probability associated with the reaction process (Rodrigues and Tome, 2007).

The reaction process

For the reaction process, the evolution of vector X is done as follows. At each time step a site i is selected at random from the lattice and updated according to the following set of rules:

(1) If the state of site i is 0, it implies that it is empty, and there is a possibility of a prey individual who occupies an adjacent site to give birth and deposit the offspring on the empty site, denotes the transitional probability that a site will be in state 1 (representing occupation by an individual of prey a) Given that it was in state 0 (empty) in the previous time step is denoted by $w_{react}(1|0) = r\delta(X_i, 0)\frac{1}{Z}\sum_j \delta(X_j, 1)$. This transitional probability per site is given by:

$$w_{react}(1|0) = r\delta(X_i, 0)\frac{1}{Z}\sum_j \delta(X_j, 1),$$

for prey 1 birth, where the summation is over the neighbourhood of site i , r is the intrinsic birth rate of prey 1, Z is the neighbourhood size, which in our paper equals 8. The function δ denotes here the Kronecker delta.

The corresponding expression relating to prey 2 births is:

$$w_{react}(2|0) = s\delta(X_i, 0)\frac{1}{Z}\sum_j \delta(X_j, 2).$$

(b) Predation and predator birth: the process of predation can result either in the emptying of a site containing a prey, or by replacing the prey on the site with a predator. If the state of site i is 1, implying it is currently occupied by an individual of prey 1. In the next time step, it will be emptied due to predation with transitional probability per site of:

$$w_{react}(0|1) = (\beta_{13} - \varphi_{13})\delta(X_i, 1)\frac{1}{Z}\sum_j \delta(X_j, 3),$$

where $w_{react}(0|1)$ represents the transitional probability that a site that was previously in state 1, is now in state 0. The site i will become occupied by predator at the next

time step with transitional probability per site of:

$$w_{react}(3|1) = \varphi_{13}\delta(X_i, 1)\frac{1}{Z}\sum_j \delta(X_j, 3),$$

where $w_{react}(3|1)$ represents the transitional probability that a site that was previously in state 1 is now in state 3. Similar transitional probabilities per site will apply if state of site i is 2, as follows:

$$w_{react}(0|2) = (\beta_{23} - \varphi_{23})\delta(X_i, 2)\frac{1}{Z}\sum_j \delta(X_j, 3),$$

$$w_{react}(3|2) = \varphi_{23}\delta(X_i, 2)\frac{1}{Z}\sum_j \delta(X_j, 3).$$

(c) Death of predator: when the state of a site i is 3, this reactive process involves spontaneous death of predator with probability:

$$w_{react}(0|3) = \kappa\delta(X_i, 3),$$

where κ is predator's death rate.

(d) Harvesting of prey 1 in patch 1: if site(i) has state 1 and resides in the harvestable patch 1, it will have state 0 due to harvesting in the next time step with probability per patch 1 site given by:

$$w_{react}(harvest)(1|0) = \delta(X_i, 1)\delta(X_i, Patch\ 1)\frac{v}{R_1}$$

where R_1 is the number of sites in patch 1 with state 1 and v is the constant quota harvest rate.

The migration process

Now, we consider the prey migration process. The process involves two adjacent sites. In this paper, it is represented by a random movement, where a prey individual moves from the site it occupies to an adjacent empty site.

(1) Migration of prey out to an empty site: if the selected site i has state 1, its state is exchanged with that of a neighbouring site of state 0. The transitional probability $w_{diff}(01|10)$ represents an exchange between two cells, the first one being occupied by prey 1, and the second one being empty. After the time step, the first cell will be empty, and the second will be occupied. The transitional probability related to this process is given by:

$$w_{diff}(01|10) = \mu_1\delta(X_i, 1)\frac{1}{Z}\sum_j \delta(X_j, 0)$$

The summation being over the neighbourhood of site i , and μ_1 being the prey 1 migration rate. Similarly,

$$w_{diff}(02|20) = \mu_2 \delta(X_i, 2) \frac{1}{Z} \sum_j \delta(X_j, 0)$$

(2) Migration of prey into an empty site: if the selected site i is empty (with state 0), its state is exchanged with that of a neighbouring site of either state 1 or state 2. The transitional probability $w_{diff}(10|01)$ represents an exchange between two cells, the first one being empty, and the second one being occupied by prey 1. After the time step, the first cell will be occupied, and the second one will be empty. The transitional probabilities related to this process are given by:

$$w_{diff}(10|01) = \mu_1 \delta(X_i, 0) \frac{1}{Z} \sum_j \delta(X_j, 1)$$

Similarly,

$$w_{diff}(20|02) = \mu_2 \delta(X_i, 0) \frac{1}{Z} \sum_j \delta(X_j, 2)$$

The mean field analysis

The evolution of this model depends on the initial distribution of species on the lattice, the size of the lattice and the values of parameters and rates used. The evolution being probabilistic, we can investigate the behavior of the model by carrying out a large number of time series simulations.

However, when the number of species individuals and the lattice size is large, one can use simplifying assumptions in an approach called the mean field approximation method. In this method, we assume that all the individual organisms in the habitat are independent and any organism can interact with another irrespective of position. We also assume that we cannot distinguish objects that are in the same states. Using these assumptions, the rates of change of state numbers will be functions of the total number of sites with various states in the lattice, and for a finite lattice, we will subsequently be able to operate with what is called the occupation vector \mathbf{m} which is the vector of proportions of objects in each state.

The justification for using the mean field approximation method is based on the so-called mean field convergence result. This theorem states that as N tends to infinity, the mean field method provides the approximate limiting distribution of the objects in the lattice in form of proportions (Bobbio et al., 2006).

The requirements are: for all local states i, j and the occupation vector \mathbf{m} , and as $N \rightarrow \infty$, $P_{i,j}^N(\mathbf{m})$ converges uniformly in \mathbf{m} to some $P_{i,j}(\mathbf{m})$ which is a continuous function of \mathbf{m} . If this requirement is satisfied, the occupancy vector converges almost surely to a

deterministic limit. This means that for each local state i the fraction $\{\mathbf{m}\}_i^N(t)$ of objects with state i at time t is known with probability one, as $t \rightarrow \infty$. For large N we can now approximate the stochastic process for the occupancy vector by a deterministic process (Bobbio et al., 2006).

The mean field approximation method is an approximate method. It gives us an insight on the behaviour of a dynamic system with spatial interactions at a relatively low cost. It requires the creation of an occupancy vector \mathbf{m} , a vector showing the proportions of the number of states in the entire lattice.

Let $M_t = (E, R, S, P)$ be the number of sites with states 0, 1, 2 and 3 in the lattice of size N . We note that the number of empty sites E will be given by $E = N - (R + S + P)$. The variable R is partitioned into R_1 and R_2 , where $R = R_1 + R_2$. R_1 represents the number of prey 1 in patch 1. R_2 represents the number of prey 1 in patch 2, where no harvesting is done. Similar partitions are done for E, S and P .

The occupancy vector is given by:

$$\mathbf{m} = \frac{1}{N} M_t = \frac{1}{N} (E, R, S, P) = (e, x, y, z)$$

where $(e, x, y, z) = \left(\frac{E}{N}, \frac{R}{N}, \frac{S}{N}, \frac{P}{N}\right)$.

The corresponding occupancies representing states of sites in patch 1, namely E_1, R_1, S_1, P_1 , are (e_1, x_1, y_1, z_1) .

Formation of equation system

We now form ordinary differential equations of the temporal evolution rates of the occupancy matrix. The interactions are between sites over the entire lattice, and not just the neighbouring sites.

As an illustration, let us consider the formation of the expression for $\frac{dx}{d\tau}$, where τ is the time variable. The temporal rate of change of x is due to prey growth, predation and harvest. The rate of change due to prey growth in the lattice is determined using the prey 1 occupancy x , empty sites occupancy e and the intrinsic growth rate r . By mass action, we obtain the first term in the rate of change, namely $rx e$. The rate of change of x due to predation is a result of mass action of occupancies representing prey 1 and the predator multiplied by the predation rate; hence, we add the second term $-\beta_{13} x z$. The negative sign shows that this predation effect tends to reduce the population of x . The third term h represents constant harvesting rate.

This paper investigates both reaction and migration effects on occupancy rates. The probability of reaction to take place at a time step is given by c . Migration within the habitat has no effect on total prey populations. Hence, the temporal evolution rate of the proportion of prey 1 in the habitat is given by the differential equation:

$$\frac{dx}{d\tau} = c[rx e - \beta_{13}xz - h] \quad (1)$$

Replacing e by $1 - x - y - z$, Equation 1 becomes:

$$\frac{dx}{d\tau} = c[rx(1 - x - y - z) - \beta_{13}xz - h]$$

Using a similar argument, we form other equations in the differential system as follows:

$$\frac{dy}{d\tau} = c[ry(1 - x - y - z) - \beta_{23}yz] \quad (2)$$

$$\frac{dz}{d\tau} = c[\varphi_{13}xz + \varphi_{23}yz - \kappa z] \quad (3)$$

$$\frac{dx_1}{d\tau} = c[rx e_1 - \beta_{13}x_1z] - h + m_1(1 - c)[e_1(x - x_1) - x_1(e - e_1)] \quad (4)$$

$$\frac{dy_1}{d\tau} = c[sy e_1 - \beta_{23}y_1z] + m_2(1 - c)[e_1(y - y_1) - y_1(e - e_1)] \quad (5)$$

$$\frac{dz_1}{d\tau} = c[\varphi_{13}xz_1 + \varphi_{23}yz_1 - \kappa z_1] \quad (6)$$

Equation 5 includes the term $m_1(1 - c)[e_1(x - x_1) - x_1(e - e_1)]$ which represents the migration effect on prey occupancy rates. Migration affects prey population in patch 1 only if it is between sites from different patches. So, we regard mass action between empty sites in one patch and prey-occupied sites in the other patch, multiplied by migration rate m_1 . A similar argument is used for Equation 6.

We carry out rescaling to reduce the number of parameters in the system of Equations 1 to 6 as follows:

$$t = c\tau, \mu_1 = m_1 \frac{1 - c}{c}, \mu_2 = m_2 \frac{1 - c}{c}$$

The result is the following system:

$$\frac{dx}{dt} = rx(1 - x - y - z) - \beta_{13}xz - h$$

$$\frac{dy}{dt} = ry(1 - x - y - z) - \beta_{23}yz$$

$$\frac{dz}{dt} = \varphi_{13}xz + \varphi_{23}yz - \kappa z$$

$$\frac{dx_1}{dt} = rx e_1 - \beta_{13}x_1z - h + \mu_1(e_1x - ex_1)$$

$$\frac{dy_1}{dt} = sy e_1 - \beta_{23}y_1z + \mu_2(e_1y - ey_1)$$

$$\frac{dz_1}{dt} = \varphi_{13}xz_1 + \varphi_{23}yz_1 - \kappa z_1 \quad (7)$$

We note that e, x, y, z, e_1, x_1 and z_1 represent the proportion of lattice occupied by the relevant species. This means:

$$x, y, z, e \geq 0, x + y + z + e = 1, x_1 \leq x, y_1 \leq y, z_1 \leq z, e_1 \leq e, x_1 + y_1 + z_1 + e_1 = \alpha \leq 1$$

The sizes of the occupancies in patch 2 can be found by using the differences, that is,

$$x_1 + x_2 = x \Rightarrow \frac{dx_2}{dt} = \frac{dx}{dt} - \frac{dx_1}{dt}$$

and similarly for variables y and z .

MODEL ANALYSIS

The system of Equations 7 is analyzed for equilibrium points. The following equilibrium points are identified.

Case 1: Prey 2 vanishes at equilibrium ($y^* = 0$)

By setting the derivatives equal to zero, we solve the equation system (Equation 7) and get:

$$x^* = \frac{\kappa}{\varphi_{13}}, z^* = \frac{1}{r + \beta_{13}} \left(r \left(1 - \frac{\kappa}{\varphi_{13}} \right) - \frac{h \varphi_{13}}{\kappa} \right), x_1^* = \frac{x^*(\alpha - z_1^*)(r + \mu_1) - h}{\mu_1(1 - z^*) + rx^* + \beta_{13}z^*} \quad (8)$$

For positive x_1^*, z_1^* , the harvest quota rate must obey the condition:

$$h \leq r \frac{\kappa}{\varphi_{13}} \left(1 - \frac{\kappa}{\varphi_{13}} \right), h < \frac{\kappa}{\varphi_{13}} (\alpha - z_1^*)(r + \mu_1) \quad (9)$$

To determine the stability of the equilibrium points, we solve for eigenvalues of corresponding Jacobian matrix:

$$= \begin{pmatrix} r(1 - 2x^* - z^*) - \beta_{13}z^* & -x^*(r + \beta_{13}) & 0 & 0 \\ \varphi_{13}z^* & \varphi_{13}z^* - \kappa & 0 & 0 \\ (r + \mu_1)(\alpha - z_1^*) - rx_1^* & x_1^*(\mu_1 - \beta_{13}) & -rx^* - \beta_{13}z^* - \mu_1(1 - z^*) & -x^*(r + \mu_1) \\ \varphi_{13}z_1^* & 0 & 0 & \varphi_{13}z^* - \kappa \end{pmatrix}$$

One of the eigenvalues was computed as:

$$\lambda_3 = -rx^* - \beta_{13}z^* - (1 - z^*)$$

which is always negative. We get another eigenvalue $\lambda_4 = 0$. The zero eigenvalue implies the equilibrium is not a point, but a curve in space which is a function of z_1^* . Removing the corresponding row and column for this eigenvalue, we remain with the submatrix:

$$J_2 = \begin{pmatrix} r(1 - 2x^* - z^*) - \beta_{13}z^* & -x^*(r + \beta_{13}) \\ \varphi_{13}z^* & 0 \end{pmatrix}$$

This sub-matrix has a positive determinant, $Det = \varphi_{13}x^*z^*(r + \beta_{13})$ and the trace given by $trace = r(1 - 2x^* - z^*) - \beta_{13}z^*$. According to Routh-Hurwitz criteria, for both eigenvalues to have negative real parts in a 2×2 matrix, the trace must be negative implying:

$$r(1 - 2x^* - z^*) - \beta_{13}z^* < 0$$

Substituting the value of z^* from Equation 8, the following is obtained:

$$h < r \left(\frac{\kappa}{\varphi_{13}} \right)^2 \tag{10}$$

The results of this analysis can be summed up in the following lemma.

Lemma 1

(1) The feasible harvest rate h for a stable positive long term prey population outside reserve obeys the following conditions:

$$h \leq \frac{\kappa}{\varphi_{13}} (\alpha - z_1^*) (r + \mu_1),$$

$$h \leq r \frac{\kappa}{\varphi_{13}} \left(1 - \frac{\kappa}{\varphi_{13}} \right),$$

$$h < r \left(\frac{\kappa}{\varphi_{13}} \right)^2$$

(2) The prey occupancy in entire habitat at equilibrium is given by:

$$x^* = \frac{\kappa}{\varphi_{13}}$$

(3) The prey occupancy at equilibrium in harvestable patch is given by:

$$x_1^* = \frac{x^*(\alpha - z_1^*)(r + \mu_1) - h}{\mu_1(1 - z^*) + rx^* + \beta_{13}z^*}$$

$$\text{where } z^* = \frac{1}{r + \beta_{13}} \left(r \left[1 - \frac{\kappa}{\varphi_{13}} \right] - \frac{\varphi_{13}h}{\kappa} \right).$$

Figure 1 shows the results of simulating the system in MATLAB using parameter values as shown in Table 1. Figure 1 shows that the total prey population stabilizes at the same value,

$$x^* = \frac{\kappa}{\varphi_{13}} = 0.625$$

for varying constant harvest rates below a threshold

given by Equations 11, namely,

$$h_m = r \frac{\kappa}{\varphi_{13}} \left(1 - \frac{\kappa}{\varphi_{13}} \right) = 0.094$$

This value is defined as the prey threshold harvest rate. It is noted that below this threshold harvest rate, the prey population in harvestable patch stabilizes at different values for varying harvest levels. When the harvest rate exceeds the threshold, the prey population in harvestable patch decreases until it eventually vanishes. The equilibrium values of x_1^* and z_1^* decrease with increasing harvesting levels provided the levels are below the harvesting level for stability.

Case 2: Predator vanishes at equilibrium ($z^* = 0$)

Solving the equation system (Equation 7) with the derivatives set at 0, and $z = 0$ we get $x^* + y^* = 1, h = 0$. In this case prey 1 and prey 2 together fill the entire habitat and there is no equilibrium point for positive harvest rates.

Case 3: The coexistence scenario: $\{x \neq 0, y \neq 0, z \neq 0\}$.

We now consider the system of Equations 9 after substituting the values $e^* = 1 - x^* - y^* - z^*$, and $e_1^* = \alpha - x_1^* - y_1^* - z_1^*$. The equations thus obtained are:

$$rx^*(1 - x^* - y^* - z^*) - \beta_{13}x^*z^* - h = 0 \tag{11}$$

$$sy^*(1 - x^* - y^* - z^*) - \beta_{23}y^*z^* = 0 \tag{12}$$

$$\varphi_{13}x^*z^* + \varphi_{23}y^*z^* - \kappa z^* = 0 \tag{13}$$

$$x^*(\alpha - x_1^* - y_1^* - z_1^*) - \beta_{13}x_1^*z_1^* - h + \mu_1[x^*(\alpha - y_1^* - z_1^*) - x_1^*(1 - y^* - z^*)] = 0 \tag{14}$$

$$sy^*(\alpha - x_1^* - y_1^* - z_1^*) - \beta_{23}y_1^*z_1^* + \mu_2[y^*(\alpha - x_1^* - z_1^*) - y_1^*(1 - x^* - z^*)] = 0 \tag{15}$$

$$\varphi_{13}x^*z_1^* + \varphi_{23}y^*z_1^* - \kappa z_1^* = 0 \tag{16}$$

From Equation 13 one gets:

$$y^* = (\kappa - \varphi_{13}x^*)/\varphi_{23} \tag{17}$$

This condition put in Equation 16 makes z_1^* a free variable; hence, can be regarded as a parameter. This leaves us with a system of five equations (Equation 11 to 16). The first three equations are devoid of x_1^*, y_1^* and z_1^* ; hence, can be addressed in isolation.

From Equations 17 and 18, we get:

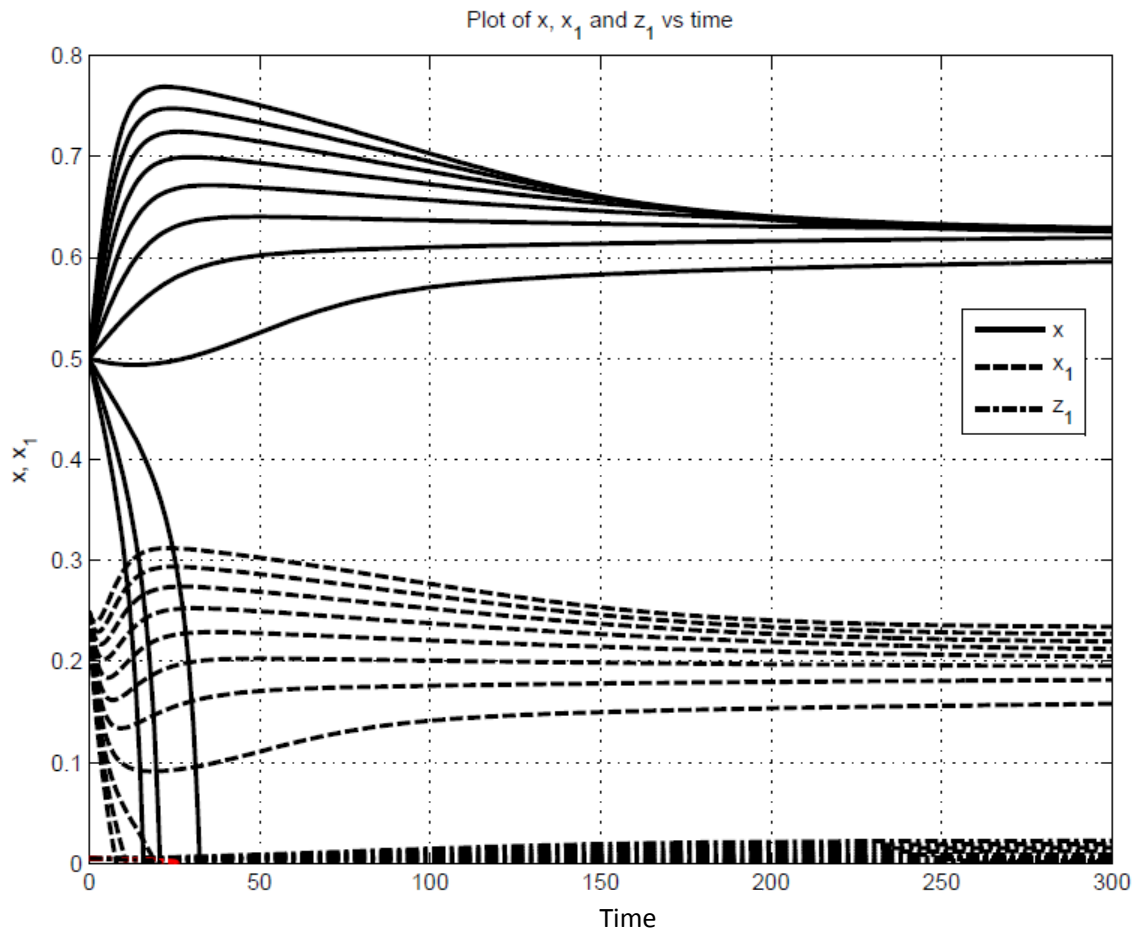


Figure 1. Effect of harvesting on prey 1 population, in the case of a one prey, one predator system using parameter values in Table 1.

Table 1. Parameter values used for the simulation in Figure 2.

Parameter	Value	Source
α	0.5	Variable ($0 < \alpha < 1$)
r	0.4	Behrensmeier and Hill (2008)
s	0.33	Behrensmeier and Hill (2008)
μ	0.1	Base value
κ	1/16	www.jungledomain.org
h	0.01 - 0.11	Base value
β_{13}, β_{23}	0.8	Fey and Green (2006)
Φ_{13}	0.100	Fey and Green (2006)
Φ_{23}	0.125	Fey and Green (2006)

$$z^* = \frac{sh}{x^*(\beta_{23}r - \beta_{13}s)} \tag{18}$$

Note the condition for positive z^* is:

$$\frac{\beta_{23}}{s} > \frac{\beta_{13}}{r} \tag{19}$$

The ratios $\frac{\beta_{13}}{r}$ and $\frac{\beta_{23}}{s}$ are called survival rates of prey 1 and prey 2, respectively. Hence, a condition for a positive z^* at equilibrium is for the survival rate of prey 2 to exceed that of prey 1.

Solving for x^* from Equations 11, 12 and 13, we get

Table 2. Conditions for real positive values of x^*

Condition for A	Condition for B	Condition for h	Positive roots
If $A > 0$	Then $B > 0$	$h < \frac{B^2(\beta_{23}r - \beta_{13}s)}{4A \varphi_{23}(s + \beta_{23})}$	$x^* = \frac{(B \pm \sqrt{B^2 - 4AC})}{2A}$
If $A = 0$	Then $B > 0$	-	C/B
If $A < 0$	Then $B > 0$	-	$x^* = \frac{(B - \sqrt{B^2 - 4AC})}{2A}$

the quadratic equation with form:

$$A(x^*)^2 - B(x^*) + C = 0,$$

where:

$$A = \varphi_{23} - \varphi_{13}, B = \varphi_{23} - \kappa, C = \frac{\varphi_{23}h(s + \beta_{23})}{\beta_{23}r - \beta_{13}s}$$

with solution:

$$x^* = \frac{B \pm \sqrt{B^2 - 4AC}}{2A} \tag{20}$$

Clearly Equation 19 implies $C > 0$.

Table 2 gives a summary of conditions for Equation 20 to have real positive solutions for x^* .

The corresponding equilibrium points for y^* and z^* can be found by Equations 17 and 18, respectively. To determine the corresponding equilibrium values for x_1^*, y_1^* as a function of z_1^* , we solve the linear simultaneous Equations 14 and 15 rearranged as follows:

$$\begin{aligned} x_1^* (1 + \beta_{13}z^* + \mu_1[1 - y^* - z^*]) + y_1^*(1 + \mu_1x^*) &= (1 + \mu_1x^*)(\alpha - z_1^*) - h \\ x_1^* (1 + \mu_2y^*) + y_1^* (1 + \beta_{23}z^* + \mu_2[1 - x^* - z^*]) &= (1 + \mu_2y^*)(\alpha - z_1^*) \end{aligned}$$

Using Cramer's rule this solves to:

$$x_1^* = \frac{[(1 + \mu_1x^*)(\alpha - z_1^*) - h](1 + \beta_{23}z^* + \mu_2[1 - x^* - z^*])}{z^*} \tag{21}$$

$$x_1^* = \frac{[(1 + \mu_1x^*)(\alpha - z_1^*) - h](1 + \beta_{23}z^* + \mu_2[1 - x^* - z^*]) - (1 + \mu_1x^*)(1 + \mu_2y^*)(\alpha - z_1^*)}{Det} \tag{22}$$

where the determinant *Det* is given by Equation 23.

$$\begin{aligned} Det = (1 - x^* - y^* - z^*)(\mu_1 + \mu_2 + \mu_1\mu_2(1 - z^*)) &+ (z^*)^2\beta_{13}\beta_{23} \\ + z^*[\beta_{13}(1 + \mu_1(1 - z^* - y^*)) &(1 + \mu_2(1 - x^* - z^*))] \end{aligned} \tag{23}$$

This value, being the sum of positive only terms for feasible values of the variables, is always positive. For

the value of x_1^* in Equation 21 to be positive, its numerator should also be positive, that is:

$$\begin{aligned} ((1 + \mu_1x^*)(\alpha - z_1^*) - h)(1 + \beta_{23}z^* + \mu_2[1 - x^* - z^*]) &- (1 + \mu_1x^*)(1 + \mu_2y^*)(\alpha - z_1^*) > 0 \end{aligned}$$

Making h the subject of the aforementioned equation, the following expression is obtained:

$$h < \frac{(1 + \mu_1x^*)(\alpha - z_1^*)(\beta_{23}z^* + \mu_2[1 - x^* - y^* - z^*])}{(1 + \beta_{23}z^* + \mu_2[1 - x^* - z^*])}$$

This is an involving expression as h is an element in the expression for x^*, y^* and z^* .

Similarly, for a positive y_1^* in Equation 22, its numerator needs to be positive too, that is:

$$\begin{aligned} (1 + \beta_{13}z^* + \mu_1[1 - y^* - z^*])(1 + \mu_2y^*)(\alpha - z_1^*) &- (1 + \mu_2y^*)((1 + \mu_1x^*)(\alpha - z_1^*) - h) > 0 \end{aligned}$$

On making h the subject, the expression becomes:

$$h > -(\alpha - z_1^*)(\beta_{13}z^* + \mu_1[1 - x^* - y^* - z^*])$$

As the right hand side of the aforementioned expression is always negative, the expression is true for feasible positive harvest rates.

Local stability of the coexistence equilibrium point

Now, we investigate the local stability of the equilibrium points. We do this by determining the eigenvalues of the Jacobian matrix of the equation system (Equation 8). A stationary point is stable if all eigenvalues are negative. The Jacobian of the system evaluated at equilibrium becomes:

$$J = \begin{pmatrix} F_{1,x} & F_{1,y} & F_{1,z} & 0 & 0 & 0 \\ F_{2,x} & F_{2,y} & F_{2,z} & 0 & 0 & 0 \\ F_{3,x} & F_{3,y} & 0 & 0 & 0 & 0 \\ F_{4,x} & F_{4,y} & F_{4,z} & F_{4,x_1} & F_{4,y_1} & F_{4,z_1} \\ F_{5,x} & F_{5,y} & F_{5,z} & F_{5,x_1} & F_{5,y_1} & F_{5,z_1} \\ F_{6,x} & F_{6,y} & F_{6,z} & F_{6,x_1} & F_{6,y_1} & 0 \end{pmatrix}$$

The eigenvalues of the matrix J are the combination of the eigenvalues of:

$$J_2 = \begin{pmatrix} F_{1,x} & F_{1,y} & F_{1,z} \\ F_{2,x} & F_{2,y} & F_{2,z} \\ F_{3,x} & F_{3,y} & 0 \end{pmatrix} \text{ and } J_3 = \begin{pmatrix} F_{4,x_1} & F_{4,y_1} & F_{4,z_1} \\ F_{5,x_1} & F_{5,y_1} & F_{5,z_1} \\ F_{6,x_1} & F_{6,y_1} & 0 \end{pmatrix}$$

calculated at the equilibrium point.

Expanding J_2 and using Equations 11 and 12, we get:

$$J_2 = \begin{pmatrix} \frac{h}{x^*} - rx^* & -rx^* & -x^*(r + \beta_{13}) \\ -sy^* & -sy^* & -y^*(s + \beta_{23}) \\ \varphi_{13}z^* & \varphi_{23}z^* & 0 \end{pmatrix}$$

The characteristic equation of J_2 matrix is calculated as:

$$\lambda^3 + D\lambda^2 + E\lambda + F = 0$$

where

$$D = rx^* + sy^* - \frac{h}{x^*}$$

$$E = \varphi_{13}x^*z^*(r + \beta_{13}) + \varphi_{23}y^*z^*(s + \beta_{23}) - \frac{h}{x^*}sy^*$$

$$F = x^*y^*z^*(r\beta_{23} - s\beta_{13})(\varphi_{23} - \varphi_{13}) - \varphi_{23}\frac{h}{x^*}y^*z^*(s + \beta_{23})$$

Note that $F < 0$ if:

$$A = (\varphi_{23} - \varphi_{13}) \leq 0 \quad (24)$$

Substituting $\frac{h}{x^*} = r(1 - x^* - y^* - z^*) - \beta_{13}z$ as denoted in Equation 11, we obtain:

$$\begin{aligned} D &= rx^* + sy^* + \beta_{13}z^* - r(1 - x^* - y^* - z^*), \\ E &= \varphi_{13}x^*z^*(r + \beta_{13}) + \varphi_{23}y^*z^*(s + \beta_{23}) + s\beta_{13}y^*z^* \\ &\quad - rsy^*(1 - x^* - y^* - z^*), \\ F &= x^*y^*z^*(r\beta_{23} - s\beta_{13})(\varphi_{23} - \varphi_{13}) - \varphi_{23}y^*z^*(s + \beta_{23})(\beta_{13}z^* \\ &\quad - r(1 - x^* - y^* - z^*)) \end{aligned}$$

By Routh-Hurwitz criteria applied in a 3×3 matrix, stability is assured if $D > 0, E > 0, F > 0$, and $DE - F > 0$. We note that in our characteristic equation $D > 0, E > 0, F > 0$ for sufficiently small values of $(1 - x^* - y^* - z^*)$. This implies D, E, F tend to positivity as the habitat occupancy approaches its carrying capacity.

We also note that $A = (\varphi_{23} - \varphi_{13}) \leq 0$ makes $F < 0$ as per Equation 24, and hence, is a condition for instability of equilibrium point. Considering $DE - F$, one gets:

$$DE - F = \left(rx^* + sy^* - \frac{h}{x^*} \right) \left(\varphi_{13}x^*z^*(r + \beta_{13}) + \varphi_{23}y^*z^*(s + \beta_{23}) - \frac{h}{x^*}sy^* \right)$$

$$\begin{aligned} & - \left(x^*y^*z^*(r\beta_{23} - s\beta_{13})(\varphi_{23} - \varphi_{13}) \right. \\ & \quad \left. - \varphi_{23}\frac{h}{x^*}y^*z^*(s + \beta_{23}) \right) \\ &= \varphi_{13}r^2(x^*)^2z^* + \varphi_{23}s^2(y^*)^2z^* \\ & \quad + z^*(\varphi_{13}rx^* + \varphi_{23}sy^*)(\beta_{13}x^* + \beta_{23}y^*) \\ & \quad + (\varphi_{23} + \varphi_{13})rsx^*y^*z^* + \frac{h^2}{(x^*)^2}sy^* \\ & \quad + \beta_{13}z^*(rsx^*y^* + \varphi_{13}rx^*z^* + s^2(y^*)^2 + \beta_{13}\varphi_{13}x^*) \\ & \quad - r(1 - x^* - y^* - z^*)(rsx^*y^* + \varphi_{13}rx^*z^* + s^2(y^*)^2 \\ & \quad + \beta_{13}\varphi_{13}x^*) \end{aligned}$$

This implies that the value of $DE - F > 0$ for sufficiently small $(1 - x^* - y^* - z^*)$.

Let us now consider J_3 . Its characteristic equation can be written in the form of:

$$\lambda^3 + K\lambda^2 + L\lambda + M = 0$$

where:

$$\begin{aligned} K &= rx^* + sy^* + z^*(\beta_{13} + \beta_{23}) + \mu_1(1 - y^* - z^*) \\ & \quad + \mu_2(1 - x^* - z^*) \\ L &= \varphi_{13}(r + \mu_1)x^*z_1^* + \varphi_{23}(s + \mu_2)y^*z_1^* \\ & \quad + (r + \mu_1)(s + \mu_2)x^*y^* \\ & \quad + [rx^* + \beta_{13}z^* + \mu_1(1 - y^* - z^*)][sy^* + \beta_{23}z^* \\ & \quad + \mu_2(1 - x^* - z^*)] \\ M &= \varphi_{13}(r + \mu_{13})x^*z_1^*[\beta_{23}z^* + \mu_{23}(1 - x^* - y^* - z^*)] \\ & \quad + \varphi_{23}(s + \mu_{23})y^*z_1^*[\beta_{13}z^* + \mu_{13}(1 - x^* - y^* - z^*)] \end{aligned}$$

According to the Routh-Hurwitz criterion applied on a 3×3 matrix, for all the eigenvalues of J_3 to have negative real parts, the condition $K > 0, L > 0, M > 0$ must be obeyed. In the aforementioned expressions for K, L and M , this condition is obeyed. A further condition for such eigenvalues is $KL - M > 0$.

$$\begin{aligned} KL - M &= [rx^* + \beta_{13}z^* + \mu_1(1 - y^* - z^*)]^2[sy^* + \beta_{23}z^* \\ & \quad + \mu_2(1 - x^* - z^*)] \\ & \quad + [rx^* + \beta_{13}z^* + \mu_1(1 - y^* - z^*)][sy^* + \beta_{23}z^* \\ & \quad + \mu_2(1 - x^* - z^*)]^2 \\ & \quad + [rx^* + \beta_{13}z^* + \mu_1(1 - y^* - z^*) + s^*y^* + \beta_{23}z \\ & \quad + \mu_2(1 - x^* - z^*)] \\ & \quad (r + \mu_1)(s + \mu_2)x^*y^* \\ & \quad + \varphi_{13}(r + \mu_1)x^*z_1^*[rx^* + \beta_{13}z^* + \mu_1(1 - y^* - z^*) - y^*(s \\ & \quad + \mu_2)] \\ & \quad + \varphi_{23}(s + \mu_2)y^*z_1^*[sy^* + \beta_{23}z^* + \mu_2(1 - x^* - z^*) \\ & \quad - x^*(r + \mu_1)] \end{aligned}$$

If this condition of $KL - M > 0$ is also obeyed, then we have all eigenvalues of J_3 negative. Most of the terms of the expansion for $KL - M$ are positive, so, unless there are very significant differences between growth rates s and r , or when migration rates μ_1 and μ_2 are high, we have $KL - M > 0$.

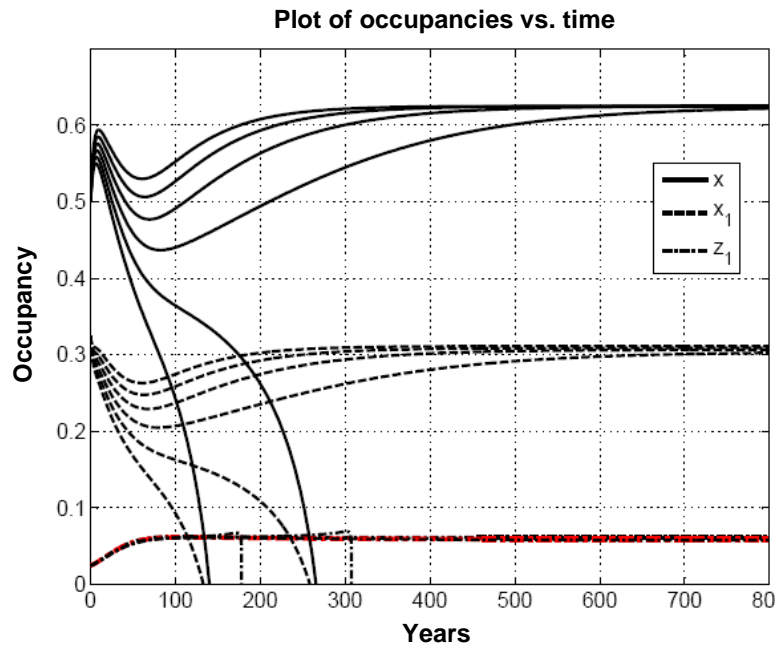


Figure 2. The effect of harvesting in a two prey, one predator dynamic system assuming parameter values depicted in Table 1.

We summarize our results in the following lemma.

Lemma 2

For a stable positive real valued equilibrium, the conditions are:

$$(1) \quad h < \frac{(1+\mu_1 x^*)(\alpha-z_1^*)(\beta_{23} z^* + \mu_2 [1-x^*-y^*-z^*])}{1 + \beta_{23} z^* + \mu_2 [1-x^*-z^*]}$$

This expression ensures positivity of x_1^* . It is a involving expression, because h occurs also in the expressions for x^*, y^* and z^* . However, for insignificant migration rates it simplifies to,

$$h < \frac{(\alpha - z_1^*)\beta_{23}z^*}{1 + \beta_{23}z^*}$$

(2) For a positive z^* , the equation states that:

$$\frac{\beta_{23}}{s} > \frac{\beta_{13}}{r}$$

(3) For a real x^* ,

$$0 < h \leq \frac{(\varphi_{23} - \kappa)^2(\beta_{23}r - \beta_{13}s)}{4\varphi_{23}(s + \beta_{23})(\varphi_{23} - \varphi_{13})}$$

(4) $A = \varphi_{23} - \varphi_{13} > 0$, that is, the biomass conversion rate of prey 2 must exceed that of prey 1.

(5) For stability, the value of $(1 - x^* - y^* - z^*)$ must be sufficiently small. This implies that stability is enhanced as the total species population approaches the carrying capacity of the habitat.

Figure 2 depicts the simulation on MATLAB using parameter values as per Table 1. From Figure 2, one can see that below a threshold value which is a function of parameter values, prey 1 eventually attains a stable equilibrium both in the habitat and in the patches. Above the threshold, prey 1 population outside reserve eventually vanishes. However, this threshold value is considerably lower than the one in the case of only one harvestable prey (Case 1).

This shows that the presence of the non harvested prey has reduced the constant harvest threshold for stability by a considerable factor.

Lattice gas model simulation

In the lattice gas model, in contrast to the mean field approximation method, species interactions are local: individuals interact only with other individuals within their neighbourhood. Migration at the boundary between patches affects prey occupancy values. The model operates within feasible variable values, ensuring they are always positive and do not exceed the carrying

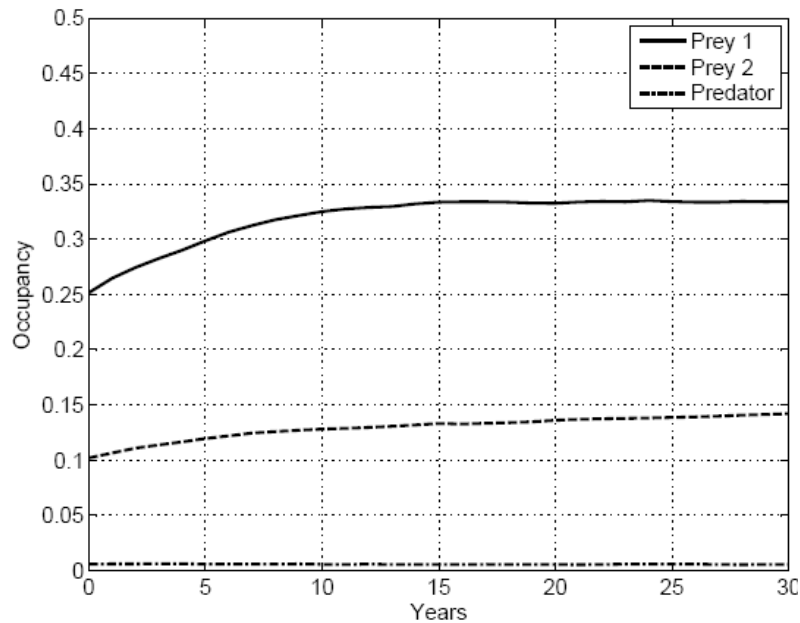


Figure 3. Time run for species populations in harvestable patch for a sustainable harvest rate, $h_m = 0.004$.

capacity of the lattice or corresponding patch.

The model is implemented using a MATLAB program. The model was executed repeatedly using differing initial values and harvest rates and run for several time steps. Parameter values used are per Table 1.

SIMULATION RESULTS

Species coexistence scenario

In the scenario where all three species have positive values, it was possible to maintain a constant harvest level of at least 30 time steps under some parameter conditions. A similar conclusion was obtained using the mean field approximation method. The maximum sustainable harvest level for the parameter values used was very low, about $h_m = 0.004$. Figure 3 depicts the situation.

At higher harvest levels, or outside the parameter conditions, the non harvested prey rapidly replaced the harvested prey, and the harvested prey vanished in finite time. This is as shown in Figure 4.

Effect of migration rate

Figure 5 shows the time series prey 1 occupancy in patch 1 with similar initial conditions but differing migration rates of 0.100 and 0.500. The graph shows that a five-fold increase in migration rate has a small effect on the prey 1 population size.

Effect of migration rate

Figure 5 shows the time series prey 1 occupancy in patch 1 with similar initial conditions but differing migration rates of 0.100 and 0.500. The graph shows that a five-fold increase in migration rate has a small effect on the prey 1 population size.

Harvesting of both prey

This paper assumed that one prey is not being harvested. If we consider a situation where both prey are harvested, that is, when we do not have a non-harvested prey, equilibrium is attained for a much larger maximum harvest rate. In this particular parameter set in the simulation depicted in Figure 6 with both prey harvested at the same rate, the maximum harvest rate is about 0.045, about ten times that obtained on an identical parameter set, when only one of the prey was harvested and under less stringent parameter conditions. Figure 6 shows a typical time series run for constant harvest rate of 0.040 and 0.045.

CONCLUSIONS AND RECOMMENDATIONS

In this paper a lattice gas mathematical model of a two competing prey, one predator dynamic system with reserve and a constant quota harvesting rate on one of the prey outside the reserve has been developed. The model has been analyzed using the mean field

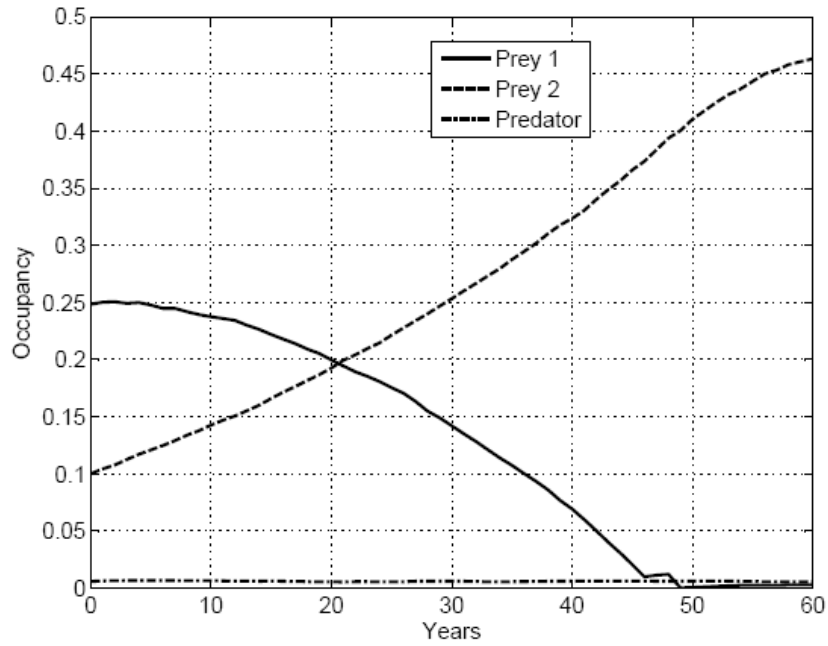


Figure 4. Harvest rate leading to extinction of prey 1 in harvestable patch, $h_m = 0.025$.

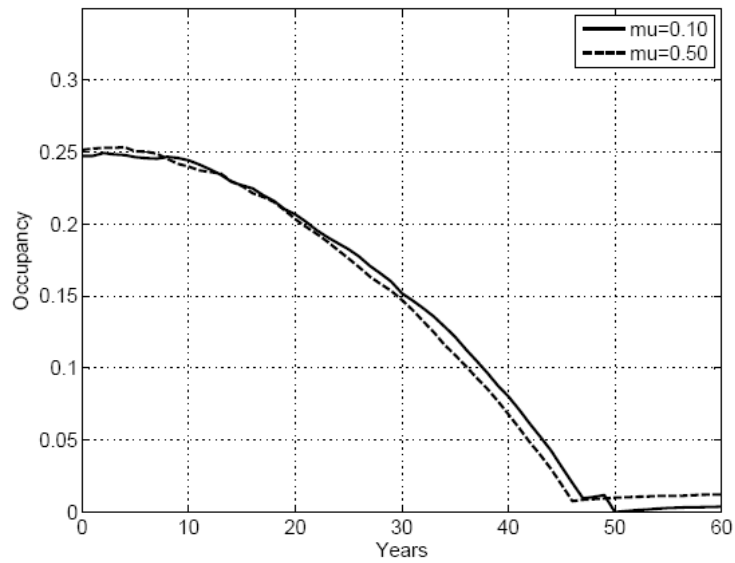


Figure 5. Effect of different migration rates on prey 1 occupancy in harvestable patch.

approximation method and by simulation.

It has been demonstrated that, given two competing prey and a predator, a constant harvest rate can lead to a stable prey occupancy, if a set of conditions pertaining to species parameters was maintained. These conditions include the harvested prey to have a higher survival rate than the non harvested prey, and the predator biomass

conversion rate for non harvested prey to exceed that of the harvested one. The equilibrium also requires that the total prey population approach the carrying capacity of the habitat.

The stable prey occupancy is attained when the harvest rate is below a threshold value, which happens to be a low harvest rate. When the harvest rate exceeds this

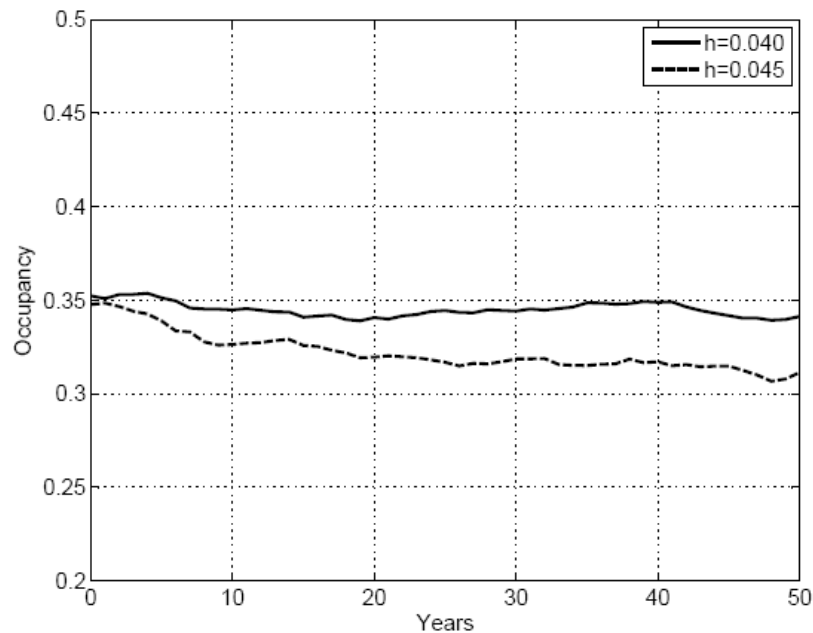


Figure 6. Constant harvest for both prey allows a higher threshold harvest value. Time run for harvest rates of harvest rates 0.040 and 0.045.

threshold, the rate of harvesting of the prey prevents the harvested prey to attain positive growth rates. This causes the harvested prey population to fall to extinction in finite time, to be replaced by the non harvested prey.

It should be noted that Qu et al. (2008) found out that for constant harvest rates, the system is unstable. In our model, however, in which we include a non harvested competing prey species, we attain stability albeit at low harvest rates.

We have shown that there was no equilibrium for any positive constant harvest rate in the absence of the predator. When predator was absent, the harvestable prey eventually was driven to extinction, being replaced by the non harvested prey. This showed that predation had a stabilizing effect on the system.

The paper shows that the threshold harvest value obtained in the case of a single prey and one predator is considerably higher to that obtained when there are two competing prey.

There is a need for regular wild animal population census that will help in specifying species growth and interaction parameters, and will assist in determining ecologically sound harvesting quotas. Harvesting quotas, thus, set must be strictly enforced, because harvesting above these quota levels might lead to extinction of some animal species.

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