

A PREY-PREDATOR MODEL WITH DIFFUSION AND A SUPPLEMENTARY RESOURCE FOR THE PREY IN A TWO-PATCH ENVIRONMENT ¹

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Abstract. In this paper, a prey-predator dynamics, where the predator species partially depends upon the prey species, in a two patch habitat with diffusion and there is a non-diffusing additional resource for the prey population, is modeled and analyzed. It is shown, that there exists a positive, monotonic, continuous steady state solution with continuous matching at the interface for both the species separately. Further, we obtain conditions for asymptotic stability for both linear and nonlinear cases.

Key words: Population diffusion, patchiness, supplementary resource, steady state solution, stability

1. Introduction

Mathematical ecology has its roots in population ecology, which treats the increase and fluctuation of population. An interesting problem in mathematical ecology is to study the growth and co-existence of species with diffusion in both homogeneous and patchy habitats. As noted before the diffusion, when it occurs, plays the role of increasing stability in a system of interacting populations [8, 10, 23, 24, 25, 27]. Some researchers have given elaborate survey of models with diffusion in both homogeneous and heterogeneous environment [14, 15, 16, 23] and also surveyed the literature related to models with diffusion and reported the effects of dispersal and spatial heterogeneity on stability of both single species and for predator-prey system [4, 5, 18]. In [21] a prey-predator model with functional response and diffusion is considered and it is shown, that if the equilibrium state is linearly stable, a sub-region

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of the positive quadrant can be found in the phase plane where it is non-linearly stable with or without diffusion.

It may be noted here that in the above study the role of alternative or supplementary resource on equilibrium levels of populations as well as on their stability has not been discussed, although the study of resource-based interacting population biology is an interesting area of research in population dynamics. Some experimental investigations on micro-organisms using the chemostat [11, 22] have been conducted and perhaps the best laboratory idealization of nature for population studies has been described in [28]. Several mathematical models of such systems, involving competition and other types of non-interacting populations, which depend upon growth limiting nutrient in a chemostat with constant input and variable washout rates have been studied in [1, 2, 13, 17]. Also some other mathematical investigations related to two competing populations which are wholly dependent on a self-renewable resource in a habitat without diffusion have been presented [9, 12, 19]. But very little attention has been given in the resource-based prey-predator system with diffusion [6]. The effect of a predator resource on a diffusive Predator-Prey system, showing the stabilizing role of diffusion have been studied.

In this paper, therefore, a logistically growing two species prey-predator type model is considered. A self-renewable supplementary resource for prey population and diffusion in a two-patch habitats is proposed and the stability of both the linear and nonlinear systems is discussed. Both the reservoir and no-flux boundary conditions are considered. It is shown that the effect of explicit dependence of the prey population on an alternative supplementary resource in the two patches may increase the level of steady state distribution for prey in the entire habitat. The model is proposed by keeping in view the depletion of forest resources biomass (prey species) with partially re-plantation of forest resource (i.e. supplementary resource) due to increased forest resource. Dependence or independence on industrialization and population (predator species) has caused patchiness in the Doon Valley situated at the foot hills of Himalayas in India [26].

This paper is organized as follows: first we write the prey-predator model with a self-renewable supplementary resource for the prey in a two-patch habitat. In the next section we study our main model in a two-patch habitat for both non-uniform and uniform steady state cases under both reservoir and no-flux boundary conditions.

2. The Mathematical Model

We consider a dynamic model of two logistically growing animal (such as deer and wolf) species with prey-predator type interaction and diffusion in a two-patch forest habitat by assuming that the second species uses the first species as an alternative resource. In such a case the rate of change of density of the first species decreases due increase in the density of the second species, but the density of the second species increases due to the increase in the density of the first species in both the patches. Let $x_i(s, t)$ and $y_i(s, t)$ be the densities of first and second species in the i -th patch respectively. Now if we supply a supplementary resource $R_i(s, t)$ for the prey population $x_i(s, t)$ in the entire habitat, then in presence of resource biomass the growth

rates of prey populations increases. We also assume that there is no explicit diffusion in the resource biomass. Then the model can be written as the following system of autonomous partial differential equations:

$$\frac{\partial R_i}{\partial t} = a_i R_i \left(1 - \frac{R_i}{C_i}\right) - \alpha_i R_i x_i, \quad i = 1, 2, \quad (2.1)$$

$$\frac{\partial x_i}{\partial t} = x_i \mathbf{g}_i(x_i) - y_i \mathbf{p}_i(x_i) + \theta \alpha_i R_i x_i + D_{1i} \frac{\partial^2 x_i}{\partial s^2}, \quad (2.2)$$

$$\frac{\partial y_i}{\partial t} = y_i \mathbf{f}_i(y_i) + \gamma_i y_i \mathbf{p}_i(x_i) + D_{2i} \frac{\partial^2 y_i}{\partial s^2}, \quad 0 \leq s \leq L_2, \quad (2.3)$$

where the i -th patch is assumed to lie along the spatial length $L_{i-1} \leq s \leq L_i$ ($L_0 = 0$), C_i , $i = 1, 2$ are the carrying capacity of the supplementary resource in the i -th patch and θ is the conversion rate of biomass constant by the prey populations, respectively. The functions $\mathbf{g}_i(x_i)$ and $\mathbf{f}_i(y_i)$ are the respective specific growth rates, $\mathbf{p}_i(x_i)$ are the interaction rates (predator response functions) and D_{1i} , D_{2i} are the diffusion coefficient of x_i and y_i in the i -th patch respectively. The constants α_i , $i = 1, 2$ are positive interaction rate coefficients of the prey species with the supplementary resource and γ_i , $i = 1, 2$ are conversion rates coefficient in the i -th patch.

We assume the following assumption for $\mathbf{g}_i(x_i)$, $\mathbf{f}_i(y_i)$, and $\mathbf{p}_i(x_i)$:

$$AH_1 : \begin{cases} \mathbf{g}_i(x_i), \mathbf{f}_i(y_i), \mathbf{p}_i(x_i) \in C^2[0, \infty), \\ \mathbf{g}_i(0) > 0, \mathbf{f}_i(0) > 0, \mathbf{p}_i(0) = 0, \\ \text{for } x_i > 0, \mathbf{g}'_i(x_i) \leq 0, \mathbf{p}'_i(x_i) > 0, \\ \text{for } y_i > 0, \mathbf{f}'_i(y_i) \leq 0. \end{cases}$$

When the environment has a carrying capacity K_i and M_i respectively for prey and predator populations in the i -th patch, then

$$\mathbf{g}_i(K_i) = 0, \quad \mathbf{f}_i(M_i) = 0, \quad \text{for } i = 1, 2.$$

Further we assume that:

$$AH_2 : \begin{cases} \exists R_i^*, x_i^*, y_i^* > 0, \text{ such that } R_i^* = C_i[a_i - \alpha_i x_i^*]/a_i, \\ x_i^* \mathbf{g}_i(x_i^*) - y_i^* \mathbf{p}_i(x_i^*) + \theta \alpha_i R_i^* x_i^* = 0, \\ \mathbf{f}_i(y_i^*) + \gamma_i \mathbf{p}_i(x_i^*) = 0. \end{cases}$$

The model is studied using one set of boundary conditions, i.e., reservoir or no-flux conditions. In the case of reservoir boundary conditions, we take

$$x_1(0, t) = x_1^*, \quad x_2(L_2, t) = x_2^*, \quad (2.4)$$

$$y_1(0, t) = y_1^*, \quad y_2(L_2, t) = y_2^* \quad (2.5)$$

and in the case of no-flux boundary conditions we consider

$$\frac{\partial x_1(0, t)}{\partial s} = 0, \quad \frac{\partial x_2(L_2, t)}{\partial s} = 0, \quad (2.6)$$

$$\frac{\partial y_1(0, t)}{\partial s} = 0, \quad \frac{\partial y_2(L_2, t)}{\partial s} = 0. \quad (2.7)$$

We also assume the continuity and flux matching conditions at the interface $s = L_1$. The continuity conditions at the interface $s = L_1$ are the following:

$$x_1(L_1, t) = x_2(L_1, t), \quad y_1(L_1, t) = y_2(L_1, t), \quad R_1(L_1, t) = R_2(L_1, t). \quad (2.8)$$

The continuous flux matching conditions at the interface $s = L_1$ for $x_i(s, t)$ and $y_i(s, t)$ are given by

$$D_{11} \frac{\partial x_1(L_1, t)}{\partial s} = D_{12} \frac{\partial x_2(L_1, t)}{\partial s}, \quad (2.9)$$

$$D_{21} \frac{\partial y_1(L_1, t)}{\partial s} = D_{22} \frac{\partial y_2(L_1, t)}{\partial s}. \quad (2.10)$$

Finally the model is completed by assuming some positive initial distribution of each species, for $i = 1, 2$, that is,

$$x_i(s, 0) = \chi_i(s) > 0, \quad L_{i-1} < s < L_i, \quad (2.11)$$

$$y_i(s, 0) = \delta_i(s) > 0, \quad L_{i-1} < s < L_i, \quad (2.12)$$

$$R_i(s, 0) = R_{0i}(s) > 0, \quad L_{i-1} < s < L_i. \quad (2.13)$$

3. Analysis of the Model in Two Patch Habitat

Our aim is to analyze the long time behavior of the system in both uniform and nonuniform cases. In next two subsection we will study the model (2.1) – (2.13), in the case of nonuniform and uniform steady state.

3.1. The Non-uniform Steady State

Let u_i , v_i and w_i are the steady state solutions of the prey populations x_i , predator populations y_i and the supplementary resource R_i . Then the steady state system becomes:

$$w_i = \frac{C_i}{a_i} [a_i - \alpha_i u_i], \quad (3.1)$$

$$D_{1i} \frac{d^2 u_i}{ds^2} + u_i \mathbf{g}_i(u_i) - v_i \mathbf{p}_i(u_i) + \theta \alpha_i w_i u_i = 0, \quad (3.2)$$

$$D_{2i} \frac{d^2 v_i}{ds^2} + v_i \mathbf{f}_i(v_i) + \gamma_i v_i \mathbf{p}_i(u_i) = 0. \quad (3.3)$$

Now substituting the value of w_i from (3.1) into (3.2) and (3.3), we get:

$$D_{1i} \frac{d^2 u_i}{ds^2} + u_i \mathcal{G}_i(u_i) - v_i \mathbf{p}_i(u_i) = 0, \quad (3.4)$$

$$D_{2i} \frac{d^2 v_i}{ds^2} + v_i \mathbf{f}_i(v_i) + \gamma_i v_i \mathbf{p}_i(u_i) = 0, \quad (3.5)$$

where

$$\mathcal{G}_i(u_i) = \mathbf{g}_i(u_i) + \theta\alpha_i \frac{C_i}{a_i}(a_i - \alpha_i u_i), \quad i = 1, 2.$$

Since

$$\mathcal{G}_i(0) = \mathbf{g}_i(0) + C_i\theta\alpha_i > 0, \quad \mathcal{G}'_i(u_i) = \mathbf{g}'_i(u_i) - \frac{C_i\theta\alpha_i^2}{a_i} < 0, \quad i = 1, 2.$$

Hence the behavior the steady state system (3.4) and (3.5) with same set of boundary conditions identical to the case when there is no supplementary resource for the prey populations. Further, we assume

$$AH_3 : \begin{cases} \exists x_i^*, y_i^* > 0, & x_i^* \mathcal{G}_i(x_i^*) - y_i^* \mathbf{p}_i(x_i^*) = 0, \\ \mathbf{f}_i(y_i^*) + \gamma_i \mathbf{p}_i(x_i^*) = 0. \end{cases} \quad (3.6)$$

Remark 1. We are only interested to find the positive steady state of the system. Therefore, it follows from (3.1), $u_i < a_i/\alpha_i$ and hence $\mathcal{G}_i(u_i) \geq \mathbf{g}_i(u_i)$, $\forall u_i$. Now, from (3.6) we get

$$y_i^* = \frac{x_i^* \mathcal{G}_i(x_i^*)}{\mathbf{p}_i(x_i^*)} > y_i^{**}, \quad x_i^* > x_i^{**},$$

where the non-zero positive x_i^{**} and y_i^{**} are equilibrium value of the above prey-predator system without supplementary resource, given by

$$x_i^{**} \mathbf{g}_i(x_i^{**}) - y_i^{**} \mathbf{p}_i(x_i^{**}) = 0, \quad (3.7)$$

$$\mathbf{f}_i(y_i^{**}) + \gamma_i \mathbf{p}_i(x_i^{**}) = 0. \quad (3.8)$$

Hence in presence of a supplementary resource for the prey population, the level of steady state distributions of both the species are higher at each location in the habitat.

Example 1. Now, we discuss a numerical example in which the behavior of the steady state solutions of the above system is studied. The results are compared with the case of a prey-predator system without supplementary resource. We consider the following particular form of functions:

$$\mathbf{g}_i(u_i) = r_i \left(1 - \frac{u_i}{K_i}\right), \quad \mathbf{f}_i(v_i) = s_i \left(1 - \frac{v_i}{M_i}\right), \quad \mathbf{p}_i(u_i) = e_i u_i, \quad i = 1, 2.$$

For simplicity let assume that the supplementary resource initially is distributed uniformly, i.e. $C_1 = C_2 = C$. Then the steady state system (3.4) and (3.5), becomes

$$\begin{cases} D_{1i} \frac{d^2 u_i}{ds^2} + u_i \left[r_i \left(1 - \frac{u_i}{K_i}\right) + \frac{\theta\alpha_i C}{a_i}(a_i - \alpha_i u_i) \right] - e_i v_i u_i = 0, \\ D_{2i} \frac{d^2 v_i}{ds^2} + s_i v_i \left(1 - \frac{v_i}{M_i}\right) + \gamma_i e_i v_i u_i = 0 \end{cases} \quad (3.9)$$

with reservoir boundary conditions

$$\begin{aligned} u_1(0) &= x_1^*, & u_2(L_2) &= x_2^*, \\ v_1(0) &= y_1^*, & v_2(L_2) &= y_2^*, \end{aligned} \quad (3.10)$$

where x_i^*, y_i^* are from (3.6), and the continuity-flux matching conditions at the interface $s = L_1$ are given as

$$\begin{aligned} D_{11} \frac{du_1}{ds}(L_1) &= D_{12} \frac{du_2}{ds}(L_1), & D_{21} \frac{dv_1}{ds}(L_1) &= D_{22} \frac{dv_2}{ds}(L_1), \\ u_1(L_1) &= u_2(L_1), & v_1(L_1) &= v_2(L_1). \end{aligned} \quad (3.11)$$

The equations (3.9) – (3.11) are solved numerically by using finite-difference method, for the following set of dimensionless values

$$\begin{aligned} L_1 &= 10, & L_2 &= 20, & D_{11} &= 0.8, & D_{12} &= 0.9, & D_{21} &= 0.8, & D_{22} &= 0.9, \\ r_1 &= 0.03, & r_2 &= 0.025, & a_1 &= 1.0, & a_2 &= 1.0, & s_1 &= 0.03, & s_2 &= 0.01, \\ e_1 &= 0.00005, & e_2 &= 0.00005, & K_1 &= 100, & K_2 &= 125, & M_1 &= 75, & M_2 &= 50, \\ \alpha_1 &= 0.00005, & \alpha_2 &= 0.00002, & C &= 60, & \gamma_1 &= 0.4, & \gamma_2 &= 1.0, & \theta &= 0.7. \end{aligned}$$

By using above values of the parameters, we get

$$\begin{aligned} x_1^* &= 87.2 > x_1^{**} = 80.77, & x_2^* &= 118.58 > x_2^{**} = 109.09, \\ y_1^* &= 118.60 > y_1^{**} = 115.385, & y_2^* &= 168.58 > y_2^{**} = 159.09. \end{aligned}$$

We can easily verify that in presence of a supplementary resource for the prey, the level of steady state distributions of both species are higher at each location of the habitat compared to the case without supplementary resource for prey population (see Fig. 1). Moreover the steady state distribution is continuous and monotonic function.

Now, we consider the following assumptions: For every

$$\begin{aligned} \min\{x_1^{**}, x_2^{**}\} &\leq u_i \leq \max\{x_1^{**}, x_2^{**}\}, \\ \min\{y_1^{**}, y_2^{**}\} &\leq v_i \leq \max\{y_1^{**}, y_2^{**}\}, \quad i = 1, 2 \end{aligned}$$

we have that:

$$\begin{aligned} (u_i - x_i^{**})[u_i \mathcal{G}_i(u_i) - v_i \mathbf{P}_i(u_i)] &< 0, \quad \forall u_i \neq x_i^{**}, \\ (v_i - y_i^{**})[v_i \mathbf{f}_i(v_i) + \gamma_i v_i \mathbf{P}_i(u_i)] &< 0, \quad \forall v_i \neq y_i^{**}. \end{aligned}$$

Under these conditions u_i and v_i both will be positive through out the habitat. We now consider without loss of generality $0 < x_1^{**} < x_2^{**}$ and $0 < y_1^{**} < y_2^{**}$. Therefore $x_1^{**} \leq u_i \leq x_2^{**}$ and $y_1^{**} \leq v_i \leq y_2^{**}$. Again, from (3.4) and (3.5) under reservoir boundary conditions, let $p_i(s, \alpha_i)$ and $q_i(s, \beta_i)$ are unique solutions of u_i and v_i respectively, for $i = 1, 2$, such that

$$\begin{aligned} \frac{\partial p_1}{\partial s}(0, \alpha_1) &= \alpha_1, & p_1(0, \alpha_1) &= x_1^{**}, & \frac{\partial p_2}{\partial s}(L_2, \alpha_2) &= \alpha_2, & p_2(L_2, \alpha_2) &= x_2^{**}, \\ \frac{\partial q_1}{\partial s}(0, \beta_1) &= \beta_1, & p_1(0, \beta_1) &= y_1^{**}, & \frac{\partial p_2}{\partial s}(L_2, \beta_2) &= \beta_2, & p_2(L_2, \beta_2) &= y_2^{**}. \end{aligned}$$

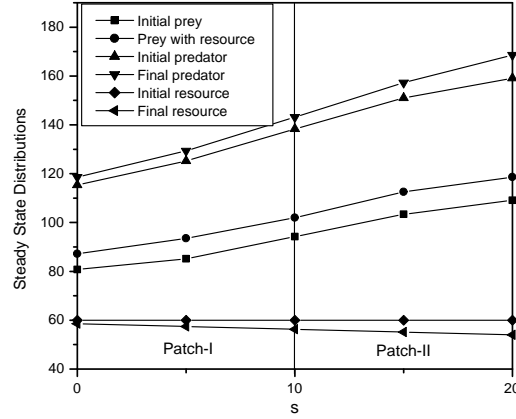


Figure 1. The steady state solutions for both the species, with and without supplementary resource for the prey.

Similarly, for no-flux boundary condition, let $p_i(s, \alpha_i)$ and $q_i(s, \beta_i)$ are unique solutions of u_i and v_i respectively, for $i = 1, 2$, such that

$$\begin{aligned} \frac{\partial p_1}{\partial s}(0, \alpha_1) = 0, \quad p_1(0, \alpha_1) = \alpha_1, \quad \frac{\partial p_2}{\partial s}(L_2, \alpha_2) = 0, \quad p_2(L_2, \alpha_2) = \alpha_2, \\ \frac{\partial q_1}{\partial s}(0, \beta_1) = 0, \quad q_1(0, \beta_1) = \beta_1, \quad \frac{\partial p_2}{\partial s}(L_2, \beta_2) = 0, \quad p_2(L_2, \beta_2) = \beta_2. \end{aligned}$$

Then the existence of the monotonic solutions are established in both the reservoir and no-flux boundary conditions, if we can show that there exists α_i and β_i , for $i = 1, 2$, such that

$$\begin{aligned} p_1(L_1, \alpha_1) = p_2(L_1, \alpha_2), \quad q_1(L_1, \beta_1) = q_2(L_1, \beta_2), \\ D_{11} \frac{\partial p_1}{\partial s}(L_1, \alpha_1) = D_{12} \frac{\partial p_2(L_1, \alpha_2)}{\partial s}, \quad D_{21} \frac{\partial q_1(L_1, \beta_1)}{\partial s} = D_{12} \frac{\partial q_2(L_1, \beta_2)}{\partial s}. \end{aligned}$$

In order to construct our required solutions for reservoir boundary conditions, we need some preliminary lemmas, in the same manner as in [3, 4].

Lemma 1. If $\alpha_1, \beta_1 > 0$, then

$$\frac{\partial p_1(s, \alpha_1)}{\partial s} > \alpha_1, \quad \frac{\partial q_1(s, \beta_1)}{\partial s} > \beta_1, \quad \text{on } 0 < s \leq L_1.$$

Lemma 2. If $\alpha_2, \beta_2 > 0$, $0 < p_2 < x_2^{**}$ and $0 < q_2 < y_2^{**}$, then

$$\frac{\partial p_2(s, \alpha_2)}{\partial s} > \alpha_2, \quad \frac{\partial q_2(s, \beta_2)}{\partial s} > \beta_2, \quad L_1 \leq s < L_2.$$

Lemma 3. Let us define $F_{1i}(\alpha_i)$ by $F_{1i}(\alpha_i) = p_i(L_1, \alpha_i)$. Then there exists $\hat{\alpha}_i > 0$ such that

$$F_{11} : [0, \hat{\alpha}_1] \rightarrow [x_1^{**}, x_2^{**}], \quad F_{12} : [0, \hat{\alpha}_2] \rightarrow [x_2^{**}, x_1^{**}].$$

Lemma 4. Let us define $F_{2i}(\beta_i)$ by $F_{2i}(\beta_i) = q_i(L_1, \beta_i)$. Then there exists $\hat{\beta}_i > 0$ such that

$$F_{21} : [0, \hat{\beta}_1] \rightarrow [y_1^{**}, y_2^{**}], \quad F_{22} : [0, \hat{\beta}_2] \rightarrow [y_2^{**}, y_1^{**}].$$

Similar type of four lemmas we can established for the steady state system with the no-flux boundary conditions. Hence we state the following theorem.

Theorem 1. (i) There exists a positive, continuous, monotonic solution of system (3.4) with continuous flux at L_1 .

(ii) There exists a positive, continuous, monotonic solution of system (3.5) with continuous flux at L_1 .

Now we consider the stability analysis of the system (2.1) – (2.3), (2.8) – (2.13) with reservoir boundary conditions (2.4) and (2.5). First we state the local stability of the system by the following theorem.

Theorem 2. The steady-state, continuous, monotonic solutions of the system (2.1) – (2.3) with reservoir boundary conditions and continuous flux at the interface $s = L_1$ are locally asymptotically stable provided the following conditions are satisfied:

$$\begin{aligned} \mathcal{X}_i &\leq 0, \quad \mathcal{Y}_i \leq 0, \quad \mathcal{Z}_i \leq 0, \\ \mathcal{U}_i^2 &\leq 4\mathcal{X}_i\mathcal{Y}_i, \quad \mathcal{X}_i\mathcal{Y}_i\mathcal{Z}_i \leq \mathcal{Y}_i\mathcal{W}_i^2 + \mathcal{Z}_i\mathcal{U}_i^2, \end{aligned} \quad (3.12)$$

where

$$\begin{aligned} \mathcal{X}_i &= \mathbf{g}_i(u_i) + u_i\mathbf{g}'_i(u_i) - v_i\mathbf{p}'_i(u_i) + \theta\alpha_i w_i, \\ \mathcal{Y}_i &= \mathbf{f}_i(v_i) + v_i\mathbf{f}'_i(v_i) + \gamma_i\mathbf{p}_i(u_i), \quad \mathcal{W}_i = \frac{\alpha_i}{2}[\theta u_i - w_i], \\ \mathcal{Z}_i &= a_i \left(1 - \frac{2w_i}{C_i}\right) - \alpha_i u_i, \quad \mathcal{U}_i = \frac{1}{2}[\gamma_i v_i \mathbf{p}'_i(u_i) - \mathbf{p}_i(u_i)], \end{aligned}$$

for $x_1^* \leq u_i \leq x_2^*$, $y_1^* \leq v_i \leq y_2^*$, where x_i^* and y_i^* are given by (3.6).

Proof. We linearize (2.1), (2.2) and (2.3) by using

$$\begin{aligned} R_i(s, t) &= w_i(s) + r_i(s, t), \\ x_i(s, t) &= u_i(s) + n_i(s, t), \quad y_i(s, t) = v_i(s) + m_i(s, t), \end{aligned} \quad (3.13)$$

then we obtain the system

$$\begin{cases} \frac{\partial r_i}{\partial t} = r_i \left[a_i \left(1 - \frac{2w_i}{C_i} \right) - \alpha_i u_i \right] - n_i \alpha_i w_i, \\ \frac{\partial n_i}{\partial t} = n_i [\mathbf{g}_i(u_i) + u_i \mathbf{g}'_i(u_i) - v_i \mathbf{p}'_i(u_i) + \theta \alpha_i w_i] \\ \quad - m_i \mathbf{p}_i(u_i) + r_i \theta \alpha_i u_i + D_{1i} \frac{\partial^2 n_i}{\partial s^2}, \\ \frac{\partial m_i}{\partial t} = m_i [\mathbf{f}_i(v_i) + v_i \mathbf{f}'_i(v_i) + \gamma_i \mathbf{p}_i(u_i)] + n_i \gamma_i v_i \mathbf{p}'_i(u_i) + D_{2i} \frac{\partial^2 m_i}{\partial s^2}. \end{cases} \quad (3.14)$$

Using (3.13) the following boundary and matching conditions are obtained:

$$\begin{aligned} n_1(0, t) = 0 = n_2(L_2, t), \quad m_1(0, t) = 0 = m_2(L_2, t), \\ n_1(L_1, t) = n_2(L_1, t), \quad m_1(L_1, t) = m_2(L_1, t), \\ D_{11} \frac{\partial n_1}{\partial s}(L_1, t) = D_{12} \frac{\partial n_2}{\partial s}(L_1, t), \quad D_{21} \frac{\partial m_1}{\partial s}(L_1, t) = D_{22} \frac{\partial m_2}{\partial s}(L_1, t). \end{aligned}$$

Now we consider the following positive definite function,

$$V(t) = \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} \frac{1}{2} (n_i^2 + m_i^2 + r_i^2) ds. \quad (3.15)$$

Differentiating (3.15) with respect to t , we get

$$\dot{V}(t) = \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} \left(n_i \frac{\partial n_i}{\partial t} + m_i \frac{\partial m_i}{\partial t} + r_i \frac{\partial r_i}{\partial t} \right) ds.$$

By using (3.14) we get

$$\begin{aligned} \dot{V}(t) &= \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} n_i^2 [\mathbf{g}_i(u_i) + u_i \mathbf{g}'_i(u_i) - v_i \mathbf{p}'_i(u_i) + \theta \alpha_i w_i] ds + \sum_{i=1}^2 \\ &\quad \times \int_{L_{i-1}}^{L_i} m_i^2 [\mathbf{f}_i(v_i) + v_i \mathbf{f}'_i(v_i) + \gamma_i \mathbf{p}_i(u_i)] ds + \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} r_i^2 \left[a_i \left(1 - \frac{2w_i}{C_i} \right) \right. \\ &\quad \left. - \alpha_i u_i \right] ds + \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} n_i m_i [-\mathbf{p}_i(u_i) + \gamma_i v_i \mathbf{p}'_i(u_i)] ds + \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} n_i r_i \alpha_i \\ &\quad \times [\theta u_i - w_i] ds + \sum_{i=1}^2 D_{1i} \int_{L_{i-1}}^{L_i} n_i \frac{\partial^2 n_i}{\partial s^2} ds + \sum_{i=1}^2 D_{2i} \int_{L_{i-1}}^{L_i} m_i \frac{\partial^2 m_i}{\partial s^2} ds. \end{aligned}$$

Therefore,

$$\begin{aligned} \dot{V}(t) &= \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} [\mathcal{X}_i n_i^2 + \mathcal{Y}_i m_i^2 + \mathcal{Z}_i r_i^2 + 2\mathcal{U}_i n_i m_i + 2\mathcal{W}_i r_i n_i] ds \\ &\quad - \sum_{i=1}^2 D_{1i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial n_i}{\partial s} \right)^2 ds - \sum_{i=1}^2 D_{2i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial m_i}{\partial s} \right)^2 ds, \quad (3.16) \end{aligned}$$

where the functions $\mathcal{X}_i, \mathcal{Y}_i, \mathcal{Z}_i, \mathcal{U}_i$, and \mathcal{W}_i are as follows,

$$\begin{aligned}\mathcal{X}_i &= \mathbf{g}_i(u_i) + u_i \mathbf{g}'_i(u_i) - v_i \mathbf{p}'_i(u_i) + \theta \alpha_i w_i, \\ \mathcal{Y}_i &= \mathbf{f}_i(v_i) + v_i \mathbf{f}'_i(v_i) + \gamma_i \mathbf{p}_i(u_i), \quad \mathcal{Z}_i = a_i \left(1 - \frac{2w_i}{C_i}\right) - \alpha_i u_i, \\ \mathcal{U}_i &= \frac{1}{2} [\gamma_i v_i \mathbf{p}'_i(u_i) - \mathbf{p}_i(u_i)], \quad \mathcal{W}_i = \frac{\alpha_i}{2} [\theta u_i - w_i]\end{aligned}$$

hence \dot{V} is negative definite, if conditions (3.12) of the theorem are satisfied for $i = 1, 2$. ■

Next, we state the corresponding nonlinear stability conditions of the system.

Theorem 3. *The steady-state, continuous, monotonic solutions of nonlinear system (2.1) – (2.3), (2.8) – (2.13) with reservoir boundary conditions (2.4) – (2.5) are asymptotically stable in the sub-region*

$$\mathbf{R} = \{x_1^* \leq x_i, \quad u_i \leq x_2^*, \quad y_1^* \leq y_i, \quad v_i \leq y_2^*, \quad i = 1, 2\},$$

provided the following conditions are satisfied:

$$\begin{aligned}\mathcal{N}_{xi} &\leq 0, \quad \mathcal{N}_{yi} \leq 0, \quad \mathcal{N}_{zi} \leq 0, \\ \mathcal{N}_{ui}^2 &\leq 4\mathcal{N}_{xi}\mathcal{N}_{yi}, \quad \mathcal{N}_{xi}\mathcal{N}_{yi}\mathcal{N}_{zi} \leq \mathcal{N}_{yi}\mathcal{N}_{wi}^2 + \mathcal{N}_{zi}\mathcal{N}_{ui}^2,\end{aligned}\tag{3.17}$$

where

$$\begin{aligned}\mathcal{N}_{xi} &= \frac{x_i \mathbf{g}_i(x_i) - u_i \mathbf{g}_i(u_i)}{x_i - u_i} - y_i \frac{\mathbf{p}_i(x_i) - \mathbf{p}_i(u_i)}{x_i - u_i} + \theta \alpha_i R_i, \\ \mathcal{N}_{yi} &= \frac{y_i \mathbf{f}_i(y_i) - v_i \mathbf{f}_i(v_i)}{y_i - v_i} + \gamma_i \mathbf{p}_i(u_i), \\ \mathcal{N}_{zi} &= a_i \left(1 - \frac{R_i + w_i}{C_i}\right) - \alpha_i u_i, \quad \mathcal{N}_{wi} = \frac{\alpha_i}{2} [\theta u_i - R_i], \\ \mathcal{N}_{ui} &= \frac{1}{2} \left[\gamma_i y_i \frac{\mathbf{p}_i(x_i) - \mathbf{p}_i(u_i)}{x_i - u_i} - \mathbf{p}_i(u_i) \right].\end{aligned}$$

Proof. By using (3.13), we get from (2.1), (2.2) and (2.3)

$$\frac{\partial r_i}{\partial t} = r_i \left[a_i \left(1 - \frac{R_i + w_i}{C_i}\right) - \alpha_i u_i \right] - n_i \alpha_i R_i,\tag{3.18}$$

$$\begin{aligned}\frac{\partial n_i}{\partial t} &= n_i \left[\frac{x_i \mathbf{g}_i(x_i) - u_i \mathbf{g}_i(u_i)}{x_i - u_i} - y_i \frac{\mathbf{p}_i(x_i) - \mathbf{p}_i(u_i)}{x_i - u_i} + \theta \alpha_i R_i \right] \\ &\quad - m_i \mathbf{p}_i(u_i) + r_i \theta \alpha_i u_i + D_{1i} \frac{\partial^2 n_i}{\partial s^2},\end{aligned}\tag{3.19}$$

$$\begin{aligned}\frac{\partial m_i}{\partial t} &= m_i \left[\frac{y_i \mathbf{f}_i(y_i) - v_i \mathbf{f}_i(v_i)}{y_i - v_i} + \gamma_i \mathbf{p}_i(u_i) \right] \\ &\quad + n_i \left[\gamma_i y_i \frac{\mathbf{p}_i(x_i) - \mathbf{p}_i(u_i)}{x_i - u_i} \right] + D_{2i} \frac{\partial^2 m_i}{\partial s^2}.\end{aligned}\tag{3.20}$$

Here also we consider the same positive definite function as in the case of linear stability. By using (3.18), (3.19) and (3.20), we get

$$\begin{aligned}
\dot{V}(t) &= \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} n_i^2 \left[\frac{x_i \mathbf{g}_i(x_i) - u_i \mathbf{g}_i(u_i)}{x_i - u_i} - y_i \frac{\mathbf{p}_i(x_i) - \mathbf{p}_i(u_i)}{x_i - u_i} + \theta \alpha_i R_i \right] ds \\
&+ \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} m_i^2 \left[\frac{y_i \mathbf{f}_i(y_i) - v_i \mathbf{f}_i(v_i)}{y_i - v_i} + \gamma_i \mathbf{p}_i(u_i) \right] ds \\
&+ \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} r_i^2 \left[a_i \left(1 - \frac{R_i + w_i}{C_i} \right) - \alpha_i u_i \right] ds + \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} n_i m_i \\
&\times \left[\gamma_i y_i \frac{\mathbf{p}_i(x_i) - \mathbf{p}_i(u_i)}{x_i - u_i} - \mathbf{p}_i(u_i) \right] ds + \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} r_i n_i \alpha_i [\theta u_i - R_i] ds \\
&+ \sum_{i=1}^2 D_{1i} \int_{L_{i-1}}^{L_i} n_i \frac{\partial^2 n_i}{\partial s^2} ds + \sum_{i=1}^2 D_{2i} \int_{L_{i-1}}^{L_i} m_i \frac{\partial^2 m_i}{\partial s^2} ds.
\end{aligned}$$

Therefore,

$$\begin{aligned}
\dot{V}(t) &= \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} [\mathcal{N}_{x_i} n_i^2 + \mathcal{N}_{y_i} m_i^2 + \mathcal{N}_{z_i} r_i^2 + 2\mathcal{N}_{u_i} n_i m_i + 2\mathcal{N}_{w_i} r_i n_i] ds \\
&- \sum_{i=1}^2 D_{1i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial n_i}{\partial s} \right)^2 ds - \sum_{i=1}^2 D_{2i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial m_i}{\partial s} \right)^2 ds, \quad (3.21)
\end{aligned}$$

where the functions \mathcal{N}_{x_i} , \mathcal{N}_{y_i} , \mathcal{N}_{z_i} , \mathcal{N}_{u_i} and \mathcal{N}_{w_i} are given by (3.18). Hence \dot{V} is negative definite if the conditions (3.17) hold for $i = 1, 2$. ■

It can be noted that, if we linearize the conditions of Thm.3, then we get the conditions of Thm. 2.

The same theorems are true for the system (2.1) – (2.3), (2.8) – (2.13) with no-flux boundary conditions (2.6) and (2.7).

3.2. The Uniform Equilibrium State

Similar as in the previous case, the main purpose of this section to find the conditions for local and global stability of the uniform equilibrium state of the system

$$x_i(s, t) \equiv K^*, \quad y_i(s, t) \equiv M^*, \quad R_i(s, t) \equiv C^*, \quad 0 \leq s \leq L_2, \quad t \geq 0$$

under both sets of boundary conditions.

Theorem 4. *The equilibrium (C^*, K^*, M^*) is locally asymptotically stable, if $H_i^* + \theta \alpha_i C^* \leq 0$, for $i = 1, 2$, where H_i^* is given by*

$$H_i^* = \mathbf{g}_i(K^*) + K^* \mathbf{g}'_i(K^*) - M^* \mathbf{p}_i(K^*) \quad (3.22)$$

and the following conditions are satisfied

$$(\gamma_i M^* \mathbf{p}'_i(K^*) - \mathbf{p}_i(K^*))^2 \leq 4(H_i^* + \theta \alpha_i C^*) M^* \mathbf{f}'_i(M^*), \quad i = 1, 2. \quad (3.23)$$

Proof. We linearize the system (2.1) – (2.3) by using

$$\begin{aligned} R_i(s, t) &= C^* + r_i(s, t), \\ x_i(s, t) &= K^* + n_i(s, t), \quad y_i(s, t) = M^* + m_i(s, t), \end{aligned} \quad (3.24)$$

then we get

$$\begin{cases} \frac{\partial r_i}{\partial t} = r_i \left[-\frac{a_i C^*}{C_i} \right] - n_i \alpha_i C^*, \\ \frac{\partial n_i}{\partial t} = n_i [\mathbf{g}_i(K^*) + K^* \mathbf{g}'_i(K^*) - M^* \mathbf{p}'_i(K^*) + \theta \alpha_i C^*] \\ \quad - m_i \mathbf{p}_i(K^*) + r_i \theta \alpha_i K^* + D_{1i} \frac{\partial^2 n_i}{\partial s^2}, \\ \frac{\partial m_i}{\partial t} = m_i M^* \mathbf{f}'_i(M^*) + n_i \gamma_i M^* \mathbf{p}'_i(K^*) + D_{2i} \frac{\partial^2 m_i}{\partial s^2}. \end{cases} \quad (3.25)$$

We consider the following positive definite function

$$V = \frac{1}{2} \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} [(x_i - K^*)^2 + (y_i - M^*)^2 + d_i (R_i - C^*)^2], \quad (3.26)$$

where $d_i, i = 1, 2$ are positive constants. Differentiating (3.26) and using (3.25), we get

$$\begin{aligned} \dot{V} &= \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} n_i^2 (H_i^* + \theta \alpha_i C^*) ds + \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} m_i^2 M^* \mathbf{f}'_i(M^*) ds \\ &\quad + \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} r_i^2 \left[-\frac{d_i a_i C^*}{C_i} \right] ds + \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} n_i m_i (-\mathbf{p}_i(K^*) \\ &\quad + \gamma_i M^* \mathbf{p}'_i(K^*)) ds + \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} n_i r_i (\alpha_i \{\theta K^* - d_i C^*\}) ds \\ &\quad + \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} D_{1i} n_i \frac{\partial^2 n_i}{\partial s^2} ds + \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} D_{2i} m_i \frac{\partial^2 m_i}{\partial s^2} ds. \end{aligned} \quad (3.27)$$

Using integration by parts and for both types of boundary conditions, we get

$$\begin{aligned} \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} D_{1i} n_i \frac{\partial^2 n_i}{\partial s^2} ds &= - \sum_{i=1}^2 D_{1i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial n_i}{\partial s} \right)^2 ds, \\ \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} D_{2i} m_i \frac{\partial^2 m_i}{\partial s^2} ds &= - \sum_{i=1}^2 D_{2i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial m_i}{\partial s} \right)^2 ds. \end{aligned}$$

We choose $d_i, i = 1, 2$, such that, coefficients of $n_i r_i$ become zero, i.e. $d_1 = d_2 = \theta K^* / C^*$. Therefore it follows from (3.27) that \dot{V} is negative definite, if the conditions $H_i^* + \theta \alpha_i C^* \leq 0$ and (3.23) are satisfied. ■

Theorem 5. Let $H_i^* + \theta\alpha_i C^* > 0$. Then the equilibrium (C^*, K^*, M^*) is locally asymptotically stable, if the conditions (3.23) and the following inequality hold:

$$H_i^* + \theta\alpha_i C^* \leq D_{1i} \frac{\pi^2}{(L_i - L_{i-1})^2}, \quad i = 1, 2.$$

Proof. From (3.28) and using Poincare's inequality we get

$$D_{1i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial n_i}{\partial s} \right)^2 ds \leq D_{1i} \frac{\pi^2}{(L_i - L_{i-1})^2} \int_{L_{i-1}}^{L_i} n_i^2 ds.$$

Therefore from (3.27) we get

$$\begin{aligned} \dot{V} &\leq \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} n_i^2 x \left(H_i^* + \theta\alpha_i C^* - D_{1i} \frac{\pi^2}{(L_i - L_{i-1})^2} \right) ds \\ &+ \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} m_i^2 M^* \mathbf{f}'_i(M^*) ds + \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} r_i^2 \left(-\frac{d_i a_i C^*}{C_i} \right) ds \\ &+ \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} n_i m_i \left(-\mathbf{p}_i(K^*) + \gamma_i M^* \mathbf{p}'_i(K^*) \right) ds - \sum_{i=1}^2 D_{2i} \int_{L_{i-1}}^{L_i} \left(\frac{\partial m_i}{\partial s} \right)^2 ds. \end{aligned}$$

Hence the theorem is proved. ■

We now state the global stability of the uniform steady state.

Theorem 6. The uniform steady-state (C^*, K^*, M^*) is globally asymptotically stable if

$$\mathcal{A}_i(x_i) = \frac{x_i \mathbf{g}_i(x_i) - M^* \mathbf{p}_i(x_i)}{x_i - K^*} + \theta\alpha_i C^* < 0, \quad \forall x_i \neq K^*, \quad (3.28)$$

$$\left(\gamma_i \frac{\mathbf{p}_i(x_i) - \mathbf{p}_i(K^*)}{x_i - K^*} - \frac{\mathbf{p}_i(x_i)}{x_i} \right)^2 \leq 4 \frac{\mathcal{A}_i(x_i)}{x_i} \left(\frac{\mathbf{f}_i(y_i) - \mathbf{f}_i(M^*)}{y_i - M^*} \right), \quad (3.29)$$

$$\begin{aligned} &\frac{\mathcal{A}_i(x_i)}{x_i} \left(\frac{\mathbf{f}_i(y_i) - \mathbf{f}_i(M^*)}{y_i - M^*} \right) \left(\frac{a_i}{C_i} \right) \\ &\leq \left(\frac{\mathbf{f}_i(M^*) - \mathbf{f}_i(y_i)}{y_i - M^*} \right) (\alpha_i^2 (\theta - R_i)^2) + \frac{a_i}{C_i} \left(\frac{\mathcal{A}_i(x_i)}{x_i} \right)^2. \end{aligned} \quad (3.30)$$

Proof. Let us consider the following positive definite function

$$\begin{aligned} V(x, y, R) &= \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} \left(x_i - K^* - K^* \ln \frac{x_i}{K^*} \right) ds + \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} \left(y_i - M^* \right. \\ &\left. - M^* \ln \frac{y_i}{M^*} \right) ds + \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} \left(R_i - C^* - C^* \ln \frac{R_i}{C^*} \right) ds. \end{aligned} \quad (3.31)$$

Differentiating (3.31) with respect to t and using (2.1) – (2.3) we get

$$\begin{aligned}
\dot{V}(s, t) &= \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} \left(\frac{x_i - K^*}{x_i} \right) \frac{\partial x_i}{\partial t} ds + \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} \left(\frac{y_i - M^*}{y_i} \right) \frac{\partial y_i}{\partial t} ds \\
&+ \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} \left(\frac{R_i - C^*}{R_i} \right) \frac{\partial R_i}{\partial t} ds = \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} \frac{(x_i - K^*)^2}{x_i} \\
&\times \left(\frac{x_i \mathbf{g}_i(x_i) - M^* \mathbf{p}_i(x_i)}{x_i - K^*} + \theta \alpha_i C^* \right) ds + \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} (y_i - y^*)^2 \\
&\times \left(\frac{\mathbf{f}_i(y_i) - \mathbf{f}_i(M^*)}{y_i - M^*} \right) ds - \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} (R_i - C^*)^2 \left(-\frac{a_i}{C_i} \right) ds \\
&+ \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} (x_i - K^*)(y_i - M^*) \left(\gamma_i \frac{\mathbf{p}_i(x_i) - \mathbf{p}_i(K^*)}{x_i - K^*} - \frac{\mathbf{p}_i(x_i)}{x_i} \right) ds \\
&+ \sum_{i=1}^2 \int_{L_{i-1}}^{L_i} (x_i - K^*)(y_i - M^*) \alpha_i (\theta - R_i) ds \\
&+ \sum_{i=1}^2 D_{1i} \int_{L_{i-1}}^{L_i} \frac{x_i - K^*}{x_i} \frac{\partial^2 x_i}{\partial s^2} ds + \sum_{i=1}^2 D_{2i} \int_{L_{i-1}}^{L_i} \frac{y_i - M^*}{y_i} \frac{\partial^2 y_i}{\partial s^2} ds.
\end{aligned}$$

Using both set of boundary and flux matching conditions

$$\begin{aligned}
(x_1(0, t) - K^*) \frac{\partial x_1}{\partial s}(0, t) &= 0, \quad (x_2(L_2, t) - K^*) \frac{\partial x_2}{\partial s}(L_2, t) = 0, \\
(y_1(0, t) - M^*) \frac{\partial y_1}{\partial s}(0, t) &= 0, \quad (y_2(L_2, t) - M^*) \frac{\partial y_2}{\partial s}(L_2, t) = 0
\end{aligned}$$

we get

$$\begin{aligned}
\sum_{i=1}^2 D_{1i} \int_{L_{i-1}}^{L_i} \frac{x_i - K^*}{x_i} \frac{\partial^2 x_i}{\partial s^2} ds &= - \sum_{i=1}^2 D_{1i} \int_{L_{i-1}}^{L_i} \frac{K^*}{x_i^2} \left(\frac{\partial x_i}{\partial s} \right)^2 ds, \\
\sum_{i=1}^2 D_{2i} \int_{L_{i-1}}^{L_i} \frac{y_i - M^*}{y_i} \frac{\partial^2 y_i}{\partial s^2} ds &= - \sum_{i=1}^2 D_{2i} \int_{L_{i-1}}^{L_i} \frac{M^*}{y_i^2} \left(\frac{\partial y_i}{\partial s} \right)^2 ds.
\end{aligned}$$

Now if conditions (3.28), (3.29) and (3.30) hold, then $\dot{V}(x, y) < 0$, and $\dot{V}(C^*, K^*, M^*) = 0$. Therefore $\dot{V}(x, y)$ is negative definite over $R > 0$, $x > 0$, $y > 0$ with respect to $R_i^* = C^*$, $x_i^* = K^*$, $y_i^* = M^*$, proving the theorem. ■

Remark 2. We conclude that the role of supplementary resource is to increase the level of nonuniform steady state distributions of both the species at each location of the linear habitat. Further, the number of conditions for stability is increased compared to the case with no supplementary resource for prey and the role of patchiness is destabilizing in present of supplementary resource.

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Plėšrūno-aukos modelis su difuzija ir papildomu resursu aukai dviejų sričių areale

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Šiame straipsnyje modeliuojama ir analizuojama plėšrūnų ir aukų dinamika, laikant, kad plėšrūnų populiacija dalinai priklauso nuo aukų skaičiaus. Arealą sudaro dvi sritys, kuriose vyksta populiacijų individų difuzija, be to, aukoms yra išskirtas nedifunduojantis resursas.

Įrodyta, kad egzistuoja teigiamas, monotoniškas, tolydus stacionarusis sprendinys, tenkinantis tolydumo sąlygą abiem populiacijoms atskirai. Gautos asimptotinio stabilumo sąlygos tiesiniu ir netiesiniu atvejais.