

MODELLING THE INTERACTION OF TWO PREDATORS COMPETING FOR A PREY IN A DIFFUSIVE SYSTEM

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In this paper, a mathematical model based on the dynamics of Gause-type model with diffusion is proposed and analyzed. We consider a resource based ecological model where two predators are competing with interference for a limited prey. Criteria for local stability, instability and global stability are obtained in the absence of diffusion. It is shown that, in the absence of intraspecific interaction of the predator species, the interior equilibrium becomes unstable. It is also shown that an unstable equilibrium state may be stabilized by increasing diffusion coefficients appropriately.

Key Words : Predator-Prey System; Interference; Stability; Diffusion

1. INTRODUCTION

Mechanistic theories of interacting populations using mathematical models have been of great interest in the past few decades and have been investigated by several researchers (Albercht *et al.*¹, Dubey², Freedman and Waltman⁷, Goh^{8&9}, Gopalsamy¹⁰, Harrison¹¹, Hsu¹³⁻¹⁶, Kazarinoff and Driessche¹⁹, May²¹). The question of two predator species competing for a single prey has occupied an important place in the ecological literature (Freedman and Waltman⁷, Harrison¹¹, Hsu¹⁵, Mitra *et al.*²⁴). In particular, Hsu¹⁵ proposed and analyzed a mathematical model with two predator species exploiting a single prey. He found that when the interspecific interference coefficient is small, in purely exploitation competition, the winner competes its rival successfully. However, if the interference is large enough, then the competitive outcome depends upon the initial population of predator species. In this study, the effect of intraspecific interference has not been investigated. Freedman and Waltman⁷ considered three population models, i.e., two competing predators feeding on a single prey and a single predator feeding on two competing prey populations. They derived the persistence criteria of the system. Gopalsamy¹⁰ established a model of two consumer species and one resource species, and obtained sufficient conditions for the three species system to converge as $t \rightarrow \infty$ to an equilibrium point. Mitra *et al.*²⁴ studied the permanent coexistence and global stability of a simple Lotka-Volterra type mathematical model of a living resource supporting two competing predators. They showed that the permanent coexistence of the system depend on the threshold of the ratio between the coefficients of numerical responses of the two consumers. In our previous work², a mathematical model has been proposed and analyzed in which two species utilize a common resource and one of the species is itself an alternative resource for the other. Here, in this paper we develop a mathematical model in a three dimensional system to study the interaction of two predators competing for a limited prey. We consider the growth rates of prey and predator species as nonlinear with crowding effects. We

also consider in our model the effect of diffusion on the stability of the system similar to the work of Freedman *et al.*⁶, Jorne¹⁷, Jorne and Carmi¹⁸, Nallaswamy and Shukla²², Rothe²³. In the absence of diffusion, our model generalizes the results of Hsu¹⁵ and Mitra *et al.*²⁴ In the presence of diffusion our results agree with those of Freedman and Shukla⁵, Hastings¹², Shukla *et al.*²⁵, Shukla and Shukla²⁶, Shukla and Verma²⁷. We investigate the local and global behavior of the uniform steady state of the proposed system by constructing a suitable Liapunov's function (La Salle and Lefschetz²⁰).

2. MATHEMATICAL MODEL

Consider an ecosystem where we wish to model the interaction of two predators competing for a limited prey with diffusion. The predator species compete not only by lowering the growth rate of population of the shared prey but also by interfering with its rival and with members of their own populations. We consider the interference coefficients as α_{ij} measuring the damage effect of predator species j on predator species i and γ_i measuring the damage effect from its own species. Then the dynamics of the system can be written as

$$\begin{aligned}\frac{\partial N}{\partial t} &= Ng(N, K) - b_1 x_1 p_1(N) - b_2 x_2 p_2(N) + D \nabla^2 N, \\ \frac{\partial x_1}{\partial t} &= x_1 (\beta_1 p_1(N) - \delta_1 - \gamma_1 x_1 - \alpha_{21} x_2) + d_1 \nabla^2 x_1\end{aligned}\quad \dots (2.1)$$

and

$$\frac{\partial x_2}{\partial t} = x_2 (\beta_2 p_2(N) - \delta_2 - \gamma_2 x_2 - \alpha_{12} x_1) + d_2 \nabla^2 x_2.$$

We impose the following boundary and initial conditions on system (2.1) as

$$\begin{aligned}N(0, u, v) &= \phi(u, v) \geq 0, x_i(0, u, v) = \psi_i(u, v) \geq 0, \\ \frac{\partial N}{\partial n} &= \frac{\partial x_i}{\partial n} = 0, i = 1, 2,\end{aligned}\quad \dots (2.2)$$

where n is the unit outward normal to the region ∂R . ϕ and ψ_i ($i = 1, 2$) are the smooth initial functions. R is a simply connected domain in the $u - v$ plane with piecewise smooth boundary ∂R .

In model (2.1), $\nabla^2 \equiv \frac{\partial^2}{\partial u^2} + \frac{\partial^2}{\partial v^2}$ is the Laplacian diffusion operator and $N(t, u, v)$, $x_i(t, u, v)$ ($i = 1, 2$) are the population density of prey species and i th predator species respectively, at time $t \geq 0$ and coordinates $(u, v) \in R$.

The function $g(N, K)$ is the specific growth rate of the prey species. It increases as the carrying capacity K of the prey species increases and decreases as the density of the prey increases. Hence, we assume

$$g(0, 0) > 0, \frac{\partial g(N, K)}{\partial N} < 0, \frac{\partial g(N, K)}{\partial K} > 0, \dots (2.3)$$

and there exists a $x = K$ such that $g(K, K) = 0$.

The function $p_i(N)$ is the functional response of the i th predator and it satisfies

$$P_i(0) = 0, p_i'(N) > 0, \text{ for } N \geq 0, i = 1, 2. \dots (2.4)$$

Here, D, d_1, d_2 are diffusion coefficients of $N(t), x_1(t), x_2(t)$ in R respectively. b_i is the feeding rate per predator (predator species i) per unit prey consumed, β_i is the birth rate per predator (predator species i) per unit prey consumed, δ_i is the death rate of the predator species i .

It may be pointed out here that if we take

$$\gamma_1 = \gamma_2 = D = d_1 = d_2 = 0, g(N, K) = r \left(1 - \frac{N}{K} \right) \dots (2.5)$$

and $p_1(N) = N = p_2(N)$,

where r is a positive constant, then model (2.1) reduces to Hsu¹⁵.

3. MODEL WITHOUT DIFFUSION

We consider the model without diffusion (i.e., $D = d_1 = d_2 = 0$) as follows

$$\begin{aligned} \dot{N} &= Ng(N, K) - b_1x_1p_1(N) - b_2x_2p_2(N), \\ \dot{x}_1 &= x_1(\beta_1p_1(N) - \delta_1 - \gamma_1x_1 - \alpha_{21}x_2), \\ \dot{x}_2 &= x_2(\beta_2p_2(N) - \delta_2 - \gamma_2x_2 - \alpha_{12}x_1) \end{aligned} \dots (3.1)$$

and

$$N(0) \geq 0, x_i(0) \geq 0 (i = 1, 2).$$

Before analysis we state one important lemma as follows, the proof of which directly follows from system (3.1).

Lemma 3.1 — A necessary condition for either predator species x_i to survive is

$$\beta_i p_i(K) > \delta_i, i = 1, 2.$$

Existence of Equilibria :

Putting $\frac{dZ}{dt} = 0$ ($Z = N, x_1, x_2$) and solving (3.1) we get the following possible non-negative equilibria, namely, $E_0(0, 0, 0), E_1(K, 0, 0), E_2(\bar{N}, \bar{x}_1, 0), E_3(\tilde{N}, 0, \tilde{x}_2), E^*(N^*, x_1^*, x_2^*)$. The equilibria E_0 and E_1 clearly exist. We shall show the existence of the other equilibria as follows.

Existence of $E_2(\bar{N}, \bar{x}_1, 0)$:

Here \bar{N} and \bar{x}_1 are the positive solutions of the following equations :

$$x_1 = \frac{Ng(N, K)}{b_1 p_1(N)} \quad \dots (3.1a)$$

and

$$\delta_1 + \gamma_1 x_1 = \beta_1 p_1(N). \quad \dots (3.1b)$$

From (3.1a) we note the following :-

When

$$N \rightarrow K, x_1 \rightarrow 0, \quad \dots (3.2a)$$

$$N \rightarrow 0, x_1 \rightarrow \frac{g(0, K)}{b_1 p_1'(0)} > 0, \quad \dots (3.2b)$$

$$\frac{dx_1}{dN} = \frac{1}{b_1 p_1^2(N)} \left[g(N, K) (p_1(N) - N p_1'(N)) + N p_1(N) \frac{\partial g(N, K)}{\partial N} \right], \quad \dots (3.2c)$$

$$\lim_{N \rightarrow K} \frac{dx_1}{dN} = \frac{K}{b_1 p_1(K)} \left[\frac{\partial g(K, K)}{\partial N} \right] < 0. \quad \dots (3.2d)$$

From (3.2c) we note that $\frac{dx_1}{dN}$ may be positive or negative.

However, it is negative in the neighbourhood of the point $N = K$.

Further, $\frac{dx_1}{dN}$ is negative provided

$$\frac{1}{g(N, K)} \frac{\partial g(N, K)}{\partial N} < \frac{N p_1'(N) - p_1(N)}{N p_1(N)}. \quad \dots (3.3)$$

From (3.1b) we note the following :

When

$$N \rightarrow K, x_1 \rightarrow \frac{1}{\gamma_1} (\beta_1 p_1(K) - \delta_1) > 0, \quad \dots (3.4a)$$

and

$$N \rightarrow 0, x_1 \rightarrow -\frac{\delta_1}{\gamma_1} < 0, \quad \dots (3.4b)$$

$$\frac{dx_1}{dN} = \frac{\beta_1 p'(N)}{\gamma_1} > 0. \quad \dots (3.4c)$$

From the above analysis we note that the two isocline (3.1a) and (3.1b) intersect at a unique point (\bar{N}, \bar{x}_1) under condition (3.3). Thus E_2 exists if condition (3.3) holds. This implies that if inequality (3.3) is satisfied, then the prey species survives with the first predator, whereas the second predator is driven to extinction.

Remark 1 : If $p_1(N) = N$, then condition (3.3) is automatically satisfied.

Existence of $E_3(\tilde{N}, 0, \tilde{x}_2)$:

Here \tilde{N} and \tilde{x}_2 are the positive solutions of the following equations :

$$x_2 = \frac{Ng(N, K)}{b_2 p_2(N)}, \quad \dots (3.5a)$$

and

$$\delta_2 + \gamma_2 x_2 = \beta_2 p_2(N). \quad \dots (3.5b)$$

As in the existence of E_2 , one can see that the equilibrium E_3 exists if the following inequality holds at E_3 ,

$$\frac{1}{g(N, K)} \frac{\partial g(N, K)}{\partial N} < \frac{Np_2'(N) - p_2(N)}{Np_2(N)}. \quad \dots (3.5c)$$

Thus, if condition (3.5c) holds, then the prey species survives with its second predator, whereas the first predator dies out.

Existence of $E^*(N^*, x_1^*, x_2^*)$:

Here N^* , x_1^* and x_2^* are the positive solutions of the following algebraic equations :

$$Ng(N, K) - b_1 x_1 p_1(N) - b_2 x_2 p_2(N) = 0, \quad \dots (3.6a)$$

$$\beta_1 p_1(N) - \delta_1 - \gamma_1 x_1 - \alpha_{21} x_2 = 0 \quad \dots (3.6b)$$

and

$$\beta_2 p_2(N) - \delta_2 - \gamma_2 x_2 - \alpha_{12} x_1 = 0. \quad \dots (3.6c)$$

Solving (3.6a) and (3.6b), we get

$$x_1 = \frac{\mu_1}{\mu_2} \quad \dots (3.7a)$$

and

$$x_2 = \frac{\mu_3}{\mu_2}, \quad \dots (3.7b)$$

where

$$\mu_1 = b_2 p_2(N) (\beta_1 p_1(N) - \delta_1) - \alpha_{21} Ng(N, K), \quad \dots (3.8a)$$

$$\mu_2 = \gamma_1 b_2 p_2(N) - \alpha_{21} b_1 p_1(N) \quad \dots (3.8b)$$

and
$$\mu_3 = \gamma_1 Ng(N, K) - b_1 p_1(N) (\beta_1 p_1(N) - \delta_1). \quad \dots (3.8c)$$

We note that $x_1 > 0$ if either

$$(i) \mu_1 > 0, \mu_2 > 0, \quad \dots (3.9a)$$

or
$$(ii) \mu_1 < 0, \mu_2 < 0, \quad \dots (3.9b)$$

hold.

Similarly, $x_2 > 0$ if either

$$(i) \mu_3 > 0, \mu_2 > 0, \quad \dots (3.10a)$$

or
$$(ii) \mu_3 < 0, \mu_2 < 0 \quad \dots (3.10b)$$

hold.

Substituting (3.7a) and (3.7b) into (3.6c) and taking

$$F(N) = \frac{1}{\gamma_1 b_2 p_2(N) - \alpha_{21} b_1 p_1(N)} \left[(\gamma_1 b_2 p_2(N) - \alpha_{21} b_1 p_1(N)) (\beta_2 p_2(N) - \delta_2) - (\gamma_1 \gamma_2 - \alpha_{12} \alpha_{21}) Ng(N, K) + (\beta_1 p_1(N) - \delta_1) (\gamma_2 b_1 p_1(N) - \alpha_{12} b_2 p_2(N)) \right] \dots (3.11)$$

we note that

$$F(0) = \frac{1}{\gamma_1 b_2 p_2'(0) - \alpha_{21} b_1 p_1'(0)} \left[(\gamma_1 b_2 p_2'(0) - \alpha_{21} b_1 p_1'(0)) (-\delta_2) - (\gamma_1 \gamma_2 - \alpha_{12} \alpha_{21}) g(0, K) + (\gamma_2 b_1 p_1'(0) - \alpha_{12} b_2 p_2'(0)) (-\delta_1) \right], \quad \dots (3.12a)$$

$$F(K) = \frac{1}{\gamma_1 b_2 p_2(K) - \alpha_{21} b_1 p_1(K)} \left[(\gamma_1 b_2 p_2(K) - \alpha_{21} b_1 p_1(K)) (\beta_2 p_2(K) - \delta_2) + (\gamma_2 b_1 p_1(K) - \alpha_{12} b_2 p_2(K)) (\beta_1 p_1(K) - \delta_1) \right] \quad \dots (3.12b)$$

and

$$F'(N) = \beta_2 p_2'(N) + \frac{\gamma_1 b_2 p_2'(N) - \alpha_{21} b_1 p_1'(N)}{(\gamma_1 b_2 p_2(N) - \alpha_{21} b_1 p_1(N))^2} [(\gamma_1 \gamma_2 - \alpha_{12} \alpha_{21}) Ng(N, K)$$

$$\begin{aligned}
 & - (\gamma_2 b_1 p_1(N) - \alpha_{12} b_2 p_2(N) (\beta_1 p_1(N) - \delta_1)] \\
 & \frac{1}{\gamma_1 b_2 p_2(N) - \alpha_{21} b_1 p_1(N)} \left[(\gamma_1 \gamma_2 - \alpha_{12} \alpha_{21}) \left(g(N, K) + N \frac{\partial g(N, K)}{\partial N} \right) \right. \\
 & - (\beta_1 p_1(N) - \delta_1) (\gamma_2 b_1 p_1'(N) - \alpha_{12} b_2 p_2'(N)) \\
 & \left. - \beta_1 p_1'(N) (\gamma_2 b_1 p_1(N) - \alpha_{12} b_2 p_2(N)) \right]. \quad \dots (3.12c)
 \end{aligned}$$

From (3.12) we note that $F(0)$, $F(K)$ and $F'(N)$ may be positive or negative. However, there exists a positive unique solution $N = N^*$ of (3.11) in the interval $0 < N^* < K$ such that $F(N^*) = 0$, if the following inequalities hold :

$$F(0) < 0, F(K) > 0, F'(N) > 0. \quad \dots (3.13)$$

Knowing the value of N^* , x_1^* and x_2^* can then be computed from (3.7a) and (3.7b) respectively. Thus the interior equilibrium E^* exists of (3.9), (3.10) and (3.13) hold.

Remark 2 : If we take the particular functions and values of the parameters as defined in eq. (2.5), then we note the following :

$$\begin{aligned}
 F(0) &= \delta_2 - \frac{\alpha_{12}}{b_1 \alpha_{21}} (\alpha_{21} r + b_2 \delta_1) < 0, \\
 F(K) &= (\beta_2 K - \delta_2) + \frac{b_2 \alpha_{12}}{b_1 \alpha_{21}} (\beta_1 K - \delta_1) > 0, \text{ for } \beta_i K > \delta_i, i = 1, 2
 \end{aligned}$$

and

$$F'(N) = \beta_2 + \frac{\alpha_{12}}{b_1 \alpha_{21}} \left(b_2 \beta_1 + \frac{\alpha_{21} r}{K} \right) > 0.$$

This shows that there exists a unique $N = N^*$ in the interval $0 < N^* < K$ such that $F(N^*) = 0$.

We also have

$$x_1^* = \frac{1}{b_1 \alpha_{21}} \left(\alpha_{21} r \left(1 - \frac{N^*}{K} \right) - b_2 (\beta_1 N^* - \delta_1) \right)$$

and

$$x_2^* = \frac{1}{\alpha_{21}} (\beta_1 N^* - \delta_1).$$

Thus, $x_1^* > 0$ and $x_2^* > 0$ if

$$\alpha_{21} r \left(1 - \frac{N^*}{K} \right) > b_2 (\beta_1 N^* - \delta_1) > 0.$$

The above results are similar to Hsu¹⁵.

Stability of Equilibria :

The local stability of the equilibria can be studied by computing variational matrices (Freedman⁴) corresponding to each equilibrium. From these matrices we note the following results:

1. $E_0(0, 0, 0)$ is a saddle point whose unstable manifold is locally in the N direction and stable manifold is locally in the $x_1 - x_2$ plane.

2. From Lemma 3.1, we note that if $\delta_i > \beta_i p_i(K)$, then no predator will survive. In such a case $E_1(K, 0, 0)$ is locally asymptotically stable. If $\delta_i < \beta_i p_i(K)$, then both predator will survive and $E_1(K, 0, 0)$ will be a saddle point with stable manifold locally in the N -direction and with unstable manifold locally in the $x_1 - x_2$ plane.

3. $E_2(\bar{N}, \bar{x}_1, 0)$ is locally asymptotically stable if

$$\beta_2 p_2(\bar{N}) - \delta_2 - \alpha_{12} \bar{x}_1 < 0 \text{ and } \bar{H} = g(\bar{N}, K) + \bar{N} \frac{\partial g(\bar{N}, K)}{\partial N} - b_1 \bar{x}_1 p_1'(\bar{N}) < 0.$$

4. $E_3(\tilde{N}, 0, \tilde{x}_2)$ is locally asymptotically stable if

$$\beta_1 p_1(\tilde{N}) - \delta_1 - \alpha_{21} \tilde{x}_2 < 0 \text{ and } \tilde{H} = g(\tilde{N}, K) + \tilde{N} \frac{\partial g(\tilde{N}, K)}{\partial N} - b_1 \tilde{x}_1 p_1'(\tilde{N}) < 0.$$

In the following theorems we are able to write down conditions for local stability and instability of E^* . The proofs of these theorems follow from Routh-Hurwitz criteria, and hence we omit them.

We first write the following notations:

$$A_1 = -H^* + \gamma_1 x_1^* + \gamma_2 x_2^*, \quad \dots (3.14a)$$

$$A_2 = -H^* (\gamma_1 x_1^* + \gamma_2 x_2^*) + (\gamma_1 \gamma_2 - \alpha_{12} \alpha_{21}) x_1^* x_2^* + b_1 \beta_1 x_1^* p_1(N^*) p_1'(N^*) \\ + b_2 \beta_2 x_2^* p_2(N^*) p_2'(N^*), \quad \dots (3.14b)$$

$$A_3 = -(\gamma_1 \gamma_2 - \alpha_{12} \alpha_{21}) H^* x_1^* x_2^* + \beta_2 p_2'(N^*) x_1^* x_2^* (\gamma_1 b_2 p_2(N^*) - \alpha_{21} b_1 p_1(N^*)) \\ + \beta_1 p_1'(N^*) x_1^* x_2^* (\gamma_2 b_1 p_1(N^*) - \alpha_{12} b_2 p_2(N^*)) \quad \dots (3.14c)$$

and

$$H^* = g(N^*, K) + N^* \frac{\partial g(N^*, K)}{\partial N} - b_1 x_1^* p_1'(N^*) - b_2 x_2^* p_2'(N^*). \quad \dots (3.14d)$$

Theorem 3.1 — Let $\gamma_1 = \gamma_2 = 0$. Then E^* is unstable.

This result is same as obtained by Hsu¹⁵.

Theorem 3.2 — *Let the following inequalities hold*

$$A_i > 0 \ (i = 1, 2, 3) \text{ and } A_1 A_2 - A_3 > 0. \quad \dots (3.15)$$

Then E^ is locally asymptotically stable.*

In the following theorem we show that E^* is globally asymptotically stable. We first state the following lemma which establishes a region of attraction for system (3.1). The proof of this lemma is easy and hence is omitted.

Lemma 3.2 — *The set*

$$\Omega = \left\{ (N, x_1, x_2) : 0 \leq N \leq K, 0 \leq x_i \leq \frac{1}{\gamma_i} (\beta p_i(K), -\delta_i), i = 1, 2 \right\}$$

is a region of attraction for all solutions initiating in the positive orthant.

Theorem 3.3 — *In addition to the assumptions (2.3)-(2.5), let $g(N, K)$, and $p(N)$ satisfy the following conditions in Ω*

$$G_m \leq -\frac{\partial g(N, K)}{\partial N} \leq G_M, \rho_i \leq p'_i(N) \leq \rho_{i+2}, i = 1, 2 \quad \dots (3.16)$$

for some positive constants $G_m, G_M, \rho_i, \rho_{i+2}$ ($i = 1, 2$).

If the following inequality holds

$$(c_2 \alpha_{12} + c_1 \alpha_{21})^2 < c_1 c_2 \gamma_1 \gamma_2, \quad \dots (3.17)$$

where

$$c_1 = \frac{b_1 p_1(N^*)}{\beta_1 \rho_3 N^*}, c_2 = \frac{b_2 p_2(N^*)}{\beta_1 \rho_3 N^*}, \quad \dots (3.18)$$

then E^* is globally asymptotically stable with respect to all solutions initiating in the positive orthant.

PROOF : We consider the following positive definite function around E^* ,

$$\begin{aligned} V(N, x_1, x_2) = & N - N^* - N^* \ln(N/N^*) + c_1(x_1 - x_1^* - x_1^* \ln(x_1/x_1^*)) \\ & + c_2(x_2 - x_2^* - x_2^* \ln(x_2/x_2^*)). \end{aligned} \quad \dots (3.19)$$

Differentiating V with respect to t along the solutions of (3.1) we get after some algebraic manipulations

$$\begin{aligned} \dot{V} \leq & -\lambda(N) (N - N^*)^2 - c_1 \gamma_1 (x_1 - x_1^*)^2 - c_2 \gamma_2 (x_2 - x_2^*)^2 \\ & + (c_1 \beta_1 \mu_1(N) - b_1 p_1(N^*)/N^*) (N - N^*) (x_1 - x_1^*) \\ & + (c_2 \beta_2 \mu_2(N) - b_2 p_2(N^*)/N^*) (N - N^*) (x_2 - x_2^*) \\ & + (c_2 \alpha_{12} + c_1 \alpha_{21}) (x_1 - x_1^*) (x_2 - x_2^*), \end{aligned} \quad \dots (3.20)$$

where

$$\lambda(N) = \begin{cases} -\left[\frac{g(N, K) - g(N^*, K)}{N - N^*} \right], & N \neq N^* \\ -\frac{\partial g(N^*, K)}{\partial N}, & N = N^* \end{cases}$$

and

$$\mu_i(N) = \begin{cases} \frac{p_i(N) - p_i(N^*)}{N - N^*}, & N \neq N^* \\ p_i'(N^*), & N = N^* \end{cases}$$

From (3.16) and the mean value theorem we note that,

$$G_m \leq |\lambda(N)| \leq G_M, \rho_i \leq |\mu_i(N)| \leq \rho_{i+2}, \quad i = 1, 2.$$

Now \dot{V} can further be written as the sum of quadratics,

$$\begin{aligned} \dot{V} \leq & -\frac{1}{2} a_{11} (N - N^*)^2 + a_{12} (N - N^*) (x_1 - x_1^*) - \frac{1}{2} a_{22} (x_1 - x_1^*)^2 \\ & - \frac{1}{2} a_{22} (x_1 - x_1^*)^2 + a_{23} (x_1 - x_1^*) (x_2 - x_2^*) - \frac{1}{2} a_{33} (x_2 - x_2^*)^2 \\ & - \frac{1}{2} a_{33} (x_2 - x_2^*)^2 + a_{31} (x_1 - x_1^*) (N - N^*) - \frac{1}{2} a_{11} (N - N^*)^2, \end{aligned} \quad \dots (3.21)$$

where

$$a_{11} = \lambda(N), \quad a_{22} = c_1 \gamma_1, \quad a_{33} = c_2 \gamma_2,$$

$$a_{12} = c_1 \beta_1 \mu_1(N) - b_1 p_1(N^*)/N^*,$$

$$a_{23} = (c_2 \alpha_{12} + c_1 \alpha_{21})$$

and

$$a_{31} = c_2 \beta_2 \mu_2(N) - b_2 p_2(N^*)/N^*.$$

Sufficient conditions for \dot{V} to be negative definite are that the following inequalities hold

$$a_{12}^2 < a_{11} a_{22}, \quad \dots (3.22a)$$

$$a_{23}^2 < a_{22} a_{33} \quad \dots (3.22b)$$

and

$$a_{31}^2 < a_{33} a_{11}. \quad \dots (3.22c)$$

By choosing c_1 and c_2 as defined in (3.18) we note that conditions (3.22a) and (3.22c) are automatically satisfied. Further, (3.17) \Rightarrow (3.22b). Thus, we conclude that \dot{V} is a Liapunov function with respect to E^* , whose domain contains the region Ω , proving the theorem.

4. MODEL WITH DIFFUSION

In this section we consider complete model (2.1)-(2.2). We note that $N=N^*, x_1=x_1^*, x_2=x_2^*$ are the uniform steady state for system (2.1)-(2.2). We wish to show that if E^* is asymptotically stable for system (3.1), then the corresponding uniform steady state is also asymptotically stable for system (2.1)-(2.2). Further, we will also show that by increasing diffusion coefficients to sufficiently large values an unstable equilibrium state can be stabilized. Now we prove it by considering the following Liapunov function,

$$W(t) = \int \int_R V(N(u, v, t), x_1(u, v, t), x_2(u, v, t)) dA, \tag{4.1}$$

where V is defined in eq. (3.19)

Now the time derivative of W along the solutions of (2.1)-(2.2) is given by

$$\begin{aligned} \dot{W}(t) &= \int \int_R \left(\frac{\partial V}{\partial N} \frac{\partial N}{\partial t} + \frac{\partial V}{\partial x_1} \frac{\partial x_1}{\partial t} + \frac{\partial V}{\partial x_2} \frac{\partial x_2}{\partial t} \right) dA \\ &= I_1 + I_2, \end{aligned} \tag{4.2}$$

where

$$I_1 = \int \int_R \dot{V}(N(u, v, t), x_1(u, v, t), x_2(u, v, t)) dA \tag{4.3}$$

and

$$I_2 = \int \int_R \left(D \frac{\partial V}{\partial N} \nabla^2 N + d_1 \frac{\partial V}{\partial x_1} \nabla^2 x_1 + d_2 \frac{\partial V}{\partial x_2} \nabla^2 x_2 \right) dA. \tag{4.4}$$

We first assume that \dot{V} does not change its sign in R .

We now note the following properties of V , namely —

1. $\frac{\partial V}{\partial N} \Big|_{\partial R} = \frac{\partial V}{\partial x_i} \Big|_{\partial R} = 0$ for all points of R ($i = 1, 2$). ... (4.5)

2. $\frac{\partial^2 V}{\partial N \partial x} = \frac{\partial^2 V}{\partial x_1 \partial x_2} = \frac{\partial^2 V}{\partial x_2 \partial N} = 0$ (4.6)

3. $\frac{\partial^2 V}{\partial N^2} > 0, \frac{\partial^2 V}{\partial x_i^2} > 0$ ($i = 1, 2$). ... (4.7)

From Green's first identity, we have

$$\begin{aligned} \int_R \int \frac{\partial V}{\partial N} \nabla^2 N \, dA &= \int_{\partial R} \frac{\partial V}{\partial N} \frac{\partial N}{\partial n} \, ds - \int_R \int \left[\nabla \left(\frac{\partial V}{\partial N} \right) \cdot \nabla N \right] \, dA \\ &= - \int_R \int \left[\nabla \left(\frac{\partial V}{\partial N} \right) \cdot \nabla N \right] \, dA, \text{ using (2.2).} \end{aligned} \quad \dots (4.8)$$

But we have

$$\nabla \left(\frac{\partial V}{\partial N} \right) = \frac{\partial^2 V}{\partial N^2} \frac{\partial N}{\partial u} \hat{i} + \frac{\partial^2 V}{\partial N^2} \frac{\partial N}{\partial v} \hat{j}.$$

Hence, (4.8) reduces to

$$\int_R \int \frac{\partial V}{\partial N} \nabla^2 N \, dA = - \int_R \int \frac{\partial^2 V}{\partial N^2} \left[\left(\frac{\partial N}{\partial u} \right)^2 + \left(\frac{\partial N}{\partial v} \right)^2 \right] \, dA \leq 0. \quad \dots (4.9a)$$

Similarly, we get

$$\int_R \int \frac{\partial V}{\partial x_i} \nabla^2 x_i \, dA = - \int_R \int \frac{\partial^2 V}{\partial x^2} \left[\left(\frac{\partial x_i}{\partial u} \right)^2 + \left(\frac{\partial x_i}{\partial v} \right)^2 \right] \, dA \leq 0. \quad \dots (4.9b)$$

This implies that $I_2 \leq 0, i = 1, 2$.

Thus from (4.2) we get

$$\begin{aligned} \dot{W}(t) &\leq \int_R \int \dot{\psi}(N(u, v, t), x_1(u, v, t), x_2(u, v, t)) \, dA \\ &\quad - \frac{DN^*}{K^2} \int_R \int \left[\left(\frac{\partial N}{\partial u} \right)^2 + \left(\frac{\partial N}{\partial v} \right)^2 \right] \, dA \\ &\quad - \sum_{i=1,2} \frac{d_i x_i^* \gamma_i^2}{(\beta p_i(K) - \delta_i)^2} \int_R \int \left[\left(\frac{\partial x_i}{\partial u} \right)^2 + \left(\frac{\partial x_i}{\partial v} \right)^2 \right] \, dA. \end{aligned} \quad \dots (4.10)$$

From (4.10) we note that if $\dot{\psi}$ is negative definite, then \dot{W} is also negative definite. This shows that if the equilibrium E^* of the model (3.1) is globally stable, then the corresponding uniform steady state E^* of the initial-boundary value problems (2.1)-(2.2) is also globally stable. Further, we also note that if $\dot{\psi}$ is positive definite, then by increasing D, d_1, d_2 to sufficiently large values, \dot{W} can be made negative definite. This implies that if the positive equilibrium E^* of the model with no diffusion is unstable, then the corresponding uniform steady state of the model with diffusion can be made stable by increasing diffusion coefficients to sufficiently large values.

Now we consider the region R to be rectangular habitat given by

$$R = \{(u, v) : 0 \leq u \leq a, 0 \leq v \leq b\}.$$

In this case, we note from (4.4) and (4.9) that I_2 can be written as

$$\begin{aligned} I_2 = & -D \int_0^b \int_0^a \frac{\partial^2 V}{\partial N^2} \left[\left(\frac{\partial(N-N^*)}{\partial u} \right)^2 + \left(\frac{\partial(N-N^*)}{\partial v} \right)^2 \right] du dv \\ & - d_1 \int_0^b \int_0^a \frac{\partial^2 V}{\partial x_1^2} \left[\left(\frac{\partial(x_1-x_1^*)}{\partial u} \right)^2 + \left(\frac{\partial(x_1-x_1^*)}{\partial v} \right)^2 \right] du dv \\ & - d_2 \int_0^b \int_0^a \frac{\partial^2 V}{\partial x_2^2} \left[\left(\frac{\partial(x_2-x_2^*)}{\partial u} \right)^2 + \left(\frac{\partial(x_2-x_2^*)}{\partial v} \right)^2 \right] du dv. \end{aligned} \quad \dots (4.11)$$

Letting $z = u/a$ we get

$$\int_0^b \int_0^a \left(\frac{\partial(N-N^*)}{\partial u} \right)^2 du dv = \frac{1}{a} \int_0^b \int_0^1 \left(\frac{\partial(N-N^*)}{\partial z} \right)^2 dz dv.$$

Now utilizing the known inequality (see Denn³, p. 225)

$$\int_0^1 \left(\frac{\partial x}{\partial u} \right)^2 du \geq \pi^2 \int_0^1 x^2 du,$$

in (4.11), we get

$$\begin{aligned} \int_0^b \int_0^a \left(\frac{\partial(N-N^*)}{\partial u} \right)^2 du dv & \geq \frac{\pi^2}{a} \int_0^b \int_0^a (N-N^*)^2 dz dv \\ & = \frac{\pi^2}{a^2} \int \int_R (N-N^*)^2 dA. \end{aligned} \quad \dots (4.12)$$

Similarly

$$\int_0^b \int_0^a \left(\frac{\partial(N-N^*)}{\partial v} \right)^2 du dv \geq \frac{\pi^2}{b^2} \int \int_R (N-N^*)^2 dA. \quad \dots (4.13)$$

Thus, $\dot{W} = I_1 + I_2$ can be estimated as,

$$\dot{W} \leq \int \int_R \dot{V} dA - \left[\frac{(a^2 + b^2)\pi^2}{a^2 b^2} \left(\frac{DN^*}{K^2} (N - N^*)^2 + \frac{c_1 d_1 x_1^* \gamma_1}{(\beta_1 p_1(K) - \delta_1)^2} (x_1 - x_1^*)^2 + \frac{c_2 d_2 x_2^* \gamma_2}{(\beta_2 p_2(K) - \delta_2)^2} (x_2 - x_2^*)^2 \right) \right] dA. \quad \dots (4.14)$$

From (4.14) we note that if \dot{V} is positive definite, then by increasing diffusion coefficients D, d_1, d_2 to sufficiently large values \dot{W} can be made a negative definite. Thus an unstable equilibrium can be made stable by increasing diffusion coefficients appropriately.

Remark 3 : From Theorem 3.1, we note that if $\gamma_1 = 0 = \gamma_2$, then the interior equilibrium E^* of model (3.1) is unstable. Then from (4.10) and (4.14) we note that, sufficiently rapid diffusion by the prey species will stabilize the unstable equilibrium E^* .

5. SIMULATION ANALYSIS

In this section, a numerical example is presented to explain the applicability of the results discussed above. We take the following particular form of the functions $g(N, K), p_1(N)$ and $p_2(N)$ in model (3.1):

$$g(N, K) = r(1 - N/K), p_1(N) = N = p_2(N). \quad \dots (5.1)$$

We choose the following values of the various parameters in model (3.1) and in eq. (5.1),

$$r = 35.0, b_1 = 2.0, b_2 = 1.8, K = 60.0,$$

$$\beta_1 = 1.0, \delta_1 = 1.5, \gamma_1 = 5.0, \alpha_{21} = 1.5,$$

$$\beta_2 = 1.05, \delta_2 = 0.6, \gamma_2 = 3.5, \alpha_{12} = 1.8.$$

With the above set of values of parameters, it can be seen that the conditions (3.9), (3.10) and (3.13) for the existence of the interior equilibrium E^* are satisfied, and E^* is given by

$$N^* = 28.20468, x_1^* = 3.37458, x_2^* = 6.55450.$$

It can also be checked that the conditions (3.15) in Theorem 3.2 are satisfied. This shows that E^* is locally asymptotically stable.

It can also be verified that condition (3.17) in Theorem 3.3 is satisfied which shows that E^* is globally asymptotically stable.

6. SUMMARY

In this paper, a mathematical model has been considered to study the growth and survival of two predator species competing for a single limited prey in a diffusive system. The growth rates of the

interacting populations are assumed to be nonlinear and the dynamics of the system is of Gause-type. In the absence of diffusion, criteria for local stability, instability and global stability have been obtained. It has been shown that the intraspecific interference coefficients of the competing predators play a crucial role in stabilizing the interior equilibrium of the system. If the intraspecific interference coefficients of the competing predators are zero, then interior equilibrium becomes unstable. In the case of diffusion it has been shown that if the interior equilibrium E^* of model (3.1) is asymptotically stable, then the uniform steady state E^* of system (2.1)-(2.2) must be asymptotically stable. It has also been noted that when the interior equilibrium E^* of model (3.1) is unstable, then the uniform steady state E^* of system (2.1)-(2.2) can be made stable by increasing diffusion coefficients appropriately under certain conditions. Thus it has been concluded that the solutions of the model with diffusion approach to its equilibrium faster than the case of no diffusion.

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