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MATHEMATICAL MODEL OF POPULATION INTERACTIONS WITH DISPERSAL: STABILITY OF TWO HABITATS WITH A PREDATOR

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A system of differential equations of dispersion between two populations in habitats separated by a barrier with a predator feeding indiscriminately on these populations is considered. A region in the $\epsilon_1 - \epsilon_2$ plane where equilibrium points exist, is studied. The stability properties of these equilibrium points are investigated.

1. INDRODUCTION

The subject of the effect of dispersal of populations is a topic of considerable ecological interest[1-4]. Holt[4] has considered a two patch model and a migrating predator from an optimal habitat selection point of view. Hasting[3] focused on spatial diffusion but also had a two patch model and showed the stabilizing effect of high dispersal rates.

The view of the problem taken in this paper, as in Freedman and Waltman[1] and Freedman *et al.*[2], is that "pressure" to disperse is given as a (monotone increasing) function of population size but that dispersal is inhibited by the difficulty of leaving the habitat which we, in turn, think of as surmounting a "barrier". It turns out that the more reasonable parameter is inverse barrier strength. This view appeared in Freedman and Waltman[1]. When this (vector) parameter is zero, dispersal is impossible (the barrier is infinite) and each population grows to its carrying capacity.

By the implicit function theorem, Freedman and Waltman[1] showed that, for small values of this parameter, the equilibrium was continuous and they approximated this equilibrium as an expansion in the parameter. This was done in Freedman and Waltman[1] for two habitats and a common barrier strength.

Freedman *et al.*[2] discussed both the two habitats and n-habitats cases each permitted to have a different level of difficulty in its "escape" barrier. In addition, once the population has left its present habitat it may not successfully reach a new one (predation harvesting, or for other reasons). In the analysis, by Freedman *et al.*[2] they regarded the probability of a successful transition between habitats as given and analyzed the question of the existence of the equilibrium as a function of the inverse barrier strength. Under reasonable biological hypotheses and one technical hypothesis, they determined the region exactly for two habitats and, in general case of n habitats.

2. The Model and Equilibria

In this section we shall consider the case where a population is able to disperse among 2-different habitats at some cost to the population in the sense that the probability of survival during a change of habitat may be less than one. This situation is described by a system of two prey and one predator of the form

$$\left.\begin{aligned} x_1' &= \alpha_1 x_1\left(1 - \frac{x_1}{k_1}\right) - \beta_1 x_1 y - \epsilon_1 x_1 + \epsilon_2 p_{21} x_2 \\ x_2' &= \alpha_2 x_2\left(1 - \frac{x_2}{k_1}\right) - \beta_2 x_2 y - \epsilon_2 x_2 + \epsilon_1 p_{12} x_1 \\ y' &= y(-\gamma + \delta_1 x_1 + \delta_2 x_2) \end{aligned}\right\} \quad \ldots(2.1)$$

with $p_{12} + p_{21} \leqslant 1$ and $x_i(0) > 0$, $i = 1, 2$ and $y(0) > 0$.

x_i represents the same population (prey) in the two different habitats; y is a predator feeding indiscriminately on the two prey x_1 and x_2; β_1 and β_2 measure the feeding rates of the predator on the two prey x_1 and x_2 respectively; γ is the death rate of the predator; δ_1 and δ_2 the conversion rates of prey to predator; ϵ_1 and ϵ_2 not necessarily small, but positive and represent inverse barrier strength in going out of the first habitat and the second habitat; and p_{ij} is the probability of successful transition from ith habitat to jth habitat (where $i \neq j$).

System (2.1) has been discussed by Freedman and Waltman[1] in the special case $p_{12} = p_{21} = 1$ and $\epsilon_1 = \epsilon_2 = \epsilon$ (the case of a common barrier strength) and for sufficiently small positive ϵ (the case of strong barrier). In our paper ϵ_1 and ϵ_2 are positive but not necessarily small. We seek to find the region in the $\epsilon_1 - \epsilon_2$ plane where an interior equilibrium exists and to determine its stability properties. Also, the system (2.1) is discussed by Freedman *et al.*[2] in general case but without predator.

Let $E^*(\epsilon_1, \epsilon_2) \equiv (x_1^*(\epsilon_1, \epsilon_2), x_2^*(\epsilon_1, \epsilon_2), y^*(\epsilon_1, \epsilon_2))$ denote an equilibrium point in positive octant, if it exists. Then, we have the following theorems:

Theorem 2.1—$E^*(0, 0)$ exists if:

$$\left.\begin{aligned} &-\frac{\alpha_2 \gamma}{\beta_2 \delta_2 k_2} < \frac{\alpha_1}{\beta_1} - \frac{\alpha_2}{\beta_2} < \frac{1}{\beta_1 \delta_1 k_1} \\ \text{and}\quad &\delta_1 k_1 + \delta_2 k_2 > \gamma \end{aligned}\right\} \quad \ldots(2.2)$$

where

$$\left.\begin{aligned} x_1^*(0,0) &= \frac{k_1(\alpha_1 \beta_2 \delta_2 k_2 - \alpha_2 \beta_1 \delta_2 k_2 + \alpha_2 \beta_1 \gamma)}{\alpha_1 \beta_2 \delta_2 k_2 + \alpha_2 \beta_1 \delta_1 k_1}, \\ x_2^*(0,0) &= \frac{k_2(\alpha_2 \beta_1 \delta_1 k_1 - \alpha_1 \beta_2 \delta_1 k_1 + \alpha_1 \beta_2 \gamma)}{\alpha_1 \beta_2 \delta_2 k_2 + \alpha_2 \beta_1 \delta_1 k_1}, \\ y^*(0,0) &= \frac{\alpha_1 \alpha_2 (\delta_1 k_1 + \delta_2 k_2 - \gamma)}{\alpha_1 \beta_2 \delta_2 k_2 + \alpha_2 \beta_1 \delta_1 k_1}. \end{aligned}\right\} \quad \ldots(2.3)$$

Theorem 2.2—(a) E^* $(0, \epsilon_2)$ exists if :

and

$$\left.\begin{aligned} &\frac{\beta_1 \delta_1 k_1}{\beta_2 \delta_2 k_2} < \frac{\alpha_1}{\alpha_2}\left[\frac{\delta_1 k_1}{\gamma} - 1\right] \\ &0 < \epsilon_2 < \beta_2\left[\frac{\alpha_2}{\beta_2} - \frac{\alpha_1}{\beta_1} + \frac{\alpha_1 \gamma}{\beta_1 \delta_1 k_1}\right] \end{aligned}\right\} \qquad \text{...(2 4)}$$

(b) E^* $(\epsilon_1, 0)$ exists if :

and

$$\left.\begin{aligned} &\frac{\beta_2 \delta_2 k_2}{\beta_1 \delta_1 k_1} < \frac{\alpha_2}{\alpha_1}\left[\frac{\delta_2 k_2}{\gamma} - 1\right] \\ &0 < \epsilon_1 < \beta_1\left[\frac{\alpha_1}{\beta_1} - \frac{\alpha_2}{\beta^2} + \frac{\alpha_2 \gamma}{\beta_2 \delta_2 k_2}\right] \end{aligned}\right\}. \qquad \text{...(2.5)}$$

Theorem 2.3— E^* (ϵ_1, ϵ_2) exists if either

$$0 < \epsilon_1 < \alpha_1\left(1 - \frac{\gamma}{\delta_1 k_1}\right) \text{ or } 0 < \epsilon_2 < \alpha_2\left(1 - \frac{\gamma}{\delta_2 k_2}\right). \qquad \text{...(2.6)}$$

Proof of Thorem 2.1—Theorem 2.1 is stated in Freedman and Waltman[1] and its proof is a routine algebraic manipulation for solution of the algebraic system

$$\left.\begin{aligned} &\alpha_1 x_1\left(1 - \frac{x_1}{k_1}\right) - \beta_1 x_1 y = 0 \\ &\alpha_2 x_2\left(1 - \frac{x_2}{k_2}\right) - \beta_2 x_2 y = 0 \\ &\delta_1 x_1 + \delta_2 x_2 = \gamma. \end{aligned}\right\} \qquad \text{...(2.7)}$$

Proof of Theorem 2.2 : At $\epsilon_1 = 0$, equilibria are solutions of following system of equations :

$$\left.\begin{aligned} &\alpha_1 x_1\left(1 - \frac{x_1}{k_1}\right) - \beta_1 x_1 y + \epsilon_2 p_{21} x_2 = 0 \\ &\alpha_2\left(1 - \frac{x_2}{k_2}\right) - \beta_2 y - \epsilon_2 = 0 \\ &\delta_1 x_1 + \delta_2 x_2 = \gamma. \end{aligned}\right\} \qquad \text{...(2.8)}$$

From the second equation, we have

$$\beta_2 y = \alpha_2 - \epsilon_2 - \frac{\alpha_2 x_2}{k_2} \qquad \text{...(2.9)}$$

and from the third equation, we have

$$x_1 = \frac{\gamma - \delta_2 x_2}{\delta_1}. \qquad \text{...(2.10)}$$

Substituting x_1 and y in the first equation yields :

$$-\alpha_1 \beta_2 k_2 (\gamma - \delta_2 x_2)(\delta_1 k_1 - \gamma + \delta_2 x_2) + \beta_1 \delta_1 k_1 (\gamma - \delta_2 x_2)$$

$$[(\alpha_2 - \epsilon_2) k_2 - \alpha_2 x_2] - \beta_2 k_1 k_2 \delta_1^2 p_{21} \epsilon_2 x_2 = 0,$$

this takes the form

$$a x_2^2 + b x_2 + c = 0$$

where

$$a = [\alpha_1 \beta_2 \delta_2 k_2 + \alpha_2 \beta_1 \delta_1 k_1] \delta_2$$

$$-b = \gamma [\alpha_1 \beta_2 \delta_2 k_2 + \alpha_2 \beta_1 \delta_1 k_1] + \delta_2 k_2 [\alpha_2 \beta_1 \delta_1 k_1 - \alpha_1 \beta_2 \delta_1 k_1 + \alpha_1 \beta_2 \gamma] + \delta_1 k_1 k_2 \epsilon_2 [\beta_2 \delta_1 p_{21} - \beta_1 \delta_2]$$

and

$$c = [\alpha_2 \beta_1 - \alpha_1 \beta_2] \delta_1 k_1 k_2 \gamma + \alpha_1 \beta_2 k_2 \gamma^2 - \beta_1 k_1 k_2 \delta_1 \gamma \epsilon_2.$$

From (2.10) for $x_1 > 0$ must be $x_2 < \gamma/\delta_2$.

Let $f(x_2) \equiv a x_2^2 + b x_2 + c$, then

$$f\left(\frac{\gamma}{\delta_2}\right) = \frac{\gamma^2}{\delta_2^2} a + \frac{\gamma}{\delta_2} b + c.$$

Substituting and simplifying we get

$$f\left(\frac{\gamma}{\delta_2}\right) = -\frac{\beta_2 \delta_1^2 k_1 k_2 p_{21} \epsilon_2}{\delta_2} < 0.$$

And $\quad f(0) = c$. Thus $0 < x_2 < \gamma/\delta_2$. ...(2.11)

If $c > 0$, that is if

$$\epsilon_2 < \beta_2 \left(\frac{\alpha_2}{\beta_2} - \frac{\alpha_1}{\beta_1} + \frac{\alpha_1 \gamma}{\beta_1 \delta_1 k_1} \right). \qquad \text{...(2.12)}$$

From (2.9), we have

$$\beta_2 k_2 y = (\alpha_2 - \epsilon_2) k_2 - \alpha_2 x_2$$

$$> (\alpha_2 - \epsilon_2) k_2 - \frac{\alpha_2 \gamma}{\delta_2} \text{ by (2.11)}$$

$$> \alpha_2 k_2 - \frac{\alpha_2 \gamma}{\delta_2} - \beta_2 k_2 \left(\frac{\alpha_2}{\beta_2} - \frac{\alpha_1}{\beta_1} + \frac{\alpha_1 \gamma}{\beta_1 \delta_1 k_1} \right)$$

$$= \frac{\alpha_1 \beta_2 k_2}{\beta_1} - \frac{\alpha_1 \beta_2 k_2 \gamma}{\beta_1 \delta_1 k_1} - \frac{\alpha_2 \gamma}{\delta_2}.$$

Thus, for $y > 0$, must be

$$\frac{\alpha_1}{\beta_1} > \gamma \left[\frac{\alpha_1}{\beta_1 \delta_1 k_1} + \frac{\alpha_2}{\beta_2 \delta_2 k_2} \right]$$

or

$$\frac{\beta_1 \delta_1 k_1}{\beta_2 \delta_2 k_2} < \frac{\alpha_1}{\alpha_2} \left[\frac{\delta_1 k_1}{\gamma} - 1 \right].$$

This completes the proof of (a), and the proof of (b) is analogus.

Proof of *Theorem* 2.3

This is the case where $\epsilon_1 > 0$ and $\epsilon_2 > 0$. Equilibria are solutions of the following system of equations:

$$\left.\begin{aligned} &\alpha_1 x_1 \left(1 - \frac{x_1}{k_1}\right) - \epsilon_1 x_1 + \epsilon_2 p_{21} x_2 = \beta_1 x_1 y \\ &\alpha_2 x_2 \left(1 - \frac{x_2}{k_2}\right) - \epsilon_2 x_2 + \epsilon_1 p_{12} x_1 = \beta_2 x_2 y \\ &\delta_1 x_1 + \delta_2 x_2 = \gamma. \end{aligned}\right\} \quad \ldots(2.13)$$

Substituting the second and the third equations in the first equation of system (2.13) and simplifying we have

$$\beta_2 x_2 \left[\frac{\alpha_1}{\delta_1} (-\gamma \delta_2 x_2) - \frac{\alpha_1}{\delta_1^2 k_1} (\gamma - \delta_2 x_2)^2 - \frac{\epsilon_1}{\delta_1} (\gamma - \delta_2 x_2) \right.$$

$$\left. + \epsilon_2 p_{21} x_2 \right] = \frac{\alpha_2 \beta_1}{\delta_1 k_2} x_2 [k_2 - x_2] [\gamma - \delta_2 x_2] - \frac{\epsilon_2 \beta_1}{\delta_1} x_2$$

$$(\gamma - \delta_2 x_2) + \frac{\epsilon_1 \beta_1 p_{12}}{\delta_1^2} (\gamma - \delta_2 x_2)^2.$$

After simplification, we get the form

$$a x_2^3 + b x_2^2 + c x_2 + D = 0$$

where

$$a = \frac{\alpha_1 \beta_2 \delta_2}{k_1} + \frac{\alpha_2 \beta_1 \delta_1}{k_2}$$

$$b = \alpha_1 \beta_2 \delta_1 + \beta_1 \delta_1 \epsilon_2 + \beta_1 \delta_2 p_{12} \epsilon_1 - \beta_2 \delta_1 \epsilon_1 - \alpha_2 \beta_1 \delta_1$$

$$- \frac{2\alpha_1 \beta_2 \gamma}{k_1} - \frac{\alpha_2 \beta_1 \delta_1 \gamma}{\delta_2 k_2} - \frac{\beta_2 \delta_1^2 p_{21} \epsilon_2}{\delta_2}$$

$$c = -\frac{\alpha_1 \beta_2 \delta_1 \gamma}{\delta_2} + \frac{\alpha_2 \beta_1 \delta_1 \gamma}{\delta_2} + \frac{\beta_2 \delta_1 \gamma \epsilon_1}{\delta_2} + \frac{\alpha_1 \beta_2 \gamma^2}{\delta_2 k_1} - \frac{\beta_1 \delta_1 \gamma \epsilon_2}{\delta_2} - 2\beta_1 \gamma p_{12} \epsilon_1$$

and

$$D = \frac{\beta_1 \gamma^2 p_{12} \epsilon_1}{\delta_2}.$$

Let

$$f(x_2) \equiv a x_2^3 + b x_2^2 + c x_2 + D.$$

Then, we have :

$$f(0) = D > 0$$

and

$$f\left(\frac{\gamma}{\delta_2}\right) = \frac{\gamma^3}{\delta_2^3} a + \frac{\gamma^2}{\delta_2^2} b + \frac{\gamma}{\delta_2} c + D.$$

Substituting and simplifying, we have

$$f\left(\frac{\gamma}{\delta_2}\right) = -\frac{\beta_2 \delta_1^2 \gamma^2 p_{21} \epsilon_2}{\delta_2^3} < 0.$$

Then, $0 < x_2 < \gamma/\delta_2$. Similarly, $0 < x_1 < \gamma/\delta_1$.

From the second equation of system (2.13), we have :

$$\begin{aligned} \beta_2 x_2 y &= \left[\alpha_2 - \epsilon_2 - \frac{\alpha_2}{k_2} x_2\right] x_2 + \frac{\gamma p_{12} \epsilon_1}{\delta_1} - \frac{\delta_2 p_{12} \epsilon_1}{\delta_1} x_2 \\ &> \left[\alpha_2 - \epsilon_2 - \frac{\alpha_2 \gamma}{\delta_2 k_2}\right] x_2 + \frac{\gamma p_{12} \epsilon_1}{\delta_1} - \frac{\delta_2 p_{12} \epsilon_1}{\delta_1} \frac{\gamma}{\delta_2} \\ &= \left[\alpha_2 - \epsilon_2 - \frac{\alpha_2 \gamma}{\delta_2 k_2}\right] x_2. \end{aligned}$$

Then, $\beta_2 y > \alpha_2 - \epsilon_2 - \frac{\alpha_2 \gamma}{\delta_2 k_2}$. Thus, for $y > 0$, must be

$$\epsilon_2 < \alpha_2 \left[1 - \frac{\gamma}{\delta_2 k_2}\right].$$

Similarly, $\epsilon_1 > \alpha_1 \left[1 - \frac{\gamma}{\delta_1 k_1}\right]$. This completes the proof of Theorem 2.3.

3. Stability

Having established the existence of an equilibrium $E^*(\epsilon_1, \epsilon_2)$, we proceed to examine its stability properties. In fact we have the following theorems :

Theorem 3.1—$E^*(0,0)$ is asymptotically stable.

Theorem 3.2—(a) $E^*(0, \epsilon_2)$ is asymptotically stable if $\beta_1 \geqslant \beta_2$:

(b) $E^*(\epsilon_1, 0)$ is asymptotically stable If $\beta_2 > \beta_1$.

Theorem 3.3—$E^*(\epsilon_1, \epsilon_2)$ is asymptotically stable if $\beta_1 = \beta_2$.

Proof : The first step is to compute the variational matrix of $E^*(\epsilon_1, \epsilon_2)$, which takes the form

$$V(\epsilon_1, \epsilon_2) = \begin{bmatrix} \alpha_1\left(1 - \frac{x_1}{k_1}\right) - \beta_1 y - \epsilon_1 - \frac{\alpha_1 x_1}{k_1} & \epsilon_2 p_{21} & -\beta_1 x_1 \\ \epsilon_1 p_{12} & \alpha_2(1-(x_2/k_2)) - \beta_2 y - \epsilon_2 - \frac{\alpha_2 x_2}{k_2} & -\beta_2 x_2 \\ \delta_1 y & \delta_2 y & 0 \end{bmatrix} \quad \ldots(3.1)$$

Making use of the system (2.13), the variational matrix takes the form

$$V(\epsilon_1, \epsilon_2) = \begin{bmatrix} -\epsilon_2 p_{21}\frac{x_2}{x_1} - \frac{\alpha_1 x_1}{k_1} & \epsilon_2 p_{21} & -\beta_1 x_1 \\ \epsilon_1 p_{12} & -\epsilon_1 p_{12}\frac{x_1}{x_2} - \frac{\alpha_2 x_2}{k_2} & -\beta_2 x_2 \\ \delta_1 y & \delta_2 y & 0 \end{bmatrix} \quad \ldots(3.2)$$

The corresponding characteristic equation is given by

$$\left[\lambda + \frac{\alpha_1 x_1}{k_1} + \epsilon_2 p_{21}\frac{x_2}{x_1}\right]\left[\lambda\left(\lambda + \frac{\alpha_2 x_2}{k_2} + \epsilon_1 p_{12}\frac{x_1}{x_2}\right) + \beta_2\delta_2 x_2 y\right]$$

$$- \epsilon_1 p_{12}[\epsilon_2 p_{21}\lambda - \beta_1\delta_2 x_1 y] + \delta_1 y\Big[\epsilon_2 p_{21}\beta_2 x_2 + \beta_1 x_1$$

$$\times\left(\lambda + \frac{\alpha_2 x_2}{k_2} + \epsilon_1 p_{12}\frac{x_1}{x_2}\right)\Big] = 0. \qquad (3.3)$$

Equation (3.3) can be written in the form

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$$

where

$$a_1 = \frac{\alpha_1 x_1}{k_1} + \frac{\alpha_2 x_2}{k_2} + \epsilon_1 p_{12}\frac{x_1}{x_2} + \epsilon_2 p_{12}\frac{x_2}{x_1}$$

$$a_2 = \frac{\alpha_1\alpha_2 x_1 x_2}{k_1 k_2} + \beta_1\delta_1 x_1 y + \beta_2\delta_2 x_2 y + \frac{\epsilon_1\alpha_1 p_{12} x_1^2}{k_1 x_2}$$

(*equation continued on p.* 212)

$$+ \frac{\epsilon_2 \alpha_2 p_{21} x_2^2}{k_2 x_1}.$$

and

$$a_3 = \beta_1 \delta_1 x_1 y \left[\frac{\alpha_2 x_2}{k_2} + \epsilon_1 p_{12} \frac{x_1}{x} \right] + \beta_2 \delta_2 x_2 y \left[\frac{\alpha_1 x_1}{k_1} + \epsilon_2 p_{12} \frac{x_2}{x_1} \right] + \epsilon_1 \beta_1 \delta_2 p_{12} x_1 y + \epsilon_2 \beta_2 \delta_1 p_{21} x_2 y.$$

Since both a_1 and a_3 are positive, then utilizing the Rough-Hurwize criteria, we get $E^* (\epsilon_1, \epsilon_2)$ is asymptotically stable if $a_1 a_2 - a_3 > 0$. After simplification we have:

$$a_1 a_2 - a_3 = a_1 \left[\frac{\alpha_1 \alpha_2 x_1 x_2}{k_1 k_2} + \frac{\epsilon_1 \alpha_1 p_{12} x_1^2}{k_1 x_2} + \frac{\epsilon_2 \alpha_2 p_{21} x_2^2}{k_2 x_1} \right] + \delta_1 y \left[\frac{\alpha_1 \beta_1 x_1^2}{k_2} + (\beta_1 - \beta_2) \epsilon_2 p_{21} x_2 \right] + \delta_2 y \left[\frac{\alpha_2 \beta_2 x_2^2}{k_2} + (\beta_2 - \beta_1) \epsilon_1 p_{12} x_1 \right]. \qquad \ldots(3.4)$$

From (3.4), it is clear that if $\epsilon_1 = \epsilon_2 = 0$, then $a_1 a_2 = a_3 > 0$ and hence $E^* (0, 0)$ is asymptotically stable. This proves Theorem 3.1.

Also $a_1 a_2 - a_3 > 0$ if $\epsilon_1 = 0$ and $\beta_1 \geqslant \beta_2$ or $\epsilon_2 = 0$ and $\beta_2 \geqslant \beta_1$ This proves Theorem 3.2.

Finally, $a_1 a_2 - a_2 > 0$ if $\beta_1 = \beta_2$ for every positive values of ϵ_1 and ϵ_2 and this proves Theorem 3.3.

Corollary —From the proofs of Theorems 2.3 & 3.3 it is easy to deduce the ultimate sizes of the two populations when $E^* (\epsilon_1, \epsilon_2)$ is asymptotically stable; for the prey x_i $(i = 1, 2)$ must be $0 < x_i < \gamma/\delta_i$ where $\delta_1 x_1 + \delta_2 x_2 = \gamma$ that is x_1, x_2 belong to the open straight line segment AB where A $(\gamma/\delta_{1,0})$ and $B(0, \gamma/\delta_2)$ Finally, for the predator y must be

$$y > \frac{1}{\beta} \max \left(\alpha_1 \epsilon_1 - \frac{\alpha_1 \gamma}{\gamma_1 k_1}, \alpha_2 - \epsilon_2 - \frac{\alpha_2 \gamma}{\delta_2 k_2} \right)$$

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