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An analytic and numerical study of a population density-dependent migration of a predator-prey system

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Abstract

We formulate a population-density-dependent migration of a predator and prey between two patches. The migration is influenced by prey and predator densities such that when the predator population is huge, the migration of prey population is more likely to occur. We also assume that migration is dependent on factors other than predation. Each patch display a limit cycle behaviour of the predator and prey interaction. Migration is on a fast timescale as compared to the inter-species interaction within a patch, thus we reduce the system from four ordinary differential equation to two by aggregation. Furthermore, we non-dimensionalize the aggregated model to reduce the number of parameters for ease of analysis. The analysis of the aggregated model shows three fixed points. Two are unstable, the third where there is co-existence of both species, its instability or stability is parameterdependent. For some certain parameter values, we get a limit cycle. This limit cycle is a synchronous state, that is observable in both patches.

Key words: *Aggregation; Non-dimensionalization; Limit cycle; Synchronization*

Mathematics Subject classification(2020): 34D25, 34D20, 37N25.

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I. Introduction

The classical predator-prey models for instance lotka-volterra is used to describe the dynamics of homogeneous environment. However, in some instances the environment is heterogeneous and may be divided by barriers such as rivers, mountains e.t.c., forming patches in the ecosystem. This phenomena requires representation using discrete patches connected by migration [7, 12, 8, 6]. The density-dependent migration is a common phenomenon in a two-patch system because of the constant migration of the predator and prey populations. The migration happens when species move from one patch to another either in search of food resources or due to predation. In this study, the prey migration is based on the quality of the patch resources and predation. This is dictated by the availability of food, water, mates e.t.c. The predator movement is determined by the presence of the prey in each patch. Predator-prey models that include spatial heterogeneity and dispersal have been widely used to the persistence and oscillatory dynamics of populations see [1, 6, 9, 5, 11, 12]. Apima et al.[1] proposed a two-patch predator-prey framework that incorporates logistic growth of the prey and 1 a constant time delay in the migration. Their model captures the influence of migration timing on the stability of species interaction, with the prey exhibiting logistic growth and predation represented through nonlinear functional responses. The delayed migration terms reflect the ecological reality that dispersal is rarely instantaneous, accounting for lags due to search-time or environmental barriers. A limitation of this study, however, lies in the assumption that the prey's carrying capacity is identical in both patches. In real ecosystems, patch environments differ significantly in terms of resources, vegetation and habitat structure, making uniform carrying capacity an oversimplication. Another limitation of constant time-delaymigration models is their inability to reflect adaptive dispersal behaviours. In nature, species movement often depends on local densities, resource availability, or predation pressure, rather than fixed delays alone. This makes it realistic and ecologically meaningful to study predator-prey interactions under density-dependent migration in a two-patch system. Density-dependent dispersal allows individual to migrate in response to local crowding, prey availability, or predator risk, thereby offering a more dynamic mechanism of population regulation. Investigating such mechanism provides insights into how species persist across heterogeneous landscape, how cycle emerges or stabilizes, and how migration strategies influence coexistence in fragmented habitats. This is the realistic and a common phenomenon in the ecosystem. We will study population densitydependent migration of a predator-prey system in two patches.

II. Formulation of the Model

A predator-prey density-dependent predator-prey model incorporating migration and interaction takes the following form:

$$\begin{aligned}\frac{dn_i}{d\tau} &= M(p_j,p_i,n_i,n_j)+\varepsilon n_i[r(1-\frac{n_i}{K_i})-\frac{\kappa p_i}{n_i+D}],\\ \frac{dp_i}{d\tau} &= K(p_j,p_i)+\varepsilon p_i[s(1-\frac{hp_i}{n_i})],\ \ i,j=1,2,\end{aligned} \tag{1}$$

where $M(p_j,p_i,n_i,n_j) := m(p_j)n_j - m(p_i)n_i$ and $K(p_j,p_i) := k(p_j-p_i)$, with $m(p_i)=\alpha p_i+\alpha_0$. The constants α and α_0 denote the prey migration induced by the predator attack and the quality of the carrying capacity in addition to other resources respectively. The $n_i := n_i(t)$ and $p_i := p_i(t)$ represent the prey and predator densities in patch i respectively at time t. The parameters r and s represent the prey and predator intrinsic growth rates respectively. The environmental carrying capacity of the prey in patch i is denoted by K_i. The parameter κ is the rate at which the prey is captured by the predator while D is a predation parameter. Mortality rate of the predator population is represented by h. Over the fast time scale $\tau=\frac{t}{\varepsilon}$(where t represents the slow time scale and the expression ε is a dimensionless parameter).
Schematically, the migration of the two species between the patches can be represented by Figure 1. From Figure 1, n_i and p_i represents the prey and predator population in patch i while $m(p_i)$ denote the rate of migration of prey induced by the predator p_i and the parameter k represents the rate of migration of predator species.

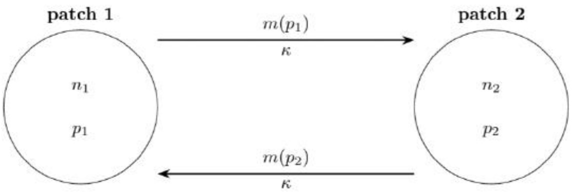

Figure 1: Movement of two species between two patches

III. Aggregation and Non-dimensionalization

For ease of analysis of Equation (1), we reduce the Ordinary Differential Equation (ODE) from a system of four to a system of two equations. This is done by building an aggregated model.

$$\begin{aligned}\frac{dn_1}{d\tau} &= m(p_2)n_2-m(p_1)n_1+\varepsilon n_1[r(1-\frac{n_1}{K_1})-\frac{\kappa p_1}{n_1+D}],\\ \frac{dn_2}{d\tau} &= m(p_1)n_1-m(p_2)n_2+\varepsilon n_2[r(1-\frac{n_2}{K_2})-\frac{\kappa p_2}{n_2+D}],\\ \frac{dp_1}{d\tau} &= kp_2-kp_1+\varepsilon p_1[s(1-\frac{h_1p_1}{n_1})],\\ \frac{dp_2}{d\tau} &= kp_1-kp_2+\varepsilon p_2[s(1-\frac{h_2p_2}{n_2})].\end{aligned} \tag{2}$$

To achieve aggregation we ignore the small terms of the order of ε in Equation (2).
We work out the steady states of the migratory part of Equation (2), which is on a fast time scale, and it yields:-

$$n_1^* = n_2^* = \frac{n}{2}, \; p_1^* = p_2^* = \frac{p}{2}. \tag{3}$$

Adding the first and the second equation of Equation (2), which describe prey population and the third to the fourth equation of Equation (2) which describes predator population and using Equation (3) we obtain:

$$\begin{aligned} \dot{n} &= n[r(1-\frac{n}{K}) - \frac{\kappa p}{n+\hat{D}}], \\ \dot{p} &= p[s(1-\frac{hp}{n})]. \end{aligned} \tag{4}$$

where $K := \frac{4K_1K_2}{K_1+K_2}$ and $\hat{D} := 2D$. We non-dimensionalize Equation (4) to further reduce the number of parameters. It is convenient to express n and p as fractions of the predator-free carrying capacity K by the following scaling: $x(\hat{t}) := \frac{n(t)}{K}$, $y(\hat{t}) := \frac{hp(t)}{K}$, $\hat{t} := rt$, $a := \frac{k}{hr}$, $b := \frac{s}{r}$, $d := \frac{\hat{D}}{K}$.
After substituting and cancelling out parameters and variables, Equation (4) takes the form:

$$\begin{aligned} \frac{dx}{d\hat{t}} &= x(1-x) - \frac{axy}{x+d} =: f(x,y), \\ \frac{dy}{d\hat{t}} &= by(1-\frac{y}{x}) =: g(x,y). \end{aligned} \tag{5}$$

This is the non-dimensionalized system where the variables x, y and parameters a, b and d are dimensionless.

IV. Long-term solutions

We now analyze the long-term behaviour of Equation (5). This is achieved by finding the stability of the fixed points of the rescalled model and analyzing them. We also study how the fixed points depend on parameters a, b and d. The fixed points of Equation (5) are given as:-

$$E_0 := (0,0), \; E_1 := (1,0) \; and \; E_2 := (x^*, y^*) \; with \; y^* = x^*$$

where x^* satisfies the Equation (6) obtained by solving the non-zero solution of the first equation in Equation (5)

$$x^2 - (1-a-d)x - d = 0. \tag{6}$$

Since we are handling prey and predator population, we take the non-negative solution. Therefore the realistic is the non-negative root of Equation (6)

To analyze the stability or instability of fixed points of Equation (5) we compute the Jacobian matrix which will allows us to check the stability or instability of the fixed point E_2.
The Jacobian $J(x,y)$ is given by

$$J(x,y) = \begin{bmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{bmatrix} = \begin{bmatrix} 1 - x - \frac{ay}{x+d} + x(-1 + \frac{ay}{(x+d)^2}) & \frac{-ax}{x+d} \\ \frac{by^2}{x^2} & b(1-\frac{y}{x}) - \frac{by}{x} \end{bmatrix}. \tag{7}$$

At the fixed point $E_0 := (0,0)$, the linearization method fails to conclusively categorize the fixed point therefore, we resort to using liapunov function theorem to help us establish the stability or instability of the system at the fixed point.

Let $\mathbb{U} := \{x : |x| < 1\}$ for some $r > 0$, $V(x,y) := x^2 + y^2$, be a real-valued function. $V : \mathbb{U} \to \mathbb{R}$. Clearly a real $V(0) = 0$, $\dot{V} > 0$; that is, V is strictly increasing. Therefore $V(x,y)$ is a Liapunov function defined on $\mathbb{U}$.
Computing $\dot{V}$ along the solution trajectory, with $y = 0$ and $0 < x < 1$, we obtain $\dot{V}(x,0) = 2x^2(1-x) > 0$. Thus, by *Chetaev's theorem* see for instance [10], $E_0(0,0)$ is an unstable fixed point.

At the fixed point E_1, we have;

$$J(E_1) \;=\; \begin{bmatrix} -1 & \frac{-a}{1+d} \\ 0 & b \end{bmatrix}. \tag{8}$$

From Equation (8) we can see that the determinant $\delta = -b$ and trace $\tau = b - 1$. Therefore, the system at E_1 is a saddle which is always unstable, see for instance [13].

At the fixed point E_2 we have :-

$$J(E_2) \;=\; \begin{bmatrix} x[\frac{ax}{(x+d)^2} - 1] & \frac{-ax}{x+d} \\ b & -b \end{bmatrix}. \tag{9}$$

We compute the determinant (δ) and the trace (τ) of $J(E_2)$ to check the stability or instability of the fixed point E_2.
The determinant δ of $J(E_2)$ is given by:-

$$\delta : \;=\; [\frac{ad}{(x+d)^2} + 1]bx, \tag{10}$$

while the trace (τ) of $J(E_2)$ is :-

$$\tau : \;=\; [\frac{ax}{(x+d)^2} - 1]x - b. \tag{11}$$

For stability, we require that $\delta > 0$ and $\tau < 0$. We see from Equation (10) that $\delta > 0$ for all parameters $(a,\ b,\ d)$ and thus we only have to analyze the trace (τ)in Equation (10). Using Equation (5) and (6) in Equation (10), we see that for $\delta > 0$, we have

$$b > [a - \{(1-a-d)^2 + 4d\}^{1/2}][\frac{1 + a + d - \{(1-a-d)^2 + 4d\}^{1/2}}{2a}]. \tag{12}$$

Where Equation (12) establishes a three-dimensional surface in the (a,b,d) parameter space. After computation, we see that the term $1 + a + d - \{(1-a-d)^2 + 4d\}^{1/2}$ is a monotonic decreasing function of d and always positive . Also, the term $\{(1-a-d)^2 + 4d\}^{1/2}$ is also monotonic decreasing function for $0 < a < 1/2$ and all $d > 0$, the stability condition in Equation (12) is achieved with any $b > 0$. In other words, the steady state (x^*, y^*) is linearly stable for parameter values $a > 0,\ b > 0,$ and $\ d > 0$.

4.1 Existence of a limit cycle

We use vector fields and nullclines to describe and analyze Equation (5) so as to show the existence of a limit cycle. This is achieved by drawing the phase plane-curves of $f(x,y) = 0$ and $g(x,y) = 0$ of Equation (5). Simulating the vector component of Equation (5) with parameter-values $a = 1$, $b = 0.08$ and $d = 0.07$ yields Figure 2.

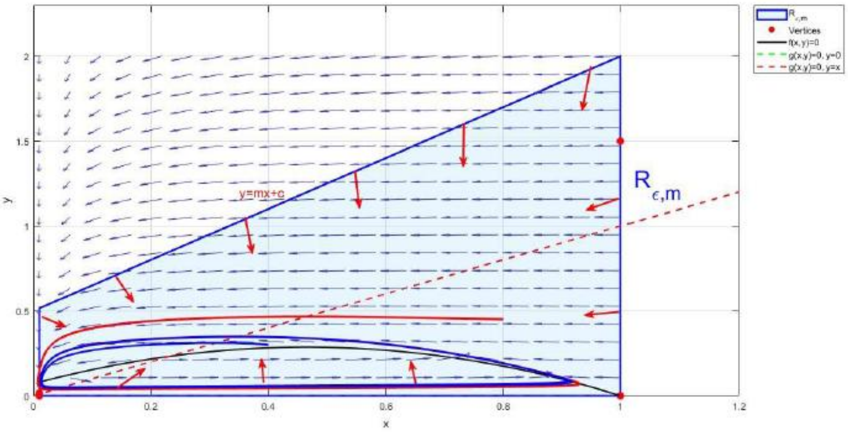

Figure 2: The invariant region with nullclines and vector fields

Let us define the region $R_{\varepsilon,m} := \{(x,y) \in \mathbb{R}^2_+ \,|\, \varepsilon \leq x \leq 1,\ 0 \leq y \leq mx + c\}$, where $m > 1$, $c > 0$, $\varepsilon \in (0,1)$ are some finite constants. Clearly $R_{\varepsilon,m}$ is a closed and compact region in $\mathbb{R}^2_+$ that contains the fixed point E_2. We wish to show that R_ε, m is positively invariant with respect to the flow defined by Equation (5). We show that the vector field in Equation (5) points inwards or tangent along all segments of the boundary of $R_{\varepsilon,m}$.

When $x = 1$, $0 \leq y \leq m + c$, we have that $\dot{x} = 1(1-1) - \frac{a \cdot 1 \cdot y}{1+d} = -\frac{ay}{1+d} \leq 0$, and $\dot{y} \leq 0$. Hence, the vector field points leftward into $R_{\varepsilon,m}$ or is tangent when $y = 0$. On the line $y = mx + c$, $\varepsilon \leq x \leq 1$, we have that $\dot{y} := (1-m) < 0$ since $m > 1$ and $\dot{x} :=> 0$ provided $y < \frac{1}{a}$ and $d < ay$. In a similar manner, when $y = 0$, $\varepsilon \leq x \leq 1$ then, $\dot{y} = 0$, and $\dot{x} = x(1-x) \geq 0$. Consequently, the flow is tangent to the line $y = 0$ axis or directed into $R_{\varepsilon,m}$, and trajectories cannot cross into $y < 0$. On the curve $x = \varepsilon, 0 \leq y \leq m\varepsilon + c$ we have $\dot{x} := \varepsilon(1-\varepsilon) - \frac{a\varepsilon y}{\varepsilon + d} \geq 0$ since $\varepsilon \in (0,1)$ and $\dot{y} := by(1 - \frac{y}{\varepsilon}) \leq 0$. The second term is of order $O(\varepsilon^2)$, which is negligible compared to $\varepsilon(1-\varepsilon)$. Hence, for sufficiently small $\varepsilon > 0$, we obtain $\dot{x} > 0$, and the vector field points rightward into $R_{\varepsilon,m}$. The vector field points inward or is tangent along all boundary segments of $R_{\varepsilon,m}$. Therefore, $R_{\varepsilon,m}$ is compact and positively invariant. Any trajectory that enters or originates within $R_{\varepsilon,m}$ remains in this region for all forward time $t \geq 0$. Therefore the $R_{\varepsilon,m}$ is positively invariant with respect to the flow defined by Equation (5)

At the interior equilibrium $E_2 = (x^*, x^*)$ the Jacobian matrix has determinant $\delta = \left(\frac{ad}{(x^*+d)^2} + 1\right) bx^* > 0$, and trace $\tau = \left(\frac{ax^*}{(x^*+d)^2} - 1\right) x^* - b$, as recorded in Equations (10) and(11). Since $\delta > 0$ automatically, linear instability of E_2 is achieved by choosing $b > 0$ small enough so that $\tau > 0$, that is,.$0 < b < \left(\frac{ax^*}{(x^*+d)^2} - 1\right)x^*$. Whenever the bracketed expression is positive, such b exist. This provides an open condition on the parameter pair (a,d). Biologically, if the prey-predator interaction strength near coexistence satisfies $\frac{ax^*}{(x^*+d)^2} > 1$, then, by selecting predator turnover b sufficiently small, the coexistence point E_2 becomes an unstable node or focus. The flow is continuously differentiable (C^1) on $R_{\varepsilon,m}$, and the only equilibrium point in the interior is E_2, which has been shown to be unstable. Therefore, the ω-limit set of any trajectory starting in $R_{\varepsilon,m}$ that does not reach the boundary cannot be empty, cannot consist of a single equilibrium, and cannot exhibit chaotic behavior in the plane. By the *Poincar'e-Bendixson theorem* see for instance [13], the ω-limit set must therefore be a nontrivial periodic orbit lying entirely within $R_{\varepsilon,m}$. This confirms the existence of a limit cycle, as illustrated in Figures 2.

4.2 Conclusion

From the model presented, the analysis in Section 4 established the existence of three equilibria: the trivial equilibrium point $E_0 = (0,0)$, the prey-only equilibrium point $E_1 = (1,0)$ and the co-existence equilibrium $E_2 = (x^*, y^*)$. The trivial and prey-only equilibria were found to be unstable, with E_0 as a source and E_1 as a saddle point. The coexistence equilibrium, however, displayed stability or instability depending on the values of the parameters a,b and d demonstrating the crucial role of ecological and migratory conditions in determining whether the two species persist together. This sensitivity of the co-existence state emphasizes how density-dependent migration, predation pressure, and intrinsic growth interact to shape the long-term dynamics of predator-prey systems. Moreover, the construction of a positively invariant region in the phase plane, as shown in Figure 2, confirmed that all trajectories remain bounded and confined to biologically feasible states. This invariance provided the foundation for invoking the *Poincar'e-Bendixson theorem*, which, combined with nullcline and vector field analysis, guaranteed the existence of a nontrivial periodic orbit. Consequently, the system admits a limit cycle, signifying sustained oscillations of predator and prey populations over time. These oscillations are synchronous across the two patches, reflecting the ecological reality that migration and dispersal mechanisms can coordinate species dynamics across fragmented habitats.

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