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Density Dependent Delayed Migration for Rosenzweig-Macaurther Model with Holling Type II Predator Functional Response

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Authors' contributions

This work was carried out in collaboration among all authors. SBA designed the study, performed the statistical analysis, wrote the protocol, and wrote the first draft of the manuscript. GOL and NJK managed the analyses of the study. All authors read and approved the final manuscript.

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Abstract

The model describing the interaction between the predator and prey species is referred to as a predator-prey model. The migration of these species from one patch to another may not be instantaneous. This may be due to barriers such as a swollen river or a busy infrastructure through the natural habitat. Recent predator-prey models have either incorporated a logistic growth for the prey population or a time delay in migration of the two species. Predator-prey models with logistic growth that integrate time delays in density-dependent migration of both species have been given little attention. A Rosenzweig-MacAurther model with density-dependent migration and time delay in the migration of both species is developed and analyzed in this study. The Analysis of the model when the prey migration rate is greater than or equal to the prey growth rate, the two species will coexist, otherwise, at least one species will become extinct. A longer delay slows down the rate at which the predator and prey population increase or decrease, thus affecting the population density of these species. The prey migration due to the predator density

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does not greatly affect the prey density and existence compared to the other factors that cause the prey to migrate. These factors include human activities in the natural habitats like logging and natural causes like bad climatic conditions, limited food resources and overpopulation of the prey species in a patch among others.

Keywords: Rosenzweig-MacAurther model; delay, variable migration.

2010 Mathematics Subject Classification: 53C25; 83C05; 57N16.

1 Introduction

Classical predator prey systems like the Lotka-Volterra model describe how the predator and prey species interact [1, 2, 3]. The model assumed that in the absence of the predator species, the prey will grow unboundedly. The Rosenzweig-Macarthur model improved the Lotka-Volterra model by including a carrying capacity for the prey species to account for the fact that the prey will grow governed by the available sustaining resources in the absence of the predation in a homogeneous environment [4, 5, 6, 7, 8, 9]. A homogeneous environment is considered in the classical predator-prey system, but in real life, the environment is heterogeneous and its connected by migration [1, 2, 10]. Migration of these species from one patch to another occurs due to a number of factors like lack of food, intraspecific competition, climatic conditions, overpopulation in a patch, lack of security among others [11, 12, 13, 14]. The rate of migration can either be constant or it variable [15, 16, 17]. For constant migration, the number of species moving per unit time is a constant fraction of the population of the species in a given patch [15]. Since the migration of the prey is largely due to predators. Similarly, since the predator migration is dependent on the availability of food (the prey), then the predator migration rate will be dependent on the density of the prey [15].

Time delays are inevitable since most decisions depend on past events or experiences [18]. Most models for instance Abdllaoui et. al [17] and Mchich et. al [19] assume that this migration is instantaneous. In a heterogeneous environment, a time delay in migration is the time taken by a species before they migrate from one patch to another after facing an unfavorable condition in the initial patch like adverse weather conditions or natural habitat land allocation to human settlement, agriculture or infrastructure [14, 15, 20].

2 The Model

In this paper we study the model considered by Samuel *et. al* [15] and take the migration rates as done by Abdllaoui *et al* [17], let the prey migration rate be given by $\alpha_i p_i + \alpha_0$ and the predator migration rate be given by $\frac{1}{\beta_i n_i + \beta_0}$, i = 1, 2. The model equation becomes

$$\dot{n}_{i}(t) = (\alpha_{j}p_{j} + \alpha_{0})n_{j}(t - \tau) - (\alpha_{i}p_{i} + \alpha_{0})n_{i} + n_{i}\left(r_{i}(1 - \frac{n_{i}}{K}) - \frac{A_{i}p_{i}}{n_{i} + B_{i}}\right),$$

$$\dot{p}_{i}(t) = \frac{p_{j}(t - \tau)}{\beta_{j}n_{j} + \beta_{0}} - \frac{p_{i}}{\beta_{i}n_{i} + \beta_{0}} + \frac{p_{i}n_{i}}{B_{i} + n_{i}} - d_{i}p_{i} \quad i, j = 1, 2, \quad i \neq j$$
(2.1)

In the absence of the predation, due to intraspecific competition, the prey population migrates at the same constant rate, α_0 . In the absence of the prey density, predators move from patch to patch at the same constant rate, $\frac{1}{\beta_0}$. We use the Holling type II predator functional response since the prey consumption is governed by the prey density.

3 Model Analysis

Let $Z_i(t) := \left(n_1(t), p_1(t)\right), i = 1, 2$, then Equation (2.1) becomes,

$$\dot{Z}_i(t) = (Z_j(t-\tau) - Z_i(t))\gamma + f_i(Z_i(t)), \quad i \neq j,$$
(3.1)

where, γ denotes the migration rates and

$$f_i(Z_i(t)) = \left(n_i \left(r_i(1 - \frac{n_i}{K}) - \frac{A_i p_i}{n_i + B_i}\right) \\ \frac{p_i n_i}{B_i + n_i} - d_i p_i.$$

Let $Z(t) := (Z_1(t), Z_2(t))$ and $f(Z(t), Z(t - \tau))$ represent the vector field on the right hand side of Equation (3.1), thus Equation (3.1) becomes,

$$\dot{Z}(t) = f(Z(t), Z(t-\tau)).$$
 (3.2)

Let $C = \mathcal{C}([-\tau, 0], \mathbb{R}^4)$ be a Banach space equipped with the sup norm, $\|\phi\| = \sup |\phi(\theta)| \le r, (0 \le r < \infty)$, for $\theta \in [-\tau, 0]$ and where $|\phi(\theta)|$ denotes a Euclidean norm of $\phi(\theta)$. Let the initial condition be given by,

$$\varphi(t) := Z(t) \mid_{[-\tau,0]},\tag{3.3}$$

where $\varphi \in C$. Since $f(Z(t), Z(t - \tau)) \in C(\mathbb{R}^4 \times C, \mathbb{R}^4)$, Equation (3.2) subject to Equation (3.3) has a unique solution. For more on existence and uniqueness of solutions, see for instance Hale & Lunel [21].

We wish to exploit the symmetries in the coupling terms of the linear part of Equation (3.1), that is;

$$\dot{Z}_i(t) = (Z_j(t-\tau) - Z_i(t))\gamma, \quad i, j = 1, 2, i \neq j,$$
(3.4)

which can be represented by two invariant manifolds. This is motivated by findings of Huang [22] which states that for large predator migration rate, the pattern is formed by persistent asymmetry, in particular prey missing in some patches and for small predator migration rate, predator and prey are present everywhere.

We now show that Equation (3.4) is exponentially bounded to show that the solutions will always be bounded.

Lemma 3.1. The solution of Equation (3.4) subject to the initial condition in Equation (3.3) for $t \ge 0$, satisfies,

$$|Z(t)| \le (1+A\tau)e^{2At} |\varphi|, \qquad (3.5)$$

where | . | denotes a sup norm in \mathbb{R} as well as a matrix norm.

The proof of Lemma (3.1) can be found in Samuel *et. al* [15].

With the assumption that the predator and prey species are of the same type regardless of the patch, we take $r_1 = r_2 := r$, $a_1 = a_2 := a$, $b_1 = b_2 := b$ and $s_1 = s_2 := s$, $A_1 = A_2 := A$ and $B_1 = B_2 := B$. As suggested by Samuel *et. al* [15], we have two manifolds; the symmetric manifold

where $Z_1(t) = Z_2(t)$ and the asymmetric manifold where $Z_1(t) = -Z_2(t)$. Therefore, we will study the dynamics of these two invariant manifolds using the following transformation,

$$u_{1} := \frac{1}{2}(n_{1} + n_{2}), \ v_{1} := \frac{1}{2}(p_{1} + p_{2}),$$

$$u_{2} := \frac{1}{2}(n_{1} - n_{2}), \ v_{2} := \frac{1}{2}(p_{1} - p_{2}).$$
 (3.6)

In the symmetric manifold, the population density in the first patch is the same as the population density the the second patch while in the asymmetric manifold, the population density in the first patch is not the same as the population density in the second patch.

Using Equation (3.6) in Equation (2.1), we obtain,

$$\dot{u}_{1} = (u_{1}(t-\tau) - u_{1})(\alpha_{0} + \alpha v_{1}) + \alpha(u_{2}(t-\tau) - u_{2})v_{2} + f_{1}(u_{i}, v_{i}), \dot{v}_{1} = \frac{-(\beta_{0}(v_{1} - v_{1}(t-\tau)) + \beta(u_{1}(v_{1} - v_{1}(t-\tau)) - u_{2}(-v_{2} + v_{2}(t-\tau)))))}{(\beta(u_{1} - u_{2}) + \beta_{0})(\beta(u_{1} + u_{2}) + \beta_{0})} + g_{1}(u_{i}, v_{i}), \dot{u}_{2} = -(u_{2}(t-\tau) + u_{2})(\alpha_{0} + \alpha v_{1}) - \alpha(u_{1}(t-\tau) + u_{1})v_{2} + f_{2}(u_{i}, v_{i}), \dot{v}_{2} = \frac{-(-\beta u_{2}(v_{1} - v_{1}(t-\tau)) + (\beta_{0} + \beta(u_{1})(v_{2} - v_{2}(t-\tau)))))}{(\beta(u_{1} - u_{2}) + \beta_{0})(\beta(u_{1} + u_{2}) + \beta_{0})} + g_{2}(u_{i}, v_{i}).$$

$$(3.7)$$

where $u_i = u_i(t)$ and v_i

$$= v_i(t), \ i = 1, 2, \ f_1(u_i, v_i) = \frac{r}{K} \left(Ku_1 - u_1^2 - u_2^2 \right) - A \left(\frac{Bu_1 v_1 + u_1^2 v_1 - u_2 (-u_2 v_1 + Bv_2)}{(u_1 + B)^2 - u_2^2} \right), \ f_2(u_i, v_i)$$

$$= \frac{r}{K} \left(Ku_2 - 2u_1 u_2 \right) - A \left(\frac{Bu_2 v_1 + u_1 (B + u_1) v_2 - u_2^2 v_2}{(u_1 + B)^2 - u_2^2} \right), \ g_1(u_i, v_i) = \frac{Bu_2 v_2 + (u_1 (B + u_1) - u_2^2) v_1}{(B + u_1)^2 - u_2^2} - dv_1,$$
and $g_2(u_i, v_i) = \frac{Bu_2 v_1 + (u_1 (B + u_1) - u_2^2) v_2}{(B + u_1)^2 - u_2^2} - dv_2.$

Using the linear subspace of \mathbb{R}^4

$$\Theta = \{ (Z_1(t), Z_2(t)), Z_i(t) \in \mathbb{R}^2 : Z_1(t) - Z_2(t) = 0 \}, \Pi = \{ (Z_1(t), Z_2(t)), Z_i(t) \in \mathbb{R}^2 : Z_1(t) + Z_2(t) = 0 \},$$
(3.8)

let $U_i = (u_i, v_i)^T$ i = 1, 2, the Π and Θ manifolds reduce to two dimensional systems of the form

$$\dot{U}_{1} = \begin{pmatrix} \alpha_{0} & 0\\ 0 & \frac{\beta_{0}}{(\beta u_{1} + \beta_{0})^{2}} \end{pmatrix} U_{1}(t - \tau) + \begin{pmatrix} -\alpha_{0} + r - \frac{ru_{1}}{K} & \alpha u_{1}(t - \tau) - \left(\alpha u_{1} + \frac{-A}{u_{1} + B}\right) u_{1} \\ 0 & -\frac{\beta_{0}}{(\beta u_{1} + \beta_{0})^{2}} + \frac{u_{1}}{u_{1} + B} - d \end{pmatrix} U_{1}$$
(3.9)

and

$$\dot{U}_2 = \begin{pmatrix} -\alpha_0 & 0\\ 0 & \frac{\beta_0}{\beta_0^2 - \beta^2 u_2^2} \end{pmatrix} U_2(t-\tau) + \begin{pmatrix} r - \alpha_0 & \frac{Au_2^2}{B^2 - u_2^2}\\ 0 & \frac{\beta_0}{\beta_0^2 - \beta^2 u_2^2} - \frac{u_2^2}{B^2 - u_2^2} - d \end{pmatrix} U_2$$
(3.10)

respectively. Next we examine the stability of solutions on the two manifolds, this will help us predict long-term behaviours of solutions of Model (2.1).

3.1 Asymmetric manifold

The following theorem is used to show the behaviour of solutions for equation (3.9),

Theorem 3.2. For all values of $\frac{1}{\beta_0}$ and d, equation (3.9) has

- (i) a sink at the origin for $\alpha_0 > r$,
- (ii) a saddle at the origin for either $\alpha_0 < r$,
- (iii) a periodic solution $\alpha_0 = r$

Proof. Let $U_1(t) = e^{\lambda t} C_1$, then we obtain the following characteristic equation from equation (3.9),

$$(\alpha_0 e^{-\lambda \tau} - \alpha_0 + r - \lambda)(\frac{1}{\beta_0}(e^{-\lambda \tau} - 1) - d - \lambda) = 0$$
(3.11)

Using the first factor of equation (3.11), we have

$$(\alpha_0 e^{-\lambda\tau} - \alpha_0 + r - \lambda) = 0 \tag{3.12}$$

Let

$$z = (\lambda + \alpha_0 - r)\tau \tag{3.13}$$

Then equation (3.12) becomes

$$=\alpha_0 \tau e^{-z} e^{(-r+\alpha_0)\tau} \tag{3.14}$$

The following lemma found in [23] will be used to analyze equation 3.14

z

Lemma 3.3. The equation $z = be^{-z}$ has simple pure imaginary roots, $z = i(\pi/2 + 2m\pi)$, for $b = -(\pi/2 + 2m\pi)$, z = 0, for b = 0, $z = i(\pi/2 + (2m + 1)\pi)$, for $b = (\pi/2 + (2m + 1)\pi)$, where m = 0, 1, 2, ... and there are no other purely imaginary roots.

Using Lemma (3.3) where $b = \alpha_0 \tau e^{-(r-\alpha_0)\tau} > 0$, we get $z = i(\pi/2 + (2m+1)\pi$ for $\alpha \tau e^{-(r-\alpha_0)\tau} = (\pi/2 + (2m+1)\pi)$. Equation (3.13) becomes

$$\lambda = i\alpha_0 e^{-(r-\alpha_0)\tau} - \alpha_0 + r \tag{3.15}$$

Equation (3.15) has

- (i) roots with positive real parts for $\alpha_0 < r$
- (ii) roots with negative real parts for $\alpha_0 > r$
- (iii) purely imaginary roots for $\alpha_0 = r$.

For the second factor of equation (3.11),

$$\left(\frac{1}{\beta_0}(e^{-\lambda\tau} - 1) - d - \lambda\right) = 0.$$
(3.16)

Let

$$z = (\lambda + \frac{1}{\beta_0} + d)\tau \tag{3.17}$$

From Lemma (3.3), equation (3.17) becomes

$$\lambda = \frac{i}{\beta_0} e^{(\frac{1}{\beta_0} + d)\tau}) - \frac{1}{\beta_0} - d$$
(3.18)

Equation (3.17) has roots with negative real parts for all values of $\frac{1}{\beta_0}$ and d. The results for equation (3.9) therefore becomes

(i) a saddle at the origin for $\alpha_0 < r$, that means that, when the prey migration rate is less than the prey growth rate, then either,

- (a) both species will be wiped out after some time. This is due to the fact that the prey migrate in low rates after facing an unfavorable condition like a predator attack or famine. Since most prey remain in the initial patch, they are still prone to more unfavorable conditions which affect their population density and leads the prey density in that patch to tend to extinction. This makes the predator density also to go to extinction.
- (b) the predator population is wiped out and the prey density grows bounded by the carrying capacity. This is due to the fact that as the prey population decreases, this makes the predator population to be led to extinction. Then the prey population grows bounded by the carrying capacity in the absence of the predator population.
- (ii) a sink at the origin for $\alpha_0 > r$, that implies that, when the constant prey migration rate is greater than the prey growth rate, the two species will coexist. This is as a result of the prey migrating in high rates to safety after facing an unfavorable condition in their initial patch. This in turn will always provide a source of food to the predator density.
- (iii) a center for $\alpha_0 = r$, that means that, when the constant prey migration rate is the same as the prey growth rate then a periodic solution occurs. The two populations will rise and fall almost dependently. The prey and predator densities will be dependent on the other species, the prey population is governed by both the predator density and the availability of sustainable resources in a given patch while the predator species is dependent on the availability of their food source.

3.2 Numerical analysis for Asymmetric manifold

The following parameter values, adapted from Samuel *et. al.* [15], are used in simulating the results of equation (3.9), $\alpha = 0.4$, K = 250, $\beta = 2.792403$, r = 0.6, B = 3, d = 0.4, $u_2 = 240$ and $v_2 = 80$. Simulations for the asymmetric manifold gives,



When the prey migration rate is less than the intrinsic growth rate ($\alpha_0 < r$), the predator density becomes extinct leading to the prey density growing bounded by the carrying capacity as seen in Figure 1 and Figure 2. This is an unstable case since one of the species is wiped out. A longer delay, as shown in Figure 2, slows down the rate at which the predator population declines.



When prey migration rate is greater than the intrinsic growth rate $(\alpha_0 > r)$, the two population densities coexist and depend on each other as shown in Figure 3 and Figure 4. The prey population is affected by the availability of sustaining resources and security while the predator population is mainly affected by the availability of the prey. We see when the predator density density is high, this negatively affects the prey density which in turn reduces, since predator attacks will be many. With a reduction in the prey density, the predator density also reduces due to their diminished source of food. This implies that predator attacks for the prey species will be minimized, thus the prey density increases. An increase in the prey population makes the predator density to grow. With a high predator density, the cycle occurs again. A longer delay slows down the increase or decrease of the predator and prey species.



In Figure 5 and 6, the prey migration rate is equal to the intrinsic growth rate ($\alpha_0 = r$). Oscillations occur where the rise and fall of densities of both species occurs dependently. These two populations depend on the available sustaining resources. A longer delay slows down the change in the predator and prey densities.

3.3 Symmetric manifold

Similarly, the following theorem is used to show the behavior of solutions for equation (3.10),

Theorem 3.4. For all values of $\frac{1}{\beta_0}$ and d, equation (3.10) has

- (i) a sink at the origin for $\alpha_0 > r$,
- (ii) a saddle at the origin for either $\alpha_0 < r$,

(iii) a periodic solution $\alpha_0 = r$

Proof. Let $U_2(t) = e^{\lambda t} C_2$, then the following characteristic equation is obtained from equation (3.10),

$$(-\alpha e^{-\lambda\tau} - \alpha_0 + r - \lambda)(\frac{1}{\beta_0}(e^{-\lambda\tau} - 1) - d - \lambda) = 0$$
(3.19)

Using the first factor of equation (3.19), we have

$$(-\alpha e^{-\lambda\tau} - \alpha_0 + r - \lambda) = 0 \tag{3.20}$$

Let

$$z = (\lambda + \alpha_0 - r)\tau \tag{3.21}$$

Then equation (3.20) becomes

$$z = -\alpha \tau e^{-z} e^{(\alpha_0 - r)\tau} \tag{3.22}$$

Using Lemma (3.3), where $b = -\alpha \tau e^{(\alpha - r)\tau} < 0$, in Equation (3.22) we get $z = i(\pi/2 + 2m\pi)$ for $-\alpha \tau e^{-r\tau} = -(\pi/2 + 2m\pi)$. Equation (3.21) becomes

$$\lambda = i\alpha_0 e^{(-r+\alpha_0)\tau} - \alpha_0 + r \tag{3.23}$$

Equation (3.23) has

- (i) roots with positive real parts for $\alpha_0 < r$
- (ii) roots with negative real parts for $\alpha_0 > r$
- (iii) purely imaginary roots for $\alpha_0 = r$.

For the second factor of equation (3.19),

$$\left(\frac{1}{\beta_0}(e^{-\lambda\tau} - 1) - d - \lambda\right) = 0.$$
(3.24)

Let

$$z = (\lambda + \frac{1}{\beta_0} + d)\tau \tag{3.25}$$

From Lemma (3.3), equation (3.25) becomes

$$\lambda = \frac{i}{\beta_0} e^{(\frac{1}{\beta_0} + d)\tau} - \frac{1}{\beta_0} - d$$
(3.26)

Equation (3.26) has roots with negative real part for all values of $\frac{1}{\beta_0}$ and d.

For all $\frac{1}{\beta_0}$ and d, the results for equation (3.19) therefore becomes

- (i) a saddle at the origin for either $\alpha_0 < r$, that means that, when the prey migration rate is less than the prey growth rate, then either,
 - (a) both species will be wiped out after some time. Since the prey density do not migrate in high rates after facing an adverse condition, they remain prone to that adverse condition which may make the prey density in that patch to be extinct. Extinction of the prey density leads the predator density to extinction.
 - (b) the prey density grows logistically after the predator population is led to extinction. As the predator density makes the prey density to decline, this makes the predator density also to decline possibly to extinction as a result of a depleted source of food. Then the prey population grows governed by the available sustaining resources in the absence of the predator population.

- (ii) a sink at the origin for $\alpha_0 > r$, that implies that, when the constant prey migration rate is greater than the prey growth rate, the two species will coexist. This is as a result of the prey moving in high rates after facing an adverse condition, and this makes the prey density not to be wipes out. With the prey density surviving, a food source to the predator density is always guaranteed thus making the two species to coexist.
- (iii) a periodic solution for $\alpha_0 = r$, that means that, when the constant prey migration rate is the same as the prey growth rate, then a periodic solution occurs.

3.4 Numerical analysis for Symmetric manifold

The following parameter values, adapted from Samuel *et. al.* [15], are used in simulating the results of equation (3.10), $\beta = 2.792403$, B = 3, d = 0.4, r = 0.6, $u_2 = 240$ and $v_2 = 80$. Simulations for the symmetric manifold gives,



When the prey migration rate is less than the intrinsic growth rate ($\alpha_0 < r$), the predator density becomes extinct while the prey density grows in patch two hence the negative populations shown in Figure 7 and Figure 8. A longer delay makes the prey density in patch two increase as seen in Figure 8. This is as a result of the prey migrating in low quantities and take time to migrate to patch one, thus an increase of the prey species in patch two. The predator in patch one will have a limited supply of food thus reducing their density.



In Figure 9 and Figure 10, the prey migration rate is greater than the intrinsic growth rate ($\alpha_0 > r$). The two densities stabilize at zero after some time. Since the prey migrate in large quantities, we therefore see the prey population decreasing at a very fast rate: most of the prey population migrates from patch one to patch two thus the negative population. Some of the prey density also migrates back to patch one and with time the prey population in the two patches. The predator population migrates slowly to patch two from patch one, to a point where the predator populations in the two patches is equal. A shorter delay makes the population to stabilize at a slightly faster rate as shown Figure 9 compared to Figure 10.



In Figure 11 and Figure 12, the prey migration rate is equal to the intrinsic growth rate ($\alpha_0 = r$). Both species stabilize at zero, meaning they will coexist. As the predator density tends to zero, the prey density tends away from zero (the prey density in patch two grows) then after some time it tends to zero. Since the prey migration rate is the same as the intrinsic growth rate, the prey migrate in large quantities as seen in the sharp decline of the prey species in patch one and the increase in the prey population in patch two. The predator population density also tends to zero as times increases, meaning the predator density will be equal in the two patches. A longer delay slows down the rate at which the prey population stabilizes.

4 Conclusion

The results from this study show that:

- (i) When the prey migration rate is greater than or equal to the prey growth rate, the two species will coexist. When the prey migration rate is less than the prey growth rate, at least one species will become extinct.
- (ii) A longer delay slows down the rate at which the predator and prey population increase or decrease, thus affecting the population density of these species.
- (iii) The prey migration due to the predator density does not greatly affect the prey density and existence compared to the other factors that cause the prey to migrate. These factors include human activities in the natural habitats like logging and natural causes like bad climatic conditions, limited food resources and overpopulation of the prey species in a patch among others.

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Competing Interests

Authors have declared that no competing interests exist.

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