DYNAMICS IN A ROSENZWEIG-MACARTHUR PREDATOR-PREY SYSTEM WITH QUIESCENCE

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Abstract. A system of four coupled ordinary differential equations is considered, which are coupled through migration of both prey and predator model with logistic type growth. Combined effect of quiescence provides a more realistic way of modeling the complex dynamical behavior. The global stability and Hopf bifurcation solutions are investigated.

1. Introduction. Quiescence (or Dormancy) is a strategy that is useful in a risky environment for species. A simple game-theoretic argument makes this transparent. Quiescent phases occur in population models in various ways and under various names such as quiescent state (see [15]), dormancy (see [12]), resting phase (see [16]), ecological refuge. It is generally understood that such phases may have drastic effects on the dynamics.

Quiescent phases have been introduced in a variety of biological models. In [13], the effects of quiescent phases on invasion speeds have been investigated, in [8] transport equations with quiescent phases have been studied. [12] and [15] extended chemostat models by a quiescent phase. Neubert, et al. in [14] studied a predator-prey system, in which the predator can leave the habitat and return. As seen from the prey the predator would enter a quiescent phase. The authors showed that the quiescent phase stabilizes against predator-prey oscillations. The effect of quiescent phases on exponential solutions of homogeneous systems has been studied in [6]. Introducing a quiescent phase does not essentially change the set of equilibria. Hadeler and Lewis (2002)(see [7]) presented and discussed briefly a model which describes a population where the individuals alternate between mobile and non-mobile states, and only the mobile reproduce. Later, Zhang and Zhao (2007)(see [20]) established the existence of the asymptotic speed of spread. For a class of systems modeling random dispersal of the pollutant while ignoring the small mobility of the infective human population, a detailed analysis of the

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steady-state bifurcation pattern is performed for the case of homogeneous Dirichlet boundary conditions applied at the endpoints of a one-dimensional interval by phase plane methods (see [2, 3]). But there are very few stability/bifurcation and global dynamical behavior results for the emergence of predator-prey system combining quiescence.

While one could conjecture that adding a quiescent phase should have similar effects as a delay, e.g. causing oscillations in negative feedback situations, the opposite is true. Introducing quiescent phases damps oscillations or even causes them to disappear (see [5]). The aim of this paper is to study the Rosenzweig-MacArthur predator-prey system with quiescence. This yields a system of four coupled ordinary differential equations, which are coupled through migration of both prey and predator(see [1]):

\[
\begin{align*}
X' &= f(X,Y) - p_1 X + q_1 Z, \\
Y' &= g(X,Y) - p_2 Y + q_2 W, \\
Z' &= -q_1 Z + p_1 X, \\
W' &= -q_2 W + p_2 Y,
\end{align*}
\] (1)

And

\[
f(X,Y) = X \left(1 - \frac{X}{K}\right) - \frac{mXY}{1+X}, \quad g(X,Y) = \frac{mXY}{1+X} - eY,
\] (2)

where \(X\) and \(Y\) express the prey and predator or population sizes at time \(t > 0\). The variable \(Z\) and \(W\) denote the prey and predator in the quiescent phase. The \(p_1, p_2\) are the rates at which the prey and predator, respectively, go quiescent. The \(q_1, q_2\) are the rates at which the prey and predator, respectively, return to the active state. All these rates are positive.

It is known that it usually poses more difficulties for the stability and bifurcation analysis to 4-dimensional ODE. Analysis of global dynamical behavior will bring some more technical hurdles. Here we further develop the methods in [5, 9] to overcome these difficulties, our analysis improved the results in [1, 5].

The rest of the paper is organized as follows. In Section 2, we first recall some well known stability results on the system without quiescence. Based on this, the global stability analysis is carried out in Section 3. Discussion on Hopf bifurcations and numerical simulations are given in Section 4 and Section 5.

2. Analysis without quiescence. First we recall some well known results on the system without quiescence(see [4, 9, 11, 17, 19]):

\[
\begin{align*}
X' &= X \left(1 - \frac{X}{K}\right) - \frac{mXY}{1+X}, \\
Y' &= \frac{mXY}{1+X} - eY,
\end{align*}
\] (3)

The system of (3) has three non-negative constant equilibrium solution \((0,0),(K,0), (\lambda,v_\lambda)\), where

\[
\lambda = \frac{e}{m - e}, \quad v_\lambda = \frac{(K - \lambda)(1 + \lambda)}{Km}
\]

The coexistence equilibrium \((\lambda,v_\lambda)\) is in the first quadrant if and only if \(0 < \lambda < K\). This system has been thoroughly studied in existing papers.

1. when \(\lambda \geq K\), \((K,0)\) is globally asymptotically stable;
2. when \(K - 1 \leq \lambda < K\), \((\lambda,v_\lambda)\) is globally asymptotically stable;
3. \( \lambda = \frac{K - 1}{2} \) is the unique bifurcation point where a subcritical Hopf bifurcation occurs;

4. when \( 0 < \lambda < \frac{K - 1}{2} \), there is a globally asymptotically stable periodic orbit.

Note that if \((X, Y)\) is a stationary state of the system without quiescence (3), then \((X, Y, p_1X/q_1, p_2Y/q_2)\) is a stationary state of the system with quiescence (1). We are interested in the change of the dynamics when coupled by the quiescence.

3. **Global stability.** It is known that system (3) has a globally stable equilibrium: \((K, 0)\) or \((\lambda, v_\lambda)\) for different ranges of \(\lambda\). We would like to know whether \((K, 0, p_1K/q_1, 0)\) and \((\lambda, v_\lambda, p_1\lambda/q_1, p_2v_\lambda/q_2)\) are globally stable for the quiescent model of (1). To prove the global stability, we will follow the methods introduced in [10] and construct Lyapunov functions.

**Theorem 3.1.** Suppose that \(p_1, q_1, p_2, q_2, m, K, e > 0\). If \( \lambda \geq K \), then \((K, 0, p_1K/q_1, 0)\) is globally asymptotically stable for system (1).

**Proof.** We define Lyapunov functions

\[
V_1(X, Y) =\int_K^X \frac{g(\xi) - g(K)}{g(\xi)} \, d\xi + Y, \tag{4}
\]

and

\[
V_2(Z, W) =\int_K^Z \frac{g(q_1\xi/p_1) - g(K)}{g(q_1\xi/p_1)} \, d\xi + W. \tag{5}
\]

Then taking derivatives with respect to time \( t \), we get

\[
\frac{d}{dt} V_1(X(t), Y(t)) = \frac{g(X) - g(K)}{g(X)} \frac{dX}{dt} + \frac{dY}{dt} = (g(X) - g(K)) h(X) + Y(g(K) - e) + \frac{g(X) - g(K)}{g(X)} [-p_1X + q_1Z] + [-p_2Y + q_2W],
\]

where \( h(X) = \frac{(X + 1)(K - X)}{Km} \), and

\[
\frac{d}{dt} V_2(Z(t), W(t)) = \frac{g(q_1Z/p_1) - g(K)}{g(q_1Z/p_1)} \frac{dZ}{dt} + \frac{dW}{dt} = \frac{g(q_1Z/p_1) - g(K)}{g(q_1Z/p_1)} [p_1X - q_1Z] + [p_2Y - q_2W].
\]

We construct a Lyapunov function \( V(X, Y, Z, W) = V_1(X, Y) + V_2(Z, W) \) for the quiescent model from (4) and (5), and we get

\[
\frac{d}{dt} V(X(t), Y(t), Z(t), W(t)) = \frac{d}{dt} V_1(X(t), Y(t)) + \frac{d}{dt} V_2(Z(t), W(t)) = (g(X) - g(K)) h(X) + Y(g(K) - e) + \frac{g(X) - g(K)}{g(X)} [-p_1X + q_1Z] + [-p_2Y + q_2W]
\]

\[
= (g(X) - g(K)) h(X) + Y(g(K) - e) + \frac{g(K)}{g(X)} [p_1X - q_1Z] - \frac{g(K)}{g(q_1Z/p_1)} [p_1X - q_1Z] + \frac{1}{g(X)} - \frac{1}{g(q_1Z/p_1)}.
\]
When $\lambda \geq K$, $(g(X) - g(K))h(X) \leq 0$ for all $X \geq 0$; Notice $g$ is an increasing function, then $(g(K) - e)Y = (g(K) - g(\lambda))Y \leq 0$ for all $Y \geq 0$; Finally the last term $p_1g(K)[X - q_1Z/p_1][1/g(X) - 1/(g(q_1Z/p_1))] \leq 0$ because $g$ is increasing. Therefore, $\dot{V} \leq 0$ for any solution orbit $(X(t), Y(t), Z(t), W(t))$ of (1). Moreover, $\dot{V} = 0$ if and only if $X(t) = K, Y(t) = 0, Z(t) = Kp_1/q_1, W(t) = 0$. Then from LaSalle's invariance principle (see [18]), $(X(t), Y(t), Z(t), W(t)) \to (K, 0, Kp_1/q_1, 0)$ as $t \to \infty$.

Next we consider the case when $K - 1 \leq \lambda < K$. The equilibrium solution considered here is $(\lambda, v_\lambda, p_1\lambda/q_1, p_2v_\lambda/q_2)$, where $\lambda = \frac{e}{m - e}$ and $v_\lambda = \frac{(\lambda + 1)(K - \lambda)}{mK}$.

**Theorem 3.2.** If $K - 1 \leq \lambda < K$, then $(\lambda, v_\lambda, p_1\lambda/q_1, p_2v_\lambda/q_2)$ is globally asymptotically stable in $\mathbb{R}^+_K$ for system (1).

**Proof.** We define Lyapunov functions

$$V_3(X, Y) = \int_\lambda^X \frac{g(\xi) - e}{g(\xi)} \, d\xi + \int_{v_\lambda}^Y \frac{Y - v_\lambda}{\eta} \, d\eta,$$

and

$$V_4(Z, W) = \int_\lambda^Z \frac{g(q_1\xi/p_1) - e}{g(q_1\xi/p_1)} \, d\xi + \int_{v_\lambda}^Z \frac{(q_2\eta/p_2) - v_\lambda}{q_2\eta/p_2} \, d\eta.$$

Then take derivatives with respect to time $t$, we get

$$\frac{d}{dt}V_3(X(t), Y(t)) = \frac{g(X) - e}{g(X)} \frac{dX}{dt} + \frac{Y - v_\lambda}{Y} \frac{dY}{dt}$$
$$= (g(X) - e)(h(X) - Y) + (Y - v_\lambda)(g(X) - e)$$
$$+ \frac{g(X) - e}{g(X)}[-p_1X + q_1Z] + \frac{Y - v_\lambda}{Y}[-p_2Y + q_2W]$$
$$= (g(X) - e)(h(X) - Y) + (Y - h(\lambda))(g(X) - e)$$
$$+ \frac{g(X) - e}{g(X)}[-p_1X + q_1Z] + \frac{Y - v_\lambda}{Y}[-p_2Y + q_2W]$$

where $h(X) = \frac{(X + 1)(K - X)}{K}$, and

$$\frac{d}{dt}V_4(Z(t), W(t)) = \frac{g(q_1Z/p_1) - e}{g(q_1Z/p_1)} \frac{dZ}{dt} + \frac{q_2W/p_2 - v_\lambda}{q_2W/p_2} \frac{dY}{dt}$$
$$= \frac{g(q_1Z/p_1) - e}{g(q_1Z/p_1)}[p_1X - q_1Z] + \frac{q_2W/p_2 - v_\lambda}{q_2W/p_2}[p_2Y - q_2W].$$

We construct a Lyapunov function $\tilde{V}(t) = V_3(X, Y) + V_4(Z, W)$ for the quiescent model from (6) and (7), and we get

$$\frac{d}{dt}\tilde{V}(X(t), Y(t), Z(t), W(t)) = \frac{d}{dt}V_3(X(t), Y(t)) + \frac{d}{dt}V_4(Z(t), W(t))$$
$$= (g(X) - e)(h(X) - Y) + (Y - h(\lambda))(g(X) - e) + \frac{e}{g(X)}[p_1X - q_1Z].$$
\[
- \frac{e}{g(q_1 Z/p_1)} [p_1 X - q_1 Z] + \frac{v_\lambda}{Y} [p_2 Y - q_2 W] - \frac{v_\lambda}{q_2 W/p_2} [p_2 Y - q_2 W]
\]
\[
= (g(X) - e) (h(X) - h(\lambda)) + (Y - h(\lambda)) (g(X) - e)
\]
\[
+ p_1 e [X - q_1 Z/p_1] \left[ \frac{1}{g(X)} - \frac{1}{g(q_1 Z/p_1)} \right] + p_2 v_\lambda (Y - q_2 W/p_2) \left[ \frac{1}{Y} - \frac{1}{q_2 W/p_2} \right].
\]

When \( K - 1 \leq \lambda < K \), \( g(X) \) is increasing while \( h(X) \) is decreasing, which makes the first two terms both less or equal to 0. The last two terms are also less or equal to 0. Then we know
\[
\frac{d}{dt} V_3(X(t), Y(t)) + \frac{d}{dt} V_4(Z(t), W(t)) \leq 0.
\]

We can again apply the LaSalle invariance principle in [18] to show that the positive equilibrium \((\lambda, v_\lambda, p_1 \lambda/q_1, p_2 v_\lambda/q_2)\) is globally stable in \( \mathbb{R}_+^4 \).

Fig 1 and Fig 2 illustrate the global stability of equilibrium, where \( p_1, q_1, p_2 \) and \( q_2 \) can be chosen to any positive number.

**Figure 1.** Graphs of solutions. Here \( K = 2 \), \( m = 2 \), \( p_1 = 1 \), \( q_1 = 0.9 \), \( p_2 = 2 \), \( q_2 = 3 \) and \( e = 1.4 \). (left): \((K, 0)\) is globally asymptotically stable for (3); (right): \((K, 0, p_1 K/q_1, 0)\) is also globally asymptotically stable for (1).

**Figure 2.** Graphs of solutions. Here \( K = 2 \), \( m = 2 \), \( p_1 = 1 \), \( q_1 = 0.9 \), \( p_2 = 2 \), \( q_2 = 3 \) and \( e = 1.1 \). (left): \((\lambda, v_\lambda)\) is globally asymptotically for (3); (right): \((\lambda, v_\lambda, p_1 \lambda/q_1, p_2 v_\lambda/q_2)\) is also globally asymptotically for (1).
4. Linear stability and instability. In an effort to examine the local stability of the four dimensional ODE model (1), after computing the Jacobian matrix of the system (1) at the coexistence equilibrium \((\lambda, v, p_1\lambda/q_1, p_2v\lambda/q_2)\), we consider the characteristic polynomial of order four depending on many parameters in the following equation:

\[
\mu^4 + A_3\mu^3 + A_2\mu^2 + A_1\mu + A_0 = 0,
\]

where

\[
\begin{align*}
A_3(A) &= s_1 + s_2 - A, & A_2(A) &= s_1s_2 - (q_1 + s_2)A - BC, \\
A_1(A) &= -BC(q_1 + q_2) - q_1s_2A, & A_0 &= -BCq_1q_2, \\
s_1 &= p_1 + q_1, & s_2 &= p_2 + q_2, \\
A &= \frac{\lambda(K - 1 - 2\lambda)}{K(1 + \lambda)}, & B &= -e, & C &= \frac{K - \lambda}{K(1 + \lambda)}.
\end{align*}
\]

The variables \(A_i\) \((i = 0, 1, 2, 3)\) are crucial to determine the stability/instability of the equilibrium \((\lambda, v, p_1\lambda/q_1, p_2v\lambda/q_2)\). For the explicit analysis, we take \(q_1, q_2, p_1, p_2, K\) and \(m\) as fixed, \(A\) (or equivalent to \(e\)) as parameters. This parameter choice amounts to fixing the values of the growth rate and the carrying capacity of the prey and allowing the predator effectiveness to vary.

After analyzing the Routh-Hurwitz conditions, Belinsky and Hadeler (see [1]) obtained that the stability domain of the system with quiescence (1) can be described by \(\Sigma_1 \cup \Sigma_2\):

\[
\Sigma_1 = \{-\infty < A \leq 0, \ -BC > 0\},
\]

and

\[
\Sigma_2 = \{0 \leq A < A^H, \ -BC > 0\},
\]

where, for any given \(-BC > 0\), \(A^H\) is the smallest positive root of the cubic equation:

\[
H(A) = (q_1 + q_2)(p_1 + p_2 - A)(BC)^2 - BC[(q_1 + q_2)((s_1 + s_2)(s_1s_2 - (q_1 + s_2)A) + q_1s_2A) - q_1s_2A((s_1 + s_2)(s_1 + s_2 - A)^2q_1q_2) - q_1s_2A((s_1 + s_2 - A)(s_1s_2 - (q_1 + s_2)A) + q_1s_2A)].
\]

Here we will show that the cubic polynomial \(H(A)\) indeed has at least one positive root, thus \(A^H > 0\) exists.

**Lemma 4.1.** Suppose that \(p_1, q_1, p_2, q_2, m, K > 0\) are fixed. Then \(H(A) = 0\) has a smallest positive root \(A^H\) in \((0, s_1 + s_2)\).

**Proof.** Recalling that \(B = -e < 0\) for any \(e > 0\), we have

\[
H(0) = (q_1 + q_2)(p_1 + p_2)(BC)^2 - BC(q_1 + q_2)(s_1 + s_2)s_1s_2 > 0.
\]

While

\[
H(s_1 + s_2) = (q_1 + q_2)(p_1 + p_2 - (s_1 + s_2))(BC)^2 - (q_1 + q_2)q_1s_2(s_1 + s_2)BC - [q_1s_2(s_1 + s_2)]^2,
\]
which can be regarded as a quadratic polynomial with respect to $BC$. It is remarkable that the discriminant $\Delta$ of the quadratic polynomial is

$$\Delta = [(q_1 + q_2)q_1s_2(s_1 + s_2)2 + 4(q_1 + q_2)(p_1 + p_2 - (s_1 + s_2))q_1s_2^2(s_1 + s_2)^2$$

$$= (q_1 + q_2)(q_1 + q_2 + 4(p_1 + p_2 - (s_1 + s_2))[q_1s_2(s_1 + s_2)]^2$$

$$= -(3q_1 + 3q_2)[q_1s_2(s_1 + s_2))^2 < 0$$

for any $q_1, q_2, p_1, p_2 > 0$. Hence $H(s_1 + s_2) < 0$ for any $BC$. Then the intermediate value theorem implies that $H$ has at least one positive root $A$ in $(0, s_1 + s_2)$ and the smallest one is denoted by $A^H$.

Lemma 4.1 extends the stability domain of the system without quiescence (3) into $A > 0$. Notice that the system without quiescence has the Hopf bifurcation value $A = 0$, but this Hopf bifurcation value is now shifted to a positive $A$ and we will specify the Hopf bifurcation value $A^H$ for the system (1).

**Theorem 4.2.** Let $A^H$ be the smallest positive root of $H(A) = 0$. Then $H(A^H) = 0$ has a pair of purely imaginary roots $\pm ki$ where $k = \sqrt{A_1(A^H)}/A_3(A^H)$. Moreover, if

$$\alpha = 4q_1s_2 + 4A_1A_0A_3 - 2A_1^2A_2 - 3A_1A_3(q_1 + q_2) + 3A_1\alpha_3^2 - 2q_1s_2A_2A_3 \neq 0,$$

then $A = A^H$ is a Hopf bifurcation value of system (1) and there is a small amplitude periodic solutions bifurcating from equilibrium $(\lambda, v_\lambda, p_1\lambda/q_1, p_2v_\lambda/q_2)$.

**Proof.** We search for purely imaginary roots of the characteristic equation (8). Substituting $\mu = ki$ into (8) and simplifying, we have

$$\begin{cases} k^4 - A_2k^2 + A_0 = 0, \\
-A_3k^2 + A_1 = 0. \end{cases}$$

(9)

Thus, a pair of imaginary eigenvalues exists if the parameters satisfy the condition

$$A_1^2 - A_1A_2A_3 + A_0A_3^2 = 0.$$  

(10)

After straightforward calculations, we find that

$$-H(A, q_1, q_2, p_1, p_2) = A_1^2 - A_1A_2A_3 + A_0A_3^2.$$

Therefore, the smallest root $A^H$ of $H(A) = 0$ is nicely the Hopf bifurcation point of (1).

From Lemma 4.1 and the expression $k^2 = A_1/A_3 > 0$, we have $A_i > 0(i = 0, 1, 2, 3)$, which also restricts the Hopf bifurcation parameter range of $A^H$ to

$$0 < A^H < \frac{s_1s_2 - BC}{q_1 + s_2}. \quad (11)$$

Considering $\mu$ as a function of $A$, and differentiating the characteristic equation (8) with respect to $A$, we obtain

$$\frac{d\mu(A)}{dA} = \frac{q_1s_2\mu - A_1 + \mu^3 + (q_1 + s_2)\mu^2}{4\mu^4 + 3A_3\mu^2 + 2A_2\mu}. \quad (12)$$

Substituting $\mu = ki$ into (12), we obtain

$$\frac{d\mu(A)}{dA} = \frac{[-(q_1 + s_2)k^2 - A_1] + [q_1s_2k - A_1k^3]i}{-3A_3k^3 + (2A_2k - 4k^3)i}. \quad (13)$$
After straightforward calculations, we have
\[ \text{Re} \left( \frac{d\mu(A)}{dA} \right) = \frac{k^2 \alpha}{a^2 + b^2}, \]
where
\[ a = 2A_2k - 4k^3, \quad b = -3A_3k^2. \]
We have \( \text{Re} \left( \frac{d\mu(A)}{dA} \right) \neq 0 \) since \( \alpha \neq 0 \), which implies that the transversal condition is satisfied. The proof is complete.

Remark 1. The expression of \( H(A,q_1,q_2,p_1,p_2) \) is essential in searching for the Hopf bifurcation point \( A \). In fact, we can also find other Hopf bifurcation parameters value such as \( q_1,q_2,p_1,p_2 \) by using the similar method in Lemma 4.1 and Theorem 4.2, which also can be captured in section 5 by numerical simulations. We take \( A \) as the main bifurcation parameter for the better clear comparison with the bifurcation value for the system without quiescence.

5. Numerical simulations. We will use several numerical simulations to illustrate and explore the impact of quiescence generated by the models (1) in different parameter regimes identified in the paper. The Matcont computing package in Matlab is implemented to solve the system (1).

1. Theorem 4.2 presents the parameter regimes in which the Hopf bifurcation value \( A^H \) of system (1) is positive (and it is obviously larger than the Hopf bifurcation value \( A^H_2 = 0 \) of system (3)), which can be illustrated in the followings. We take the same parameters as \( K = 2, m = 2 \) in both systems. Then the Hopf bifurcation point of (3) is \( e \approx 0.6667 \) (or equivalent to \( A^H_2 = 0 \)). While the Hopf bifurcation point of (1) is \( e \approx 0.6465 \) (or equivalent to \( A^H \approx 0.0072 \)) with \( p_1 = 1, q_1 = 0.5, p_2 = 2, q_2 = 3 \), see Figure 3.

![Figure 3](image)

**Figure 3.** (left): The Bifurcation graphs of (3); (right): The Bifurcation graphs of (1).

2. The unstable coexistence equilibrium of (3) will become stable with the quiescence. We take \( e = 0.66 \) and the other parameters same as Figure 3. In fact, \( e = 0.66 \) lies in between the Hopf bifurcation value \( e \approx 0.6667 \) of (3) and the Hopf bifurcation value \( e \approx 0.6465 \) of (1). Thus the oscillation can be
obtained in system (3) without quiescence but the global stability of positive equilibrium for (1) with quiescence, see Figure 4.

3. The stability also changes with the “behavioural” parameters $p_i$ and $q_i$, $i = 1, 2$. In fact, we fix all parameters $K = 2$, $m = 2$, $e = 0.3$, $p_1 = 1$, $p_2 = 2$, $q_2 = 3$ and vary $q_1$. Figure 5 shows that $(\lambda, v, p_1\lambda/q_1, p_2v/\lambda/q_2)$ will increase the stability with the decreasing of $q_1$. It can be found the Hopf bifurcation value of (1) is $q_1 \approx 1.6961$.

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