DYNAMICS OF CONSUMER-RESOURCE SYSTEMS WITH CONSUMER’S DISPERAL BETWEEN PATCHES

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Abstract. This paper considers consumer-resource systems with Holling II functional response. In the system, the consumer can move between a source and a sink patch. By applying dynamical systems theory, we give a rigorous analysis on persistence of the system. Then we show local/global stability of equilibria and prove Hopf bifurcation by the Kuznetsov Theorem. It is shown that dispersal in the system could lead to results reversing those without dispersal. Varying a dispersal rate can change species’ interaction outcomes from coexistence in periodic oscillation, to persistence at a steady state, to extinction of both species. By explicit expressions of stable equilibria, we prove that dispersal can make the consumer reach overall abundance larger than if non-dispersing, and there exists an optimal dispersal rate that maximizes the abundance. Asymmetry in dispersal can also lead to those results. It is proven that the overall abundance is a ridge-like function (surface) of dispersal rates, which extends both previous theory and experimental observation. These results are biologically important in protecting endangered species.

1. Introduction. With the uncontrolled land-usage of human, more and more habitats of species are fragmented. The fragmentation threatens survival of many endangered species [5]. Making ecological corridors between fragmented patches would reduce the threat. By the corridors, the species can disperse and colonize new patches or recolonize old patches. For example, Zhang et al. [29] reported that in their experiments with yeast (Saccharomyces cerevisiae, a consumer), the manipulated movement of yeast between patches makes it survive in some patches where it cannot survive in the absence of movement. However, the corridors may also enhance the threat. By the corridors, the species may move from suitable to unsuitable patches with low reproductive rates. Indeed, Aström and Pütt [3] showed that the corridors might have negative effects on the overall abundance in laboratory experiments with oribatid mites. Thus, it is significant to study whether or not making ecological corridors enhances total abundance of species.

Holt [12] studied dispersal of species between a source and a sink patch. Here, a patch is called a source (resp. a sink) if the species can (resp. cannot) survive on it. For example, a refuge is a source for an endangered species, while the fragmented

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poor habitat may be a sink. By analyzing the one-species model, Holt showed that when the dispersal rate is small and the absolute magnitude of the death rate in the sink is less than the intrinsic rate of increase in the source population, the species persists in both patches and passive dispersal into the sink increases total population abundance. Wu et al. [27] studied a specific case of Holt’s model, and showed that total population abundance of the species increases when dispersal increases with a relatively small rate, then approaches a maximum, and finally decreases. This hump-shaped response was confirmed in real observations. Indeed, in their laboratory experiments, Zhang et al. [30] checked total population abundances with four different dispersal rates, namely 0%, 6%, 10%, 20%, and found that the maximum was attained at 6%. Moreover, Zhang et al. [28] reported that the increased “extra individuals” through dispersal resided in the poor patches in experiments. For additional relevant literature, we refer to [8-18].

In real situations, a species often coexists with others and has various relationships with them. Ruiz-Herrera and Torres [21] studied dispersal in two-species systems with relationship of predation/competition. In their study on predator-prey systems with the predator’s dispersal, they showed that when the dispersal is small, there are precise thresholds that determine when dispersal makes the predator reach overall abundance higher than if non-dispersing. While Ruiz-Herrera and Torres provided interesting predictions, they assumed that the functional response in predation is linear and the dispersal is symmetric, which means that the dispersal rate from one patch to the other is equal to that in the opposite direction. In nature, the functional response can be nonlinear (e.g., with saturated response), and the dispersal can be asymmetric. Thus, it is necessary to study dispersal systems with asymmetric dispersal, where the functional response is nonlinear.

In this paper, we consider consumer-resource systems with Holling II functional response. In the system, the consumer can move between a source and a sink. By applying dynamical systems theory, we show nonnegativeness and boundedness of solutions of the model, and give a rigorous analysis on persistence of the system (see Proposition 1 and Theorem 3.1 and Fig. 1). Then we show local/global stability of equilibria by using both the graph method and Lyapunov theory (see Theorems 3.2-3.3). We prove periodic oscillations by computing the first Lyapunov coefficient (see Theorem 4.3 and Fig. 2). It is shown that dispersal in the system can lead to results reversing those without dispersal: (a) Dispersal can change species’ coexistence in periodic oscillation without dispersal to species’ persistence at a steady state; (b) Dispersal can change species’ persistence, to extinction of the predator, and even to extinction of both species. Varying a dispersal rate (resp. one parameter) can lead to transition of species’ interaction outcomes between coexistence in periodic oscillation, persistence at a steady state, extinction of the predator, and extinction of both species in a smooth fashion (see Section 6 and Figs. 1,5). By explicit expressions of stable equilibria, we prove that dispersal can make the consumer reach overall abundance larger than if non-dispersing, and there exists an optimal dispersal that maximizes the abundance. Meanwhile, the dispersal always makes the resource species reach a density higher than if non-dispersing. Asymmetry in dispersal can also lead to the results. It is proven that the overall abundance is a ridge-like function (surface) of dispersal rates, which extends both previous theory and experimental observation (see Section 5 and Figs. 3-4). Numerical simulations illustrate and extend our results.
The paper is organized as follows. In the next section, we describe the model. Section 3 proves persistence of the system, Section 4 shows Hopf bifurcation, while total population abundance is analyzed in Section 5. Discussion and application are in Section 6.

2. Model. In this section, we describe the consumer-resource model with dispersal. Let \( M \) represent the resource and \( N \) the consumer. Species \( M \) lives in patch 1 all the time, while the consumer \( N \) can move between patch 1 and 2. When the predation in patch 1 has saturated responses, the consumer-resource system can be described by

\[
\frac{dM}{dt} = rM(1 - \frac{M}{K} - \frac{a_{12}N_1}{b + M}) \\
\frac{dN_1}{dt} = N_1(-r_1 + \frac{a_{21}M}{b + M}) + D_2N_2 - D_1N_1 \\
\frac{dN_2}{dt} = -r_2N_2 + D_1N_1 - D_2N_2
\]

(1)

where \( M \) represents population density of the resource in patch 1, and \( N_i \) is that of the consumer in patch \( i, i = 1, 2 \). Parameter \( r \) represents the intrinsic growth rate of resource in patch 1, and \( K \) is the carrying capacity. Parameter \( r_i \) represents the death rate of consumer in patch \( i \). The consumer consumes the resource with functional response \( \frac{ra_{12}MN_1}{b + M} \) (Holling II) and contributes to its growth with \( \frac{a_{21}MN_1}{b + M} \). Here, parameter \( ra_{12} \) measures the saturated consumption ratio, \( a_{21} \) is the conversion ratio, and \( b \) is the half-saturation density. Parameter \( D_1 \) represents the dispersal rate of consumer from patch 1 to 2, and \( D_2 \) is that from patch 2 to 1. All parameters in (1) are positive. We consider solutions of (1) with nonnegative initial values, i.e., \( M(0) \geq 0, N_i(0) \geq 0 \).

Since variables \( M(t) \) and \( N_i(t) \) represent population densities, they must be nonnegative. They should be bounded because any density in nature cannot reach infinity. The following result shows these properties.

**Proposition 1.** Solutions of system (1) are nonnegative and bounded.

*Proof.* Since the boundary plane \( M = 0 \) is an invariant set of system (1), each orbit of (1) cannot pass through the plane \( M = 0 \), which implies that \( M(t) \geq 0 \) as \( t > 0 \).

On the boundary plane \( N_1 = 0 \), we have \( dN_1/dt = D_2N_2 \geq 0 \). If \( N_2 > 0 \), then \( dN_1/dt > 0 \), which implies \( N_1(t) > 0 \) as \( t > 0 \). If \( N_2 = 0 \), we have \( N_1 = N_2 = 0 \), and we can see that all solutions of (1) on the \( M \)-axis converge to equilibrium \( P_1(K, 0, 0) \), which implies that \( N_1(t) \equiv 0 \) as \( t > 0 \). Thus, we obtain \( N_1(t) \geq 0 \) as \( t > 0 \).

On the boundary plane \( N_2 = 0 \), we have \( dN_2/dt = D_1N_1 \geq 0 \). A similar discussion could show \( N_2(t) \geq 0 \) as \( t > 0 \). Thus, solutions of system (1) are nonnegative.

From the first equation of (1) we have

\[
\frac{dM}{dt} \leq rM(1 - \frac{M}{K}).
\]

The comparison theorem [10] implies \( \limsup_{t \to \infty} M(t) \leq K \). Then there exists \( \delta_0 > 0 \) and \( T_0 > 0 \) such that when \( t > T_0 \), we have \( M(t) \leq K + \delta_0 \).
From (1) we have
\[
\frac{d}{dt} \left( \frac{a_{21}}{a_{12}} M + N_1 + N_2 \right) = \frac{a_{21}}{a_{12}} M \left( 1 - \frac{M}{K} \right) - r_1 N_1 - r_2 N_2 \\
\leq \frac{a_{21}}{a_{12}} M \left( 1 - \frac{M}{K} \right) - \tilde{r} (N_1 + N_2 + \frac{a_{21}}{ra_{12}} M) + \frac{\tilde{r} a_{21}}{ra_{12}} M
\]
where \( \tilde{r} = \min\{r_1, r_2\} \). Then we have
\[
\frac{d}{dt} \left( \frac{a_{21}}{ra_{12}} M + N_1 + N_2 \right) \leq \tilde{K} - \tilde{r} (N_1 + N_2 + \frac{a_{21}}{ra_{12}} M)
\]
with
\[
\tilde{K} = \frac{a_{21}}{a_{12}} (1 + \frac{\tilde{r}}{r}) (K + \delta_0).
\]
Citing the comparison theorem again, we have
\[
\limsup_{t \to \infty} \left( \frac{a_{21}}{ra_{12}} M + N_1 + N_2 \right) \leq \frac{\tilde{K}}{\tilde{r}}
\]
which implies that solutions of (1) are bounded and system (1) is dissipative.

When there is no dispersal, i.e., \( D_1 = D_2 = 0 \), we have \( \lim_{t \to \infty} N_2(t) = 0 \) by the third equation of system (1). Then all solutions of (1) converge to the boundary \( N_2 = 0 \), and system (1) becomes:
\[
\begin{align*}
\frac{dM}{dt} &= r M \left( 1 - \frac{M}{K} - \frac{a_{12} N_1}{b + M} \right) \\
\frac{dN_1}{dt} &= N_1 \left( -r_1 + \frac{a_{21} M}{b + M} \right).
\end{align*}
\]
(2)

There are two boundary equilibria \( O(0,0), \bar{P}_1(K,0) \) in system (2). A possible positive equilibrium \( \bar{P}^+ (M^+, N_1^+) \) of (2) satisfies
\[
M^+ = \frac{br_1}{a_{21} - r_1}, \quad N_1^+ = \frac{b + M^+}{a_{12}} \left( 1 - \frac{M^+}{K} \right).
\]

Dynamics of system (2) are well known, which are shown as follows [11].

**Proposition 2.** \( i \) If
\[
a_{21} \leq \frac{r_1 (K + b)}{K},
\]
equilibrium \( \bar{P}_1(K,0) \) of system (2) is globally asymptotically stable in \( \operatorname{int} \mathbb{R}^2_+ \).

\( ii \) If
\[
a_{21} > \frac{r_1 (K + b)}{K},
\]
\[
(K - b) a_{21} \leq r_1 (K + b),
\]
equilibrium \( \bar{P}^+ (M^+, N_1^+) \) of system (2) is globally asymptotically stable in \( \operatorname{int} \mathbb{R}^2_+ \).

\( iii \) If
\[
(K - b) a_{21} > r_1 (K + b),
\]
equilibrium \( \bar{P}^+ \) is unstable and system (2) admits a periodic solution, which is globally asymptotically stable in \( \operatorname{int} \mathbb{R}^2_+ - \{ \bar{P}^+ \} \).
3. **Persistence.** In this section, we show persistence of system (1) and prove local/global stability of equilibria. Denote

\[
\begin{align*}
D_1^+ &= \frac{a_21 K - r_1}{K + b} \frac{r_2 + D_2}{r_2}, \quad D_1^0 = \frac{a_21(K - b)}{K + b} \frac{r_2 + D_2}{r_2}, \\
D_1^- &= \frac{a_21(K - b)}{K} - r_1 \frac{r_2 + D_2}{r_2}, \quad c = r_1 + \frac{r_2 D_1}{r_2 + D_2}.
\end{align*}
\]

Then \( D_1^+ > 0 \) if condition (4) holds; \( D_1^0 > 0 \) if condition (6) holds; \( D_1^+ > D_1^0 > D_1^- \) if \( K - b > 0 \).

**Theorem 3.1.** Let (4) hold.

(i) If \( D_1 < D_1^+ \), system (1) is uniformly persistent as shown in Figs. 1a-c.

(ii) If \( D_1 > D_1^+ \), the boundary equilibrium \( P_1(K, 0, 0) \) is globally asymptotically stable in \( \text{int}R_3^+ \), and system (1) is not persistent as shown in Fig. 1d.

**Proof.** From (4), we have \( D_1^+ > 0 \).

(i) On the boundary \( M = 0 \), it is obvious that all solutions of (1) converge to equilibrium \( O \).

On the boundary \( N_1 = 0 \), we have \( dN_1/dt = D_2 N_2 \geq 0 \). If \( N_2 > 0 \), then \( dN_1/dt > 0 \), which implies that no positive solution of (1) would approach the boundary \( N_1 = 0 \). If \( N_2 = 0 \), then we have \( N_1 = N_2 = 0 \), and we can see that all solutions of (1) on the M-axis converge to equilibrium \( P_1(K, 0, 0) \). Thus, no positive solution of (1) would approach the boundary \( N_1 = 0, N_2 > 0 \).

On the boundary \( N_2 = 0 \), we obtain \( dN_2/dt = D_1 N_1 \geq 0 \). A similar discussion could show that no positive solution of (1) would approach the boundary \( N_1 > 0, N_2 = 0 \). Thus, in order to show persistence of (1), we need to prove that the boundary equilibria \( O \) and \( P_1 \) have no stable manifold in \( \text{int}R_3^+ \), which is shown as follows.

The Jacobian matrix of (1) at \( O \) is

\[
J_0 = \begin{pmatrix}
r & 0 & 0 \\
0 & -r_1 - D_1 & D_2 \\
0 & D_1 & -r_2 - D_2
\end{pmatrix}.
\]

Then \( J_0 \) has an eigenvalue \( \mu_1 = r > 0 \). The other two eigenvalues \( \mu_2, \mu_3 \) satisfy

\[
\mu^2 + \alpha_0 \mu + \beta_0 = 0
\]

with

\[
\alpha_0 = r_1 + D_1 + r_2 + D_2 > 0, \quad \beta_0 = (r_1 + D_1)(r_2 + D_2) - D_1 D_2 > 0,
\]

which means that \( \text{Re} \mu_2 < 0, \text{Re} \mu_3 < 0 \). Thus, equilibrium \( O \) is a saddle point, and has the boundary \( M = 0 \) as its stable manifold and the M-axis as its unstable manifold, which means that \( O \) has no stable manifold in \( \text{int}R_3^+ \).

The Jacobian matrix of (1) at \( P_1 \) is

\[
J_1 = \begin{pmatrix}
-r & -r_2 a_21 \frac{K}{b + K} & 0 \\
0 & -r_1 - D_1 + a_21 \frac{K}{b + K} & D_2 \\
0 & D_1 & -r_2 - D_2
\end{pmatrix}.
\]

Then \( J_1 \) has an eigenvalue \( \lambda_1 = -r < 0 \) and the corresponding eigenvector is \( v_1(1,0,0) \), which means that the M-axis is its stable manifold. The other two
eigenvalues $\lambda_2, \lambda_3$ satisfy

$$\lambda^2 + \alpha_1 \lambda + \beta_1 = 0$$

with

$$\alpha_1 = r_1 + D_1 - a_{21} \frac{K}{b + K} + r_2 + D_2, \quad \beta_1 = (r_1 + D_1 - a_{21} \frac{K}{b + K})(r_2 + D_2) - D_1 D_2.$$

Then we obtain $\beta_1 < 0$ by $D_1 < D_1^+$, which means that $\lambda_2 \lambda_3 < 0$ and equilibrium $P_1$ is a saddle point. Without loss of generality, we assume $\lambda_2 < 0 < \lambda_3$. A direct computation shows that the eigenvalue $\lambda_2 < 0$ has an eigenvector $v_2(v_{21}, v_{22}, v_{23})$ with

$$v_{21} = 0, \quad v_{22} = -D_2, \quad v_{23} = \frac{1}{2}(r_2 + D_2 + a_{21} \frac{K}{b + K} - r_1 - D_1 + \sqrt{\alpha_1^2 - 4\beta_1}).$$

Since

$$\alpha_1^2 - 4\beta_1 - (r_2 + D_2 + a_{21} \frac{K}{b + K} - r_1 - D_1)^2 = 4D_1 D_2 > 0,$$

we obtain $v_{23} > 0$, which implies that eigenvector $v_2$ isn’t directed toward $\text{int}\mathbb{R}_+^3$.

Similarly, the eigenvalue $\lambda_3 > 0$ has an eigenvector $v_3(v_{31}, v_{32}, v_{33})$ with

$$v_{31} = 0, \quad v_{32} = D_2, \quad v_{33} = \frac{1}{2}(-r_2 - D_2 - a_{21} \frac{K}{b + K} + r_1 + D_1 + \sqrt{\alpha_1^2 - 4\beta_1}).$$

From (9) we obtain $v_{31} > 0$, which means that eigenvector $v_3$ is directed toward $\text{int}\mathbb{R}_+^3$. Thus, $P_1$ has no stable manifold in $\text{int}\mathbb{R}_+^3$.

Since the boundary equilibria $O$ and $P_1$ cannot be in a heteroclinic cycle in $\mathbb{R}_+^3$, we obtain uniform persistence of system (1) by the Acyclicity Theorem [4].

(ii) Since $D_1 > D_1^+$, there is $\delta_0 > 0$ such that $D_1 > D_1^+$ with

$$\bar{D}_1^+ = (\frac{a_{21} \bar{K}}{K + b} - r_1) \frac{r_2 + D_2}{r_2}, \quad \bar{K} = K + \delta_0.$$

From the first equation of (1), we have

$$\frac{dM}{dt} \leq r M (1 - \frac{M}{K})$$

which means $\limsup_{t \to \infty} M(t) \leq K$ by the comparison theorem (Hale, 1969). Let $(M(t), N_1(t), N_2(t))$ be a solution of (1) with $M(0) = M^0 > 0, N_i(0) = N_i^0 > 0, i = 1, 2$. Then there exists $T > 0$ such that $M(t) < K$ if $t > T$.

From the second and third equation of (1), we have

$$\frac{dN_1}{dt} \leq N_1(-r_1 + a_{21} \frac{\bar{K}}{b + \bar{K}}) + D_2 N_2 - D_1 N_1$$

$$\frac{dN_2}{dt} \leq -r_2 N_2 + D_1 N_1 - D_2 N_2. \tag{10}$$

Consider a new system

$$\frac{dn_1}{dt} = (-r_1 - D_1 + \frac{a_{21} \bar{K}}{b + \bar{K}}) n_1 + D_2 n_2$$

$$\frac{dn_2}{dt} = D_1 n_1 - (r_2 + D_2) n_2 \tag{11}$$

with $n_i(0) = N_i^0 > 0, i = 1, 2$. System (11) is linear with coefficient matrix $\bar{A}$. Since $D_1 > \bar{D}_1^+$, we have

$$\text{tr} \bar{A} = -D_1 + \frac{a_{21} \bar{K}}{b + \bar{K}} - r_1 - (r_2 + D_2) < -(r_2 + D_2) < 0, \quad \det \bar{A} = r_2 (D_1 - \bar{D}_1^+) > 0,$$
which means equilibrium \((0, 0)\) of system \((11)\) is globally asymptotically stable and 
\[ \lim_{t \to \infty} n_i(t) = 0. \] 
As system \((11)\) is cooperative, we have 
\[ \limsup_{t \to \infty} N_i(t) \leq 0 \] 
([22], Appendix B). Thus, 
\[ \lim_{t \to \infty} N_i(t) = 0 \] 
equilibrium \(P_1(K, 0, 0)\) of system \((1)\) is globally asymptotically stable.

**Corollary 1.** Let \((3)\) hold. The boundary equilibrium \(P_1(K, 0, 0)\) is globally asymptotically stable in \(\text{int} \mathbb{R}_+^3\), and system \((1)\) is not persistent.

**Proof.** From \((1)\), we have 
\[ a_{21} \leq r_1(K + b)/K \] 
and 
\[ D_1^+ \leq 0. \] 
If \(D_1 > 0\), then \(D_1 > D_1^+\). By a proof similar to that for Theorem 3.1(ii), we obtain that \(P_1\) is globally asymptotically stable. If \(D_1 = 0\) and \(D_2 \geq 0\), then \(N_2 \to 0\) by the third equation of \((1)\), which means \(N_1 \to 0\) and \(M \to K\) by the first and second equations of \((1)\) and Proposition 2(i). Thus, \(P_1\) is globally asymptotically stable.

Theorem 3.1 makes sense biologically. From \((4)\), we have 
\[ a_{21} > r_1(K + b)/K. \] 
When there is no dispersal, the consumer persists in patch 1 by Proposition 2(iii). When there is dispersal and the dispersal from the source to sink is small (i.e., \(D_1 < D_1^+\)), the consumer persists in both patches. The biological reason is that individuals that die in the sink are compensated by those moving from the source, which leads to the consumer’s persistence in both patches. However, when the dispersal is large (i.e., \(D_1 > D_1^+\)), the consumer goes to extinction in both patches. The underlying reason is that too many individuals move from the source to sink to die, which results in the extinction.

Corollary 1 displays that if the consumer cannot persist in the system without dispersal, it will go to extinction in both patches with any dispersal. Indeed, from \((3)\), we have \(a_{21} \leq r_1(K + b)/K\), which means that when there is no dispersal, the consumer will go to extinction in patch 1 by Proposition 2(i). When there is dispersal, Corollary 1 shows that the consumer goes to extinction for any dispersal. This is consistent with our intuition since dispersal leads to movement of the consumer to a sink, which accelerates its extinction in the source and then results in its extinction in both patches.

When \(D_1 < D_1^+\), the dissipativity and uniform persistence of the system now guarantee (see [4]) that system \((1)\) has a positive equilibrium \(P^*(M^*, N_1^*, N_2^*)\), which satisfies

\[
1 - \frac{M^*}{K} - \frac{a_{12}N_1^*}{b + M^*} = 0
\]

\[
N_1^*(-r_1 + \frac{a_{21}M^*}{b + M^*} + D_2N_2^* - D_1N_1^* = 0
\]

\[
-r_2N_2^* + D_1N_1^* - D_2N_2^* = 0
\]

so that

\[
M^* = \frac{bc}{a_{21} - c}, \quad N_1^* = \frac{b + M^*}{a_{12}}(1 - \frac{M^*}{K}), \quad N_2^* = \frac{D_1}{r_2 + D_2}N_1^*.
\] (12)

A direct computation shows that \(D_1 < D_1^+\) if and only if \(a_{21} > c, M^* < K\). Therefore, we conclude the following result.

**Proposition 3.** Let \((4)\) hold. System \((1)\) has a positive equilibrium \(P^*\) if and only if \(D_1 < D_1^+\). The positive equilibrium of \((1)\) is unique when it exists.
The Jacobian matrix of (1) at $P^*(M^*, N_1^*, N_2^*)$ is

$$J^* = \begin{pmatrix}
    rM^*(-\frac{1}{K} + \frac{a_{12}N_1^*}{(b + M^*)^2}) & -a_{12}\frac{rM^*}{b + M^*} & 0 \\
    a_{21}N_1(\frac{1}{(b + M^*)^2}) & -r_1 - D_1 + \frac{a_{21}M^*}{b + M^*} & D_2 \\
    0 & D_1 & -r_2 - D_2
\end{pmatrix}.  \quad (13)
$$

The characteristic equation of $J^*$ is

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

where

$$a_1 = re_1 + e_2, \quad a_2 = r(e_3 + e_1e_2), \quad a_3 = re_3(r_2 + D_2)$$

$$a_1a_2 - a_3 = r[e_3\frac{D_1D_2}{r_2 + D_2} + e_2^2e_1 + re_1(e_3 + e_1e_2)] \quad (14)$$

with

$$e_1 = \frac{c + a_{21}}{a_{21}K}M^* - \frac{c}{a_{21}}, \quad e_2 = r_2 + D_2 + \frac{D_1D_2}{r_2 + D_2} > 0, \quad e_3 = \frac{bc}{b + M^*(1 - \frac{M^*}{K})}.$$

From $D_1 < D_1^+$, we have $M^* < K$ and then $e_3 > 0, a_3 > 0$. By the Hurwitz Criteria, we conclude the following result.

**Theorem 3.2.** Assume

$$a_{21} > r_1(K + b)/K, \quad D_1 < D_1^+, \quad a_1 > 0, \quad a_1a_2 - a_3 > 0. \quad (15)$$

Then the positive equilibrium $P^*$ is locally asymptotically stable.

Finally, we give sufficient conditions for global stability of $P^*$.

**Theorem 3.3.** Let (4) hold. If $D_1^* < D_1 < D_1^+$, the positive equilibrium $P^*(M^*, N_1^*, N_2^*)$ of system (1) is globally asymptotically stable in $\mathbb{R}^3_+$.

**Proof.** From $a_{21} > r_1(K + b)/K$ we have $D_1^+ > 0$. From $D_1 < D_1^+$, we have $a_{21} > a_1$ and system (1) has a positive equilibrium $\tilde{P}^*(M^*, N_1^*, N_2^*)$.

Choose a Lyapunov function as follows:

$$V(M, N_1, N_2) = \delta \int_{M^*}^{M} \frac{M - M^*}{M} \, dM + \int_{N_1^*}^{N_1} \frac{N_1 - N_1^*}{N_1} \, dN_1 + \int_{N_2^*}^{N_2} \frac{N_2 - N_2^*}{N_2} \, dN_2,$$

where $\delta$ is a positive constant to be determined. Along any trajectory of system (1), we have

$$\frac{dV}{dt} = \delta r(M - M^*)[1 - \frac{M}{K} - \frac{a_{12}N_1}{b + M}] + (N_1 - N_1^*)(-r_1 + a_{21}\frac{M}{b + M})$$

$$+ \frac{N_1 - N_1^*}{N_1}(D_2N_2 - D_1N_1) + \frac{D_2N_2^2}{D_1N_1^*}N_2 - N_2^*(\frac{-r_2N_2 + D_1N_1 - D_2N_2}{N_2})$$

$$= \delta r(M - M^*)[1 - \frac{M - M^*}{K} + \frac{a_{12}N_1^*}{b + M^*} + \frac{N_1^*(M - M^*) - (b + M^*)(N_1 - N_1^*)}{(b + M)(b + M^*)}]$$

$$+ (N_1 - N_1^*)(a_{21}\frac{M^*}{b + M^*} - \frac{M^*}{N_1^*}N_2 - \frac{N_2^*}{N_1^*}N_2)$$

$$+ \frac{D_2N_2^2}{N_2^*}(N_2 - N_2^*)(\frac{N_1}{N_2} - \frac{N_1^*}{N_2^*})$$

$$= -\delta r\frac{1}{K} - \frac{a_{12}N_1^*}{(b + M^*)(b + M^*)}(M - M^*)^2$$

$$+ [a_{21}b - \delta a_{12}(b + M^*)]\frac{(M - M^*)(N_1 - N_1^*)}{(b + M)(b + M^*)} - \frac{D_2}{N_1^*N_2N_2^*}(N_1N_2^* - N_2N_1^*)^2.$$
From $D_1 > D^-_1$, we have
\[
\frac{1}{K} > \frac{a_{12}N^*_1}{b(b + M^*)}.
\]
Choose
\[
\delta = \frac{a_{21}b}{a_{12}r(b + M^*)}.
\]
Then we obtain $\frac{dV}{dt} \leq 0$ and $\frac{dV}{dt} = 0$ if and only if $M = M^*, \frac{N_1}{N^*_1} = \frac{N_2}{N^*_2}$, which implies $N_1 = N^*_1, N_2 = N^*_2$ by (12). Therefore, LaSalle’s Invariance Principle implies that $P^*$ is globally asymptotically stable in int $\mathbb{R}^3_+$. This completes the proof.

4. Periodic oscillation. In this section, we show periodic oscillations in system (1) by using the following result.

**Theorem 4.1.** [18] Let $\dot{x} = F(x)$ be an $n$-dimensional differential system with $F \in C^4$, in which $P^*$ is an equilibrium. Let the first three terms of the Taylor approximation of $F$ at $P^*$ be written as
\[
F(x) = Ax + \frac{1}{2}B(x,x) + \frac{1}{3!}C(x,x,x) + O(|x|^4).
\]
Assume that the Jacobian matrix $A$ has a pair of purely imaginary eigenvalues $\pm \omega i$. Let $q$ be the normalized eigenvector of $A$ corresponding to the eigenvalue $\omega i$ with $q \cdot \bar{q} = 1$, where $\bar{q}$ is the conjugate vector of $q$. Let $p$ be the adjoint eigenvector such that $A^T p = -\omega i p$ with $\bar{p} \cdot q = 1$. Let $I$ be the $n \times n$ identity matrix. Then the first Lyapunov coefficient $l_1(P^*)$ of the system $\dot{x} = F(x)$ at equilibrium $P^*$ is
\[
l_1(P^*) = \frac{1}{2\omega} \text{Re} \left[ \bar{p} \cdot C(q,q,\bar{q}) - 2\bar{p} \cdot B(q,A^{-1}B(q,\bar{q})) + \bar{p} \cdot B(\bar{q},(2\omega iI - A))^{-1}B(q,\bar{q}) \right].
\]
\[(16)\]

When $l_1(P^*) < 0$, supercritical bifurcation occurs: equilibrium $P^*$ is a weak focus of the differential system restricted to the central manifold at $P^*$, associated to the pair of complex eigenvalues which cross the imaginary axis, and the emerging limit cycle from $P^*$ is stable. When $l_1(P^*) > 0$, the limit cycle that emerges from $P^*$ is unstable, where subcritical bifurcation occurs.

For convenience, we re-parameterize the trajectories of system (1) by introducing a variable $\tau$ such that $\frac{dt}{d\tau} = b + M$. Setting $M(t) = M(\tau(t)), N_1(t) = N_1(\tau(t)), N_2(t) = N_2(\tau(t))$ and using the chain rule, we obtain the following polynomial differential system
\[
\begin{align*}
\frac{dM}{d\tau} &= rM[(b + M)(1 - \frac{M}{K}) - a_{12}N_1] \\
\frac{dN_1}{d\tau} &= N_1[\frac{1}{r_1}N_1(b + M) + a_{21}M] + (D_2N_2 - D_1N_1)(b + M) \\
\frac{dN_2}{d\tau} &= (\frac{1}{r_2}N_2 + D_1N_1 - D_2N_2)(b + M).
\end{align*}
\]
\[(17)\]
When $D_1 < D_1^+$, there is a positive equilibrium $P^*(M^*, N_1^*, N_2^*)$ in (1), which is also a positive equilibrium of (17). Denote

$$a_1^* = (r_2 + D_2 + \frac{D_1 D_2}{r_2 + D_2})(b + M^*) - rM^*e_4, \quad e_4 = 1 - \frac{b + 2M^*}{K}$$

$$a_2^* = rM^*[ba_1(1 - \frac{M^*}{K}) - e_4(r_2 + D_2 + \frac{D_1 D_2}{r_2 + D_2})(b + M^*)]$$

$$a_3^* = rsa_1 M^*(1 - \frac{M^*}{K})(r_2 + D_2)(b + M^*) > 0.$$  \hspace{1cm} (18)

Then $e_4 > 0$ if and only if $D_1 < D_1^0$.

Prior to stating and proving our main result in this section, we prove the following lemma.

**Lemma 4.2.** Let (6) hold. Let $D_1 < D_1^0$ and $a_2^* > 0$.

(i) System (17) has a positive equilibrium $P^*(M^*, N_1^*, N_2^*)$, which is independent of the parameter $r$, i.e., $P^*$ is fixed when $r$ varies.

(ii) There exists a unique value $r^* > 0$ such that when $r = r^*$, the Jacobian matrix $A$ of system (17) at $P^*$ has a pair of imaginary conjugate eigenvalues, $\pm \omega i$ and the third eigenvalue, $\alpha < 0$.

(iii) When $r < r^*$, all eigenvalues of matrix $A$ have negative real parts and equilibrium $P^*$ is asymptotically stable. When $r > r^*$, the matrix $A$ has a pair of eigenvalues $\mu \pm \omega i$ with $\mu > 0$ and the third eigenvalue $\alpha < 0$, and equilibrium $P^*$ is a saddle point.

**Proof.** (i) From (6), we have $D_1^0 > 0$. From $D_1 < D_1^0$, we have $e_4 > 0$, $D_1 < D_1^+$, which implies that there exists a unique positive equilibrium $P^*(M^*, N_1^*, N_2^*)$ in (1) and (17) by Proposition 3. From explicit expressions of $M^*, N_1^*$ and $N_2^*$ in (12), the positive equilibrium $P^*$ is independent of the parameter $r$.

(ii) By (12), the Jacobian matrix of (17) at $P^*(M^*, N_1^*, N_2^*)$ is

$$A = \begin{pmatrix}
\frac{rM^*e_4}{bao_1(1 - \frac{M^*}{K})} & -\frac{a_1}{a_2} & 0 \\
0 & -\frac{D_1 D_2}{r_2 + D_2}(b + M^*) & D_2(b + M^*) \\
0 & -\frac{D_1}{D_1(b + M^*)} & -(r_2 + D_2)(b + M^*)
\end{pmatrix}. \hspace{1cm} (19)$$

Then the characteristic equation of $A$ is

$$f(\lambda) = \lambda^3 + a_1^* \lambda^2 + a_2^* \lambda + a_3^* = 0.$$  \hspace{1cm} (20)

Assume that $\alpha$ and $\omega > 0$ satisfy

$$f(\lambda) - (\lambda - \alpha)(\lambda + \omega i)(\lambda - \omega i) = 0.$$  \hspace{1cm} (21)

Then $\alpha, \omega$ and the parameter value $r$ must satisfy

$$\alpha = -a_1^*, \quad \omega^2 = a_2^*, \quad \alpha \omega^2 = -a_3^*.$$  \hspace{1cm} (22)

From $D_1 < D_1^0$, we have $e_4 > 0$ and

$$\alpha = -\frac{a_3^*}{a_2^*} < 0, \quad \omega^2 = a_2^*, \quad \alpha \omega^2 = -a_3^*.$$  \hspace{1cm} (23)

Then the expressions of $a_2^*, a_3^*$ are independent of parameter $r$. From the proof of (ii) we obtain that if $r = r^*$, then $a_1^*a_2^* - a_3^* = r(a_1^*a_2^* - a_3^*) = 0$. Since the function $a_1^* = a_1^*(r)$ is monotonically decreasing with
Theorem 4.3. Let (6) hold. Let \( D_1 < D_0^* \) and \( a_2^* > 0 \). Let parameter \( r \) in (17) vary but fix other parameters. Then system (17) has a fixed positive equilibrium \( s \) of \( q \) with \( A \) of matrix expression for \( \omega, r \). Then supercritical bifurcation occurs at \( P^* \) and \( r = r^* \) when the first Lyapunov coefficient \( l_1(P^*) < 0 \), and a stable limit cycle emerges when \( r > r^* \).

Proof. In order to directly apply the Kuznetsov Theorem, we compute the linear \( A \), quadratic \( B \), and cubic \( C \) parts by the Taylor series of system (17) at \( P^* \), when \( \omega, r^* \) and \( \alpha \) satisfy (20). The explicit form of the matrix \( A \) is given in (19). The expression for \( B \) at the points \( x(x_1, x_2, x_3) \) and \( y(y_1, y_2, y_3) \) is

\[
B(x, y) = (B_1(x, y), B_2(x, y), B_3(x, y))
\]

with

\[
B_1(x, y) = 2r(1 - \frac{b + 3M^*}{K})x_1y_1 - a_12r(x_1y_2 + x_2y_1)
\]

\[
B_2(x, y) = (a_{21} - r - D_1)(x_1y_2 + x_2y_1) + D_2(x_1y_3 + x_3y_1)
\]

\[
B_3(x, y) = D_1(x_1y_2 + x_2y_1) - (r + D_2)(x_1y_3 + x_3y_1).
\]

The corresponding expression for \( C \) at the points \( x(x_1, x_2, x_3), y(y_1, y_2, y_3) \) and \( z(z_1, z_2, z_3) \) is

\[
C(x, y, z) = (C_1(x, y, z), C_2(x, y, z), C_3(x, y, z))
\]

with

\[
C_1(x, y, z) = \frac{6r}{K}x_1y_1z_1, \quad C_2(x, y, z) = 0, \quad C_3(x, y, z) = 0.
\]

Now we proceed to compute the normalized vectors \( q, \bar{q}, p \) and \( \bar{p} \). The eigenvector \( q \) of \( A \) corresponding to the eigenvalue \( \omega i \) is

\[
q = \frac{1}{s_0} \left( \frac{a_{12}rM^*[(r_2 + D_2)(b + M^*) + \omega i]}{[(r_2 + D_2)(b + M^*) + \omega i][rM^*e_4 - \omega i]} \right),
\]

where \( s_0 > 0 \) with

\[
s_0^2 = a_{12}^2r^2M^*[(r_2 + D_2)^2(b + M^*)^2 + \omega^2] + [rM^*e_4(r_2 + D_2)(b + M^*) + \omega^2]^2
\]

\[
+ \omega^2[rM^*e_4 - (r_2 + D_2)(b + M^*)]^2 + D_1^2(b + M^*)^2[rM^*e_4^2 + \omega^2].
\]

The adjoint eigenvector \( p \) associated with \( A^T \) (the transpose matrix of \( A \)) is

\[
p = \frac{s_0}{s_1} \left( \frac{ba_{21}(1 - \frac{M^*}{K})[(r_2 + D_2)(b + M^*) - \omega i]}{[(r_2 + D_2)(b + M^*) - \omega i][rM^*e_4 - \omega i]} \right)
\]

where

\[
s_1 = ba_{21}rM^*(1 - \frac{M^*}{K})[(r_2 + D_2)(b + M^*) - \omega i]^2
\]

\[
- [(r_2 + D_2)(b + M^*) - \omega i]^2rM^*e_4 + \omega i]^2 - D_1D_2(b + M^*)^2[rM^*e_4 + \omega i]^2.
\]

By the Kuznetsov Theorem, a Hopf bifurcation occurs at \( P^* \) and \( r = r^* \) when the first Lyapunov coefficient \( l_1(P^*) \neq 0 \). By Lemma 4.2(iii), we obtain the result.

\[\square\]
Numerical simulations illustrate the result in Theorem 4.3. Indeed, let
\[ r_1 = 0.2, \ r_2 = 0.1, \ a_{12} = 0.9, \ a_{21} = 0.8, \ b = 1, \ K = 4, \ D_1 = 0.3, \ D_2 = 0.1. \] (21)
By (20), we have \( r^* = 0.2718, \ \omega = 0.2979 \) and \( P^* = (0.7778, 1.5912, 2.3868) \). By
(16), a long but straightforward computation on the software MatLab shows that the first Lyapunov coefficient \( l_1(P^*) = -0.0263 < 0 \). By Theorem 4.3, system (1) admits a stable limit cycle when \( r > r^* \). Therefore, we conclude the following result.

**Corollary 2.** Let (21) hold. Then supercritical bifurcation occurs at \( P^* \) and \( r = 0.2718 \), while a stable limit cycle emerges when \( r > 0.2718 \), as shown in Fig. 2.

5. **Total population abundance.** In this section, we show that dispersal can make the consumer approach a total population abundance higher than if it were non-dispersing.

When there is no dispersal and conditions (4)-(5) hold, system (1) becomes (2), and system (2) has a stable positive equilibrium \( \bar{T}^+(r^*; N_1^+, N_2^+) \) as shown in Proposition 2. Then population abundances of the resource and consumer are

\[ \bar{T}_0 = M^* = \frac{br_1}{a_{21} - r_1}, \ \bar{T}_0 = N_1^+ = \frac{a_{21}b[Ka_{21} - (b + K)r_1]}{a_{12}K(a_{21} - r_1)^2}. \]

When there is dispersal and condition (15) holds, system (1) has a stable positive equilibrium \( P^*(M^*, N_1^+, N_2^+) \) as shown in Theorem 3.2. Let \( D_3 = 1/(r_2 + D_2) \). Then \( c = r_1 + r_2D_1D_3 \) and total population abundances of the resource and consumer are

\[ \bar{T}_1(D_1, D_2) = M^* = \frac{bc}{a_{21} - c}, \]
\[ T_1(D_1, D_2) = N_1^+ + N_2^+ = (1 + D_1D_3) \frac{a_{21}b[Ka_{21} - c(b + K)]}{a_{12}K(a_{21} - c)^2} \] (22)
so that

\[ F(D_1, D_2) = \bar{T}_1(D_1, D_2) - \bar{T}_0 = \frac{b}{a_{21}/c - 1} - \frac{b}{a_{21}/r_1 - 1}, \]
\[ F(D_1, D_2) = T_1(D_1, D_2) - T_0 = \frac{a_{21}bD_1D_3(m - nD_1D_3)}{a_{12}K(a_{21} - r_1)^2(a_{21} - c)^2} \] (23)
with

\[ m = (a_{21} - r_1)^2[Ka_{21} - (b + K)r_1] - r_2(a_{21} - r_1)[a_{21}(b - K) + r_1(b + K)], \]
\[ n = (b + K)(a_{21} - r_1)^2r_2 + [Ka_{21} - (b + K)r_1]^2 > 0. \]

Denote
\[ r_2^0 = \frac{(a_{21} - r_1)[Ka_{21} - (b + K)r_1]}{a_{21}(b - K) + r_1(b + K)} \]
when \( a_{21}(b - K) + r_1(b + K) \neq 0. \)

**Proposition 4.** Let (4), (5) and (15) hold. Then \( a_{21}(b - K) + r_1(b + K) \geq 0. \)

(i) \( \bar{T}_1 > \bar{T}_0. \)

(ii) Assume \( a_{21}(b - K) + r_1(b + K) > 0. \) If \( r_2 < r_2^0 \) and \( D_1 < \frac{m}{n}(r_2 + D_2) \), then \( \bar{T}_1 > \bar{T}_0. \) Otherwise, \( \bar{T}_1 \leq \bar{T}_0. \)

(iii) Assume \( a_{21}(b - K) + r_1(b + K) = 0. \) If \( D_1 < \frac{m}{n}(r_2 + D_2) \), then \( \bar{T}_1 > \bar{T}_0. \) Otherwise, \( \bar{T}_1 \leq \bar{T}_0. \)
Proof. From (4) and (5), we have $K_{a_21} - r_1(b + K) > 0$ and $a_{21}(b - K) + r_1(b + K) \geq 0$.  

(i) From $c > r_1$ and (23), we have $F(D_1, D_2) > 0$, which means $T_1 > T_0$.  

(ii) From (23), we have $m > 0$ when $r_2 < r_2^0$. Thus, $F(D_1, D_2) > 0$ if $D_1 D_3 < \frac{m}{n}$, which means $T_1 > T_0$. If $D_1 D_3 \geq \frac{m}{n}$, then $F(D_1, D_2) \leq 0$, which means $T_1 \leq T_0$. When $r_2 \geq r_2^0$, we have $m \leq 0$ and then $F(D_1, D_2) < 0$, which means $T_1 < T_0$. This completes the proof for (ii).  

(iii) From (23) we obtain $m > 0$. By a proof similar to that for (ii), we obtain the result in (iii).  

Proposition 4 makes sense biologically. We focus on dispersal $D_1$, while a similar discussion can be given for $D_2$ and variation of both $D_1$ and $D_2$. Let $D_2$ be fixed. Proposition 4(i) shows that dispersal $D_1$ from the source to sink always leads to increase of the resource species. The reason is that dispersal of the consumer decreases the level of top down control of the consumer on the resource, so that resource size increases. The result is that a small amount of dispersal causes very little decrease in the consumer abundance on patch 1. The total population $N_1^p + N_2^p$ thus increases for small dispersal rate when the death rate $r_2$ of consumer in the sink is low, as shown in Proposition 4(ii). The biological reason is that individuals that die in the sink are compensated by those moving from the source, which leads to the consumer’s survival in the sink and results in the increase of total population abundance. However, when the death rate is high or the dispersal is not small, the dispersal to the sink makes the consumer reach total population abundance less than if non-dispersing. The reason is that with the large dispersal, many individuals move from the source to the sink to die, which results in the decreased abundance. Moreover, by Theorem 3.1(ii), when the dispersal is large (i.e., $D_1 > D_1^+$), the consumer goes to extinction even though the resource species persists. The reason is that with the large dispersal, too many individuals move from the source to the sink to die, which results in the consumer’s extinction. A similar discussion can be given for Proposition 4(iii).

Now we show the optimal dispersal at which the consumer approaches the maximal abundance. Denote 

$$
\tilde{r}_2 = \frac{2n}{m}(a_{21} - r_1), \quad D_1 = \frac{a_{21} - r_1}{r_2 - r_2}(r_2 + D_2), \quad D_2 = \frac{\tilde{r}_2 - r_2}{a_{21} - r_1}D_1 - \tilde{r}_2,
$$

$$
D_4 = \frac{D_1}{r_2 + D_2}, \quad \tilde{D}_4 = \frac{a_{21} - r_1}{r_2 - r_2}, \quad T_{1\text{max}} = (1 + \tilde{D}_4)\frac{a_{21}b[Ka_{21} - (b + K)(r_1 + r_2 D_4)]}{a_{12}K(a_{21} - r_1 - r_2 D_4)^2}
$$

when $\tilde{r}_2 - r_2 \neq 0$.

**Proposition 5.** Let (4), (5) and (15) hold. 

(i) For a fixed $D_2 = D_2^0$, $T_1$ approaches its maximum $T_{1\text{max}}$ at an intermediate dispersal rate $D_1 = D_1^*$, and the function $T_1 = T_1(D_1)$ is hump-shaped as shown in Fig. 3a. 

(ii) For a fixed $D_1 = D_1^0$, $T_1$ approaches its maximum $T_{1\text{max}}$ at an intermediate dispersal rate $D_2 = D_2^*$, and the function $T_1 = T_1(D_2)$ can be convex as shown in Fig. 3b. 

(iii) For unfixed $D_1$ and $D_2$, $T_1$ approaches its maximum $T_{1\text{max}}$ at balanced dispersal rates $D_1 = D_4(r_2 + D_2)$, which corresponds to a straight line. The function $T_1 = T_1(D_1, D_2)$ is a twisty surface as shown in Fig. 4.
Proof. Since
\[ T_1 = T_1(D_4) = \frac{a_2 b D_4 (m - n D_4)}{a_1 K (a_21 - r_1)^2 (a_21 - r_1 - r_2 D_4)^2} + T_0 \]
we have
\[ \frac{dT_1}{dD_4} = \frac{a_2 b m}{a_1 K (a_21 - r_1)^2 (a_21 - r_1 - r_2 D_4)^2} \left( a_21 - r_1 - D_4 (\bar{r}_2 - r_2) \right). \]
Thus, if \( D_4 = \bar{D}_4 \), then \( \frac{dT_1}{dD_4} = 0 \); if \( D_4 < \bar{D}_4 \), then \( \frac{dT_1}{dD_4} > 0 \); if \( D_4 > \bar{D}_4 \), then \( \frac{dT_1}{dD_4} < 0 \), which implies that function \( T_1 = T_1(D_4) \) is concave at \( D_1 = \bar{D}_1 \), where \( T_1 \) approaches its maximum \( T_{1\text{max}} \). Thus, we obtain the result in (iii).

Since
\[ \frac{\partial T_1}{\partial D_1} = \frac{1}{r_2 + D_2} \frac{dT_1}{dD_4} = \frac{D_1}{(r_2 + D_2)^2} \frac{dT_1}{dD_4} \]
we obtain the results in (i)-(ii). \( \square \)

Proposition 5 makes sense biologically. We focus on discussion of Proposition 5(i), while similar discussions can be given for others. For a fixed dispersal rate \( D^0_1 \), when the dispersal rate \( D_1 \) from the source to sink is intermediate (i.e., \( D_1 = \bar{D}_1 \)), the consumer can approach the maximal total population abundance, while a large or small one is not the best. The reason is that a large dispersal rate (i.e., \( D_1 > \bar{D}_1 \)) results in much death in the sink, and a small one (i.e., \( D_1 < \bar{D}_1 \)) leads to a small population density in the sink, which is not the best for the increase of consumer in the sink.

For extremely large dispersal rates \( D_1, D_2 \), i.e., \( D_1 \to \infty, D_2 \to \infty \), we consider a specific case of \( D_1 = s D_2, D_2 = D \) with \( D \to \infty \), where parameter \( s \) represents the asymmetry. Then we have
\[ D_4 = \frac{D_1}{r_2 + D_2} = \frac{s D}{r_2 + D} \to s \text{ as } D \to \infty. \]
By a proof similar to those of Propositions 4-5, we obtain the following result while we omit the proof.

**Corollary 3.** Let (4), (5) and (15) hold. Then \( a_21 (b - K) + r_1 (b + K) \geq 0 \). Let \( D_1 = s D, D_2 = D \) with \( D \to \infty \),
(i) \( \bar{T}_1 > \bar{T}_0 \).
(ii) Assume \( a_21 (b - K) + r_1 (b + K) > 0 \). If \( r_2 < r_2^0 \) and \( s < \frac{m}{n} \), then \( T_1 > T_0 \) and \( T_1 \) approaches the maximum \( T_{1\text{max}} \) at \( s = \bar{D}_4 \). Otherwise, \( T_1 \leq T_0 \).
(iii) Assume \( a_21 (b - K) + r_1 (b + K) = 0 \). If \( s < \frac{m}{n} \), then \( T_1 > T_0 \) and \( T_1 \) approaches the maximum \( T_{1\text{max}} \) at \( s = \bar{D}_4 \). Otherwise, \( T_1 \leq T_0 \).

Corollary 3 shows that the asymmetry plays a role in the increase of species’ abundances when both dispersal rates are extremely large. Corollary 3(i) shows that the dispersal with any asymmetry will result in increase of the resource species. This is because any dispersal to the sink patch decreases the consumer’s density in the source and thus reduces consumer’s consumption on the resource, which leads to the increase. Corollary 3(ii) shows that when the asymmetry is small (i.e., \( s < m/n \)) and the death rate of consumer in the sink is low, total population abundance of the consumer in two patches is larger than that without dispersal. The reason is that with the small asymmetry, individuals that die in the sink can be compensated by those moving from the source. Moreover, the consumer can approach the maximal
abundance when the asymmetry is intermediate (i.e., \( s = D_4 \)), while a large or small one is not the best. However, when the asymmetry is very large (i.e., \( s > m/n \)), total population abundance of the consumer is less than that without dispersal. The reason is that with the large asymmetry, many individuals move from the source to the sink to die, which results in the decrease. On the other hand, by Theorem 3.1(ii), when the asymmetry is extremely large (i.e., \( s > \left[ a_{21}K - r_1(b+K) \right]/\left[ r_2(b+K) \right] \)), the consumer goes to extinction in both patches. The reason is that with the extremely large asymmetry, too many individuals move from the source to the sink to die, which results in the consumer’s extinction. A similar discussion can be given for Corollary 3(iii).

**Remark 1.** The condition (15) in Propositions 4-5 and Corollary 3 can be replaced with
\[
 a_{21} > r_1(K + b)/K, D_1^- < D_1^- < D_1^+ \text{ in Theorem 3.3},
\]
which can also guarantee that system (1) has a stable positive equilibrium \( P^* \).

**6. Discussion and application.** In this paper, we consider consumer-resource systems in which the consumer can move between a source and a sink. Rigorous analysis on the model demonstrates that dispersal could make the consumer approach a total population abundance larger than if it were non-dispersing, while the dispersal always makes the resource species reach a density higher than if it were non-dispersing. Our results provide new insight in effects of dispersal on consumer-resource interactions.

First, varying one dispersal rate could lead to transition of interaction outcomes from coexisting in periodic oscillations with high amplitudes to low amplitudes, to coexisting at a steady state, and to extinction of one/both species. Indeed, let
\[
 r = 1, \quad r_1 = 0.2, \quad r_2 = 0.1, \quad a_{12} = 0.9, \quad a_{21} = 0.5, \quad b = 1, \quad K = 4. \quad (24)
\]
Then condition (6) holds, which means that in the absence of dispersal, the consumer and resource are in periodic oscillations by Proposition 2. In the presence of dispersal, as shown in Fig. 1, when \( D_2 = 0.1 \) and the dispersal rate \( D_1 \) increases from 0.03, to 0.15, to 0.28, and to 0.9, interaction outcomes between the species transition from oscillating in high amplitudes to oscillating in low amplitudes, to coexisting at a steady state, and to extinction of the consumer. Further computations show that when \( D_1 (< 0.03) \) decreases, the resource’s amplitude in oscillations increases monotonically, which means extinction of the resource species when its number is less than one, and then means extinction of the consumer because of no food. Thus, both of the consumer and resource will go to extinction by the dispersal.

Second, varying one parameter in system (1) can change interaction outcomes from species’ extinction, to coexistence at steady states, and to coexistence in periodic oscillations. Indeed, as shown in Figs. 5a-d, when the conversion ratio \( a_{21} \) of consumer increases from 0.4, to 0.5, to 0.65 and to 0.8, dynamics of system (1) change from extinction of the consumer, to species’ coexistence at a steady state, to species’s coexistence in periodic oscillations with low and high amplitudes, respectively. The underlying reason is that (a) when the ratio is small, the consumer cannot survive in the system since it cannot efficiently convert its consumption into fitness. (b) When the ratio is intermediate, the consumer and resource coexist at a steady state since the intermediate ratio can lead to its persistence in the system. (c) When the ratio is large, the consumer grows rapidly and then reaches a high
population density. As a result, the density of resource will be low because of intensive consumption. Then the consumer decreases because of the reduced resource (food), which leads to the increase of resource. Again, the population density of consumer is high, hence more consumer, hence less resource, and so on. This looks like an oscillating system. (d) When the ratio is extremely large, amplitudes in the periodic oscillations would be extremely large, which may lead to extinction of the consumer when its number is less than one, or even means extinction of both species when the resource’s number is less than one.

Third, dispersal in the system can lead to results reversing previous predation theory without dispersal. (I) Dispersal can result in disappearance of periodic oscillations in the system without dispersal. Indeed, let (24) hold, which means that condition (6) is satisfied. Thus, when there is no dispersal, the two species coexist in periodic oscillations in the source by Proposition 2(iii). However, when there is dispersal with $D_1 = 0.28, D_2 = 0.1$, the species coexist at a steady state in both patches as shown in Fig. 1c, which means that the dispersal results in disappearance of periodic oscillations. The mathematical reason is that condition (6) in Proposition 2(iii) means oscillations, which can be changed to steady states by dispersal when the condition in Theorem 3.2 holds. The biological reason is that moving away from the source leads to reduced consumption on the resource, which results in disappearance of oscillations as discussed in the above paragraph in case (c). (II) Dispersal could result in extinction of the consumer even though it can persist in the system without dispersal. Indeed, let (24) hold. When there is no dispersal, the species persists as discussed in (I). However, when there is dispersal with $D_1 = 0.9, D_2 = 0.1$, the consumer goes to extinction as shown in Fig. 1d, which reverses the predation theory without dispersal. Moreover, as discussed above, when $D_2 < 0.03$ decreases in the situation of Fig. 1, the resource’s amplitude in oscillation increases monotonically, which means extinction of both species when the resource’s number is less than one. Thus, small dispersal could lead to extinction of both species, which extends previous predation theory without dispersal. (III) The consumers’ overall abundance in two patches is a ridge-like function of dispersal rate $D_2$, which is hump-shaped if $D_2 < 0.6014$ but is convex if $D_2 > 0.6014$ as shown Fig. 3b. This result extends previous conclusions that the function is hump-shaped when the dispersal between patches is symmetric.

Finally, the results in this work may provide strategies for protecting endangered species. Indeed, let (24) hold. When there is no dispersal, the resource and the (endangered) consumer coexist in periodic oscillations by Proposition 2(iii), in which average densities of the consumer and resource are $\bar{N}^+ = 1.4002, \bar{M}^+ = 1.2165$ by computations on the software MatLab. When there is dispersal with the optimal dispersals $D_1 = 0.28, D_2 = 0.1$, the species coexist at a steady state $P^*(2.1250, 1.6272, 2.2787)$ as shown in Fig. 1c, in which the consumer reaches the maximal abundance $T_{1max} = 1.6272 + 2.2787 = 3.9059$. Since

$$\frac{3.9059 - \bar{N}^+}{\bar{N}^+} = 178.95\%, \quad \frac{2.1250 - \bar{M}^+}{\bar{M}^+} = 74.68\%$$

the dispersal makes two species reach population abundances 178.95% and 74.68% larger than if non-dispersing, which efficiently protects persistence of the endangered consumer. Thus, our results suggest that ecological managers should control the dispersal rates in both directions according to Proposition 4(ii-iii), which would lead to much increase of the consumer. On the other hand, the dispersal changes dynamics of the system from coexisting in periodic oscillations to coexisting at a
steady state, which promotes stability of the system and is beneficial for survival of the endangered species because intensive oscillations may mean extinction of one/both species.

Our results are different from previous ones. Jansen [16] studied system (1) by numerical simulations. The simulations displayed that when the symmetric dispersal $D_1 = D_2$ is small, there is a stable limit cycle; When the dispersal is intermediate, the cycle shrinks to a stable equilibrium; When the dispersal is large, the equilibrium loses its stability and a stable limit cycle appears again. Huang and Diekmann [13] analyzed a predator-prey Rosenzweig-MacArthur model with predator’s dispersal between two patches. The dispersal term is derived by extending the Holling time budget argument to dispersal. Their analysis showed that the extension of the Holling time budget argument to dispersal has significant effects on the dynamics. Goldwyn and Hastings [9] studied a two-patch predator-prey system with identical weak dispersal between the patches. They showed that a difference in time scales between the predator and prey species is the most important requirement for fast convergence to spatial synchrony of oscillating populations. Feng et al. [6] explored the predator-prey dynamics in a two-patch system with migration of both species. They showed upper and lower bounds for the populations with three types of Holling functional responses. Liu [19] studied an extended model of (1), in which there is resource in patch 2. Liu showed global stability of the positive equilibrium for the symmetric case and performed simulations for the asymmetric cases and limit cycles.

Kang et al. [17] studied a Rosenzweig-MacArthur prey-predator two patch model, where the dispersal rate of predators from patch $i$ to patch $j$ depends on the prey-predator interaction term in patch $j$. Based on theoretical analysis, they showed local/global stability of boundary equilibria, and proved existence and local stability of positive equilibria. Then they showed conditions for persistence of the system. Their numerical simulations displayed that there is a stable limit cycle and there may exist multiple stable positive equilibria. When the diffusion is symmetric (i.e., $D_1 = D_2$), model (1) is a specific case of system (13) of Kang et al. (2017). Kang et al. gave an extensive study on system (13), including persistence of the prey species, global stability of the boundary equilibrium, and global stability of the positive equilibrium. When the diffusion in (1) is asymmetric (i.e., $D_1 \neq D_2$), our analysis shows new phenomena in which the asymmetry can lead to results reversing those with symmetric diffusion: (a) Varying the asymmetry (e.g., fix $D_2$ but let $D_1$ vary) can change the system from persistence to non-persistence. As shown in Theorem 3.1(i) in this work, when $D_1$ is small (i.e., $D_1 < D_1^*$), the system is uniformly persist. However, when $D_1$ is large (i.e., $D_1 > D_1^*$), the system is not persist and the boundary equilibrium $P_1(K,0,0)$ is globally asymptotically stable. (b) Varying the asymmetry can change stability of the positive equilibrium and lead to periodic oscillation. As shown in Theorem 3.4 and Lemma 4.2, varying $D_1$ can change the positive equilibrium from stable to unstable, which may lead to periodic oscillation as shown in Theorem 4.3. (c) Numerical simulation in Figs. 1 and 5 display that varying the asymmetry can lead to a variety of dynamics, from consumer extinction, to stable coexistence, to small periodic oscillations, to strong periodic oscillations that can lead to extinction of both consumer and resource.

The differences of our results from previous works are: (i) we gave a rigorous analysis on effects of dispersal/asymmetry on stability of boundary/positive equilibria and persistence of system (1). For example, Theorem 3.1 shows that if the
dispersal from the source to sink is small (i.e., $D_1 < D_1^+$), system (1) is uniformly persistent; If $D_1 > D_1^+$, the boundary equilibrium $P_1(K, 0, 0)$ is globally asymptotically stable. A similar discussion can be given for Theorem 3.3. Here, $D_1$ also represents the asymmetry in dispersal when dispersal $D_2$ in the opposite direction is fixed. (ii) The periodic oscillation in system (1) is theoretically proven in Theorem 4.3. Moreover, numerical simulations in Fig. 1 showed that varying one dispersal rate or asymmetry in dispersal could lead to transition of interaction outcomes from coexisting in periodic oscillations with high amplitudes to low amplitudes, to coexisting at a steady state, and to extinction of one/both species, which is different from Jansen’s findings with symmetric diffusion. (iii) Effect of dispersal/asymmetry on predator’s total abundance is clearly shown, and the optimal strategy for dispersal/asymmetry is derived. Moreover, the overall abundance is shown to be a ridge-like function (surface) of dispersal rates, which extends both previous theory and experimental observation.

While Ruiz-Herrera and Torres [21] focused on small dispersal and linear functional responses in source-source systems, this work analyzes general dispersal rates and Holling Type II functional responses in source-sink systems, which leads to optimal dispersals and periodic oscillations. It is worth mentioning that this work focuses on the system with source-sink patches, and systems with general dispersal rates between source-source patches and Holling Type II functional responses, may have more complex dynamics. We’ll pursue it in a future work.

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Figure 1. Effect of dispersal $D_1$ on dynamics of system (1). Fix $r = 1, r_1 = 0.2, r_2 = 0.1, a_{12} = 0.9, a_{21} = 0.5, b = 1, K = 4, D_2 = 0.1$. (a-b) Let $D_1 = 0.03$ and $D_1 = 0.15$, respectively. The resource and consumer coexist in periodic oscillations, while the amplitude decreases with the increase of $D_1$. (c) Let $D_1 = 0.28$. The resource and consumer coexist at a steady state $P^*(2.1250, 1.6272, 2.2787)$. (d) Let $D_1 = 0.9$. The consumer goes to extinction even though the resource species persists.
Figure 2. Dynamics of system (1). Let $r = 1$, $r_1 = 0.2$, $r_2 = 0.1$, $a_{12} = 0.9$, $a_{21} = 0.8$, $b = 1$, $K = 4$, $D_1 = 0.3$, $D_2 = 0.1$. Numerical simulations display that all positive solutions (except $P^*$) of systems (1) converge to the unique limit cycle and exhibit periodic oscillations.
Figure 3. Comparison of $T_1(D_1, D_2)$ and $T_0$. The red and black lines represent $T_1$ and $T_0$, respectively. Fix $r = 1, r_1 = 0.2, r_2 = 0.1, a_{12} = 2, a_{21} = 0.8, b = 1, K = 2$. (a) Fix $D_2 = 0.1$ but let $D_1$ vary. $T_1$ approaches its maximum $T_{1\text{max}} = 1.5089$ at $D_1 = 0.4276$, and the curve is hump-shaped. We have $T_1 > T_0$ if $D_1 < 0.6305$; $T_1 < T_0$ if $D_1 > 0.6305$ as shown in Proposition 4(ii). (b) Fix $D_1 = 0.86$ but let $D_2$ vary. $T_1$ approaches its maximum $T_{1\text{max}} = 1.5089$ at $D_2 = 0.3023$. The curve is hump-shaped if $D_2 < 0.6014$ but is convex if $D_2 > 0.6014$. We have $T_1 > T_0$ if $D_2 > D_2 = 0.1728$; $T_1 < T_0$ if $D_2 < 0.1728$. 
Figure 4. The surface of $T_1(D_1, D_2)$ when both $D_1$ and $D_2$ vary. Fix $r = 1, r_1 = 0.2, r_2 = 0.1, a_{12} = 2, a_{21} = 0.8, b = 1, K = 2$. Then $T_1$ approaches its maximum $T_{1\text{max}} = 1.5089$ at a line $D_1 = 0.213 + 2.137D_2$, as shown in proposition 5(iii). This figure provides an intuition of the surface of $T_1 = T_1(D_1, D_2)$, which is a combination of Figs. 3a-b, i.e., when $D_2$ is fixed, the surface becomes Fig. 3a; when $D_1$ is fixed, the surface becomes Fig. 3b.
Figure 5. Dynamics of system (1). Fix $r = 1, r_1 = 0.2, r_2 = 0.1, a_{12} = 0.9, b = 1, K = 4, D_1 = 0.28, D_2 = 0.1$. (a) Let $a_{21} = 0.4$. The consumer goes to extinction even though the resource species persists. (b) Let $a_{21} = 0.5$. The resource and consumer coexist at a steady state $P^*(2.1250, 1.6272, 2.2787)$. (c-d) Let $a_{21} = 0.65$ and $a_{21} = 0.8$, respectively. The resource and consumer coexist in periodic oscillation, while the amplitude increases with the increase of $a_{21}$. 

(a) $a_{21} = 0.4$ (b) $a_{21} = 0.5$ (c) $a_{21} = 0.65$ (d) $a_{21} = 0.8$