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THE OPTIMAL DISPERSAL STRATEGY: A TWO-PATCH MODEL WITH TRAVEL LOSS

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Abstract. The dispersal of organisms plays an important role in determining the dynamics of ecological models. Ecologically, it is of interest in understanding how dispersal strategy influences the distribution of populations. An ideal free distribution (IFD) of populations has been used to predict the distribution of organisms among patches, where a key assumption is to assume that species can move freely between patches without paying any cost. If instead one assumes that there are losses when species moves from one patch to another, then ideal free distributions may not appear. In this note, we examine a two-patch resident-mutant model with travel loss and predict the optimal dispersal strategy for resident and mutant. Moreover, such strategy which produces a non-IFD is evolutionarily stable. Some same and different features of patch models with travel loss are discussed.

1. Introduction

How organisms select their habitats is a fundamental issue in ecology. A classical theory, ideal free distribution (IFD) theory, proposed by Fretwell and Lucas [15] has been used to predict the distribution of organisms among patches, that is, at steady state individuals in each patch have the same fitness (all populations of species are at carrying capacity). IFD has been supported by some experiments in laboratory (Milinski [32]; Regelmann [35]; Korona [24]). The dispersal strategy of organisms plays a central role in ecology and evolutionary biology and affects the habitats selection for animals (Bowler and Benten [2]; Clobert et al. [8]; Levin et al. [26]). "Balanced dispersal" which means that, for each patch, the total number of immigrants is equal to the number of emigrants (Doncaster et al. [14]), can be thought of as an extension of IFD. For a single species logistic model with two patches, the dispersal strategy which leads to "balanced dispersal" results in an ideal free distribution (McPeek and Holt [31]). For more general m-species patch models in n-patch:

$$\frac{du_{ki}}{dt} = \sum_{j=1, j\neq i}^{n} \left[d^k_{ij} u_{kj} - d^k_{ji} u_{ki}\right] + f_{ki}(\mathbf{u}) u_{ki},\ i = 1, \ldots, n,\ k = 1, \ldots, m,$$

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where $\mathbf{u} := (u_{11}, u_{12}, \ldots, u_{mn})^T$ is the vector of population of all species over all patches, so an ideal free dispersal strategy relative to the stationary point $\mathbf{u}^*$ can be realized as that there is no net movement of population when $\mathbf{u} = \mathbf{u}^*$ (Cantrell et al. [5]). Namely,

$$\sum_{j=1, j\neq i}^{n} [d_{ij}^k u_{kj} - d_{ji}^k u_{ki}] = 0, \; i = 1, \ldots, n, \; k = 1, \ldots, m.$$

A key assumption of IFD is that species can move freely between patches without paying any cost. In reality, it is reasonable to take travel cost into account. As pointed by DeAngelis et al. [9], movement may leads to the loss of energy, which may increase the risk of predation so that species will die during the movement. If one assumes that there exists losses in moving from one place to another, we may expect that IFD may not exist anymore. DeAngelis et al. [9] proposed a tri-trophic model in N patches ($N \geq 2$) with travel loss. They focus on how travel loss will impact the the population distribution which is not an IFD. An "optimal" dispersal rate was also given to explain that the travel loss leads to a deviation of the population distribution from the IFD. The global stability was studied by Lou and Wu [28]. We also refer to [1, 7, 18, 22, 30, 33, 36, 37] and references therein for studies including travel loss.

It is also of ecological interest in understanding the evolution of dispersal. An interesting result reported by Hastings [20] is that for spatially variable but temporally constant environments, selection usually favors slower unconditional dispersal (see also Dockery et al. [13]; Kirkland et al. [23]). However, faster dispersal rates may be selected if the dispersal is unconditional in spatially and temporally varying environments (Hutson et al. [21]; McPeek and Holt [31]). We also refer to [3, 6, 27, 34] and references therein for partial differential models. From the viewpoint of adaptive dynamics (Dieckmann [10]; Dieckmann and R. Law [11]; Diekmann [12]; Geritz and Gyllenberg [16]; Geritz et al. [17]), an important notion related to the evolution of dispersal is called evolutionarily stable strategy (ESS). A dispersal strategy is an ESS if a population adopting this strategy cannot be invaded by a small population adopting any other strategy. It is interesting to ask under what conditions an ideal free dispersal strategy is evolutionarily stable. Cantrell et al. [5] provided certain conditions such that an ideal free dispersal strategy is actually evolutionarily stable. Some more general results has been established by Cantrell et al. [4] constructing a new Lyapunov functional. It is natural to ask if a non-ideal free dispersal strategy can be an ESS? The answer is positive (DeAngelis et al. [9]; Lou and Wu [28]). Furthermore, we may ask if this is a common feature of ecological models if travel loss is taken into account. For this, we shall examine a simple resident-mutant model with travel loss in two patches to capture this phenomenon.

The rest of this paper is organized as follows. In Section 2, we examine a simple resident-mutant model with travel loss and prove our main results. Finally, we give a brief conclusion in Section 3.

2. The two-patch model

We consider a simple logistic growth model, where the species P can disperse between two patches, and will die during dispersal. The model is formulated as

$$\begin{aligned}\frac{dP_1}{dt} &= P_1[a_1 - P_1] - m_{21}P_1 + m_{12}(1-\varepsilon_{12})P_2,\\ \frac{dP_2}{dt} &= P_2[a_2 - P_2] - m_{12}P_2 + m_{21}(1-\varepsilon_{21})P_1.\end{aligned}$$

where $P_i(t)$ denotes the population of resident in i-th patch ($i = 1,2$) and at time $t \geq 0$; the positive constant a_i measures the resource of the patch i; the positive constant m_{ij} represents dispersal rate of resident P from patch j to patch i; the constant $\varepsilon_{ij} \in (0,1)$ stands for the fractional loss of individuals during movement from patch j to patch i.

To capture some common features of resident-mutant models with travel loss, we envision that a mutant appears and play a different dispersal strategy $\widehat{m}_{ij}$. Therefore, we examine the following two-patch resident-mutant model:

$$\frac{dP_1}{dt} = P_1[a_1 - (P_1 + \widehat{P}_1)] - m_{21}P_1 + m_{12}(1-\varepsilon_{12})P_2, \tag{2.1}$$

$$\frac{dP_2}{dt} = P_2[a_2 - (P_2 + \widehat{P}_2)] - m_{12}P_2 + m_{21}(1-\varepsilon_{21})P_1, \tag{2.2}$$

$$\frac{d\widehat{P}_1}{dt} = \widehat{P}_1[a_1 - (P_1 + \widehat{P}_1)] - \widehat{m}_{21}\widehat{P}_1 + \widehat{m}_{12}(1-\varepsilon_{12})\widehat{P}_2, \tag{2.3}$$

$$\frac{d\widehat{P}_2}{dt} = \widehat{P}_2[a_2 - (P_2 + \widehat{P}_2)] - \widehat{m}_{12}\widehat{P}_2 + \widehat{m}_{21}(1-\varepsilon_{21})\widehat{P}_1, \tag{2.4}$$

with the initial condition

$$P_i(0) > 0, \widehat{P}_i(0) > 0, \quad i = 1,2,$$

where $P_i(t)$, $\widehat{P}_i(t)$ denote the number of resident and mutant, respectively, in i-th patch ($i = 1,2$) and at time $t \geq 0$; the constant $\widehat{m}_{ij}$ represents dispersal rates of mutant $\widehat{P}$ from patch j to patch i.

We adopt a similar biological assumption as in [9, 28]: due to stream flow, species is forced to disperse from patch 2 to patch 1 with a fixed rate, i.e., patch 2 is located in the upper part of a stream and patch 1 is located downstream. Then larva in patch 2 will be washed out from patch 2 and move to patch 1. So we assume that the resident larva and the mutant larva have the same dispersal rate from patch 2 to patch 1, i.e., $m_{12} = \widehat{m}_{12}$. When larva grows into adult, it is reasonable to assume the resident adults in patch 1 have different dispersal rate from the mutant adults. In conclusion, we have the following assumption:

(A) $m_{12} = \widehat{m}_{12}$ and $m_{21} \neq \widehat{m}_{21}$.

Under the assumption **(A)**, it is interesting to see if there exists an optimal dispersal rate from patch 1 to patch 2 such that the resident will not be replaced by the mutant when rare which use a different dispersal rate from patch 1 to patch 2? Our goal is to predict the exact form of the optimal dispersal rate. To do so, our approach follows from theory of adaptive dynamics (see e.g., [10, 12, 16, 17]). See also [9].

We linearize (2.1)–(2.4) at a semi-trivial stationary point $E := (P_1^*, P_2^*, 0, 0)$ for some $P_j^* > 0$ $(j = 1, 2)$. Let $\mathbf{J}$ be the Jacobian matrix for system (2.1)–(2.4) evaluated at E. By direct computations, $\mathbf{J}$ takes the form

$$\mathbf{J} = \begin{bmatrix} \mathbf{A} & \mathbf{B} \\ \mathbf{0} & \mathbf{D} \end{bmatrix},$$

where $\mathbf{0}$ denotes 2 by 2 matrix with all entries 0,

$$\mathbf{A} = \begin{bmatrix} a_1 - 2P_1^* - m_{21} & (1-\varepsilon_{12})m_{12} \\ (1-\varepsilon_{21})m_{21} & a_2 - 2P_2^* - m_{12} \end{bmatrix},$$

$$\mathbf{D} = \begin{bmatrix} a_1 - P_1^* - \widehat{m}_{21} & (1-\varepsilon_{12})m_{12} \\ (1-\varepsilon_{21})\widehat{m}_{21} & a_2 - P_2^* - m_{12} \end{bmatrix}.$$

Let λ be any eigenvalue of $\mathbf{J}$. Then

$$0 = \det(\mathbf{J} - \lambda\mathbf{I}) = \det(\mathbf{A} - \lambda\mathbf{I})\det(\mathbf{D} - \lambda\mathbf{I}).$$

Thus, we can understand the stability at E if the sign of the real parts of the eigenvalues of $\mathbf{A}$ and $\mathbf{D}$ can be obtained. Also, note that $\mathbf{A}$ is actually the Jacobian matrix of the following system

$$\frac{dP_1}{dt} = P_1[a_1 - P_1] - m_{21}P_1 + m_{12}(1-\varepsilon_{12})P_2,$$
$$\frac{dP_2}{dt} = P_2[a_2 - P_2] - m_{12}P_2 + m_{21}(1-\varepsilon_{21})P_1$$

evaluated at the coexistence state (P_1^*, P_2^*). It is well-known that the coexistence state is asymptotically stable if it exists. Therefore, to study the stability of E, it suffices to investigate the eigenvalues of $\mathbf{D}$, which is called the invasion matrix.

Taking $c > 0$ large enough such that $\mathbf{D}' := \mathbf{D} + c\mathbf{I}$ forms a nonnegative irreducible matrix. Then Perron-Frobenius theorem yields that $\mathbf{D}'$ has the largest eigenvalue. Hence $\mathbf{D}$ has the largest eigenvalue, say λ_1. The other eigenvalue is defined by λ_2 such that $\lambda_2 \le \lambda_1$.

We now start to predict the optimal dispersal strategy. Assume that there exits $m^* > 0$ such that $\lambda_1 \le 0$ for $m_{21} = m^*$ for all $\widehat{m}_{21}$ lying in a neighborhood of m_{21}. Then we can observe that

$$\lambda_1|_{\widehat{m}_{21} = m_{21}} = 0. \tag{2.5}$$

Indeed, from (2.1) and (2.2), we have

$$a_1 - P_1^* = m_{21} - (1-\varepsilon_{12})m_{12}\frac{P_2^*}{P_1^*}, \tag{2.6}$$

$$a_2 - P_2^* = m_{12} - (1-\varepsilon_{21})m_{21}\frac{P_1^*}{P_2^*}. \tag{2.7}$$

Using (2.6) and (2.7), we have

$$\det\mathbf{D}|_{m_{21}=\widehat{m}_{21}} = (a_1 - P_1^* - m_{21})(a_2 - P_2^* - m_{12}) - (1-\varepsilon_{12})(1-\varepsilon_{21})m_{12}m_{21} = 0.$$

Hence 0 is an eigenvalue of **D**. Also, it is easy to see that the all component of the eigenvector associated with the eigenvalue 0 are positive. It follows that 0 is the largest eigenvalue of **D** (Perron-Frobenius theorem), which implies (2.5). Moreover, since we assume that $\lambda_1 \le 0$ for all $\widehat{m}_{21}$ nearby $m_{21} = m^*$, it follows that

$$\frac{\partial \lambda_1}{\partial \widehat{m}_{21}}\Big|_{\widehat{m}_{21}=m_{21}=m^*} = 0. \tag{2.8}$$

Using (2.5) and (2.8), we obtain

$$\frac{\partial \det\mathbf{D}}{\partial \widehat{m}_{21}}\Big|_{m_{21}=\widehat{m}_{21}=m^*} = \frac{\partial(\lambda_1\lambda_2)}{\partial \widehat{m}_{21}}\Big|_{m_{21}=\widehat{m}_{21}=m^*} = 0$$

On the other hand, by the definition of **D**, we can also calculate

$$0 = \frac{\partial \det\mathbf{D}}{\partial \widehat{m}_{21}}\Big|_{m_{21}=\widehat{m}_{21}=m^*} = -a_2 + P_2^* + m_{12} - (1-\varepsilon_{12})(1-\varepsilon_{21})m_{12}$$

such that

$$P_2^* = a_2 + (1-\varepsilon_{12})(1-\varepsilon_{21})m_{12} - m_{12} \tag{2.9}$$

Note that (P_1^*, P_2^*) satisfies (2.1) and (2.2) with $m_{21} = m^*$. Putting (2.9) into (2.2) yields that

$$P_1^* = \frac{P_2^*(m_{12} + P_2^* - a_2)}{(1-\varepsilon_{21})m^*}. \tag{2.10}$$

Putting (2.10) into (2.1) with $m_{21} = m^*$, we obtain

$$\begin{aligned} m^* &= \frac{m_{12}}{a_1}P_2^*(1-\varepsilon_{12}) \\ &= \frac{m_{12}}{a_1}(1-\varepsilon_{12})\Big[a_2 + (1-\varepsilon_{12})(1-\varepsilon_{21})m_{12} - m_{12}\Big] \\ &= m_{12}(1-\varepsilon_{12})\frac{P_2^*}{P_1^*}. \end{aligned}$$

From the above discussion, we obtain our first result as follows:

Theorem 1. *Assume that* **(A)** *holds. Suppose that there exists* $m^* > 0$ *such that* $\lambda_1 \le 0$ *for* $m_{21} = m^*$ *and for all* $\widehat{m}_{21}$ *lying in a neighborhood of* m^**. Then*

$$m^* = \frac{m_{12}}{a_1}(1-\varepsilon_{12})\Big[a_2 + (1-\varepsilon_{12})(1-\varepsilon_{21})m_{12} - m_{12}\Big] = m_{12}(1-\varepsilon_{12})\frac{P_2^*}{P_1^*},$$

where λ_1 *is the largest eigenvalue of the invasion matrix defined above.*

Our next result shows that m^* is actually an global ESS if $m^* > 0$.

Theorem 2. *Assume that* **(A)** *holds and* $m_{21} = m^* > 0$*. Then* $E := (P_1^*, P_2^*, 0, 0)$ *is globally asymptotically stable, where*

$$(P_1^*, P_2^*) = \Big(a_1,\ a_2 + (1-\varepsilon_{12})(1-\varepsilon_{21})m_{12} - m_{12}\Big). \tag{2.11}$$

The proof of Theorem 2 can be done by using Lyapunov function method, where the Lyapunov function was introduced by Goh [19]. Together with LaSalle's invariant principle [25] (see Proposition 1 below), the global stability of E can be established. The proof basically follows the same line as in [28].

Here we need a modified version of LaSalle's invariant principle.

Proposition 1 (Theorem 1.2 of [29])**.** *Consider the system of differential equations*

$$\frac{dx}{dt} = f(x),$$

where $f : \mathbb{R}^n \to \mathbb{R}^n$ *is continuous. Suppose that* $V : G \subset \mathbb{R}^n \to \mathbb{R}$ *satisfies the followings:*

(i) V *is continuous on* G*;*
(ii) V *is not continuous at* $\bar{x} \in \bar{G}$ *(the closure of* G*) implies that* $\lim_{x\to\bar{x}, x\in G} V(x) = +\infty$*;*
(iii) $\nabla V \cdot f \le 0$ *in* G*.*

Let $\mathcal{M} := \{x | \dot{V}(x) = 0,\ x \in \bar{G}\}$ *and* $\mathcal{M}'$ *be the largest invariant set in* $\mathcal{M}$*. Then every bounded (for* $t \ge 0$*) trajectory of* $\dot{x} = f(x)$ *which remains in* G *for* $t \ge 0$ *tends to the set* $\mathcal{M}'$ *as* $t \to +\infty$*.*

We are ready to show Theorem 2.

Proof of Theorem 2. For convenience, we adopt the following notations:

$$X := (x_1, x_2, x_3, x_4)^T = (P_1, P_2, \widehat{P}_1, \widehat{P}_2)^T,$$
$$X^* := (x_1^*, x_2^*, x_3^*, x_4^*)^T = (P_1^*, P_2^*, 0, 0)^T.$$

The system (2.1)–(2.4) is written as a vector form $\dot{X} = f(X)$, where

$$f(X) := (f_1(X), f_2(X), f_3(X), f_4(X))^T.$$

Let $G := \{X|\ x_1 > 0, x_2 > 0, x_3 \geq 0, x_4 \geq 0\}$. Define $V : G \to \mathbb{R}$ by

$$V(X) := \sum_{i=1}^{2} k_i \left[x_i - x_i^* - x_i^* \ln(\frac{x_i}{x_i^*}) \right] + \sum_{i=3}^{4} k_i x_i$$

where $k_i > 0$ $(i = 1, \dots, 4)$ is defined as

$$k_1 = k_3 = 1, \quad k_2 = k_4 = \frac{1}{1 - \varepsilon_{21}}. \tag{2.12}$$

By direct calculations, we have

$$\begin{aligned} \dot{V}(X) &= \sum_{i=1}^{2} k_i \left[\dot{x}_i - x_i^* \frac{\dot{x}_i}{x_i} \right] + \sum_{i=3}^{4} k_i \dot{x}_i \\ &= \sum_{i=1}^{2} k_i (x_i - x_i^*) \frac{\dot{x}_i}{x_i} + \sum_{i=3}^{4} k_i \dot{x}_i. \end{aligned}$$

Using $\dot{x}_i = f_i(X)$ and $f_i(X^*) = 0$ for $i = 1, \dots, 4$, we obtain

$$\dot{V}(X) = \sum_{i=1}^{2} k_i (x_i - x_i^*) \left[\frac{f_i(X)}{x_i} - \frac{f_i(X^*)}{x_i^*} \right] + \sum_{i=3}^{4} k_i \left[f_i(X) - f_{i-2}(X^*) \frac{x_i}{x_{i-2}^*} \right]. \tag{2.13}$$

Recall that $x_3^* = x_4^* = 0$ and $\widehat{m}_{12} = m_{12}$, and the relation

$$m_{21} = m^* = m_{12}(1 - \varepsilon_{12}) \frac{x_2^*}{x_1^*}, \tag{2.14}$$

the second term of (2.13) can be evaluated as

$$\begin{aligned} &\sum_{i=3}^{4} k_i \left[f_i(X) - f_{i-2}(X^*) \frac{x_i}{x_{i-2}^*} \right] \\ &= k_3 \left\{ x_3[a_1 - (x_1 + x_3)] - \widehat{m}_{21} x_3 + m_{12}(1 - \varepsilon_{12}) x_4 - x_3[a_1 - (x_1^* + x_3^*)] \right\} \\ &\quad + k_4 \left\{ x_4[a_2 - (x_2 + x_4)] + \widehat{m}_{21}(1 - \varepsilon_{21}) x_3 - x_4[a_2 - (x_2^* + x_4^*)] - m_{21}(1 - \varepsilon_{21}) \frac{x_1^*}{x_2^*} x_4 \right\} \\ &= k_3 (x_3 - x_3^*) \left[-(x_1 - x_1^*) - (x_3 - x_3^*) \right] + k_4 (x_4 - x_4^*) \left[-(x_2 - x_2^*) - (x_4 - x_4^*) \right] \\ &\quad + x_3 [-k_3 \widehat{m}_{21} + k_4 \widehat{m}_{21}(1 - \varepsilon_{21})] + x_4 \left[k_3 m_{12}(1 - \varepsilon_{12}) - k_4 m_{21}(1 - \varepsilon_{21}) \frac{x_1^*}{x_2^*} \right]. \end{aligned}$$

By (2.12) and (2.14), we see that the last two terms are equal to zero.

Hence (2.13) becomes

$$\begin{aligned} \dot{V}(X) = {} & k_1 (x_1 - x_1^*) \left[-(x_1 - x_1^*) - (x_3 - x_3^*) + m_{12}(1 - \varepsilon_{12}) \left(\frac{x_2}{x_1} - \frac{x_2^*}{x_1^*} \right) \right] \\ & + k_2 (x_2 - x_2^*) \left[-(x_2 - x_2^*) - (x_4 - x_4^*) + m_{21}(1 - \varepsilon_{21}) \left(\frac{x_1}{x_2} - \frac{x_1^*}{x_2^*} \right) \right] \end{aligned}$$

$$\begin{aligned}&+k_3(x_3-x_3^*)\left[-(x_1-x_1^*)-(x_3-x_3^*)\right]\\&+k_4(x_4-x_4^*)\left[-(x_2-x_2^*)-(x_4-x_4^*)\right].\end{aligned}$$

To prove that $\dot{V}\le 0$ in G, we set $W_i := x_i - x_i^*$ for $i=1,\dots,4$ and

$$\begin{aligned}\Lambda_1 &:= k_1W_1m_{12}(1-\varepsilon_{12})\Big(\frac{x_2}{x_1}-\frac{x_2^*}{x_1^*}\Big)+k_2W_2m_{21}(1-\varepsilon_{21})\Big(\frac{x_1}{x_2}-\frac{x_1^*}{x_2^*}\Big),\\ \Lambda_2 &:= \dot{V}(X)-\Lambda_1.\end{aligned}$$

Let us focus on Λ_1 first. By simple calculations,

$$\begin{aligned}\Lambda_1 &= k_1m_{12}(1-\varepsilon_{12})W_1\left[\frac{x_2x_1^*-x_2x_1+x_2x_1-x_1x_2^*}{x_1x_1^*}\right]\\ &\quad+k_2m_{21}(1-\varepsilon_{21})W_2\left[\frac{x_1x_2^*-x_1x_2+x_1x_2-x_2x_1^*}{x_1x_1^*}\right]\\ &= -k_1m_{12}(1-\varepsilon_{12})\frac{x_2}{x_1x_1^*}W_1^2-k_2m_{21}(1-\varepsilon_{21})\frac{x_1}{x_2x_2^*}W_2^2\\ &\quad+\left[\frac{k_1m_{12}}{x_1^*}(1-\varepsilon_{12})+\frac{k_2m_{21}}{x_2^*}(1-\varepsilon_{21})\right]W_1W_2.\end{aligned}$$

Due to (2.12) and (2.14), we have

$$\Lambda_1=-\frac{k_1m_{12}(1-\varepsilon_{12})}{x_1^*}\left(\sqrt{\frac{x_2}{x_1}}W_1-\sqrt{\frac{x_1}{x_2}}W_2\right)^2\le 0; \tag{2.15}$$

and $\Lambda_1=0$ if and only if

$$\frac{x_1}{x_1^*}=\frac{x_2}{x_2^*}.$$

We now focus on Λ_2. Using (2.12), we have

$$\Lambda_2 := \dot{V}(X)-\Lambda_1=-(W_1+W_3)^2-k_2(W_2+W_4)^2\le 0 \tag{2.16}$$

and the equality holds if and only if $x_1+x_3=x_1^*$ and $x_2+x_4=x_2^*$. Due to (2.15) and (2.16), we obtain

$$\dot{V}(X)=\Lambda_1+\Lambda_2\le 0.$$

Moreover, $\dot{V}=0$ if and only if

$$\frac{x_1}{x_1^*}=\frac{x_2}{x_2^*},\ x_1+x_3=x_1^*,\ \text{and } x_2+x_4=x_2^*. \tag{2.17}$$

Hence the set $\mathscr{M}$ defined in Proposition 1 is

$$\mathscr{M}:=\{X\mid \dot{V}(X)=0\}\cap\overline{G}$$

$$= \left\{ X \,\middle|\, \frac{x_1}{x_1^*} = \frac{x_2}{x_2^*},\ x_1 + x_3 = x_1^*,\ x_2 + x_4 = x_2^*,\ x_i \geq 0\ \forall\ i \right\}.$$

Finally, we show that the largest invariant set in $\mathscr{M}$ is actually $\{E\}$. If $X(t) = (x_1(t), \ldots, x_4(t))$ is a solution of (2.1)−(2.4) and falls in $\mathscr{M}$ for $t \geq 0$. Using (2.17) and equations of x_i, it is easy to see that $X(t) \equiv E$ for all $t \geq 0$. This means that the largest invariant set in $\mathscr{M}$ is $\{E\}$. By Proposition 1, E is globally asymptotically stable. Hence the proof of Theorem 2 is complete. ☐

3. Discussion

In this note, we study a sample resident-mutant model with travel loss in two-patch environments. If resident and mutant have the same dispersal rate from patch 2 to patch 1 (due to stream flow), we predict the optimal dispersal rate $m^* > 0$ from patch 1 to patch 2 for resident which is given by

$$m^* := \frac{m_{12}}{a_1}(1-\varepsilon_{12})\Big[a_2 + (1-\varepsilon_{12})(1-\varepsilon_{21})m_{12} - m_{12}\Big]. \tag{3.1}$$

From this formula, we see that in order to $m^* > 0$, m_{12} cannot be to large. If m_{12} is large enough such that $m^* < 0$, the optimal dispersal rate can be expected to be zero. A biological reason can be presented as follows: note that m_{12} represents the stream speed (see the assumption **(A)**), too large m_{12} will increase the difficult for adult resident to move back to the upstream. In this situation, species may prefer not to move from the downstream to the upstream.

Recall that m^* can be rewritten as

$$m^* = m_{12}(1-\varepsilon_{12})\frac{P_2^*}{P_1^*}, \tag{3.2}$$

were P_i^* $(i = 1, 2)$ is given by (2.11). In fact, the formula (3.2) is actually the same as in the model of DeAngelis et al. [9] (in two-patch environments) although these models are different. On the other hand, if the resident adopts the optimal strategy, i.e., $m_{12} = m^*$, (3.2) indicates that the dispersal in the downstream equation (2.1) is balanced, but the dispersal in the upstream equation (2.1) is not. Such phenomenon is also found in [9]. Moreover, since $P_1^* = a_1$, we see that the resident in patch patch 1 reaches carrying capacity. However, $P_2^* = a_2 + (1-\varepsilon_{12})(1-\varepsilon_{21})m_{12} - m_{12}$, and $P_2^* = a_2$ only for $\varepsilon_{12} = \varepsilon_{21} = 0$. Thus, as reported in [9], the spatial distribution of populations which adopt the optimal dispersal rate m^* is an IFD if there is no travel loss; while the IFD will not appear anymore if there is travel loss.

Our second result shows that the optimal dispersal rate we predict (if it is positive) is a global ESS, which means that the resident using this dispersal strategy will not be invaded by any mutant adopting any other strategy. This result reveals that a non-ideal free dispersal strategy can be an ESS.

The explicit formula of m^* also gives a biological explanation about the evolution of dispersal. Note that m^* is strictly decreasing ε_{21} (the fraction of loss of population during the movement from patch 1 to patch 2). This means that if travel loss during the movement from patch 1 to patch 2 is very high, the species prefers not to move too much. Such result is different from the one reported in [9]. Therein, the optimal dispersal strategy m^* in two-patches case does not depend on ε_{21}. The main reason is that the model of DeAngelis et al. is a Predation-Prey model. As reported in [28], when ε_{21} increases, which means the risk of predation on the way to patch 2 increases such that the species should prefer not to move to patch 2; however, if ε_{21} increases, it can be observed that the equilibrium population of the predator in patch 2 decreases, which increases the fitness for patch 2. It suggests that species should move to patch 2. In some sense, the benefit and damage brought from the increment of ε_{21} counteract each other. For the model we study, it is not a Predation-Prey model. In fact, when ε_{21} increases, the fitness for patch 2 never changes. Hence there is no benefit for species moving to patch 2 if ε_{21} is increased. This may explain why m^* is strictly decreasing ε_{21}.

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