THE EVOLUTIONARY STABILITY OF PARTIAL MIGRATION WITH ALLEE EFFECTS

YOGESH TRIVEDI, RAM SINGH, AND ANUSHAYA MOHAPATRA

Abstract. An Allee effect occurs when the per-capita growth rate increases at low densities. Here, we investigate the evolutionary stability of a partial migration population with migrant population experiencing Allee effects. Partial migration is a unique form of phenotypic diversity wherein migrant and non-migrant individuals coexist together. It is shown that when Allee effect is incorporated, the population undergoes a bifurcation as the fraction of migrating population increases from zero to unity. Using an evolutionary game theoretic approach, we prove the existence of a unique evolutionary stable strategy (ESS). It is also shown that the ESS is the only ideal free distribution (IFD) that arises in the context of partially migrating population.

1. Introduction

Allee effect is a phenomenon, in which individual fitness increases with increasing density at low densities. Many research has shown the evidence of Allee effects and the importance of this biological phenomenon has been widely recognized in population dynamics, conservation programs, management of endangered species and ecosystem dynamics [2, 7, 10, 11, 12, 16]. Here we study the evolution of partial migration phenomenon when only migrants experience Allee effects. Migration is a diverse phenomenon, and can be categorized into a multitude of forms. The most common type of migration is known as partial migration in which some individual migrate between habitats and others remain in a single habitat during their entire life. Originally, these studies were motivated by birds, by now, partial migration has been found across many taxa, including fish, invertebrates and mammals [6, 19, 20, 23, 24]. This type of within-population diversity is thought to play an important role in population stability and resilience [31], so understanding how it is maintained by natural selection is critical for predicting how species may respond to future conditions.

There has been lot of interest in understanding such a complex system in which population consists of a mix of migratory and non-migratory individuals. Several mechanisms are studied in association with partial migration which include genetic control, density-dependence, and exogenous stochastic effects in environmental variables [6, 17, 23, 29, 30]. In general, partial migration population models with negative density dependence effects are studied and neglecting the populations that experience Allee effects [17, 21, 26, 29]. One of the most common examples of Allee effects occur when a species is subject to predation with a saturating functional response, meaning that increased population levels decrease the risk of predation. Motivated by the partially migrating fish population steelhead rainbow trout system, in which steelhead experiences predation during its ocean phase, but trout does not, and only experiences the usual negative density dependence, we study a partial migration population model where the critical component is incorporation of an Allee effect. The primary goal of this work is to investigate what will happen when the biological mechanism Allee effects is included. Is partial migration preserved? Or can it be lost? How robust is it when the underlying population model is modified to incorporate the neglected biological feature?

We investigate the evolutionary stability of the partial migration population with strong Allee effect (migrants) using evolutionary game theoretic or Darwin’s dynamics approach. This is an alternative approach to Adaptive dynamics and is based on Evolutionary Game Theory as given in [19, 20, 27, 32]. We also explore the connections between Ideal Free Distributions (IFD) arising from strategies that lead to
partial migration behavior and evolutionary stable strategies. It turns out that the strategy which is the fraction of population became migrant act as a bifurcation parameter for the model. More ever it is shown that under rather general conditions the only possible strategies corresponding to an IFD, are evolutionary stable, as well as convergent stable.

The rest of this paper is structured as follows. In Section 2 we formulate the population model and state the stability results. In Section 3 we derive an explicit formula for the ESS using evolutionary game approach. In Section 4 we discuss the results that connect IFDs and ESSs, and we conclude in Section 5 with possible future work and a brief non-mathematical discussion of the results obtained in this research.

2. THE POPULATION MODEL WITH STRONG ALLEE EFFECT

Consider the following stage structured, density-dependent and matrix population model.

\[
\begin{pmatrix}
  x_1(t+1) \\
  x_M(t+1) \\
  x_N(t+1)
\end{pmatrix} = \begin{pmatrix}
  0 & f_M(z_M(t)) & f_N(z_N(t)) \\
  \phi s_M & 0 & 0 \\
  (1-\phi)s_N & 0 & 0
\end{pmatrix}
\begin{pmatrix}
  x_1(t) \\
  x_M(t) \\
  x_N(t)
\end{pmatrix},
\]

where \(x_1(t), x_M(t)\) and \(x_N(t)\) are non-negative real numbers, respectively representing the abundances of eggs, migrant adults and non-migrant adults at time \(t\), where \(t\) is a non-negative integer. A fraction \(\phi \in [0,1]\) of eggs at time \(t\) will become migrant adults, provided they survive a season, which is captured by the survival probability \(s_M \in (0,1)\) in the model. Similarly, a fraction \(1-\phi\) of eggs will become non-migrant adults, after surviving a season, with survival probability \(s_N \in (0,1)\). The functions \(f_M(z)\) and \(f_N(z)\) are per capita fertilities of migrants and non-migrants respectively. The parameter \(\phi\) represents an allocation strategy whereby each morph (migrant or non-migrant) produces offspring that can become either type of morphs. \(z_i\), with \(i = M, N\) represents the total number of competing individuals experienced by phenotype \(i\) during reproduction, and it is given by

\[
z_M(t) = x_M(t) + px_N(t)
\]

and

\[
z_N(t) = x_N(t) + qx_M(t)
\]

with \(0 < p, q < 1\). Here, \(p\) is a parameter representing the fraction of the non-migrant population competing with each migrant adult. Similarly \(q\) represents the fraction of the migrant population that competes with each non-migrant adult.

We now describe the assumptions behind our general results:

**H1** (Migrant Allee effect) \(f_M : [0,\infty) \to [0,\infty)\) is a smooth and unimodal function. Namely there is an unique positive population density \(C_0\) such that \(f_M'(C_0) = 0\) and the maximum value of the function is \(f_M(C_0)\). \(f_M\) increases at low densities i.e. \(f_M(z) > 0\) for \(z\) sufficiently small. There is a positive equilibrium density \(A\) such that \(f_M(z) < 1\) for all \(z < A\) and \(f_M(z) > 1\) for some \(z > A\). More ever we choose \(s_M f_M(C_0) > 1\) and \(g_M(z) = zf_M(z)\) has positive derivative.

**Remark 2.1.** In the case of \(s_M f_M(C_0) < 1\), the migrant only population model has only zero equilibrium point that may lead to extinction. So the assumption \(s_M f_M(C_0) > 1\) guarantee the existence of non-zero or positive fixed points for migrant only population. The solution set of the equation \(s_M f_M(z) = 1\) is non-empty, more ever it has precisely two element say \(\hat{x}_M\) and \(\tilde{x}_M\) with \(0 < \hat{x}_M < C_0 < \tilde{x}_M\), where \(\hat{x}_M\) is referred as the carrying capacity of the migrant population.

**Example 2.2.** The most common Allee effect occurs in species subject to predation by a generalist predator with a saturating functional response. Migrant population can be modeled by the following equation

\[
f_M(z) = \frac{az}{(b+z)^2}
\]

If we choose \(a = 5\) and \(b = 1\) then the graph of the function \(f_M(z)\) is as shown in the following figure.
(H2) (Decreasing fertility) \( f_N : [0, \infty) \to (0, \infty) \) is a smooth function, with negative derivatives and \( g_N(z) := f_N(z)z \) has positive derivative. More ever \( s_N f_N(0) > 1 \). Biologically, reproduction decrease with increasing population density.

**Remark 2.3.** The condition \( s_N f_N(0) > 1 \) imply that when only non-migrant morph is present, the population persists. The equation \( s_N f_N(z) = 1 \) has a unique solution \( \bar{x}_N > 0 \) and referred as the carrying capacity of the non-migrant population.

2.1. Stability Analysis. Model (1) can be re-written more compactly in vector form as

\[
X(t + 1) = A_1(X(t), \phi)X(t),
\]

where

\[
X = \begin{pmatrix} x_1 \\ x_M \\ x_N \end{pmatrix},
A_1(X, \phi) = \begin{pmatrix} 0 & f_M(z_M) & f_N(z_N) \\ \phi s_M & 0 & 0 \\ (1 - \phi) s_N & 0 & 0 \end{pmatrix},
\]

\( z_M(t) = x_M(t) + px_N(t) \) and \( z_N(t) = x_N(t) + qx_M(t) \). By splitting \( A_1(X, \phi) \) as:

\[
A_1(X, \phi) = F + T, \quad \text{where } F = \begin{pmatrix} 0 & f_M(z_M) & f_N(z_N) \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}, \quad \text{and } T = \begin{pmatrix} 0 & 0 & 0 \\ \phi s_M & 0 & 0 \\ (1 - \phi) s_N & 0 & 0 \end{pmatrix}.
\]

By splitting \( F(I - T)^{-1} \) into \( \rho(F(I - T)^{-1}) = \phi R_0^M(z_M) + (1 - \phi) R_0^N(z_N) \) for every \( (X, \phi) \in \mathbb{R}^3_+ \times [0, 1] \).

Here, \( \rho(F(I - T)^{-1}) \) denotes the spectral radius of \( F(I - T)^{-1} \) and \( R_0^I(z_I) = s_I f_I(z_I) \) for \( I = M, N \).

**Lemma 2.4.** Suppose \( \phi = \frac{1 - s_N f_N(0)}{s_M f_M(0) - s_N f_N(0)} \), then for \( \phi \in [0, \phi_1) \), \( R_0(0, \phi) > 1 \), and for \( \phi \in (\phi_1, 1) \), \( R_0(0, \phi) < 1 \).

**Proof.** We have \( R_0(0, \phi) = \phi s_M f_M(0) \) and \( (1 - \phi) s_N f_N(0) \). The derivative of \( R_0(0, \phi) \) w.r.t \( \phi \) is \( s_M f_M(0) - s_N f_N(0) \) which is negative as \( s_M f_M(0) < 1 < s_N f_N(0) \) by hypothesis (H1) and (H2). So \( R_0(0, \phi) \) is a decreasing function of \( \phi \). More ever we have \( R_0(0, \phi_1) = 1 \) iff \( \phi = \phi_1 \), where \( \phi_1 = \frac{1 - s_N f_N(0)}{s_M f_M(0) - s_N f_N(0)} \). Hence for \( \phi \in [0, \phi_1), R_0(0, \phi) > 1 \) and for \( \phi \in (\phi_1, 1) \), \( R_0(0, \phi) < 1 \).

**Lemma 2.5.** Suppose the functions \( f_M \) and \( f_N \) satisfies the hypothesis (H1) – (H2) and suppose that \( s_N f_N(\frac{C_B}{d_1}) > 1, q s_M < s_N \) and \( p s_N < s_M \). Define \( Q_\phi(x) := \phi s_M f_M(d_1 x) + (1 - \phi) s_N f_N(d_2 x) \) where \( d_1(\phi) = \phi s_M + p(1 - \phi) s_N \) and \( d_2(\phi) = q s_M + (1 - \phi) s_N \). Exactly one solution \( \bar{x}_1(\phi) \) of the equation \( Q_\phi(x) = 1 \) will lie in the interval \( (\frac{C_B}{d_1(\phi)}, \infty) \), where \( f_M'(C_0) = 0 \).

**Proof.** Denote \( F_\phi^M(x) = 1 - \phi s_M f_M(d_1 x) \) and \( F_\phi^N(x) = (1 - \phi) s_N f_N(d_2 x) \), then we have

\[
Q_\phi(x) - 1 = F_\phi^N(x) - F_\phi^M(x).
\]
Notice that $\frac{d}{dx}(F^M_\phi) = 0$ at $\frac{C_0}{d_1}$ and $F^M_\phi$ is a unimodal function for each $\phi \in (0, 1)$ as shown in the figure (2). Also $F^N_\phi$ is a strictly decreasing function in $x$. So if $F^M_\phi(\frac{C_0}{d_1}) < F^N_\phi(\frac{C_0}{d_1})$, then the graphs of $F^M_\phi$ and $F^N_\phi$ will intersect at least at one point in the first quadrant. It is easy to check that the assumptions $s_N f_N(\frac{C_0}{p}) > 1, q s_M < s_N, p s_N < s_M$ and $s_M f_M(C_0) > 1$ together implies $F^M_\phi(\frac{C_0}{d_1}) < F^N_\phi(\frac{C_0}{d_1})$. So the equation $Q_\phi(x) = 1$ has at least one solution in positive real line. Since $F^N_\phi$ is strictly decreasing and $F^M_\phi$ is strictly increasing on $[\frac{C_0}{d_1}, \infty)$, the equation $Q_\phi(x) = 1$ has exactly one solution $\hat{x}_1(\phi)$ in $(\frac{C_0}{d_1}, \infty)$ (see figure 2).

**Remark 2.6.** Lemma (2.5) says that the number of positive solution of the equation $Q_\phi(x) = 1$ in $(\frac{C_0}{d_1(\phi)}, \infty)$ is one, however there may be one or more then one positive solution of the equation $Q_\phi(x) = 1$ in the interval $[0, \frac{C_0}{d_1})$. For simplification purpose we only focus on a class functions $f_N$, $f_M$ and other suitable parameters such that the equation $Q_\phi(x) = 1$ has at most one solution in $[0, \frac{C_0}{d_1})$ for all $\phi \in (0, 1)$ as shown in the figure (2) and also the main results in this work remain same even if the equation $Q_\phi(x) = 1$ has one or more solutions in $[0, \frac{C_0}{d_1})$.

**Remark 2.7.** The assumption $s_N f_N(\frac{C_0}{p}) > 1$ in lemma (2.5) is equivalent to $C_0 < p \bar{x}_N$, provided $q s_M < s_N$ and $p s_N < s_M$, where $f'_M(C_0) = 0$.

So we make another hypothesis as follows.

**(H3)** For each $\phi \in (0, 1)$ the equation $Q_\phi(x) = 1$ has at most one positive solution in the interval $(0, \frac{C_0}{d_1})$ as shown in the figure (2), where $Q_\phi(x)$ is the function as defined in lemma (2.5). And more ever as assumed in the lemma (2.5) choose $C_0 < p \bar{x}_N, q s_M < s_N$ and $p s_N < s_M$.

**Example 2.8.** Let $f_M(z) = \frac{7}{(1+z)^2}$, $f_N(z) = \frac{3}{1+z}$ and $s_M = 0.70, s_N = 0.85, q = 0.80, p = 0.80$. In this case we get $\phi_1 = 0.61$, so when $\phi \in [0, 0.61)$ i.e. $R_0(0, \phi) > 1$, the functions $F^M_\phi$ and $F^N_\phi$ intersect at exactly one point. And if $\phi \in (0.61, 1]$ i.e. $R_0(0, \phi) < 1$, the functions $F^M_\phi$ and $F^N_\phi$ intersect at two points. Hence the equation $Q_\phi(x) = 1$ has one positive solution for $R_0(0, \phi) > 1$, and two positive solutions for $R_0(0, \phi) < 1$. The graphs corresponding to some $\phi$ values are given below. The functions $f_N$, $f_M$ and other parameters satisfies all the hypothesis (H1) - (H3).
exactly one point. And if this case we get $R$ of the system (5), then it should satisfy the equation $Q$. Hence the equation (7) $d$ and other parameters satisfies all the hypothesis ($H1$).

Example 2.9. Let $f_M(z) = \frac{8}{(1+z)^2}$, $f_N(z) = \frac{9}{1+2z}$ and $s_M = 0.60, s_N = 0.28, q = 0.45, p = 0.90$. In this case we get $\phi = 0.60$, so when $\phi \in [0, 0.60]$ i.e. $R_0(0, \phi) > 1$, the functions $F_\phi^M$ and $F_\phi^N$ intersect at exactly one point. And if $\phi \in (0.60, 1]$ i.e. $R_0(0, \phi) < 1$, the functions $F_\phi^M$ and $F_\phi^N$ intersect at two points. Hence the equation $Q_{\phi}(x) = 1$ has one positive solution for $R_0(0, \phi) > 1$, and two positive solutions for $R_0(0, \phi) < 1$. The graphs corresponding to some $\phi$ values are given below. The functions $f_N$, $f_M$ and other parameters satisfies all the hypothesis ($H1$) - ($H3$).

2.2. The population dynamics. One can observe that if there exist a positive fixed point $x^* = (x_1^*, x_M^*, x_N^*)$ of the system (5), then it should satisfy the equation $R_0(x^*, \phi) = 1$. If we choose $d_1 = \phi s_M + p(1 - \phi)s_N$ and $d_2 = q\phi s_M + (1 - \phi)s_N$, then the first coordinate $x_1^*$ satisfy the following

$$Q_{\phi}(x) = \phi s_M f_M(d_1 x) + (1 - \phi) s_N f_N(d_2 x) = 1$$

Conversely suppose any positive $x_1^*$ satisfy the equation (7). If you choose $x^* = (x_1^*, x_M^*, x_N^*)$ with $x_M^* = \phi s_M x_1^*$ and $x_N^* = (1 - \phi)s_N x_1^*$, then $R_0(x^*, \phi) = 1$ and $x^*$ is a positive fixed point of the model (5). Since $x^*$ is uniquely defined by $x_1^*$, the number of positive solution to the equation (7) is same as the number of positive fixed point of the system (5).

We have the following result.

Theorem 2.10. Assume that the hypothesis ($H1$) - ($H3$) holds for the system (1) then following holds with $\phi_1 = \frac{1 - s_N f_N(0)}{s_M f_M(0) - s_N f_N(0)}$:

1. For $\phi \in [0, \phi_1)$, the zero fixed point is unstable and for $\phi \in (\phi_1, 1]$, it is locally stable.

2. If $\phi \in (0, 1)$, the system (1) has exactly one locally stable positive fixed point $x^*(\phi) = (x_1^*(\phi), x_M^*, x_N^*)$ with $x_1^* > \frac{C_0}{d_1}$, where $d_1 = \phi s_M + p(1 - \phi)s_N$ and $f_M'(C_0) = 0$.

3. If $\phi = 0$, then system (1) has a unique, non-zero locally stable fixed point $(\tilde{x}_1, 0, \tilde{x}_N)$, where $\tilde{x}_N > 0$ is the unique positive solution to the equation $s_N f_N(z) = 1$, and if $\phi = 1$, then system (1) has exactly one non-zero locally stable fixed point $(\tilde{x}_1, \tilde{x}_M, 0)$, where $\tilde{x}_M$ is a positive solution to the equation $s_M f_M(z) = 1$, with $f_M'(\tilde{x}_M) < 0$ and $\tilde{x}_1 = \tilde{x}_M/s_M$, $\tilde{x}_1 = \tilde{x}_N/s_N$. 

Figure 3

(a) $\phi = 0.4$ i.e. $R_0(0, \phi) > 1$

(b) $\phi = 0.75$ i.e. $R_0(0, \phi) < 1$

Figure 4

(a) $\phi = 0.50$ i.e. $R_0(0, \phi) > 1$

(b) $\phi = 0.85$ i.e. $R_0(0, \phi) < 1$
Proof. For \( \phi \in [0, \phi_1), R_0(0, \phi) > 1 \) and for \( \phi \in (\phi_1, 1), R_0(0, \phi) < 1 \) by Lemma (2.4). So for \( \phi \in (\phi_1, 1) \) the origin is a locally stable fixed point and for \( \phi \in [0, \phi_1) \), it is unstable.

**Case I :** \( \phi \in (0, 1) \).
Suppose \( R_0(0, \phi) \geq 1 \), then by lemma (2.5) and hypothesis (H3), for each \( \phi \) the system (1) has one positive fixed point \( x^*(\phi) = (x_1^*, x_M^*, x_N^*) \) with \( x_1^* > \frac{M_0}{s_M} \). The Jacobian matrix \( J \) defined at the fixed point \( (x_1^*, x_M^*, x_N^*) \) is

\[
J = \begin{pmatrix}
0 & F_1 & F_2 \\
\phi s_M & 0 & 0 \\
(1 - \phi)s_N & 0 & 0
\end{pmatrix}
\]

where \( F_1 = x_M^*(t) f_M'(z_M^*(t)) + f_M(z_M^*(t)) + q x_N^*(t)f_M'(z_N^*(t)) \) and \( F_2 = px_M^*(t)f_M'(z_M^*(t)) + x_N^*(t)f_M'(z_N^*(t)) + f_N(z_N^*(t)) \). The eigenvalues of the matrix \( J \) are found to be 0, and \( \pm \sqrt{1 + x_1^* Q_0'(x_1^*)} \). Where

\[
Q_0'(x_1^*) = d_1 \phi s_M f_M'(d_1 x_1^*) + d_2 (1 - \phi) s_N f_N'(d_2 x_1^*)
\]

with \( d_1 = \phi s_M + p(1 - \phi) s_N \) and \( d_2 = q \phi s_M + (1 - \phi) s_N \). Since the derivative of the functions \( x f_M(d_1 x) \) and \( x f_N(d_2 x) \) are positive, we have \( d_1 x_1^* f_M'(d_1 x_1^*) < |f_M'(d_1 x_1^*)| \) and \( d_2 x_1^* f_N'(d_2 x_1^*) < |f_N'(d_2 x_1^*)| \). So

\[
|d_1 \phi s_M x_1^* f_M'(d_1 x_1^*)| + |d_2 (1 - \phi) s_N x_1^* f_N'(d_2 x_1^*)| < 1.
\]

So the eigenvalue \( \lambda = |\sqrt{1 + x_1^* Q_0'(x_1^*)}| \) of the matrix \( J \) is dominant, positive and less than one as \( x_1^* Q_0'(x_1^*) < 0 \). Hence the fixed point \( (x_1^*, x_M^*, x_N^*) \) is locally asymptotically stable. Now suppose \( R_0(0, \phi) < 1 \), by lemma (2.5) and hypothesis (H3), for each \( \phi \) the system (1) has two positive fixed points say \( x^{**}(\phi) \) and \( x^*(\phi) \). Suppose \( x_1^{**} \) and \( x_1^* \) are the corresponding first coordinates with \( x_1^{**} < \frac{C_0}{1 - \phi} < x_1^* \). Similar to the previous case (for \( R_0(0, \phi) \geq 1 \)) the eigenvalues of the Jacobian of the system (1) at \( x^{**} \) are 0, and \( \pm \sqrt{1 + x_1^{**} Q_0'(x_1^{**})} \). In this case \( x_1^{**}, Q_0'(x_1^{**}) \) is positive as \( Q_0(x) - 1 \) is an increasing function at \( x_1^{**} \), so the eigenvalue \( \lambda = |\sqrt{1 + x_1^{**} Q_0'(x_1^{**})}| \) is dominant, positive and bigger than one which make the fixed point \( x^{**}(\phi) \) locally asymptotically unstable.

On the other hand \( x^* \) is locally stable using the same argument as in the case of \( R_0(0, \phi) \geq 1 \). So for each \( \phi \in (0, 1) \), the system (1) has exactly one locally stable fixed point \((x_1^*(\phi), x_M^*(\phi), x_N^*(\phi))\).

**Case II :** Suppose \( \phi = 0 \), then notice that every orbit of (1) enters the invariant part of the boundary of \( \mathbb{R}^3 \) where \( x_M = 0 \) in 1 step. The restriction of the dynamics to this part of the boundary is given by a planar system:

\[
\begin{pmatrix}
x_1(t + 1) \\
x_N(t + 1)
\end{pmatrix} = \begin{pmatrix}
0 & f_N(x_N(t)) \\
s_N & 0
\end{pmatrix} \begin{pmatrix}
x_1(t) \\
x_N(t)
\end{pmatrix}
\]

Suppose that \( (x_1^*, x_N^*) \) is a positive fixed point of the system (9) then it turns out that
\( s_N f_N(x_N^*(t)) = 1 \) which has a unique positive solution \( \bar{x}_N \). Choose \( \bar{x}_1 = \frac{\bar{x}_N}{s_N} \), clearly \((\bar{x}_1, 0, \bar{x}_N)\) the unique non-zero fixed point of the system (1) when \( \phi = 0 \). The Jacobian matrix when we linearize the system (9) near the fixed point \((\bar{x}_1, 0, \bar{x}_N)\) is given by

\[
J_1 = \begin{pmatrix}
0 & \bar{x}_N f_M'(\bar{x}_N) + f_N(\bar{x}_N) \\
s_N & 0
\end{pmatrix}
\]

The eigenvalues of the matrix \( J_1 \) are given by \( \lambda = \pm \sqrt{1 + s_N \bar{x}_N f_M'(\bar{x}_N)} \). Since the function \( z f_N(z) \) is increasing and \( f_N(z) \) is decreasing, \( |\lambda| < 1 \), so the fixed point \((\bar{x}_1, 0, \bar{x}_N)\) is linearly stable.

Now suppose \( \phi = 0 \), as similar to the case \( \phi = 0 \), the fixed point is of the form \((x_1^*, x_M^*, 0)\), where \( s_M f_M(x_M^*) = 1 \) and \( x_1^* = \frac{\bar{x}_M}{s_M} \). The equation \( s_M f_M(x_M^*) = 1 \) has two solution \( \bar{x}_M \) and \( \tilde{x}_M \) satisfying \( \bar{x}_M < C_0 < \tilde{x}_M \) which corresponds to two fixed points \( \tilde{x} \) and \( \tilde{x} \) of the system (9). The eigenvalues of the Jacobian, if we linearize the system near any fixed point \( x^* = (x_1^*, x_M^*, 0) \) are \( \lambda = \pm \sqrt{1 + s_N x_M^* f_M'(x_M^*)} \). So \( |\lambda| > 1 \) at \( x^* = \tilde{x} \) as \( f_M'(\tilde{x}_M) > 0 \), hence it is an unstable fixed point and \( |\lambda| < 1 \) at \( x^* = \bar{x}_M \) by the same argument as in the case \( \phi = 0 \) so it is a stable fixed point.

So in summary, we just proved that for each \( \phi \in [0, 1] \), there is exactly one locally stable fixed point for the system (1).
3. Evolutionary game and ESS

If Allee effect is present only in migrant population, the dynamics of the system (1) undergoes a bifurcation as the zero fixed point stability changes when parameter \( \phi \) passes through \( \phi_1 \). The goal is to investigate how the evolution of partial migration is affected when only the migrants experience Allee effects. To address this question, we will use an evolutionary Game theory approach as advocated in [9, 19, 20, 32]. In this methodology, an individual’s allocation strategy is denoted by \( v \), and the mean allocation strategy \( \phi(t) \) in the population is treated as a dynamic state variable whose dynamics are governed by Lande’s equation (or the breeder’s equation, Fisher’s equation, or the canonical equation of evolution). The methodology provides a coupled system for the population dynamics and the mean allocation strategy, known as the Darwinian dynamics:

\[
\begin{pmatrix}
  x_1(t+1) \\
  x_M(t+1) \\
  x_N(t+1)
\end{pmatrix}
= \begin{pmatrix}
  0 & f_M(z_M(t)) & f_N(z_N(t)) \\
  v s_M (1-v)s_N & 0 & 0 \\
  (1-v)s_N & 0 & 0
\end{pmatrix}
\begin{pmatrix}
  x_1(t) \\
  x_M(t) \\
  x_N(t)
\end{pmatrix}
\]

(11)

\[
\phi(t+1) = \phi(t) + \sigma^2 \frac{\partial \ln (\lambda(x(t),v))}{\partial v} \Big|_{v=\phi(t)},
\]

(12)

Equation (12) states that the change in the mean strategy is proportional to the fitness gradient. Fitness here is taken to be \( \ln (\lambda(x,v)) \), where \( \lambda(x,v) \) is the dominant eigenvalue of the matrix

\[
A_1(x,v) = \begin{pmatrix}
  0 & f_M(z_M) & f_N(z_N) \\
  v s_M & 0 & 0 \\
  (1-v)s_N & 0 & 0
\end{pmatrix}.
\]

The constant \( \sigma^2 \) is related to the (assumed constant) variance of the strategy throughout the population (equal, or proportional to the variance, depending on how the trait dynamics are derived) and is referred to as the speed of evolution.

A straightforward calculation shows that \( \lambda(x,v) \) equals the square root of the basic reproduction number associated to \( A_1(x,v) \), which we already defined in (6):

\[
\lambda(x,v) = (R_0(x,v))^{1/2}, \text{ where } R_0(x,v) := v s_M f_M(z_M) + (1-v) s_N f_N(z_N).
\]

Hence, system (11) – (12) can be re-written as:

\[
\begin{pmatrix}
  x_1(t+1) \\
  x_M(t+1) \\
  x_N(t+1)
\end{pmatrix}
= \begin{pmatrix}
  0 & f_M(z_M(t)) & f_N(z_N(t)) \\
  \phi(t)s_M (1-\phi(t))s_N & 0 & 0 \\
  (1-\phi(t))s_N & 0 & 0
\end{pmatrix}
\begin{pmatrix}
  x_1(t) \\
  x_M(t) \\
  x_N(t)
\end{pmatrix}
\]

(13)

\[
\phi(t+1) = \phi(t) + \frac{1}{2} R_0(x(t),\phi(t)) \frac{\partial R_0(x(t),v)}{\partial v} \Big|_{v=\phi(t)}.
\]

(14)

We first study this system for \( \sigma = 0 \), i.e. when there are no evolutionary forces at work:

**Theorem 3.1.** Assume that \( \sigma^2 = 0 \). Suppose that (H1) – (H3) hold,

Then the following holds:

1. For every fixed \( \phi_0 \) in (0,1), there is a positive fixed point \((x^*(\phi_0),\phi_0)\) such that every positive solution of system (13) – (14) with initial condition \((x_0,\phi_0)\) for \( x_0 \) in a neighborhood of \((x^*(\phi_0),\phi_0)\), converges to \((x^*(\phi_0),\phi_0)\). The fixed point \((x^*(\phi_0),\phi_0)\) is locally stable with respect to positive initial conditions with arbitrary positive \( x_0 \), but fixed \( \phi_0 \).

2. If \( \phi_0 = 0 \), then every positive solution of system (13) – (14) with initial condition \((x_0,\phi_0)\) for arbitrary positive \( x_0 \), converges to a unique non-zero fixed point \((\tilde{x}_1,0,\tilde{x}_N,0)\), where \( \tilde{x}_N > 0 \) is the unique positive solution to the equation \( s_N f_N(z) = 1 \), and \( \tilde{x}_1 = \tilde{x}_N/s_N \). This fixed point is linearly stable with respect to initial conditions with arbitrary positive \( x_0 \), but fixed \( \phi_0 = 0 \).

3. If \( \phi_0 = 1 \), then every positive solution of system (13) – (14) with initial condition \((x_0,\phi_0)\) for arbitrary positive \( x_0 \), converges to a unique non-zero fixed point \((\tilde{x}_1,\tilde{x}_M,0,1)\), where \( \tilde{x}_M > 0 \) is a
positive solution to the equation \( s_M f_M(z) = 1 \), and \( \dot{x}_1 = \hat{x}_M / s_M \). This fixed point is linearly stable with respect to initial conditions with arbitrary positive \( x_0 \), but fixed \( \phi_0 = 1 \).

**Proof.** The proof follows immediately from Theorem 2.10 and the fact that for each \( \phi_0 \) in \([0, 1]\), the set \( \{(x, \phi) \in \mathbb{R}_+^2 \times [0, 1] \mid \phi = \phi_0\} \) is forward invariant for solutions of system (13) – (14) when \( \sigma^2 = 0 \). ■

**Definition 3.2.** Suppose \((x^*(\phi^*), \phi^*)\) is the stable fixed point of the system (13) – (14) for \( \phi^* \) in \([0, 1]\) and for \( \sigma = 0 \). We say \( \phi^* \) is an evolutionary stable strategy (ESS) if \((x^*(\phi^*), \phi^*)\) is a locally asymptotically stable fixed point of system (13) – (14) for small positive \( \sigma^2 \neq 0 \).

This notion captures that if the population has adopted an ESS, then it can not be invaded by other population that use nearby strategies. Our next result shows the existence and uniqueness of an ESS.

**Theorem 3.3.** Assume that \( \sigma^2 > 0 \). Suppose that (H1) – (H3) hold, and the carrying capacities satisfies the inequalities: \( q\hat{x}_M < \hat{x}_N \) and \( p\hat{x}_N < \hat{x}_M \). Then the system (13) – (14) has a fixed point \((x^*(\phi^*), \phi^*)\) in \( \mathbb{R}_+^2 \), where \( x^*(\phi^*) \) is the unique stable positive fixed point of system (1) with \( \phi = \phi^* \) (see Theorem 2.10) and \( \phi^* \) is given by the following formula

\[
\phi^* = \frac{\hat{x}_M - \hat{p}\hat{x}_N}{\hat{x}_N - \hat{q}\hat{x}_M} + \frac{\hat{s}_M}{\hat{s}_N}.
\]

Moreover, \((x^*(\phi^*), \phi^*)\) is a locally asymptotically stable fixed point of system (13) – (14) for sufficiently small positive \( \sigma^2 \). So \( \phi^* \) is a unique ESS.

**Proof.** The system of equations, when evolutionary force at work are

\[
\begin{pmatrix}
    x_1(t + 1) \\
    x_M(t + 1) \\
    x_N(t + 1)
\end{pmatrix} = \begin{pmatrix}
    0 & f_M(z_M(t)) & f_N(z_N(t)) \\
    \phi(t)s_M & 0 & 0 \\
    (1 - \phi(t))s_N & 0 & 0
\end{pmatrix} \begin{pmatrix}
    x_1(t) \\
    x_M(t) \\
    x_N(t)
\end{pmatrix}
\]

\[
\phi(t + 1) = \phi(t) + \frac{\sigma^2}{2} \left. \frac{\partial R_0(x(t), v)}{\partial v} \right|_{v = \phi(t)},
\]

where \( R_0(x, v) := vs_M f_M(z_M) + (1 - v)s_N f_N(z_N) \).

Suppose \((x_1^*, x_M^*, x_N^*, \phi^*)\) is a fixed point for the system (16) – (17). We have

\[
\phi^*(t) = \phi^*(t) + \frac{\sigma^2(s_M f_M(z_M^*) - s_N f_N(z_N^*))}{2\phi^* s_M f_M(z_M^*) + (1 - \phi^*) s_N f_N(z_N^*)}
\]

which implies that \( s_M f_M(z_M^*) - s_N f_N(z_N^*) = 0 \) so \( s_M f_M(z_M^*) = s_N f_N(z_N^*) \). We also have \( R_0(x^*, \phi^*) = \phi^* (s_M f_M(z_M^*) - s_N f_N(z_N^*)) + s_N f_N(z_N^*) = 1 \)

It follows that \( s_N f_N(z_N^*) = 1 \) and \( s_M f_M(z_M^*) = 1 \). The equation \( s_N f_N(z_N) = 1 \) has unique solution say \( \hat{x}_N \) and \( s_M f_M(z_M) = 1 \) has two solution \( \hat{x}_M \) and \( \hat{x}_M \) with \( f'(\hat{x}_M) > 0 \), \( f'(\hat{x}_M) < 0 \) and \( \hat{x}_M < \hat{x}_M \). Hence either \( z_M^*(\phi) = x_M^*(\phi) + px_N^*(\phi) = \hat{x}_M \) or \( z_M^*(\phi) = \hat{x}_M \) and \( z_N^*(\phi) = x_N^*(\phi) + qx_M^*(\phi) = \hat{x}_N \). After simplifying and solving for \( x_M^* \) and \( x_N^* \) in case of \( z_M^*(\phi) = \hat{x}_M \) we get

\[
x_M^*(\phi) = \frac{\hat{x}_M - \hat{p}\hat{x}_N}{1 - pq}
\]

\[
x_N^*(\phi) = \frac{\hat{x}_N - \hat{q}\hat{x}_M}{1 - pq}
\]

it follows that:

\[
\frac{x_M^*(\phi)}{x_N^*(\phi)} = \frac{\hat{x}_M - \hat{p}\hat{x}_N}{\hat{x}_N - \hat{q}\hat{x}_M} = \frac{s_M}{s_N} \frac{1 - \phi}{1 - \phi^*}.
\]
Similarly in case of \( z^*_N(\phi) = \tilde{x}_M \), we have

\begin{equation}
\phi^* = \frac{\tilde{x}_M - p\tilde{x}_N}{\tilde{x}_N - q\tilde{x}_M} + \frac{s_M}{s_N}.
\end{equation}

Because \( \tilde{x}_M < C_0 < p\tilde{x}_N \), the corresponding fixed point is not a positive one. So we have one positive fixed point for the system \((16)-(17)\), we will show that the fixed point \((x^*(\phi^*), z^*(\phi^*))\) is local asymptotically stable. We linearize the Darwinian system \((16)-(17)\) near fixed point \((x^*(\phi^*), z^*(\phi^*))\) yielding the following Jacobian matrix:

\[
J_D(\sigma^2) = \begin{pmatrix}
0 & a & b & 0 \\
c & 0 & 0 & g \\
d & 0 & 0 & -h \\
e & f & 1 & 0
\end{pmatrix}\]

where 
\[a = f'_M(z^*_M)x^*_M + f_M(z^*_M) + x^*_N f'_N(z^*_N), q, \quad b = p f'_M(z^*_M)x^*_M + f'_N(z^*_N)x^*_N + f_N(z^*_N), \quad c = \phi^* s_M, \quad g = s_M x^*_N, \quad d = (1 - \phi^*) s_N, \quad h = s_N x^*_N, \quad e = \frac{\sigma^2}{2}(s_M f'_M(z^*_M) - s_N f'_N(z^*_N)) \quad \text{and} \quad f = \frac{\sigma^2}{2}(p s_M f'_M(z^*_M) - s_N f'_N(z^*_N)).\]

In the appendix, we have shown that the dominant eigenvalue of the matrix \(J_D(\sigma^2)\) is positive and less than one, hence the \(\phi^*\) given by the equation \((21)\) is an unique ESS.

\[\square\]

4. The ESS is an IFD in two habitat environment

Theorem \(3.3\) reveals the existence of an evolutionary stable strategy \(\phi^* \in (0, 1)\) such that for any population with the fixed strategy \(\phi^*\), can not be invaded by other population with near by strategies. However, it does not say whether that strategy which lead to stable fixed points that correspond to an ideal free distribution. The IFD has emerged in many studies on the evolution of dispersal \([3, 4, 8, 13, 15, 18, 25]\). Here we study the IFD concept for a population that exhibits partial migration. The goal of this Section is to examine this issue. The concept of an IFD is based on the ability of individuals to assess the quality of a spatial environment, yet model \((1)\) does not incorporate space explicitly. However, it does contain space implicitly, and we can re-interpret model \((1)\) as a population model that evolves in two habitats \(h_M\) and \(h_N\), representing a migratory and non-migratory habitat. To each habitat we can associate a pay-off or fitness function which depends on the density of the abundances in that habitat, at equilibrium state. A population at equilibrium is considered to be ideal free, if the finesses in both habitats are equal and maximal. In this scenario, individuals would have no incentive to move to a different habitat. In this section, we will show that the ESS is in fact an IFD, corresponding to a non-extreme value of the strategy parameter \(\phi^*\). But first, we give a mathematical definition of the IFD concept.

**Definition 4.1.** Recall from Theorem \(2.10\) that for each \(\phi \in [0, 1]\), there is one positive equilibrium state \((x^*_M(\phi), x^*_N(\phi))\) which is locally asymptotically stable for system \((1)\). We define the payoff (or fitness) function for habitat \(h_I\) to be \(R^I_0(z^*_M(\phi)) = s_I f_I(z^*_I), \) where \(I = M, N\), \(z^*_M(\phi) = x^*_M(\phi) + px^*_N(\phi)\) and \(z^*_N(\phi) = x^*_N(\phi) + qx^*_M(\phi)\). An allocation strategy \(\phi^*\) is said to be an IFD strategy for model \((1)\) if the two habitats \(h_M\) and \(h_N\) have the same payoffs at \(\phi^*\), i.e if

\[R^M_0(z^*_M(\phi^*)) = R^N_0(z^*_N(\phi^*)),\]

and if no other strategy satisfying this payoff equality condition, has a higher payoff.

**Theorem 4.2.** If the conditions of Theorem \(3.3\) hold for system \((1)\) then the ESS strategy \(\phi^*\) given by the formula \((21)\) is the only IFD.
Proof. By formula (15), we have the following;

\[ \frac{\dot{x}_M - p\tilde{x}_N}{\dot{x}_N - q\tilde{x}_M} = \frac{s_M}{s_N} \frac{\phi^*}{1 - \phi^*}. \]

Choose \( \tilde{x}_1 = \frac{\dot{x}_M - p\tilde{x}_N}{(1-pq)s_M} \) and \( \tilde{x} = (\tilde{x}_1, \frac{\dot{x}_M - p\tilde{x}_N}{1-pq}, \frac{\dot{x}_N - q\tilde{x}_M}{1-pq}) \). It is easy to check that \( R_0(\tilde{x}, \phi^*) = 1 \) so, clearly \( \tilde{x} \) is an equilibrium point of the system (1) which is positive. One can show that it is in fact locally asymptotically stable. So we have

\[ x^*_M(\phi^*) = \frac{\dot{x}_M - p\tilde{x}_N}{1 - pq} \]

Hence the pay-off functions are found to be equal:

\[ R^M_0(z^*_M(\phi^*)) = R^N_0(z^*_N(\phi^*)) = 1 = R^M_0(\tilde{x}_M) = R^N_0(\tilde{x}_N) \]

and this proves that \( \phi^* \) is indeed an IFD.

Conversely suppose \( \phi = \phi^* \) is an IFD. Then

\[ R^M_0(z^*_M(\phi^*)) = R^N_0(z^*_N(\phi^*)) \]

By the theorem (3.3), \( \phi^* \) is an ESS. 

5. Discussion

The goals of this study were twofold: investigating if the evolution of partial migration is affected when only the migrants experience Allee effects and using the evolutionary game theory approach to determine evolutionary stable strategies if any. In existing literature [14, 21, 24, 29], it is shown that negative density dependence in the fertilities alone can explain the partial migration phenomenon, provided it is attenuated with increasing sub-type abundances. The works are mostly numerical. Nevertheless, several biological features specially Allee effects of partially migrating populations have been neglected. An Allee effect is a positive association between absolute average individual fitness and population size over some finite interval. In some partially migrating population, the migrant individual experience predation during their stays at migrant habitat which may result in Allee effects. When the size of populations subject to Allee effects is low, then these populations tend towards extinction. This fact argues for a thorough understanding of Allee effects and their mechanisms in order to develop sound management practices for a number of environmental issues. So the important aspect of this work is that, we have obtained an analytical formula for the Evolutionary Stable Strategy (ESS) for the allocation strategy adopted by a partially migrating population with migrant population experiencing a strong Allee effects. This ESS is expressed in terms of the demographic model parameters for the migrant and non-migrant populations, and thus the formula can be used to predict the ESS value, whenever the life histories of the migrant and non-migrant populations are known, for example from lab or empirical data. More ever, the conditions on environmental parameters like carrying capacities under which the population will be evolutionary stable are clearly stated. Our results differ from previous studies [14, 21, 24, 29] in that partial migration as it point to more of a system of thresholds, which provides some insight into how populations may respond to future conditions when migrant undergoes Allee effects. We also investigate the connection between spatio/temporal structure and the evolution of partial migration behavior by associating the ESS to Ideal Free distribution (IFD) which happens to be a powerful tool for understanding how populations distribute themselves in heterogeneous environments. Mostly the phenomenon is studied in temporally constant environment but many environments are seasonal and changes with time. So for the future work it is motivating to investigate the phenomenon when the underlying population model is modified to incorporate time varying environments.

6. Acknowledgment

This work is funded by start up research grant, SERB (SRG/2019/002200) to AM.
7. Appendix

The dominant eigenvalue of the Jacobian of Darwinian system:

The Jacobian matrix with $\sigma^2 > 0$ is given by

$$J_D(\sigma^2) = \left( C(x^*(\phi^*), \phi^*) * 1 \right) + \sigma^2 \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix},$$

where the * represents a 3-dimensional vector whose value is unimportant at present, and the $3 \times 3$ matrix $C(x^*(\phi^*), \phi^*)$ is defined as:

$$C(x^*(\phi^*), \phi^*) = \begin{pmatrix} 0 & a & b \\ c & 0 & 0 \\ d & 0 & 0 \end{pmatrix},$$

with $a = f_M'(z_M^*)x_M^* + f_M(z_M^*) + x_N^*f_N'(z_N^*)$, $b = pf_M'(z_M^*)x_M^* + f_N(z_N^*) + x_N^*f_N'(z_N^*)$, $c = \phi^*s_M$ and $d = (1-\phi^*)s_N$. One can check that the eigenvalues of the matrix $C(x^*(\phi^*), \phi^*)$ are $0$ and $\pm \sqrt{1 + x_1^* Q(x_1^*)}$.

We have proved in the theorem (2.10) that the dominant eigenvalue $\lambda^*$ holds that: $\sqrt{1 + x_1^* Q(x_1^*)}$ is positive and less than one. Consequently, the dominant eigenvalue of $J_D(0)$ is $1$, and this eigenvalue is simple. By continuity of eigenvalues, the matrix $J_D(\sigma^2)$ will also have a real, simple and dominant eigenvalue $\lambda_p(\sigma^2)$ for all sufficiently small $\sigma^2$, such that $\lambda_p(0) = 1$. We claim that $\lambda_p(\sigma^2) < 1$, at least for all sufficiently small $\sigma^2$. To prove this, we now examine the roots of the characteristic polynomial $F(\lambda, \sigma^2) := \det(\lambda I - J_D(\sigma^2))$ associated to the matrix $J_D(\sigma^2)$.

$$J_D(\sigma^2) = \begin{pmatrix} 0 & a & b & 0 \\ c & 0 & 0 & g \\ d & 0 & 0 & -h \\ 0 & \sigma^2 e & \sigma^2 f & 1 \end{pmatrix}$$

Where $g = s_M x_M^*$, $h = s_N x_N^*$, $e = \frac{\sigma^2}{2} (s_M f_M'(z_M^*) - q s_N f_N'(z_N^*))$ and $f = \frac{\sigma^2}{2} (p s_M f_M'(z_M^*) - s_N f_N'(z_N^*))$. A tedious calculation shows that the characteristic polynomial of the matrix $J_D(\sigma^2)$ is given by:

$$F(\lambda, \sigma^2) = \lambda^4 - \lambda^3 - [\sigma^2(e g - f h) + (a c + b d)] \lambda^2 + (a c + b d) \lambda + \sigma^2 (b e - a f)(c h + d g)$$

Note that $F(\lambda, 0)$ is positive for all $\lambda > 1 = \lambda_p(0)$ (since $\lambda_p(0) = 1$ is the dominant root of $F(\lambda, 0)$, and $\lim_{\lambda \to \infty} F(\lambda, 0) = +\infty$). Moreover, $\partial F/\partial \lambda(\lambda_p(0), 0)$ must be positive because $\lambda_p(0) = 1$ is a simple root of $F(\lambda, 0)$ (this can also be shown directly by calculating this partial derivative using the expression above: $\partial F/\partial \lambda(\lambda_p(0), 0) = 1 - (a c + b d)$, and this is positive). Therefore, the claim above (namely, that $\lambda_p(\sigma^2) < 1$, for all sufficiently small $\sigma^2$) will be proved, provided we can show that for all sufficiently small $\sigma^2$, there holds that:

$$F(1, \sigma^2) > 0.$$ Evaluating $F(1, \sigma^2)$ yields:

$$F(1, \sigma^2) = \sigma^2 ((b e - a f)(c h + d g) - (e g - f h)).$$

Therefore, a sufficient condition for (25) to hold, is that:

$$(f h - e g) - ((a f - b e)(c h + d g)) > 0$$

After simplifying we found that

$$(f h - e g) - ((a f - b e)(c h + d g)) = f_M'(z_M^*) f_N'(z_N^*) s_M s_N (1 - p q) (z_N^* s_M + z_M^* s_N) > 0$$

This concludes that the dominant eigenvalue of the Jacobian matrix corresponding to the Darwinian system [16]-[17] is less than one in modulus.
References

[1] Allen, L. J., & Van den Driessche, P. (2008). The basic reproduction number in some discrete-time epidemic models. *Journal of difference equations and applications*, 14(10-11), 1127-1147.

[2] Boukal, D. S., & Berec, L. (2002). Single-species models of the Allee effect: extinction boundaries, sex ratios and mate encounters. *Journal of Theoretical Biology*, 218(3), 375-394.

[3] Cantrell, R. S., Cosner, C., Lewis, M. A., & Lou, Y. (2020). Evolution of dispersal in spatial population models with multiple timescales. *Journal of mathematical biology*, 80(1), 3-37.

[4] Cantrell, R. S., Cosner, C., & Lou, Y. (2008). Approximating the ideal free distribution via reaction–diffusion–advection equations. *Journal of Differential Equations*, 245(12), 3687-3703.

[5] Caswell, H. (2000). Matrix population models (Vol. 1). *Sunderland, MA: Sinauer*.

[6] Chapman, B. B., Brönnmark, C., Nilsson, J. Å., & Hansson, L. A. (2011). The ecology and evolution of partial migration. *Oikos*, 120(12), 1764-1775.

[7] Courchamp, F., Clutton-Brock, T., & Grenfell, B. (1999). Inverse density dependence and the Allee effect. *Trends in ecology & evolution*, 14(10), 405-410.

[8] Cressman, R., Krivan, V., & Garay, J. (2004). Ideal free distributions, evolutionary games, and population dynamics in multiple-species environments. *The American Naturalist*, 164(4), 473-489.

[9] Cushing, J. M. (1998). An introduction to structured population dynamics. *Society for industrial and applied mathematics*.

[10] Cushing, J. M. (2014). Backward bifurcations and strong Allee effects in matrix models for the dynamics of structured populations. *Journal of biological dynamics*, 8(1), 57-73.

[11] Cushing, J. M., & Hudson, J. T. (2012). Evolutionary dynamics and strong Allee effects. *Journal of biological dynamics*, 6(2), 941-958.

[12] Edelstein-Keshet, L. (2005). Mathematical models in biology. *SIAM*, Philadelphia, PA. Zbl1100, 92001.

[13] Gadgil, M. (1971). Dispersal: population consequences and evolution. *Ecology*, 52(2), 253-261.

[14] Griswold, C. K., Taylor, C. M., & Norris, D. R. (2011). The equilibrium population size of a partially migratory population and its response to environmental change. *Oikos*, 120(12), 1847-1859.

[15] Hastings, J. W. (1983). Biological diversity, chemical mechanisms, and the evolutionary origins of bioluminescent systems. *Journal of molecular evolution*, 19(5), 309-321.

[16] Courchamp, F., Berec, L., & Gascoigne, J. (2008). Allee effects in ecology and conservation. *OUP Oxford*.

[17] Kokko, H. (2007). Modelling for field biologists and other interesting people. *Cambridge University Press*.

[18] Krivan, V., Cressman, R., & Schneider, C. (2008). The ideal free distribution: a review and synthesis of the game-theoretic perspective. *Theoretical population biology*, 73(3), 403-425.

[19] Lande, R. (1976). Natural selection and random genetic drift in phenotypic evolution. *Evolution*, 314-334.

[20] Lande, R. (1982). A quantitative genetic theory of life history evolution. *Ecology*, 63(3), 607-615.

[21] De Leenheer, P., Mohapatra, A., Ohms, H. A., Lytle, D. A., & Cushing, J. M. (2017). The puzzle of partial migration: adaptive dynamics and evolutionary game theory perspectives. *Journal of Theoretical Biology*, 412, 172-185.

[22] Li, C. K., & Schneider, H. (2002). Applications of Perron–Frobenius theory to population dynamics. *Journal of mathematical biology*, 44(5), 450-462.

[23] Lundberg, P. (1988). The evolution of partial migration in birds. *Trends in ecology & evolution*, 3(7), 172-175.

[24] Lundberg, P. (2013). On the evolutionary stability of partial migration. *Journal of Theoretical Biology*, 321, 36-39.

[25] McPeek, M. A., & Holt, R. D. (1992). The evolution of dispersal in spatially and temporally varying environments. *The American Naturalist*, 140(6), 1010-1027.

[26] Mohapatra, A., Ohms, H. A., Lytle, D. A., & De Leenheer, P. (2016). Population models with partial migration. *Journal of Difference Equations and Applications*, 22(2), 316-329.

[27] Allen, B., Nowak, M. A., & Dieckmann, U. (2013). Adaptive dynamics with interaction structure. *The American Naturalist*, 181(6), E139-E163.

[28] Sloat, Matthew R. and Reeves, Gordon H. and Jonsson, Bror.(2014). Individual condition, standard metabolic rate, and rearing temperature influence steelhead and rainbow trout ( *Oncorhynchus mykiss*) life histories. *Canadian Journal of Fisheries and Aquatic Sciences* 71, 491-501.

[29] Ohms, H. A., Mohapatra, A., Lytle, D. A., & De Leenheer, P. (2019). The evolutionary stability of partial migration under different forms of competition. *Theoretical Ecology*, 12(3), 347-363.

[30] Pérez, C., Granadeiro, J. P., Dias, M. P., Alonso, H., & Catry, P. (2014). When males are more inclined to stay at home: insights into the partial migration of a pelagic seabird provided by geolocators and isotopes. *Behavioral Ecology*, 25(2), 313-319.

[31] Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., & Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, 465(7298), 609-612.

[32] Vincent, T. L., & Brown, J. S. (2005). Evolutionary game theory, natural selection, and Darwinian dynamics, *Cambridge University Press*. 
