THE EFFECTS OF DISPERsal 
ALONG ENVIRONMENTAL GRAdIENTS ON 
THE DYNAMICS OF POPULATIONS 
IN HETEROGENEOUS ENVIRONMENTS

FETHI BELGACEM AND CHRIS COSNER

ABSTRACT. In this paper we study the effects of adding a term describing drift or advection along environmental gradients to reaction-diffusion models for population dynamics with dispersal. The basic models are linear or logistic equations with diffusion and with a spatially varying linear zero order term describing the local population growth rate. The drift terms are constructed from the gradient of the local growth rate and thus describe directed movement of the population up or down the gradient of the growth rate. The effects of drift depend critically on boundary conditions. If the boundary of the region inhabited by the population acts as a barrier, then sufficiently rapid movement in the direction of the gradient of the growth rate is always beneficial. If the boundary is lethal to the population, then movement up the gradient of the growth rate may be either beneficial or harmful depending on the specific situation.

The analysis is performed by observing the effects of drift on the principal eigenvalues of certain elliptic operators. The eigenvalues determine whether a given model predicts persistence or extinction for the population it describes. The eigenvalues are estimated via a change of variables which permits the use of variational methods even though the original problems are not self-adjoint.

1. Introduction. Reaction-diffusion models have been widely used to study the effects of dispersal in population dynamics, but often the dispersal is considered to be completely random and the environment is assumed to be uniform. In this paper we examine models for situations in which the environment is assumed to be spatially heterogeneous and the population inhabiting it is assumed to have a tendency to move up or down gradients of habitat quality in addition to random (or diffusive) movement. The models are constructed by adding a drift or "advection" term to linear or logistic reaction-diffusion models for...
population growth on a bounded region or patch. The local rate of increase in population density is taken to be spatially variable and in general to change sign, reflecting the presence of both favorable and unfavorable habitat types within the overall environment. The drift vector, describing the directed component of the dispersal of the population, is taken to be a multiple of the gradient of the local population growth rate. The predictions of the models depend critically on the boundary conditions. On an environment whose boundary acts as a reflecting barrier to the population a sufficiently rapid rate of movement up the gradient of the local growth rate is always beneficial to the population. In contrast, if the boundary of a domain is assumed to be lethal to the population, there are cases where overly rapid movement up or down the growth rate gradient is always detrimental to the population, although the effects of slow movement up or down the gradient may be either beneficial or detrimental. The effect of directed motion is determined through an analysis of the principal eigenvalues describing the existence and/or stability of equilibria.

There is a substantial literature on diffusion models for dispersal of populations; see for example the discussion and references in [5, 6, 14, 15, 17, 19, 21]. The operator describing the process of diffusion is obtained as the limit of a random walk, from a stochastic differential equation describing Brownian motion, or alternatively from Fick’s law as the divergence of a flux. If the movement of the population is assumed to have a directed as well as a random component, an additional term describing the drift, advection, or taxis affecting the population must be incorporated into the operator. That term should also be in divergence form (so that the population is neither increased nor decreased by dispersal) and can also be obtained via random walks, stochastic differential equations, or Fick’s law. Derivations for models of various forms of motion with both random and directed aspects are given in [1, 16, 19, 21]. The effects of true advection via physical forces are discussed in [20]. The goal of this article is to study the effects of the taxis up or down environmental gradients in heterogeneous environments. The approach is to use the ideas of [3, 5, 6, 9, 17, 25] to formulate criteria for persistence or extinction in terms of eigenvalue problems and then to use methods from [2, 9–13, 18, 20, 24, 25, 26] to obtain information about the eigenvalues. Related results with a focus on the effects of environmental heterogeneity are discussed in
[5, 6] and additional results are given in [1].

We formulate our models and give a result which implies that in a closed environment with a reflecting boundary a strong taxis up the environmental gradient is always beneficial in Section 2. In Section 3 we derive estimates which show that the effect of a taxis up the environmental gradient may be detrimental to a population in some cases but beneficial in others if the environment has a lethal (i.e., absorbing) boundary. In Section 4 we briefly discuss the biological implications of our results.

2. Models and basic spectral theory. Diffusion processes have been widely used to model the dispersal of organisms; see, for example, [5, 6, 14, 15, 17, 19, 21]. An underlying assumption of purely diffusive models is that dispersal is random, with movements in all directions being equally likely. However, many organisms can sense their surroundings and may attempt to move in the direction of increasing favorability of the environment. A simple way to take such motion into account is to assume that the organisms exhibit a taxis in the direction of increasing environmental favorability which could be described mathematically by adding terms analogous to those introduced by drift or advection to the basic diffusion model. Specifically, we envision our population inhabiting a bounded region \( \Omega \subseteq \mathbb{R}^N \) with a population density given by \( u(x, t) \) and growing (or declining) linearly or logistically with a local growth rate \( m(x) \) which may change sign in \( \Omega \). We shall always assume that \( m(x) \) is positive on some part of \( \Omega \) since otherwise any reasonable model predicts extinction. For technical reasons we assume \( \partial \Omega \) and \( m(x) \) to be smooth. If our population moves by a combination of random diffusion and directed motion upward along the gradient of \( m(x) \) we can describe the flux of the population density by

\[
J = -D \nabla u + \alpha u \nabla m,
\]

(2.1)

see for example [1, 19], so that the linear growth model takes the form

\[
\frac{\partial u}{\partial t} = -\nabla \cdot J + m(x)u
\]

(2.2)

\[
= \nabla \cdot [D \nabla u - \alpha u \nabla m] + m(x)u
\]

in \( \Omega \times (0, \infty) \).
and the corresponding logistic model is

$$
\frac{\partial u}{\partial t} = -\nabla \cdot J + m(x)u - cu^2
$$

in $\Omega \times (0, \infty)$.

$$
= \nabla \cdot [D\nabla u - \alpha u \nabla m] + m(x)u - cu^2
$$

The constant $D$ in (2.1) is the usual diffusion rate; the constant $\alpha$ measures the rate at which the population moves up the gradient of the growth rate $m(x)$. If $\alpha < 0$, the population would move in a direction along which $m$ is decreasing, that is, away from the favorable habitat and toward regions of less favorable habitat. Note that the dispersal terms in (2.2) and (2.3) are written in divergence or "conservation law" form. This is a necessary feature of any model for dispersal in which the dispersal per se does not increase or decrease the population. We shall see that the models will be converted to nondivergence form via a change of variables which facilitates our analysis, but the new equations will not be for the original physical variable $u(x, t)$. The models (2.2) and (2.3) can also be obtained from stochastic differential equations describing Brownian motion with drift by deriving the associated Fokker-Plank equation. This is done in [1].

Associated with the models (2.2) and (2.3) are boundary conditions. We shall consider two cases: either the boundary $\partial \Omega$ is a perfect reflector so that the flux across $\partial \Omega$ is zero, or the exterior of $\Omega$ is lethal and any member of the population which encounters $\partial \Omega$ crosses into the lethal exterior region so that the population density at $\partial \Omega$ is zero. The no flux condition is

$$
-J \cdot \vec{n} = D \frac{\partial u}{\partial n} - \alpha u \frac{\partial m}{\partial n} = 0 \quad \text{on } \partial \Omega \times (0, \infty)
$$

where $\vec{n}$ is the outward pointing normal vector and $\partial / \partial n$ is the normal derivative. The case of a lethal exterior is described by the Dirichlet condition

$$
(2.5) \quad u = 0 \quad \text{on } \partial \Omega \times (0, \infty).
$$

There are some difficulties in applying standard theory directly to the models (2.2) and (2.3), especially under the boundary condition (2.4). Specifically, many results based on positive operator theory require
\( \alpha \partial n / \partial n \leq 0 \) in (2.4), and if we wish to separate dispersal terms from growth terms the zero order coefficient \(- \alpha \nabla^2 \tilde{m}\) in the dispersal terms would generally be required to be nonpositive. To avoid these problems, we make the change of variables \( v = e^{-(\alpha/D)\tilde{m}}u \). In terms of the new variables (2.2) becomes

\[
(2.6) \quad \frac{\partial v}{\partial t} = D \nabla^2 v + \alpha \nabla m \cdot \nabla v + mv \quad \text{in } \Omega \times (0, \infty)
\]

and (2.3) becomes

\[
(2.7) \quad \frac{\partial v}{\partial t} = D \nabla^2 v + \alpha \nabla m \cdot \nabla v + mv - ce^{(\alpha/D)\tilde{m}}v^2 \quad \text{in } \Omega \times (0, \infty).
\]

The boundary condition (2.4) becomes

\[
(2.8) \quad \frac{\partial v}{\partial n} = 0 \quad \text{on } \partial \Omega \times (0, \infty)
\]

while (2.5) is unchanged. Models of the form (2.6) or (2.7) with boundary conditions (2.5) or (2.8) have been widely studied and can be analyzed in terms of some associated linear eigenvalue problems. Since \( u = e^{(\alpha/D)\tilde{m}}v \) any predictions of growth or decline in (2.6) or about equilibria in (2.7) are also valid for the original models (2.2) and (2.3). The behavior of the linear model can be understood in terms of the eigenvalue problem

\[
(2.9) \quad D \nabla^2 \phi + \alpha \nabla m \cdot \nabla \phi + \lambda m \phi = \sigma \phi \quad \text{in } \Omega
\]

with \( \lambda = 1 \) subject to the boundary conditions (2.5) or (2.8) on \( \partial \Omega \). (We introduce the extra parameter \( \lambda \) for generality and for ease in stating the results about eigenvalues.) In (2.9) with boundary conditions (2.5) or (2.8) there is always a real principal eigenvalue \( \sigma_1(\alpha, \lambda) \). The eigenvalue \( \sigma_1(\alpha, \lambda) \) is real, is larger than the real part of any other eigenvalue, and is characterized by having a positive eigenfunction \( \phi_1 \). This follows from the Krein-Rutman theory of positive operators; see, for example, the discussion in [9, 23, 25, 26]. If \( \sigma_1(\alpha, \lambda) > 0 \), then the model (2.6) and hence (2.2) predicts exponential population growth, and if \( \sigma_1(\alpha, \lambda) < 0 \), then the prediction of (2.6) and (2.2) is exponential population decline toward extinction. This can be seen immediately via separation of variables. The logistic case (2.7) (and hence (2.3)) is
harder to analyze, but it turns out that its predictions of persistence or extinction are similar. We shall describe the logistic situation in more detail later, but first we introduce another eigenvalue problem related to (2.9), where the parameter $\lambda$ plays the role of eigenvalue:

$$
(2.10) \quad -D\nabla^2 \rho - \alpha \nabla m \cdot \nabla \rho = \lambda m(x) \rho \quad \text{in } \Omega.
$$

In the case of boundary condition (2.5), it follows from the results of [10] that (2.10) will always have a unique positive principal eigenvalue $\lambda_1(\alpha)$ which is characterized by having a positive eigenfunction. The case of boundary condition (2.8) is more subtle. The relevant result is

**Proposition 2.1.** The problem (2.10) subject to boundary condition (2.8) has a unique positive principal eigenvalue $\lambda_1(\alpha)$ characterized by having a positive eigenfunction if and only if

$$
(2.11) \quad \int_{\Omega} me^{(\alpha/D)m} < 0.
$$

**Proof.** This is a special case of results due to Senn and/or Hess [9, 25, 26]; see also [24]. The case $\alpha = 0$ was obtained by variational methods in [2]. The results of [25, 26] imply the existence of $\lambda_1(\alpha) > 0$ provided that $\int_{\Omega} m\psi_1 < 0$, where $\psi_1$ is the eigenvector corresponding to the principal eigenvalue of the Banach space adjoint $L^*$ of the operator $L\phi \equiv D\nabla^2 \phi + \alpha \nabla m \cdot \nabla \phi$ acting on the Sobolev space $W^{2,p}(\Omega)$, $p > N$, subject to the boundary condition (2.8). A computation shows that the adjoint operator can be realized as $L^* \psi = -\nabla \cdot [D\nabla \psi - \alpha \psi \nabla m]$ with boundary condition (2.4), and that $\psi_1 = e^{(\alpha/D)m} > 0$ is an eigenvector corresponding to the principal eigenvalue, which is zero. Thus, the results of [25, 26] yield the existence of $\lambda_1(\alpha) > 0$ subject to (2.11). Alternatively, we may observe that, by multiplying (2.10) by $e^{(\alpha/D)m}$, we obtain

$$
(2.12) \quad D\nabla \cdot e^{(\alpha/D)m} \nabla \phi + \lambda \tilde{m} \phi = 0 \quad \text{in } \Omega
$$

where $\tilde{m} = me^{(\alpha/D)m}$. It follows from [2] that (2.12) subject to boundary condition (2.8) has a positive principal eigenvalue if $\int_{\Omega} \tilde{m} dx < 0$, 

which is equivalent to (2.11). Furthermore, the variational formulation in [2] yields

\begin{equation}
\lambda_1(\alpha) = \inf_{\phi \in \Phi_1} \left[ D \int_{\Omega} e^{(\alpha/D)m} |\nabla \phi|^2 \, dx / \int_{\Omega} e^{(\alpha/D)m} m \phi^2 \, dx \right]
\end{equation}

where

\[ \Phi_1 = \left\{ \phi \in W^{2,p}(\Omega) : \partial \phi / \partial n = 0 \text{ on } \partial \Omega \right. \]
\[ \left. \text{ and } \int_{\Omega} e^{(\alpha/D)m} m \phi^2 \, dx > 0 \right\}. \]

The corresponding variational formulation for \( \lambda_1(\alpha) \) can be obtained from (2.9) in the case of boundary condition (2.5) as in [18] by replacing \( \Phi_1 \) with

\[ \Phi_0 = \left\{ \phi \in W^{2,p}(\Omega) : \phi = 0 \text{ on } \partial \Omega \right. \]
\[ \left. \text{ and } \int_{\Omega} e^{(\alpha/D)m} m \phi^2 \, dx > 0 \right\}. \]

(Of course, (2.11) is not required under boundary condition (2.5).) We shall use (2.9) and the associated variational formula for \( \lambda_1(\alpha) \) in some of our later analysis. A more detailed discussion is given in [1]. It is worth noting that the results in [10, 25] yielding the existence of \( \lambda_1(\alpha) \) also imply that the adjoint problems corresponding to (2.10) and (2.5) or (2.8) will also have \( \lambda_1(\alpha) \) as a principal eigenvalue, and that those adjoint problems involve the original elliptic operator in (2.2) and convert the boundary condition (2.8) back to (2.4). Thus, \( \lambda_1(\alpha) \) relative to boundary conditions (2.5), respectively (2.8), will also be a positive principal eigenvalue for the problem

\[-\nabla \cdot [D \nabla \rho - \alpha \rho \nabla m] = \lambda m \rho \text{ in } \Omega \]

under boundary conditions (2.5), respectively (2.4). □

The next result connects \( \lambda_1(\alpha) \) with \( \sigma_1(\alpha, \lambda) \).
Proposition 2.2. i) If \( \lambda < \lambda_1(\alpha) \) in (2.9) with either boundary condition (2.5) or with boundary condition (2.8) and with (2.11) satisfied, then \( \sigma_1(\alpha, \lambda) < 0 \).

ii) If \( \lambda = \lambda_1(\alpha) \) in (2.9) with either (2.5) or (2.8) and (2.11) satisfied, then \( \sigma_1(\alpha, \lambda) = 0 \).

iii) If \( \lambda > \lambda_1(\alpha) \) in (2.9) with either (2.5) or (2.8) and (2.11) satisfied, or if \( \lambda > 0 \), (2.8) is satisfied, and (2.11) is violated, then \( \sigma_1(\alpha, \lambda) > 0 \).

Note. This result is obtained in [25] for the boundary condition (2.8); related results for the case of boundary condition (2.5) are discussed in [5, 9]. For the model (2.6) and hence (2.2) the relevant case is \( \lambda = 1 \). If \( \sigma_1(\alpha, 1) > 0 \), the model predicts population growth. If \( \sigma_1(\alpha, 1) < 0 \) it predicts decline toward extinction.

The underlying analysis of the nonlinear models (2.7) and hence (2.3) is more complicated, but the predictions of persistence or extinction are similar. We have

Proposition 2.3. i) Suppose that either (2.5) is satisfied or (2.8) and (2.11) are satisfied.

If \( 1 \leq \lambda_1(\alpha) \), then all nonnegative solutions of (2.7) and hence of (2.3) decline toward zero as \( t \to \infty \). If \( 1 > \lambda_1(\alpha) \), then (2.7) and hence (2.3) has a unique positive equilibrium which is globally attracting among nonzero nonnegative solutions.

(ii) Suppose that (2.8) is satisfied and (2.11) is violated. In this case (2.7) and hence (2.3) has a unique positive equilibrium which is globally attracting among nonzero nonnegative solutions.

Note. Proposition 2.3 is a basic result on the behavior of a logistic equation with diffusion and drift. It is an immediate consequence of Theorem 28.1 of [9] and Proposition 2.2. Theorem 28.1 of [9] implies the existence of a unique positive equilibrium for (2.7) which is globally attracting among positive solutions provided \( \sigma_1(\alpha, 1) > 0 \) and the decay of all positive solutions of (2.7) to zero if \( \sigma_1(\alpha, 1) \leq 0 \). The sign of \( \sigma_1(\alpha, \lambda) \) is determined by the relative size of \( \lambda \) and \( \lambda_1(\alpha) \) according to Proposition 2.2, so if \( \lambda_1(\alpha) \geq 1 \) then \( \sigma_1(\alpha, 1) \leq 0 \) while if \( \lambda_1(\alpha) < 1 \)
then $\sigma_1(\alpha, 1) > 0$. Theorem 28.1 and other results of [9] are stated for periodic-parabolic problems, but elliptic problems such as (2.7) correspond to the special case where the coefficients are periodic with any period.

In the case of the Dirichlet boundary condition (2.5), Proposition 2.3 is contained in Theorem 2.4 and Corollary 3.3 of [5]. The dependence of $\lambda_1(\alpha)$ on $m$ is studied in [5]. It turns out that the quantity $\lambda_1(\alpha) - 1$ can be used to estimate the size of the equilibrium if $\lambda_1(\alpha) > 1$ or the rate of decay of solution to (2.7) toward zero if $\lambda_1(\alpha) < 1$. \hfill \Box

Results related to Proposition 2.3 are given in [3, 17, 25].

We can now draw our first biologically relevant conclusion:

**Theorem 2.4.** Under the no-flux boundary condition (2.4) the models (2.2) and (2.3) predict persistence of the population if $\alpha$ is sufficiently large, i.e., if the rate at which the population moves up the gradient of the growth rate $m(x)$ is sufficiently high.

**Proof.** As $\alpha \to \infty$, $m e^{(\alpha/D)m} \to \infty$ for $x \in \Omega$ such that $m(x) > 0$ and $m e^{(\alpha/D)m} \to 0$ for $x \in \Omega$ such that $m(x) \leq 0$. It follows that for $\alpha$ sufficiently large that (2.11) must be violated, so (2.6) and thus (2.2) will predict population growth by Proposition (2.2) (since $\sigma_1(\alpha_1, 1) > 0$ and in fact $\lambda_1(\alpha)$ becomes 0) and (2.7) and hence (2.3) will predict the existence of a positive equilibrium which is globally stable among nonzero nonnegative solutions. \hfill \Box

**Remark.** Theorem 2.4 implies that a sufficiently strong taxis or drift in the direction of more favorable habitat is always beneficial to a population inhabiting an environment with a boundary which acts as a barrier. This is in contrast with the results of [20], which imply that any constant drift is detrimental to a population inhabiting a spatially homogeneous environment with a lethal boundary.

3. **Behavior of principal eigenvalues.** The results of the preceding section imply that for a population inhabiting a heterogeneous environment whose boundary acts as a reflecting barrier, a sufficiently
strong tendency to disperse in the direction of increasing habitat quality is always beneficial to the population. In this section we consider cases where the tendency to disperse in the direction of better habitat is weak or moderate, and focus on the case where the boundary is lethal.

Our first result describes the local dependence of $\lambda_1(\alpha)$ on $\alpha$. We base our analysis on the formulations in (2.12) and (2.13).

**Theorem 3.1.** If (2.12) (equivalently (2.10)) is augmented with either boundary condition (2.5) or boundary condition (2.8) and hypothesis (2.11), then $\lambda_1(\alpha)$ depends differentiably on $\alpha$. Under boundary condition (2.5),

$$
(3.1) \quad \lambda_1'(\alpha) = \int_{\Omega} (\phi_1^2/2) \nabla \cdot e^{(\alpha/D)m} \nabla m \, dx
$$

and under boundary condition (2.8)

$$
(3.2) \quad \lambda_1'(\alpha) = \int_{\Omega} (\phi_1^2/2) \nabla \cdot e^{(\alpha/D)m} \nabla m \, dx - \int_{\partial \Omega} (\phi_1^2/2) e^{(\alpha/D)m} \frac{\partial m}{\partial n} \, ds
$$

where $\phi_1$ is the eigenfunction of (2.12) corresponding to $\lambda_1(\alpha)$ normalized so that

$$
\int_{\Omega} me^{(\alpha/D)m} \phi_1^2 \, dx = 1.
$$

**Remark.** It follows that if we start with $\alpha = 0$, i.e., with no directed motion up the environmental gradient, increasing $\alpha$ away from zero may be either harmful or beneficial to the population (i.e., may either increase or decrease $\lambda_1(\alpha)$) under boundary condition (2.5) (the case where the boundary is lethal). This can be seen by noting that if $\nabla^2 m$ is of one sign then $\lambda_1'(0)$ is of the same sign in (3.1). The mechanism which might cause an increase in $\alpha$ to harm the population would be that if $\nabla^2 m > 0$ then movement upward along $\nabla m$ might push the population toward the lethal boundary. A simple example would be $\Omega = \{(x_1, x_2) : x_1^2 + x_2^2 < 1\} \subseteq \mathbb{R}^2$ and $m(x) = x_1^2 + x_2^2 - 1/4$. The
situation is less clear under boundary condition (2.8) because of the extra term occurring in (3.2). Since \( \int_\Omega \nabla^2 m \, dx = \int_{\partial \Omega} (\partial m / \partial n) \, ds \) the terms \( \nabla^2 m \) and \( \partial m / \partial n \) cannot be globally of opposite signs, so that it is not obvious how to construct examples where the sign of \( \lambda_1(0) \) in (3.2) can be immediately determined. One special class of examples can be constructed by looking at choices of \( m \) constructed from functions \( \theta \) satisfying

\[
\nabla^2 \theta = \gamma \theta \quad \text{in } \Omega \\
\frac{\partial \theta}{\partial n} = 0 \quad \text{on } \partial \Omega.
\]

For any eigenvalue \( \gamma < 0 \) the eigenfunction \( \theta \) will change sign, and if we take \( m = \theta - \varepsilon \) then for any \( \varepsilon > 0 \) we have \( \int_\Omega m \, dx < 0 \). If we choose \( \varepsilon \) so that \( m \) is positive somewhere, then we see from (3.2) and the normalization of \( \phi_1 \) that we have

\[
\lambda_1(0) = \int_\Omega \nabla^2 m \phi_1^2 \, dx = \int_\Omega \nabla^2 \theta \phi_1^2 \, dx = \int_\Omega \gamma \theta \phi_1^2 \, dx = \int_\Omega \gamma (m + \varepsilon) \phi_1^2 \, dx = \gamma + \gamma \varepsilon \int_\Omega \phi_1^2 \, dx < 0
\]

so increasing \( \alpha \) from zero is always helpful to the population. We conjecture on biological grounds that such is the case for any choice of \( m \) under no-flux boundary conditions, but we do not know how to prove that.

**Proof of Theorem 3.1.** Let \( \theta \in (0,1) \), and define

\[
E_0 = \{ \phi \in C^{2+\theta}(\bar{\Omega}) : \phi = 0 \text{ on } \partial \Omega \} \times \mathbb{R} \\
E_1 = \{ \phi \in C^{2+\theta}(\bar{\Omega}) : \partial \phi / \partial n = 0 \text{ on } \partial \Omega \} \times \mathbb{R}.
\]

The mapping \( F(\phi, \lambda, \alpha) : E_i \times \mathbb{R} \to C^\theta(\bar{\Omega}) \times \mathbb{R} \) defined by

\[
F(\phi, \lambda, \alpha) = \left( D\nabla \cdot e^{(\alpha/D)m \nabla \phi} + \lambda me^{(\alpha/D)m \phi} \int_\Omega me^{(\alpha/D)m \phi^2} \, dx - 1 \right)
\]

is smooth, and \( \lambda \) is an eigenvalue and \( \phi \) a normalized eigenfunction of (2.12) if \( F(\phi, \lambda, \alpha) = 0 \). If we can show that the linearization \( DF \) of \( F \) with respect to \( E_i \) is a bijection at \( \lambda = \lambda_1(\alpha), \phi = \phi_1 \), where \( \phi \)}
is the eigenfunction corresponding to $\lambda_1(\alpha)$, it will follow by the open mapping theorem that $DF(\phi_1, \lambda_1(\alpha), \alpha)$ is a linear homeomorphism, and we can then conclude from the implicit function theorem that $\lambda_1(\alpha)$ and $\phi_1$ depend differentiably on $\alpha$. (Related arguments are used in [1, 4, 24].) Computation shows that the linearization $DF$ of $F$ with respect to $E_i$ is given by

$$DF(\phi, \lambda, \alpha)(w, t) = \left(D\nabla \cdot e^{(\alpha/D)m} \nabla w + \lambda m e^{(\alpha/D)m} w + t m e^{(\alpha/D)m} \phi, 2 \int_{\Omega} m e^{(\alpha/D)m} \phi_1 dx \right).$$

To see that $DF$ is injective, we note that if $DF(\phi_1, \lambda_1(\alpha), \alpha)(w, t) = (0, 0)$ then

$$(3.3) \quad D\nabla \cdot e^{(\alpha/D)m} \nabla w + \lambda_1(\alpha) m e^{(\alpha/D)m} w = -t m e^{(\alpha/D)m} \phi_1$$

in $\Omega$. Multiplying (3.3) by $\phi_1$ and integrating by parts using the divergence theorem and the boundary conditions on $\phi_1$ and $w$ yields

$$(3.4) \quad t \int_{\Omega} m e^{(\alpha/D)m} \phi_1^2 dx = 0.$$

However, the normalization of $\phi_1$ in $F(\phi_1, \lambda_1(\alpha), \alpha) = 0$ implies that the integral in (3.4) is positive, so $t = 0$. If $t = 0$ in (3.3), then $w$ is an eigenfunction for (2.12) corresponding to $\lambda_1(\alpha)$. However, the results of [10, 24, 25] imply that $\lambda_1(\alpha)$ is simple, so that $w = k \phi_1$ for some $k$. Finally,

$$2 \int_{\Omega} m e^{(\alpha/D)m} \phi_1 w = 2k \int_{\Omega} m e^{(\alpha/D)m} \phi_1^2 = 0,$$

so $k = 0$ and hence $w = 0$. To see that $DF(\phi_1, \lambda_1(\alpha), \alpha)$ is surjective, consider the problem $DF(\phi_1, \lambda_1(\alpha), \alpha)(w, t) = (f, r)$ in the form

$$(3.5) \quad D\nabla \cdot e^{(\alpha/D)m} \nabla w + \lambda_1(\alpha) m e^{(\alpha/D)m} w = f - t m e^{(\alpha/D)m} \phi_1 \quad \text{in} \quad \Omega,$$

$$(3.6) \quad 2 \int_{\Omega} m e^{(\alpha/D)m} \phi_1 w = r.$$
By the Fredholm alternative (3.4) will have solutions of the form
\[ w = z + s\phi_1 \]
with
\[ \int_{\Omega} me^{(\alpha/D)m} z\phi_1 \, dx = 0 \]
provided \( t = \int_{\Omega} f\phi_1 \, dx / \int_{\Omega} me^{(\alpha/D)m} \phi_1^2 \, dx \) so that the right side of (3.5) yields the value zero when integrated against \( \phi_1 \). Thus, we need only show that \( s \) can be chosen so that (3.6) holds; but that will be the case if \( s = r/2 \int_{\Omega} me^{(\alpha/D)m} \phi_1^2 \, dx \). Thus, \( DF(\phi_1, \lambda_1(\alpha), \lambda) \) is a bijection as required. If we now consider (2.12) differentiated with respect to \( \alpha \) and denote differentiation with a prime, we have
\[
D\nabla \cdot e^{(\alpha/D)m} \nabla \phi_1 + D\nabla \cdot (m/D)e^{(\alpha/D)m} \nabla \phi_1
+ \lambda_1(\alpha) me^{(\alpha/D)m} \phi_1' + \lambda_1(\alpha)(m^2/D)e^{(\alpha/D)m} \phi_1
+ \lambda'_1(\alpha) me^{(\alpha/D)m} \phi_1 = 0 \quad \text{in } \Omega.
\]
Multiplying by \( \phi_1 \) and using (2.12) and the boundary conditions (2.5) or (2.8) and the normalization \( \int me^{(\alpha/D)m} \phi_1^2 \, dx = 1 \) built into the equation \( F(\phi, \lambda, \alpha) = 0 \) yields
\[
\lambda'_1(\alpha) = -\int_{\Omega} \phi_1 \nabla \cdot me^{(\alpha/D)m} \nabla \phi_1 \, dx
- \lambda_1(\alpha) \int_{\Omega} (m^2/D)e^{(\alpha/D)m} \phi_1^2 \, dx.
\]
We have
\[
\phi_1 \nabla \cdot me^{(\alpha/D)m} \nabla \phi_1 = \phi_1 m \nabla \cdot e^{(\alpha/D)m} \nabla \phi_1
+ \phi_1 \nabla \phi_1 \cdot e^{(\alpha/D)m} \nabla m
= -(\lambda_1(\alpha)/D)m^2 e^{(\alpha/D)m} \phi_1^2
+ \nabla (\phi_1^2/2) \cdot e^{(\alpha/D)m} \nabla m.
\]
Substituting into (3.7) yields
\[
\lambda'_1(\alpha) = -\int_{\Omega} \nabla (\phi_1^2/2) \cdot e^{(\alpha/D)m} \nabla m \, dx.
\]
Under boundary condition (2.5) we may integrate (3.8) by parts to obtain (3.1). Boundary condition (2.8) yields (3.2). \( \square \)
Theorem 3.1 gives a description of how $\lambda_1(\alpha)$ changes with $\alpha$. It is also possible to make comparisons between $\lambda_1(\alpha)$ and other eigenvalues which may be easier to compute, or between $\lambda_1(\alpha)$ and $\lambda_1(0)$. Results of that sort are obtained in [1, 5, 20], and we shall examine some of their implications next.

**Theorem 3.2.** Suppose that $m(x)$ is nonconstant and that if $\phi_1$ is the eigenfunction corresponding to $\lambda_1(0)$ in (2.12) under boundary condition (2.5),

$$\int_{\Omega} \phi_1^2 \nabla^2 m \, dx \neq 0.$$

Under these hypotheses there exists an $\alpha \neq 0$ such that, for boundary condition (2.5), $\lambda_1(\alpha) < \lambda_1(0)$.

**Remark.** The sign of $\alpha$ depends on the sign of the integral in the hypotheses. The implication of the inequality $\lambda_1(\alpha) < \lambda_1(0)$ is that the presence of the right amount of drift upward or downward along environmental gradients will benefit the population described by our model. The case where drift downward along environmental gradients is beneficial would correspond to a situation where moving upward along the gradient of $m$ would bring the population into closer contact with the boundary $\partial \Omega$, which under condition (2.5) is assumed to be lethal.

**Proof.** If we make the change of variables $\psi = e^{(\alpha/2D)m} \phi$ in (2.13) we have

$$\int_{\Omega} m \psi^2 \, dx = \int_{\Omega} e^{(\alpha/D)m} m \phi^2 \, dx$$

and

$$\int_{\Omega} (D|\nabla \psi|^2 - \alpha \psi \nabla \psi \cdot \nabla m + (\alpha^2/4D)|\nabla m|^2 \psi^2) \, dx$$

$$= \int_{\Omega} D e^{(\alpha/D)m} |\nabla \psi|^2 \, dx.$$

Thus, for boundary condition (2.5), (2.13) becomes

(3.9)

$$\lambda_1(\alpha) = \inf_{\psi \in \Psi_0} \left[ \frac{\int_{\Omega} (D|\nabla \psi|^2 - \alpha \psi \nabla \psi \cdot \nabla m + (\alpha^2/4D)|\nabla m|^2 \psi^2) \, dx}{\int_{\Omega} m \psi^2 \, dx} \right]$$
where $\psi \in \Psi_0$ if and only if $\phi = e^{-(\alpha/2D)m}\psi \in \Phi_0$, that is,

\[
\Psi_0 = \left\{ \psi \in W^{2,p}(\Omega) : \psi = 0 \text{ on } \partial\Omega \text{ and } \int_{\Omega} m\psi^2 \, dx > 0 \right\}.
\]

(Similarly, if (2.11) holds, then we can obtain $\lambda_1(\alpha)$ for boundary condition (2.8) be replacing $\Psi_0$ in (3.9) with

\[
\Psi_1 = \left\{ \psi \in W^{2,p}(\Omega) : \partial\psi/\partial n - (\alpha/2D)\psi \partial m/\partial n = 0 \right\}.
\]

In the case where $m$ does not change sign on $\Omega$, (3.9) is a special case of the variational formulation for the principal eigenvalue of a nonselfadjoint operator obtained in [11–13]. The results of [11–13] are extended to the case where $m$ changes sign in [1]. The formulation (3.9) is used in [1, 5, 20] to obtain eigenvalue estimates. In the present context we want to examine specifically how (3.9) depends on $\alpha$. If we let $\psi_1 = \phi_1$ be the eigenfunction for $\lambda_1(0)$ under boundary condition (2.5), and break the numerator in (3.9) into the sum of the integrals of the three terms, we can factor $\alpha$ out of the second term and $\alpha^2$ out of the third and then minimize the resulting expression with respect to $\alpha$. That yields

\[
\alpha = \alpha_0 = \frac{2D \int_{\Omega} \phi_1 \nabla \phi_1 \cdot \nabla m}{\int_{\Omega} |\nabla m|^2 \phi_1^2 \, dx} = \frac{D \int \phi_1^2 \nabla^2 m \, dx}{\int_{\Omega} |\nabla m|^2 \phi_1^2 \, dx}
\]

so that

\[
\lambda_1(\alpha_0) \leq \frac{\left( \int_{\Omega} |\nabla \phi_1|^2 \, dx - \left[ D \left( \int_{\Omega} \phi_1^2 \nabla^2 m \, dx \right)^2 / \int_{\Omega} |\nabla m|^2 \phi_1^2 \, dx \right] \right)}{\int m \phi_1^2 \, dx}
\]

\[
= \lambda_1(0) - D \frac{\left( \int_{\Omega} \phi_1^2 \nabla^2 m \, dx \right)^2}{\int_{\Omega} m \phi_1^2 \, dx \int_{\Omega} |\nabla m|^2 \phi_1^2 \, dx}
\]

from which the conclusion of Theorem 3.2 follows. \quad \Box

The variational formulation (3.9) can be used to obtain bounds on $\lambda_1(\alpha)$ in certain cases by adapting the argument used in [20]. Since
the analysis is quite similar to that appearing in [5, 20] we do not give a detailed derivation but merely sketch the argument. In the case of boundary condition (2.5) in (2.12) the numerator in (3.9) may be written as

$$\int_{\Omega} (D|\nabla \psi|^2 + [(\alpha/2)\nabla^2 m + (\alpha^2/4D)|\nabla m|^2]\psi^2) \, dx.$$ (3.11)

If $\phi_1$ is the eigenfunction corresponding to $\lambda_1(0)$ and $\psi_1$ corresponds to $\lambda_1(\alpha)$ we have

$$\lambda_1(\alpha) \leq \frac{\int_{\Omega} D|\nabla \phi_1|^2 \, dx}{\int_{\Omega} m\phi_1^2 \, dx} + \frac{\int_{\Omega} [(\alpha/2)\nabla^2 m + (\alpha^2/4D)|\nabla m|^2]\phi_1^2 \, dx}{\int_{\Omega} m\phi_1^2 \, dx}$$

$$= \lambda_1(0) + \frac{\int_{\Omega} [(\alpha/2)\nabla^2 m + (\alpha^2/4D)|\nabla m|^2]\phi_1^2 \, dx}{\int_{\Omega} m\phi_1^2 \, dx}$$ (3.12)

and

$$\lambda_1(0) \leq \frac{\int_{\Omega} D|\nabla \psi_1|^2 \, dx}{\int m\psi_1^2 \, dx}$$

$$\lambda_1(\alpha) - \frac{\int_{\Omega} [(\alpha/2)\nabla^2 m + (\alpha^2/4D)|\nabla m|^2]\psi_1^2 \, dx}{\int m\psi_1^2 \, dx}.$$ (3.13)

If it happens that $[(\alpha/2)\nabla^2 m + (\alpha^2/4D)|\nabla m|^2]$ can be bounded above or below by $\gamma m$ for some $\gamma$, then (3.12) and/or (3.13) will yield bounds on $\lambda_1(\alpha)$ of the forms $\lambda_1(\alpha) \leq \lambda_1(0) + \gamma$ and $\lambda_1(\alpha) \geq \lambda_1(0) + \gamma$, respectively. In particular, if $\nabla m \neq 0$ in $\Omega$, then we have $[(\alpha/2)\nabla^2 m + (\alpha^2/4D)|\nabla m|^2] \geq \gamma m$ for $\gamma = [(\alpha/2)\inf\nabla^2 m + (\alpha^2/4D)\inf|\nabla m|^2]/\sup m$ so that by (3.13) we have $\lambda_1(\alpha) \to \infty$ as $|\alpha| \to \infty$. Thus, any sufficiently strong drift either upward or downward along $\nabla m$ will be detrimental to our population in this case. Similarly, if $\nabla^2 m \geq \gamma_0 m$ for some $\gamma_0 > 0$ (which will certainly be true if $\nabla^2 m > 0$ but may also be true in other cases) then we may use $\gamma = (\alpha\gamma_0/2)$ and (3.13) then implies $\lambda_1(\alpha) \geq \lambda_1(0) + \alpha\gamma_0/2$ so that any drift in the direction of increasing $m$ will be detrimental, and $\lambda_1(\alpha) \to \infty$ as $\alpha \to \infty$. It is important to note, however, that both the conditions $\nabla m \neq 0$ and $\nabla^2 m > \gamma_0 m$ with $\gamma_0 > 0$ rule out the possibility that $m$ has a positive maximum inside $\Omega$. That would be the situation in which drift upward along $\nabla m$ might not push the population toward the lethal boundary.
There are a number of other possible approaches to estimating $\lambda_1(\alpha)$, including the methods of [7, 8, 22]. Some of those are used in [1], but they yield qualitative conclusions about the behavior of $\lambda_1(\alpha)$ which are similar to those we have already drawn, so we do not explore them further here.

4. Biological conclusions. It was shown in [20] that any constant advection (due for example to physical forces such as winds or currents) is always detrimental to a population inhabiting and diffusing through a homogeneous region with a lethal boundary. Our results show that if the population responds to the environment by a taxis up the gradient of habitat quality, the effects are much more complicated. Theorem 2.1 implies that when the boundary of the region inhabited by a population acts as a barrier, a taxis up the environmental gradient is always beneficial if it is strong enough. Theorem 3.1 shows that a weak taxis up the environmental gradient may be either beneficial or harmful in the case where the boundary is lethal. Other results indicate that even in the case of a lethal boundary, some sort of taxis up or down the environmental gradient is often beneficial, but an overly strong taxis up or down the gradient may be harmful. It is natural to expect that a taxis in the direction of increasing habitat quality would be beneficial. An examination of the conditions under which it is predicted to be harmful suggests that the way in which movement toward more favorable habitat may be harmful is that if the more favorable habitat is near the lethal boundary of the region, movement toward better habitat may draw the population toward the boundary. Our results have implications for refuge design. If the species to be preserved actively seeks favorable habitat, then either the boundaries of the refuge should be made so that the population does not cross them, or if that is not possible and the exterior of the refuge is inhospitable to the population then the refuge should be arranged so that the most favorable habitat is located away from the boundary.

REFERENCES


21. A. Okubo, *Diffusion and ecological problems: Mathematical models*, Biomath-


Department of Mathematics, University of Miami, Coral Gables, FL 33124