

DIFFUSIVE LOGISTIC EQUATIONS WITH INDEFINITE WEIGHTS: POPULATION MODELS IN DISRUPTED ENVIRONMENTS II*

ROBERT STEPHEN CANTRELL† AND CHRIS COSNER†

Abstract. The dynamics of a population inhabiting a strongly heterogeneous environment are modeled by diffusive logistic equations of the form $u_t = \nabla \cdot (d(x, u)\nabla u) - \mathbf{b}(x) \cdot \nabla u + m(x)u - cu^2$ in $\Omega \times (0, \infty)$, where u represents the population density, $d(x, u)$ the (possibly) density dependent diffusion rate, $\mathbf{b}(x)$ drift, c the limiting effects of crowding, and $m(x)$ the local growth rate of the population. The growth rate $m(x)$ is positive on favorable habitats and negative on unfavorable ones. The environment Ω is bounded and surrounded by uninhabitable regions, so that $u = 0$ on $\partial\Omega \times (0, \infty)$. In a previous paper, the authors considered the special case $d(x, u) = d$, a constant, and $\mathbf{b} = 0$, and were able to make an analysis based on variational methods. The inclusion of density dependent diffusion and/or drift makes for more flexible and realistic models. However, variational methods are mathematically insufficient in these more complicated situations. By employing methods based on monotonicity and positive operator theory, many previous results on the dependence on m of the overall suitability of the environment can be recovered and some new results can be established concerning environmental quality dependence on \mathbf{b} . In the process, a bifurcation and stability analysis is made of the model which includes some new estimates on eigenvalues for associated linear problems.

Key words. diffusive logistic equations; heterogeneous environments; population dynamics; monotone flows; bifurcation and stability analysis; eigenvalue problems; indefinite weights

AMS(MOS) subject classifications. 35J65, 35K60, 92A15

1. Introduction. Reaction-diffusion equations have been widely used as models for populations whose densities vary with location as well as time. If the environment is strongly heterogeneous, the coefficients describing the growth and diffusion of the population may vary with location as well. In an earlier article, we studied a diffusive logistic model in which the diffusion rate of the population was constant but the growth rate was assumed to vary with position, being positive in regions of favorable habitat and negative in unfavorable regions. The present article is devoted to extending our results to models in which the diffusion rate varies with position and population density, and the population may be subject to drift in addition to pure diffusion. These more complicated models incorporate effects which are often present in real situations, and thus can give more complete descriptions of biological phenomena. Since these models are quasilinear rather than semilinear, and in general are not in variational form, the technical aspects of the analysis are somewhat different and more difficult than in the case of simple Fickian diffusion. The technical complexity is inherent in the models we consider, and cannot be avoided if we are to give a rigorous analysis. However, we have introduced into our models only the sorts of effects which theoretical ecologists have suggested to us as being especially important.

Since the implications of our analysis should be of some interest to biological scientists, we give a brief summary of them in the last section, and conclude each section of the paper with a fairly detailed discussion of the main results from a biological viewpoint. Some of the discussion overlaps that given in [6], [7], and [9]. Additional references are given in [6] and [9]. In [7] we use relatively simple mathematics to analyze a number of special cases of the general models considered here and give a

* Received by the editors July 17, 1989; accepted for publication (in revised form) June 11, 1990. This research was supported by National Science Foundation grant DMS88-02346.

† Department of Mathematics and Computer Science, University of Miami, Coral Gables, Florida 33124.

moderately detailed biological discussion of their interpretation. A reader whose primary interest is in the biological aspects of the work may find the present article more accessible after reading [7].

The situation we wish to model is that of a species inhabiting a bounded region of variable habitat, and dispersing throughout that region via a process of diffusion which may be affected by population density and location and which may also involve drift due to wind, current, or environmental gradients. The questions we address are those of deciding how environmental factors and/or the density dependence of the diffusion affect the population. Obviously, if the overall environment includes too much poor habitat the population cannot be expected to persist. However, the *arrangement* of favorable and unfavorable regions turns out to play an important role in determining the overall suitability of an environment. Questions about the effects of the arrangement of favorable and unfavorable regions are especially important in refuge theory; for example, is one large preserve likely to be more or less effective in sustaining a population than several small preserves? Of course, the answers to such questions will depend on the details of the biology but models can suggest answers in some cases and serve to sharpen discussion in others. Island biogeography theory has been widely used in the context of refuge theory. The sort of models we consider provide an alternative approach. We discuss this point in some detail and give a number of references in [6]. One object of the present work is to extend the results of [6] to include models with more complex and realistic sorts of diffusion and drift processes. Another object is to study directly the effects of density dependent diffusion and of drift. We find that density dependence in the diffusion rate may have effects similar to those of depensation in the growth dynamics, as studied in [20]. Specifically, models with density dependent diffusion may admit multiple equilibria even if the corresponding dynamics with constant diffusion yield a unique equilibrium. The effects of drift in the case of a homogeneous environment and constant diffusion are discussed in [22]. We extend some of the results of [22] to models with variable diffusion and growth coefficients, but we have so far been unable to give a complete description of the effects of drift on the population dynamics.

There is a vast literature on traveling waves in reaction-diffusion models. Most of that literature is not directly relevant to our work, because we are concerned exclusively with bounded regions. A general overview of the literature on waves is given in [10] and [28]. Some specific problems related to wavelike propagation in ecological models and to considerations of domain size are studied in [4]. Another class of models which have a more direct relation to our work are patch models, where a population is assumed to inhabit a number of discrete patches rather than a continuous region. Some topics similar to those we consider are discussed from the viewpoint of patch models in [26]. (Threshold results for propagation through an infinite number of patches are derived in [3]; the specific model in [3] arises in neurophysiology, but the same methods would also apply to ecological models.) Our present work is most closely related to the ideas discussed in [20], [22], and [27], and of course [6], [9], where the models are primarily reaction-diffusion equations on bounded spatial domains.

The viewpoint we take in our modeling is essentially that taken in the pioneering work of Skellam [27], who deduced reaction-diffusion models for population growth and dispersal from the random-walk problem, and analyzed some of those models via classical methods. A representative result is that the density u of a population with linear growth law inhabiting a uniform disc of radius r_0 surrounded by a completely inhospitable region can be described by the equation $u_t = d\Delta u + mu$ with homogeneous Dirichlet boundary conditions, and hence will grow rather than decline provided

$m - (dj_1^2/r_0^2) > 0$, where j_1 is the first zero of the Bessel function J_0 . Another way to state this result is that the population will grow if the first eigenvalue λ_1 for the problem $-d\Delta\phi = \lambda m\phi$ on the disc of radius r_0 with homogeneous Dirichlet conditions satisfies $\lambda_1 < 1$. Skellam considered several other models, the most complicated being of the general form $u_t = d\Delta u + m(x)u - c(x)u^2$. Of such models, Skellam wrote (in 1951) that "orthodox analytical methods appear inadequate." (See [27, p. 212].) Since that time, there has been much work on reaction-diffusion models for population dynamics, and a number of new analytical methods have been introduced. For general background on the modeling aspects of population dynamics, see [19] or [24]; for mathematical methods and results, see [9], [10], or [28]. In our previous article [6], we study models that include those considered by Skellam, and discuss their biological interpretation.

The models in [6] have the form

$$(1.1) \quad u_t = d\Delta u + f(x, u)u \quad \text{in } \Omega, \quad u = 0 \quad \text{on } \partial\Omega,$$

where f is decreasing in u and Ω is a bounded domain in \mathbb{R}^n , with $n \leq 3$ in applications. The intrinsic local growth rate of the population is given by $f(x, 0)$, which is assumed to change sign on Ω , with positive values indicating favorable habitat and negative ones unfavorable habitat. Our results imply that (1.1) has a unique positive steady state which is a global attractor for nonnegative, nontrivial solutions, provided the first positive eigenvalue $\lambda_1(d, f(x, 0))$ of the problem

$$-d\Delta\phi = \lambda f(x, 0)\phi \quad \text{in } \Omega, \quad \phi = 0 \quad \text{on } \partial\Omega,$$

satisfies $\lambda_1(d, f(x, 0)) < 1$. We also examined the question of how $\lambda_1(d, m(x))$ depends on the arrangement of positive and negative regions for $m(x)$. We showed that for a sequence $\{m_j(x)\}$ of weights, a necessary and sufficient condition for having

$$\lim_{j \rightarrow \infty} \lambda_1(d, m_j(x)) = \infty \quad \text{is that} \quad \limsup_{j \rightarrow \infty} \int_{\Omega} \psi m_j \leq 0$$

for any $\psi \in L^1(\Omega)$ with $\psi \geq 0$ almost everywhere. (This result is Theorem 3.1 of [6].) One implication of these results is that if the unfavorable regions are greater than or equal to the favorable ones in strength and extent, and the two sorts of regions are too closely interspersed, the population will not persist, *even though it might persist if the favorable habit formed a single larger region*. We also showed that in a certain sense, the most favorable situations will occur if there is a relatively large favorable region located some distance away from the boundary of Ω .

In the present article we consider models of the form

$$(1.2) \quad u_t = \nabla \cdot d(x, u)\nabla u - \mathbf{b} \cdot \nabla u + m(x)u - cu^2 \quad \text{in } \Omega, \quad u = 0 \quad \text{on } \partial\Omega,$$

and attempt to recover some of the results of [6]. Since the analysis of [6] was based largely on variational methods, we have had to substantially modify our techniques. In many cases, we replace ideas and results based on variational principles with others based on monotonicity or positive operator theory. Also, since we assume only $m(x) \in L^\infty(\Omega)$ (for various reasons which are discussed in [6]), we must work with weak solutions, so the standard Hopf maximum principle must generally be replaced by the maximum and comparison principles for weak solutions of elliptic equations discussed in [11, Chaps. 8, 9], or the corresponding results for the parabolic case which follow readily from similar arguments. (We do not always state this explicitly, and in some

cases we will simply cite references where the Hopf maximum principle is used but whose results extend directly to our situation via maximum principles for weak solutions.)

Models such as (1.2) display some different features than those of the form (1.1). In particular, if $d(x, u)$ is not monotone nondecreasing in u , (1.2) may have multiple positive solutions. (We give an example in § 3.) It is known that a similar phenomenon can occur in (1.1) in the presence of depensation (that is, if $f(x, u)$ is allowed to be increasing in u for some values of x and/or u) but not in the case of logistic growth. This situation is not surprising, since the equation $\nabla \cdot d(u)\nabla u + g(u) = 0$ can be converted to the form $\Delta U + G(U) = 0$ by letting $U = D(u)$ where $D(0) = 0$ and $D'(u) = d(u)$, and such a change of variables may destroy monotonicity or concavity properties of $g(u)$.

To analyze (1.2) we observe that the recent work of Hirsch [16] on monotone flows implies that the dynamics of (1.2) are determined by its steady states, we "unfold" the steady-state problem by introducing a parameter λ multiplying the undifferentiated terms, and we then analyze the steady states by using λ as a bifurcation parameter and applying the results of Rabinowitz [25]. Our main results state that under suitable restrictions on d , \mathbf{b} , and m , the problem (1.2) has a unique, stable, positive steady state provided $\lambda_1(d(x, 0), \mathbf{b}(x), m(x)) < 1$, where $\lambda_1(d, \mathbf{b}, m)$ is the first positive eigenvalue of

$$(1.3) \quad -\nabla d \nabla \phi + \mathbf{b} \cdot \nabla \phi = \lambda m \phi \quad \text{in } \Omega, \quad \phi = 0 \quad \text{on } \partial\Omega,$$

and give a partial description of how that eigenvalue depends on d , \mathbf{b} , and m . In particular, we show that under a mild coercivity assumption on the left side of (1.3), the necessary and sufficient condition for $\lambda_1(d, 0, m_j(x)) \rightarrow \infty$ as $j \rightarrow \infty$ given in Theorem 3.1 of [6] extends to the case of $\lambda_1(d(x), \mathbf{b}(x), m_j(x))$. Since environments may vary in ways best described by discontinuous functions (for example, if a field is crossed by a paved road with sharp boundaries) we consider the case of $m \in L^\infty(\Omega)$ with $m > 0$ on a set of positive measure, but with m taking both positive and negative values. In that situation, we have to extend known results somewhat to obtain the existence of a first positive eigenvalue $\lambda_1(d, \mathbf{b}, m)$. The analysis is based on work of Hess and Kato [15] and Hess [14]. Our results on the behavior of $\lambda_1(d, \mathbf{b}, m)$ overlap slightly with those of Murray and Sperr [22], who considered the case of $\lambda_1(1, \mathbf{b}, 1)$. Other results implying bounds for eigenvalues for $\lambda_1(d, \mathbf{b}, m)$ under various hypotheses are given in [12], [13], [15], and [17], but they either do not apply in our situation or do not appear to be sharp enough for our purposes. We have observed that the presence of a drift term can either raise or lower $\lambda_1(d, \mathbf{b}, m)$. Our analysis of the existence problem for positive steady states of (1.2) is fairly complete, but to obtain uniqueness we must make additional structure assumptions (specifically that either $\partial d / \partial u = 0$ or $\mathbf{b} = 0$), and there remain many open questions about the dependence of $\lambda_1(d, \mathbf{b}, m)$ on d , \mathbf{b} , and m .

The paper is structured as follows. We derive the basic existence theory for positive equilibria in § 2, and obtain conditions on the uniqueness and stability of equilibria in § 3. Many of the results are somewhat technical, but they have some interesting biological implications. In § 4 we examine how the eigenvalue $\lambda_1(d, \mathbf{b}, m)$, whose size determines whether the model predicts extinction or persistence for the population, depends on the environment, drift, and diffusion. In § 5 we obtain some population estimates, again in terms of $\lambda_1(d, \mathbf{b}, m)$. Since the answers to the questions of greatest biological interest are determined by the size of $\lambda_1(d, \mathbf{b}, m)$, we consider the results of § 4 to have the greatest applied significance because they relate $\lambda_1(d, \mathbf{b}, m)$ to the physical conditions in the model. In § 6 we give a biologically oriented summary of

our conclusions. We also conclude each section with a description of the biological interpretation of the main results of that section.

2. A qualitative overview. In this section, we consider the positive steady-state solutions of the parabolic problem

$$(2.1) \quad \begin{aligned} u_t &= \nabla \cdot (d(x, u)\nabla u) - \mathbf{b}(x) \cdot \nabla u + \lambda(m(x)u - cu^2) && \text{in } \Omega \times (0, \infty), \\ u(x, 0) &= u_0(x) \geq 0 && \text{for } x \in \Omega, \\ u(x, t) &= 0 && \text{on } \partial\Omega \times (0, \infty). \end{aligned}$$

Here, as noted in the Introduction, λ is a real parameter and we wish to observe the structure of said solutions when viewed as a subset of an appropriate function space via global bifurcation theory [25] as well as determine the stability properties of the solution when viewed as solutions to (2.1). We assume that $d \in C^2(\bar{\Omega} \times \mathbb{R})$ such that $d(x, s) \geq d_1 > 0$ for all $(x, s) \in \bar{\Omega} \times \mathbb{R}$, $\mathbf{b} \in [C^1(\bar{\Omega})]^n$, and $m \in L^\infty(\bar{\Omega})$ and consider

$$(2.2) \quad \begin{aligned} -\nabla \cdot (d(x, u)\nabla u) + \mathbf{b}(x) \cdot \nabla u &= \lambda(m(x)u - cu^2) && \text{in } \Omega, \\ u &= 0 && \text{on } \partial\Omega. \end{aligned}$$

Observe first of all that (2.2) can be expressed as

$$(2.3) \quad \begin{aligned} -\Delta u + \left[\frac{\mathbf{b}(x) \cdot \mathbf{d}_x(x, 0)}{d(x, 0)} \right] \cdot \nabla u \\ = \lambda \frac{m(x)}{d(x, 0)} u + \left[\frac{d_u(x, u)}{d(x, u)} |\nabla u|^2 + \left(\frac{\mathbf{d}_x(x, u)}{d(x, u)} - \frac{\mathbf{d}_x(x, 0)}{d(x, 0)} \right) \cdot \nabla u \right. \\ \left. + \left(\frac{1}{d(x, 0)} - \frac{1}{d(x, u)} \right) (\mathbf{b}(x) \cdot \nabla u) + \lambda \left(\frac{1}{d(x, u)} - \frac{1}{d(x, 0)} \right) m(x)u - \frac{\lambda cu^2}{d(x, u)} \right] && \text{in } \Omega, \\ u &= 0 && \text{on } \partial\Omega. \end{aligned}$$

Denote the expression in brackets in (2.3) by $H(\lambda, u)$. Then for a sufficiently large p , $H: \mathbb{R} \times W_0^{1,p}(\Omega) \rightarrow L^{p/2}(\Omega)$ is continuous and $\lim_{\|u\|_{1,p} \rightarrow 0} H(\lambda, u) / \|u\|_{1,p} = 0$, where $\|\cdot\|_{1,p}$ denotes the norm in $W_0^{1,p}(\Omega)$ and the limit is uniform for λ contained in compact intervals. (That such is the case relies on the fact $W_0^{1,p}(\Omega)$ embeds into $C_0^\alpha(\bar{\Omega})$ for sufficiently large p .) Consequently, if L denotes the elliptic operator on the left-hand side of (2.3) subject to zero Dirichlet boundary data and M/D denotes multiplication by $m(x)/d(x, 0)$, a solution u to (2.3) is equivalent to a solution u of

$$(2.4) \quad u = \lambda L^{-1} \left(\frac{M}{D} \right) u + L^{-1} H(\lambda, u).$$

Since $L^{-1}: L^{p/2}(\Omega) \rightarrow W^{2,p/2}(\Omega) \cap W_0^{1,p/2}(\Omega)$ is continuous, $W^{2,p/2}(\Omega) \cap W_0^{1,p/2}(\Omega)$ embeds compactly into $C_0^{1+\alpha}(\bar{\Omega})$, $0 < \alpha < 1$ for p sufficiently large, and $C_0^{1+\alpha}(\bar{\Omega})$ embeds into $W_0^{1,p}(\Omega)$ for any p , the right-hand side of (2.4) may be viewed as a completely continuous operator on $W_0^{1,p}(\Omega)$ for a sufficiently large p with $\lim_{\|u\|_{1,p} \rightarrow 0} \|L^{-1} H(\lambda, u)\|_{1,p} / \|u\|_{1,p} = 0$ uniformly for λ in compact intervals. Consequently, $\mathbb{R} \times W_0^{1,p}(\Omega)$ is an appropriate space in which to apply global bifurcation theory [25].

In order to invoke global bifurcation theory to guarantee the existence of a continuum of positive solutions to (2.2) in $\mathbb{R} \times W_0^{1,p}(\Omega)$, it suffices to establish that there is a unique $\lambda = \lambda_1(m) > 0$ such that

$$(2.5) \quad v = \lambda L^{-1} \left(\frac{M}{D} \right) v$$

has as generalized null space the span of a positive function. Note that (2.5) is equivalent

to

$$(2.6) \quad \begin{aligned} -\nabla \cdot (d(x, 0)\nabla v) + \mathbf{b}(x) \cdot \nabla v &= \lambda m(x)v && \text{in } \Omega, \\ v &= 0 && \text{on } \partial\Omega. \end{aligned}$$

In the special cases $\mathbf{b} \equiv \mathbf{0}$ or $m \in C(\bar{\Omega})$, the result follows from the results of [21] and [15], respectively, provided that $\{x \in \Omega: m(x) > 0\}$ has positive measure. In the case that $\mathbf{b} \neq \mathbf{0}$ and $m \in (L^\infty(\Omega) - C(\bar{\Omega}))$, to our knowledge, the result does not explicitly appear in the literature. Since such is the case and since the result is of independent interest, we include a brief proof.

THEOREM 2.1. *Suppose that d , \mathbf{b} , and m are as described above and that $\{x \in \Omega: m(x) > 0\}$ has positive measure. Then there is a unique $\lambda = \lambda_1(m) > 0$ such that*

$$(2.7) \quad \begin{aligned} -\Delta v + \left[\frac{\mathbf{b}(x) - \mathbf{d}_x(x, 0)}{d(x, 0)} \right] \cdot \nabla v &= \lambda \frac{m(x)}{d(x, 0)} v && \text{in } \Omega, \\ v &= 0 && \text{on } \partial\Omega \end{aligned}$$

has a solution $v \in C_0^{1+\alpha}(\bar{\Omega})$ with $v(x) > 0$ in Ω and $(\partial v / \partial n)(x) < 0$ on $\partial\Omega$. Moreover, $\bigcup_{r \geq 1} N\{(I - \lambda L^{-1}(M/D))^r\} = \langle v \rangle$.

Proof. The uniqueness and simplicity assertions of the theorem follow as in [15] once the existence of such a λ has been established. To this end, let $R > 0$ be such that $m(x)/d(x, 0) + R > 0$ on Ω almost everywhere and consider the operator $A_\lambda = \lambda(L + R\lambda)^{-1}(M/D + R)$, which may be viewed as a compact positive operator on $C_0^0(\bar{\Omega})$. A_λ is continuous in λ and consequently so is its spectral radius $r(A_\lambda)$ [23]. Moreover, $\lim_{\lambda \rightarrow 0} r(A_\lambda) = 0$. Hence, as in [8], the existence of an eigenvalue λ with the required properties follows from the Krein-Rutman theorem and the maximum principle as long as there is a $\lambda > 0$ so that $r(A_\lambda) \geq 1$. The assumption that $\{x \in \Omega: m(x) > 0\}$ has positive measure guarantees that (2.7) has infinitely many eigenvalues with positive real part [14, Thm. 2]. For any such eigenvalue λ^* and any associated eigenfunction v , Lemma 3 of [15] implies that

$$|v| \leq A_{\text{Re } \lambda^*} |v|.$$

Hence $r(A_{\text{Re } \lambda^*}) \geq 1$, and the result is established.

It is of substantial interest from the biological point of view not only to have the existence of an unbounded continuum of positive solutions to (2.2) but also to know there is a solution (λ, u) on the continuum for all $\lambda > \lambda_1(m)$. Such an observation requires information in addition to that provided by global bifurcation theory. The *a priori* estimates given in the following theorem are sufficient for this purpose.

THEOREM 2.2. *Suppose (λ, u) is a positive solution to (2.2) and that $\lambda \in [a, b]$, where $0 \leq a \leq b < \infty$. Then there is a constant $K > 0$ such that $\|u\|_{1,p} \leq K$.*

Proof. We know that $u \in W^{2,p}(\Omega) \cap W_0^{1,p}(\Omega)$ and consequently $u \in C_0^{1+\alpha}(\bar{\Omega})$. Hence, as in §2 of [6], the maximum principle implies that $\|u\|_\infty \leq \text{ess sup}_{x \in \bar{\Omega}} (m^+(x)/c)$. The result then will follow if we can show $\|\nabla u\|_\infty$ is bounded uniformly with respect to $\lambda \in [a, b]$.

To this end, we employ results in §§4 and 5 of Chapter 4 and in §2 of Chapter 6 of [18]. Equation (2.2) satisfies the ellipticity and structure conditions there imposed, with ellipticity (and other constants) bounded for $\lambda \in [a, b]$. Moreover, as noted, $0 \leq u(x) \leq \text{ess sup}_{x \in \bar{\Omega}} (m^+(x)/c)$. By the proof of Theorem 4.1 of [18, Chap. 4], $\text{ess sup}_\Omega |\nabla u|$ can then be bounded in terms of $\text{ess sup}_{\partial\Omega} |\nabla u|$ and integrals which are in essence $\|u\|_{2,2}^2$ and $\|u\|_{1,4}^2$. Theorem 5.1 of [18, Chap. 4] implies that these last integrals are bounded in terms of $\|u\|_\infty$ and constants depending on Ω and the coefficients of (2.2), all of which are uniformly bounded for $\lambda \in [a, b]$.

In order to see that $\text{ess sup}_{\partial\Omega} |\nabla u|$ is uniformly bounded with respect to $\lambda \in [a, b]$, we employ Lemma 4.1 of [18, Chap. 4] or Lemma 2.1 of [18, Chap. 6]. (These are two statements of the same result.) The idea behind the lemmas is Bernstein's, namely, to compare u with an appropriate auxiliary function via differential inequalities and the maximum principle to obtain bounds on $\partial u / \partial n$ on subsets of $\partial\Omega$. In [18], the classical maximum principle is used, and u is assumed to have classical second derivatives throughout Ω . However, we may replace the classical maximum principle with the maximum principle for weak solutions as stated in Chapter 8 of [11] and only require that $u \in W^{2,p}(\Omega) \cap W_0^{1,p}(\Omega)$. The bound we obtain depends only on Ω , $\|u\|_\infty$, and ellipticity and structure constants which are bounded as long as $\|u\|_\infty$ and λ are uniformly bounded so the result follows.

Consequently, there is an unbounded continuum \mathcal{C} in $\mathbb{R} \times W_0^{1,p}(\Omega)$ of positive solutions to (2.2) with the property that if $(\lambda, u) \in \mathcal{C}$ and $\lambda \in [a, b]$, where $0 \leq a < b < \infty$, there is a $K > 0$ such that $\|u\|_{1,p} \leq K$. Furthermore, it is evident that (2.2) has only the trivial solution when $\lambda = 0$. Hence, the projection $\Pi(\mathcal{C})$ into \mathbb{R} of \mathcal{C} must satisfy $(\lambda_1(m), \infty) \subseteq \Pi(\mathcal{C}) \subseteq (0, \infty)$. In particular, there is at least one positive solution of (2.2) for every $\lambda > \lambda_1(m)$.

For any fixed λ , $(\lambda, u) \in \mathcal{C}$ of course implies that u is an equilibrium solution to (2.1). It is sometimes possible to determine that u is globally asymptotically stable with respect to smooth initial data $u_0(x) \geq 0$. We first observe that if $\lambda > \lambda_1(m)$, then the zero solution of (2.2) is unstable. To this end, observe that the linearization A of $-\nabla \cdot (d(x, u)\nabla u) + \mathbf{b}(x) \cdot \nabla u - \lambda(m(x)u - cu^2)$ with respect to u at $u = 0$ is given by $A(\phi) = -\nabla \cdot (d(x, 0)\nabla \phi) + \mathbf{b}(x) \cdot \nabla \phi - \lambda m(x)\phi$ and that the zero solution is unstable provided that

$$\begin{aligned} A\phi &= \sigma\phi && \text{in } \Omega, \\ \phi &= 0 && \text{on } \partial\Omega, \end{aligned}$$

and $\phi(x) > 0$ in Ω implies that $\sigma < 0$. If $\sigma \geq 0$, then $v = \phi$ is a positive solution to the inhomogeneous boundary value problem

$$\begin{aligned} -\nabla \cdot (d(x, 0)\nabla v) + \mathbf{b}(x) \cdot \nabla v &= \lambda m(x)v + h && \text{in } \Omega, \\ v &= 0 && \text{on } \partial\Omega, \end{aligned}$$

where $h = \sigma\phi \geq 0$. As $\lambda > \lambda_1(m)$, Proposition 3 of [15] is violated. As a consequence, the zero solution of (2.2) is unstable as an equilibrium to (2.1) if $\lambda > \lambda_1(m)$, and we are able to establish the following theorem.

THEOREM 2.3. *Suppose that for some $\lambda > \lambda_1(m)$, there is a unique positive solution \bar{u} to (2.2). Then \bar{u} is a globally asymptotically stable equilibrium for (2.1) provided we require the initial data u_0 to lie in an appropriate Sobolev-Slobedickii space $W_0^{\sigma,p}$. This will be the case if $u_0 \in C_0^2(\bar{\Omega})$, for example.*

Proof. The methods of Amann [1], [2] imply that (2.1) generates a monotone flow on a Sobolev-Slobedickii space $W_0^{\sigma,p}(\Omega)$ with $W_0^{\sigma,p}(\Omega) \subseteq W^{2,p}(\Omega) \cap W_0^{1,p}(\Omega) \subseteq C^1(\bar{\Omega})$. (See also [16, Thm. 4.6]. We assume slightly less regularity than Amann since $m(x) \in L^\infty(\Omega)$, but a comparison principle for weak solutions to quasilinear parabolic problems can be readily obtained by modifying the proof of Theorem 9.5 of [11] to treat the parabolic case, so this is not a problem.) Consequently, the results of [16] are applicable in this situation. Since the zero solution of (2.2) is an unstable equilibrium and since $[0, \bar{u}]$ is an order interval containing no other equilibria, Theorem 0.6 of [16] implies that if $0 \leq \bar{u}_0(x) \leq \bar{u}(x)$ and $u_0(x) \neq 0$, then the solution $u(x, t)$ of (2.1) corresponding to $u_0(x)$ converges to $\bar{u}(x)$ as $t \rightarrow \infty$, uniformly on $\bar{\Omega}$. Moreover, for any sufficiently

large constant K , Theorem 0.7 of [16] implies that the solution $u_K(x, t)$ of (2.1) corresponding to initial condition K converges to $\bar{u}(x)$ as $t \rightarrow \infty$, uniformly on $\bar{\Omega}$. The result now follows from monotonicity, since for any smooth initial data $v(x) > 0$ and $v \neq 0$, we can find $u_0(x) \in [0, \bar{u}]$ and K sufficiently large so that $u_0(x) \leq v(x) \leq K$. We conclude this section with the following result, which is a corollary to Theorems 2.1–2.3.

THEOREM 2.4. Consider equation (2.6) and let $\lambda_1(d, \mathbf{b}, m)$ be as in Theorem 2.1. If $\lambda_1(d, \mathbf{b}, m) < 1$, then the problem (2.1) with $\lambda = 1$ has a positive equilibrium solution \bar{u} . If \bar{u} is unique, then it is globally asymptotically stable with respect to smooth initial data $u_0(x)$.

2.1. Biological interpretation. The primary result of biological interest in this section is Theorem 2.4. That result asserts that there exists a positive equilibrium density for the population being modeled provided that the eigenvalue $\lambda_1(d, \mathbf{b}, m)$ is less than 1. The significance of the result lies in the fact that $\lambda_1(d, \mathbf{b}, m)$ depends directly on the terms in the model describing biological properties of the population and the environment. Thus Theorem 2.4 provides a criterion for the possible persistence of a population in terms of diffusion, drift, and growth rates which vary with location. In some simple cases it is possible to compute $\lambda_1(d, \mathbf{b}, m)$ as the solution of an equation involving trigonometric and hyperbolic functions (which can be approximated by Newton's method). This is discussed in [7]; an example is given below.

In general, the numerical problem of finding $\lambda_1(d, \mathbf{b}, m)$ is fairly difficult but has been studied extensively. Approximation schemes for the case $\mathbf{b} = 0$ (no drift) are discussed in detail in [29]. There is a substantial literature on numerical approximation for solutions of eigenvalue problems with or without drift terms; [29] gives a large number of references. It is not surprising that the computation of the eigenvalue λ_1 may be complicated, since if λ_1 gives a reasonable synthesis of the various factors such as the size, shape, and quality of the environment and the effects of winds, currents, temperature or chemical gradients, it must reflect a large number of complex biological factors. In giving an accurate description of a complex phenomenon, a certain amount of mathematical sophistication may be required. Even so, the computational problem of finding $\lambda_1(d, \mathbf{b}, m)$ is likely to be simpler than that of evaluating the results of a comparably detailed simulation.

A major advantage of having a criterion for persistence based on $\lambda_1(d, \mathbf{b}, m)$ is that it is possible to make a number of *qualitative* statements about the ways in which changes in the environment affect a population. That is the main theme of [6] and [7] and of § 4 of this article. We discuss the topic at some length in § 4.

As an example, suppose that we consider a one-dimensional region $\Omega = (0, \ell)$, with no drift, constant diffusion rate, and a growth rate $m(x)$ which is a positive constant on a subinterval of Ω and a negative constant on the remainder of Ω . For appropriate d , this problem can easily be rescaled into the form

$$(2.8) \quad \begin{aligned} u'' + m(x)u - cu^2 &= 0 \quad \text{on } (0, 1), \\ u(0) = u(1) &= 0 \end{aligned}$$

with

$$(2.9) \quad m(x) = \begin{cases} -1, & 0 < x < a, \\ k, & a < x < a + T, \\ -1, & a + T < x < 1, \end{cases}$$

for some $T < 1$ describing the relative size of the favorable region, some $a \in [0, 1 - T]$ describing its location relative to the boundary, and some k describing the relative

quality of the favorable habitat compared with the unfavorable. (The diffusion coefficient is scaled into $m(x)$; the carrying capacity relative to habitat quality is described by c but does not directly enter the computation of λ_1 .) We show in [7] that for (2.8), (2.9), we have $\lambda_1 = \alpha^2$ where α is the smallest positive solution of

$$(2.10) \quad \cot \alpha \sqrt{k} T = \frac{k \tanh [\alpha(1-a-T)] \tanh \alpha a - 1}{\sqrt{k} [\tanh \alpha a + \tanh \alpha(1-a-T)]}.$$

Note that for a uniformly favorable environment we have $\lambda_1 = \alpha^2 = \pi^2/k$ so that we can expect persistence only for $k > \pi^2$. For $k = 16$, $T = 1$, $a = 0$ (indicating a uniformly favorable environment), we have $\lambda_1 \approx .61$. For $k = 16$, $a = .1$, $T = .8$ we find by solving (2.10) that $\lambda_1 \approx .63$. For $k = 16$, $a = .3$, $T = .4$, $\lambda_1 \approx .86$. The results of [7] show how in (2.8) a number of other forms of $m(x)$ can be treated via equations similar to (2.10).

3. Uniqueness. In this section we shall consider the question of uniqueness for positive steady states in our model. Our analysis includes some results on the direction of bifurcation with respect to the unfolding parameter λ , and on the linearized stability of the steady state. We begin with an example that shows that some restrictions are needed if uniqueness is to hold. In the general semilinear problem $\Delta u + f(x, u) = 0$, some conditions must be imposed on f to obtain uniqueness, and the problem $\nabla \cdot d(u)\nabla u + m(x)u - cu^2 = 0$ is equivalent to the semilinear problem $\Delta U + m(x)D^{-1}(U) - c[D^{-1}(U)]^2 = 0$ where $U = D(u)$ with $D'(s) = d(s)$, $D(0) = 0$; so we must expect that some conditions will be needed on $d(s)$ if the corresponding semilinear problem is to have a unique solution. The nature of those conditions is indicated by the problem

$$(3.1) \quad (d(u)u')' + \lambda(u - u^2) = 0, \quad u > 0 \quad \text{on } (0, \pi), \quad u(0) = u(\pi) = 0,$$

where $d(s) = 1 - 2d_0s$ for $0 \leq s \leq d_0/4$, $d(s)$ is smooth for $0 \leq s < \infty$, and $d(s) \geq d_1 > 0$. By the analysis in § 2, a branch of positive solutions to (3.1) bifurcates from the trivial solution at $\lambda = 1$. If we multiply the equation in (3.1) by u , integrate by parts, and use the fact that

$$\int_0^\pi u'(x)^2 dx \geq \int_0^\pi u(x)^2 dx,$$

then we obtain the relation

$$d_1 \int_0^\pi u^2 dx \leq d_1 \int_0^\pi (u')^2 dx \leq \int_0^\pi d(u)(u')^2 dx = \lambda \int_0^\pi u^2 dx - \lambda \int_0^\pi u^3 dx.$$

Since $u > 0$ on $(0, \pi)$, it follows that $\lambda \geq d_1 > 0$. Also, $0 < u < 1$ on $(0, \pi)$ by the maximum principle, so a standard application of the Rabinowitz global bifurcation theorem implies that the branch of positive solutions emanating from the zero solution at $\lambda = 1$ must meet infinity in λ . However, if we multiply (3.1) by $\sin x$ and integrate by parts, then as long as $0 \leq u \leq d_0/4$ (which will be true locally near the bifurcation point) we have

$$\begin{aligned} \lambda \int_0^\pi u \sin x dx - \lambda \int_0^\pi u^2 \sin x dx &= - \int_0^\pi (d(u)u')' \sin x dx \\ &= - \int_0^\pi u'' \sin x dx + \int_0^\pi (2d_0uu')' \sin x dx \\ &= \int_0^\pi u \sin x dx - \int_0^\pi d_0u^2 \sin x dx. \end{aligned}$$

Hence, as long as $0 < u \leq d_0/4$, we have

$$\lambda \int_0^\pi (u - u^2) \sin x \, dx = \int_0^\pi (u - u^2) \sin x \, dx + (1 - d_0) \int_0^\pi u^2 \sin x \, dx,$$

so if $d_0 > 1$, we must have $\lambda < 1$. But the branch of solutions must meet infinity in λ , so there must be a solution with $\sup u > d_0/4$ corresponding to $\lambda = 1$. It follows from the fact that the branch of positive solutions is a continuum and the leftward direction of bifurcation that for some $\varepsilon > 0$, the problem (3.1) has at least two solutions, one with $\sup u \leq d_0/4$ and one with $\sup u > d_0/4$, for $\lambda = 1 - \varepsilon$.

To avoid the phenomenon observed in this example, we must ensure that the bifurcation is to the right rather than to the left. If we have $\lambda > \lambda_1(d(x, 0), \mathbf{b}, m)$ for all positive solutions and they are all linearly stable, that is enough for uniqueness.

THEOREM 3.1. *Assume that $d(x, u)$ is of class C^1 . Suppose that for any solution of*

$$(3.2) \quad \begin{aligned} \nabla d(x, u) \nabla u - \mathbf{b}(x) \cdot \nabla u + \lambda(m(x)u - cu^2) &= 0 && \text{in } \Omega, \\ u &= 0 && \text{on } \partial\Omega, \\ \lambda > 0, \quad u > 0 &&& \text{in } \Omega, \end{aligned}$$

we have $\lambda > \lambda_1(d(x, 0), \mathbf{b}, m)$, and that the first eigenvalue of the linearized problem

$$(3.3) \quad \begin{aligned} -\nabla \cdot d(x, u) \nabla \phi - \nabla \cdot \phi \frac{\partial d(x, u)}{\partial u} \nabla u + \mathbf{b} \cdot \nabla \phi + \lambda(2cu - m)\phi &= \sigma \phi && \text{in } \Omega, \\ \phi &= 0 && \text{on } \partial\Omega \end{aligned}$$

satisfies $\sigma_1 > 0$ for any positive solution u . Then the positive solution for (3.2) is unique for any given λ .

Remarks. Combined with the comparison principle for the corresponding parabolic problem and the results of Hirsch [16], uniqueness implies stability. The condition $\sigma_1 > 0$ already implies linearized (and hence local) stability.

Proof. Choose $p > 1$ large enough that $W^{2,p}(\Omega) \cap W_0^{1,p}(\Omega)$ embeds in $C_0^{1+\alpha}(\Omega)$ and $W^{1,p/2}(\Omega)$ embeds in $C^\beta(\Omega)$ for some $\alpha, \beta \in (0, 1)$. Then the nonlinear function $F(\lambda, u) = \nabla \cdot d(x, u) \nabla u - \mathbf{b}(x) \cdot \nabla u + \lambda(m(x)u - cu^2)$ maps $\mathbb{R} \times (W^{2,p}(\Omega) \cap W_0^{1,p}(\Omega)) \rightarrow L^p(\Omega)$. The map is continuously differentiable, and the derivative with respect to the second variable is the negative of the operator on the left side of (3.3). If $\sigma_1 > 0$ in (3.3), then the linearized operator is invertible from L^p to $W^{2,p} \cap W_0^{1,p}$ by standard elliptic theory. Thus, if (λ_0, u_0) satisfies $F(\lambda, u) = 0$ and $u_0 > 0$ in Ω , then there is a bounded neighborhood U of u_0 in $W^{2,p} \cap W_0^{1,p}$, an interval $\Lambda = (\lambda_0 - \delta, \lambda_0 + \delta)$ with $\delta > 0$, and a function $g: \Lambda \rightarrow U$ such that for any $\lambda \in \Lambda$, the unique solution in U of (3.2) is $u = g(\lambda)$. Let $\lambda_k \uparrow \lambda_0 + \delta$ as $k \rightarrow \infty$. By (3.2), we have for $u_k = g(\lambda_k)$

$$(3.4) \quad \begin{aligned} u_k &= -\Delta^{-1}[(\nabla d(x, u_k) \cdot \nabla u_k - \mathbf{b} \cdot \nabla u_k + \lambda_k(mu_k - cu_k^2))/d(x, u_k)] \\ &\equiv -\Delta^{-1}w_k. \end{aligned}$$

Since U is bounded in $W^{2,p} \cap W_0^{1,p}$, so is \bar{U} ; thus the right side of (3.4) is of the form $-\Delta^{-1}w_k$, where $\{w_k\}$ is uniformly bounded in $W^{1,p/2}$. (Here the $p/2$ is due to the presence on the right side of (3.4) of terms of the form $(\partial d/\partial u)|\nabla u|^2$; also, we have used the fact that $d \geq d_1 > 0$, the embedding $W^{2,p} \cap W_0^{1,p} \hookrightarrow C_0^{1+\alpha}$, and the differentiability of d .) Our choice of p is such that $W^{1,p/2} \hookrightarrow C^\beta$, so since C^β embeds compactly in

C^0 , we may choose a subsequence and reindex so that $\{w_k\}$ converges in C^0 , and hence in L^p . Then (3.4) implies that the sequence $\{u_k\}$ converges in $W^{2,p} \cap W_0^{1,p}$, thus producing a nonnegative solution to (3.2) at $\lambda = \lambda_0 + \delta$. A similar argument applies at $\lambda = \lambda_0 - \delta$. For these values of λ , the solution can be extended further if it is positive. However, if we choose $K > 0$ sufficiently large we have from (3.2) that

$$-\nabla \cdot d(x, u) \nabla u + \mathbf{b}(x) \cdot \nabla u + Ku = [\lambda m(x) - \lambda cu + K]u \geq 0,$$

so if $u \geq 0$ and $u = 0$ somewhere in Ω , then $u = 0$ almost everywhere by the strong maximum principle for weak solutions (see [11, Thm. 8.19]). Hence, the only way that continuation in λ can fail is if λ is a bifurcation point from the branch of trivial solutions. The unique point where positive solutions can bifurcate from that branch is $\lambda = \lambda_1(d(x, 0), \mathbf{b}, m)$. It follows that if (3.2) has a positive solution u_0 for some λ_0 , then there is a curve $(\lambda, u(\lambda))$ of positive solutions passing through (λ_0, u_0) which can be extended at least until $\lambda = \lambda_1(d(x, 0), \mathbf{b}, m)$. Suppose that for some $\lambda_0 > \lambda_1(d(x, 0), \mathbf{b}, m)$ there are two distinct positive solutions of (3.2). Then each lies on an arc which extends until $\lambda = \lambda_1(d(x, 0), \mathbf{b}, m)$, and the arcs cannot intersect as long as the solutions to (3.2) remain positive. If an arc contains a positive solution to (3.2) at $\lambda = \lambda_1(d(x, 0), \mathbf{b}, m)$, then the preceding argument based on the implicit function theorem implies that there are positive solutions of (3.2) on $\lambda \in (\lambda_1 - \delta, \lambda_1)$, for some $\delta > 0$, contradicting our hypotheses. But both branches cannot connect to the zero solution at the point $\lambda = \lambda_1(d(x, 0), \mathbf{b}, m)$, since the Crandall-Rabinowitz constructive bifurcation theorem for simple eigenvalues implies that there is a unique branch of positive solutions in some neighborhood of the bifurcation point. Hence, assuming the existence of two distinct positive solutions for some λ yields a contradiction, so for any λ the positive solution of (3.2) must be unique.

Remark. A similar argument is used to obtain a uniqueness theorem for a diffusive Lotka-Volterra competition model in [5].

So far, we have been unable to establish that the hypotheses of Theorem 3.1 are satisfied, in general, for equations of the form (3.2). However, we can show that they will be met if the differential operator in (3.2) is either linear or in divergence form. The two cases require different arguments, so we consider them separately.

COROLLARY 3.2. *Suppose that $\mathbf{b} \equiv 0$ and $\partial d(x, u)/\partial u \geq 0$ for all $x \in \Omega$ and $u \in [0, \text{ess sup}(m^+/c)]$. Then (3.2) has a unique positive solution for $\lambda > \lambda_1(d(x, 0), 0, m)$.*

Proof. Suppose that (3.2) has a positive solution for some $\lambda > 0$. Multiplying by u , integrating by parts, and using the hypothesis that $d(x, u)$ is monotone increasing in u , we have

$$0 < \int_\Omega d(x, 0)|\nabla u|^2 \, dx < \int_\Omega d(x, u)|\nabla u|^2 \, dx + \lambda c \int_\Omega u^3 \, dx = \lambda \int_\Omega m(x)u^2 \, dx.$$

Since $\int_\Omega mu^2 \, dx > 0$, it follows from results in [16] that

$$\int_\Omega d(x, 0)|\nabla u|^2 \, dx \geq \lambda_1(d(x, 0), 0, m) \int_\Omega m(x)u^2 \, dx,$$

so that

$$\lambda_1(d(x, 0), 0, m) \int_\Omega mu^2 \, dx < \lambda \int_\Omega mu^2 \, dx$$

and

$$\lambda_1(d(x, 0), 0, m) < \lambda,$$

as required.

Suppose that $\phi_1 > 0$ is an eigenfunction for (3.3) corresponding to the principal eigenvalue σ_1 . Multiplying (3.3) by u and integrating by parts yields

$$\sigma_1 \int_{\Omega} u \phi_1 dx = \int_{\Omega} \left[-\nabla \cdot d(x, u) \nabla u + \frac{\partial d(x, u)}{\partial u} |\nabla u|^2 + 2\lambda c u^2 - \lambda m u \right] \phi_1 dx,$$

so by (3.2) we have

$$\sigma_1 \int_{\Omega} u \phi_1 dx = \int_{\Omega} \left[\frac{\partial d(x, u)}{\partial u} |\nabla u|^2 + \lambda c u^2 \right] \phi_1 dx > 0$$

and hence $\sigma_1 > 0$ as required.

COROLLARY 3.3. *Suppose that $d(x, u) \equiv d(x, 0)$, so that (3.2) is semilinear. Then (3.2) has a unique positive solution for $\lambda > \lambda_1(d(x, 0), \mathbf{b}, m)$.*

Proof. Suppose that (3.2) has a positive solution for some $\lambda > 0$. Then we have

$$-\nabla \cdot d(x, 0) \nabla u + \mathbf{b}(x) \cdot \nabla u = \lambda(m(x) - cu)u,$$

where $u > 0$ in Ω and $u = 0$ on $\partial\Omega$, so that

$$\lambda = \lambda_1(d(x, 0), \mathbf{b}, m - cu) > \lambda_1(d(x, 0), \mathbf{b}, m)$$

by the monotonicity of the positive principal eigenvalue with respect to the weight (see [11]). In this case, (3.2) can be written as

$$(3.5) \quad -\nabla \cdot d(x, 0) \nabla u + \mathbf{b} \cdot \nabla u + \lambda(2cu - m)u = \lambda cu > 0.$$

Since (3.5) admits a positive solution u for the positive inhomogeneous term λcu , it follows that the principal eigenvalue for the operator $L\phi \equiv -\nabla \cdot d(x, 0) \nabla \phi + \mathbf{b} \cdot \nabla \phi + \lambda(2cu - m)\phi$ must be positive. Since $\partial d(x, u)/\partial u \equiv 0$, that eigenvalue is σ_1 , so $\sigma_1 > 0$.

Remark. It would be of interest to find a natural set of conditions including those of both corollaries under which the hypotheses of Theorem 3.1 are satisfied. So far we have been unable to find such general conditions. It is well known that results for quasilinear problems not in divergence form are typically much weaker and/or more difficult than for either linear or divergence form problems (see the discussion in [7] and [14]). There are numerous open questions about uniqueness even in the case of ordinary differential equations.

3.1. Biological interpretation. The results of this section serve largely to sharpen those of the previous section by giving criteria for the uniqueness of the positive steady state for the population. Uniqueness is important in the context of our models because it implies the global stability of the positive steady state and thus the persistence of the population. Perhaps the most interesting observation from a biological viewpoint is that uniqueness may *fail* if the rate of diffusion is allowed to decrease with respect to the population density. Such a phenomenon occurs when the diffusion rate is constant but the logistic growth term is replaced by something of the form $uf(x, u)$ with $f(x, u)$ sometimes increasing with u ; in other words, in the presence of depensation in the growth rate. That observation is made in [20] in connection with a model for the population dynamics of the spruce budworm. As far as we know, it has not been observed previously that the same sort of effect can be induced by density dependent diffusion, which can sometimes produce multiple steady states even with a simple logistic growth term. In the absence of drift, we show that such an effect can only occur if the diffusion rate decreases relative to the population density at some densities. We have not been able to determine the effects of drift terms on this phenomenon. In

the case of a density independent diffusion rate, we show that a positive steady state is unique and stable if it exists, and similarly for models with no drift and a diffusion rate which increases with population density.

4. Properties of the principal eigenvalue. We have seen that under fairly general hypotheses, the condition $\lambda_1(d(x, 0), \mathbf{b}(x), m(x)) < 1$ is sufficient for the existence of a positive steady state for our model, and under somewhat stronger hypotheses the condition is also necessary and the positive steady state is unique and hence stable. Thus, it is natural to ask how $\lambda_1(d(x, 0), \mathbf{b}(x), m(x))$ depends on d , \mathbf{b} , and m . Some results for the case $d(x, 0) \equiv 1$, $m(x) \equiv 1$ are given in [21], and for the case $d(x, 0) \equiv 1$ and $\mathbf{b} \equiv 0$ in [6].

Our first result is an extension of Theorem 3.1 of [6].

THEOREM 4.1. *Suppose that $d(x) = d(x, 0) \in C^{1+\alpha}(\bar{\Omega})$, $\mathbf{b}(x) = (b_1, \dots, b_n)$ with $b_i(x) \in C^\alpha(\bar{\Omega})$ for $i = 1, \dots, n$, and $m_j(x) \in L^\infty(\Omega)$ for $j = 1, 2, \dots$. Suppose that d and \mathbf{b} are such that for any $\phi \in W_0^{1,2}(\Omega)$ we have*

$$(4.1) \quad \int_{\Omega} d |\nabla \phi|^2 + (\mathbf{b} \cdot \nabla \phi) \phi \geq d_0 \int_{\Omega} |\nabla \phi|^2$$

for some $d_0 > 0$, and for each j ,

$$(4.2) \quad \|m_j\|_\infty \leq m_0 \quad \text{and} \quad m_j > 0 \quad \text{on a set of positive measure.}$$

To have $\lim_{j \rightarrow \infty} \lambda_1(d, \mathbf{b}, m_j) = \infty$, it is necessary and sufficient that

$$(4.3) \quad \limsup_{j \rightarrow \infty} \int_{\Omega} m_j \beta \leq 0$$

for all $\beta \in L^1(\Omega)$ with $\beta \geq 0$ almost everywhere.

Proof. Suppose that (4.1), (4.2), and (4.3) hold but $\lambda_1(d, \mathbf{b}, m_j) \neq \infty$ as $j \rightarrow \infty$. We may then choose a subsequence $\{\lambda_1(d, \mathbf{b}, m_k)\}$ which is bounded. Let ϕ_k be the positive eigenfunction corresponding to $\lambda_1(d, \mathbf{b}, m_k)$ and normalized so that $\int_{\Omega} |\nabla \phi_k|^2 = 1$. Then the sequence $\{\phi_k\}$ is uniformly bounded in $W_0^{1,2}(\Omega)$, and since $W_0^{1,2}(\Omega)$ embeds compactly in $L^2(\Omega)$, we may choose a subsequence $\{\phi_l\}$ which converges in $L^2(\Omega)$ to some function ϕ . We have

$$(4.4) \quad \begin{aligned} d_0 &= d_0 \int_{\Omega} |\nabla \phi_l|^2 \leq \int_{\Omega} d(x) |\nabla \phi_l|^2 + \phi_l \mathbf{b}(x) \cdot \nabla \phi_l \\ &= \lambda_1(d, \mathbf{b}, m_l) \int_{\Omega} m_l \phi_l^2 \\ &= \lambda_1(d, \mathbf{b}, m_l) \left(\int_{\Omega} m_l (\phi_l^2 - \phi^2) + \int_{\Omega} m_l \phi^2 \right). \end{aligned}$$

Letting $l \rightarrow \infty$, the first integral in the last formula goes to zero since $\|m_l\|_\infty \leq m_0$ and $\phi_l \rightarrow \phi$ in $L^2(\Omega)$; the second goes to zero by (4.3). Since $\{\lambda_1(d, \mathbf{b}, m_l)\}$ is bounded, this implies $d_0 \leq 0$, which is a contradiction, so we must have $\lambda_1(d, \mathbf{b}, m_j) \rightarrow \infty$.

To show that our hypotheses are necessary as well as sufficient, we use a device due to Holland [17] in a form similar to that used by Hess [13] in the context of periodic-parabolic problems. (In fact, this device provides a method for estimating the size of $\lambda_1(d, \mathbf{b}, m)$ from above for fixed d , \mathbf{b} , and m , but we shall not pursue this.) Consider the problem

$$(4.5) \quad -\nabla d(x) \nabla \psi + \mathbf{b} \cdot \nabla \psi - \lambda m \psi = \mu \psi \quad \text{in } \Omega, \quad \psi = 0 \quad \text{on } \partial\Omega,$$

where $m \in L^\infty(\Omega)$ and $m > 0$ on a set of positive measure. The first eigenvalue $\mu_1(\lambda)$ admits an eigenfunction with $\psi > 0$ on Ω . Let $\theta = -\ln \psi$; then θ is defined on Ω and satisfies

$$(4.6) \quad d\Delta\theta - d|\nabla\theta|^2 - (\mathbf{b} - \nabla d) \cdot \nabla\theta - \lambda m = \mu_1(\lambda).$$

Suppose that $\phi \in C_0^\infty(\Omega)$ satisfies $\int_\Omega m\phi^2 > 0$ and $\int_\Omega \phi^2 = 1$. (We will return to the question of deciding if such functions exist later.) Multiplying (4.6) by ϕ^2 and using the divergence theorem, we have

$$(4.7) \quad \int_\Omega \nabla \cdot d\phi^2 \nabla\theta - \int_\Omega [d\phi^2 |\nabla\theta|^2 + 2d\phi \nabla\phi \cdot \nabla\theta + \phi^2 \mathbf{b} \cdot \nabla\theta] - \lambda \int_\Omega m\phi^2 = \mu_1(\lambda).$$

Another application of the divergence theorem shows that the first term in (4.7) is zero. Adding the quantity

$$\int_\Omega d|\phi \nabla\theta + [\phi \mathbf{b} + 2d\nabla\phi]/2d|^2 \geq 0$$

to the left side of (4.7) and rearranging terms, we have

$$(4.8) \quad \int_\Omega [|\phi \mathbf{b} + 2d\nabla\phi|^2/4d] - \lambda \int_\Omega m\phi^2 \geq \mu_1(\lambda).$$

If we let

$$\lambda = \Lambda(\phi, m) \equiv \int_\Omega [|\phi \mathbf{b} + 2d\nabla\phi|^2/4d] / \int_\Omega m\phi^2,$$

then (4.8) implies $\mu_1(\lambda) \leq 0$; but since $\psi > 0$, it then follows from (4.5) and the positivity lemma of [15] that $\lambda_1(d, \mathbf{b}, m) \leq \Lambda(\phi, m)$. Now suppose that $\limsup_{j \rightarrow \infty} \int_\Omega m_j \beta = \varepsilon_0 > 0$ for some $\beta \in L^1(\Omega)$ with $\beta \geq 0$ almost everywhere. Then we can take a subsequence $\{m_k\}$ so that $\int_\Omega m_k \beta \geq \varepsilon_0/2$, and we can approximate $\sqrt{\beta}$ as closely as we wish in $L^2(\Omega)$ with a function $\phi \in C_0^\infty(\Omega)$. If we choose ϕ so that $\int_\Omega |\beta - \phi^2| \leq \varepsilon_0/4m_0$, we obtain $\int m_k \phi^2 \geq \varepsilon_0/4 > 0$. It follows that for such ϕ the denominator of $\Lambda(\phi, m_k)$ is uniformly bounded away from zero, and since the numerator is independent of m , we have $\lambda_1(d, \mathbf{b}, m_k) \leq \Lambda_0 < \infty$ for some Λ_0 and all m_k in the subsequence. Hence we cannot have $\lim_{j \rightarrow \infty} \lambda_1(d, \mathbf{b}, m_j) = \infty$ if (4.3) does not hold.

Remarks. If we consider a set of weights $\{m_j\}$ with $\int m_j \geq m_1 > 0$ for all j , then (4.3) fails for $\beta = 1$, so the corresponding set of principal eigenvalues $\lambda_1(d, \mathbf{b}, m_j)$ must be bounded, since otherwise we could find a sequence m_l with $\lambda_1(d, \mathbf{b}, m_l) \rightarrow \infty$ as $l \rightarrow \infty$. There are various conditions on d and \mathbf{b} under which (4.1) must hold. For example, if we assume $d \geq d_1 > 0$ and $|\mathbf{b}| \leq b_0$, then we have for any $\varepsilon > 0$

$$\left| \int_\Omega (\mathbf{b} \cdot \nabla\phi)\phi \right| \leq \int_\Omega (\varepsilon(\mathbf{b} \cdot \nabla\phi)^2/2) + (\phi^2/2\varepsilon) \leq [(\varepsilon b_0^2/2) + (1/2\varepsilon\lambda_0)] \int_\Omega |\nabla\phi|^2$$

where $\lambda_0 = \lambda_1(1, 0, 1)$. If we minimize with respect to ε , we obtain $|\int_\Omega (\mathbf{b} \cdot \nabla\phi)\phi| \leq b_0/\sqrt{\lambda_0}$, so that (4.1) is satisfied if $d_1 > b_0/\sqrt{\lambda_0}$. If we assume $\mathbf{b} \in [C^1(\bar{\Omega})]^n$, we have

$$\int_\Omega (\mathbf{b} \cdot \nabla\phi)\phi = \frac{1}{2} \int_\Omega \mathbf{b} \cdot \nabla(\phi^2) = -\frac{1}{2} \int_\Omega (\nabla \cdot \mathbf{b})\phi^2.$$

If $\nabla \cdot \mathbf{b} \leq b_1$ and $d \geq d_1 > 0$, then (4.1) must hold provided $d_1 > b_1/2\lambda_0$.

Next we consider the problem of how \mathbf{b} affects $\lambda_1(d, \mathbf{b}, m)$. For the case where $d = 1$, $m = 1$, and $\mathbf{b} = -\nabla B$, $B \in C^2(\bar{\Omega})$, Murray and Sperr [22] showed that if γ_1, γ_2 are such that $\gamma_1 \leq \frac{1}{2}\Delta B + \frac{1}{4}|\nabla B|^2 \leq \gamma_2$, then

$$(4.9) \quad \lambda_1(1, 0, 1) + \gamma_1 \leq \lambda_1(1, \mathbf{b}, 1) \leq \lambda_1(1, 0, 1) + \gamma_2.$$

They also showed that if $\Omega \subseteq \mathbb{R}^2$ is convex, the matrix $((\partial b_i/\partial x_j))$ is positive semidefinite in Ω , $\omega = \max_{\partial\Omega} |\mathbf{b}|$, $\alpha(\lambda, \omega) = \omega((\lambda + \omega^2)^{1/2} + \omega)$, and ρ is the radius of the largest disc contained in Ω , then $\lambda_1(1, \mathbf{b}, 1)$ is greater than or equal to the first positive root λ of $\alpha(\lambda, \omega)/(\lambda + \alpha(\lambda, \omega)) = \cos(\rho\sqrt{\lambda})$.

Inequality (4.9) is obtained via a change of variables. If we have $\mathbf{b}(x)/d(x) = -\nabla B$ for some B , we can make the corresponding change of variables; letting $\psi = e^{B/2}\phi$ converts the problem $-\nabla \cdot d\nabla\phi + \mathbf{b} \cdot \nabla\phi = \lambda m\phi$ to

$$(4.10) \quad -\nabla \cdot d\nabla\psi + [(\nabla \cdot d\nabla B/2) + (d|\nabla B|^2/4)]\psi = \lambda m\psi,$$

while preserving the homogeneous Dirichlet boundary condition. If $\lambda = \lambda_1(d, \mathbf{b}, m)$ then since $\psi = e^{B/2}\phi > 0$, λ is also the first eigenvalue for (4.10), which has the variational characterization (see [21])

$$(4.11) \quad \lambda = \inf_{\substack{\psi \in W_0^{1,2}(\Omega) \\ \int_\Omega m\psi^2 > 0}} \frac{\int_\Omega [d|\nabla\psi|^2 + \gamma\psi^2]}{\int_\Omega m\psi^2},$$

where $\gamma = [(\nabla \cdot d\nabla B/2) + (d|\nabla B|^2/4)]$. In the special case $d = 1$, $m = 1$, (4.11) implies the bound (4.9). In general, if \mathbf{b} satisfies $\mathbf{b} = -d\nabla B$, with B such that $\gamma \geq 0$, then we may conclude $\lambda_1(d, \mathbf{b}, m) \geq \lambda_1(d, 0, m)$, and if $\gamma \leq 0$, $\lambda_1(d, \mathbf{b}, m) \leq \lambda_1(d, 0, m)$. Since m is indefinite, it is not clear how to obtain bounds analogous to (4.9).

In the case where \mathbf{b} is not a gradient, we can still obtain some information if $\mathbf{b} \in [C^1(\Omega)]^n$. If we multiply the equation $-\nabla \cdot d\nabla\phi + \mathbf{b} \cdot \nabla\phi = \lambda_1 m\phi$ by ϕ , integrate by parts, and use the boundary condition, we obtain

$$(4.12) \quad \int_\Omega [d|\nabla\phi|^2 - (\nabla \cdot \mathbf{b}/2)\phi^2] = \lambda_1 \int_\Omega m\phi^2.$$

If condition (4.1) is satisfied (which will clearly be the case if $\nabla \cdot \mathbf{b} \leq 0$) then we have $\int_\Omega m\phi^2 > 0$, so that we may again use the variational formulation of [21] to see that if $\nabla \cdot \mathbf{b} \leq 0$, then

$$\begin{aligned} \lambda_1(d, \mathbf{b}, m) &\geq \inf_{\substack{\psi \in W_0^{1,2}(\Omega) \\ \int_\Omega m\psi^2 > 0}} \frac{\int_\Omega [d|\nabla\psi|^2 - (\nabla \cdot \mathbf{b}/2)\psi^2]}{\int_\Omega m\psi^2} \\ &\geq \inf_{\substack{\psi \in W_0^{1,2}(\Omega) \\ \int_\Omega m\psi^2 > 0}} \frac{\int_\Omega d|\nabla\psi|^2}{\int_\Omega m\psi^2} = \lambda_1(d, 0, m). \end{aligned}$$

We have thus proved the following result.

THEOREM 4.2. *Suppose that either $\mathbf{b} \in [C^1(\bar{\Omega})]^n$ and $\nabla \cdot \mathbf{b} \leq 0$, or that $\mathbf{b} = -d\nabla B$ for some $B \in C^2(\bar{\Omega})$ such that $\gamma = [(\nabla \cdot d\nabla B/2) + (d|\nabla B|^2/4)] \geq 0$. Then $\lambda_1(d, \mathbf{b}, m) \geq \lambda_1(d, 0, m)$.*

Theorem 4.2 generalizes a result of [22] which implies that adding a constant drift term to the Laplacian always raises the principal eigenvalue. It can be shown via a perturbation argument that if $\mathbf{b} \in [C^1(\bar{\Omega})]^n$ with $\nabla \cdot \mathbf{b} > 0$, then for $\varepsilon > 0$ sufficiently small, $\lambda_1(1, \varepsilon\mathbf{b}, m) \leq \lambda_1(1, 0, m)$. The general question of deciding how $\lambda_1(d_1, \mathbf{b}_1, m_1)$ and $\lambda_1(d_2, \mathbf{b}_2, m_2)$ are related is to our knowledge an open problem.

THEOREM 4.3. Suppose that $d \geq d_1 > 0$ and that $\mathbf{b} \in [C^1(\bar{\Omega})]^n$ with $\nabla \cdot \mathbf{b} \leq 0$. Let $M(x)$ be any solution to

$$(4.13) \quad \nabla \cdot d \nabla M + \mathbf{b} \cdot \nabla M + (\nabla \cdot \mathbf{b})M = m.$$

Suppose $M_1 \geq \sup_{\Omega} M$ and $M_2 \geq \text{ess sup}_{\Omega} (-Mm)$. If $M_2 \leq 0$, then $\lambda_1(d, \mathbf{b}, m) \geq 1/2M_1$. If $M_2 > 0$, then

$$\lambda_1(d, \mathbf{b}, m) \geq \frac{-2M_1 + [4M_1^2 + (8M_2/d_1 \lambda_1(1, 0, 1))]^{1/2}}{(4M_2/d_1 \lambda_1(1, 0, 1))}.$$

Remarks. Observe that no boundary condition is imposed on M in (4.13). Since $\nabla \cdot \mathbf{b} \leq 0$, there will exist a solution for any reasonable boundary data.

Proof. Suppose ϕ satisfies

$$(4.14) \quad \begin{aligned} -\nabla \cdot d \nabla \phi + \mathbf{b} \cdot \nabla \phi &= \lambda_1(d, \mathbf{b}, m)m\phi & \text{in } \Omega, \\ \phi &= 0 & \text{on } \partial\Omega. \end{aligned}$$

Then we have via integration by parts

$$0 = \int_{\Omega} M(\nabla \cdot d \nabla \phi^2) - \phi^2(\nabla \cdot d \nabla M).$$

Since

$$\begin{aligned} \nabla \cdot d \nabla \phi^2 &= 2\phi \nabla \cdot d \nabla \phi + 2d|\nabla \phi|^2 \\ &= 2\phi \mathbf{b} \cdot \nabla \phi - 2\lambda_1 m \phi^2 + 2d|\nabla \phi|^2 \end{aligned}$$

and

$$\int_{\Omega} 2M\phi(\mathbf{b} \cdot \nabla \phi) = \int_{\Omega} M\mathbf{b} \cdot \nabla \phi^2 = - \int_{\Omega} \phi^2[\nabla M \cdot \mathbf{b} + M \nabla \cdot \mathbf{b}],$$

it follows that

$$(4.15) \quad 0 = 2 \int_{\Omega} Md|\nabla \phi|^2 - \int_{\Omega} \phi^2[\nabla \cdot d \nabla M + \mathbf{b} \cdot \nabla M + (\nabla \cdot \mathbf{b})M] - 2\lambda_1 \int_{\Omega} Mm\phi^2.$$

From (4.14) it follows that

$$\begin{aligned} \lambda_1 \int_{\Omega} m\phi^2 &= \int_{\Omega} [d|\nabla \phi|^2 + (\mathbf{b} \cdot \nabla \phi)\phi] \\ &= \int_{\Omega} [d|\nabla \phi|^2 - (\nabla \cdot \mathbf{b}/2)\phi^2] > 0, \end{aligned}$$

and we may assume that ϕ is normalized so that $\lambda_1 \int_{\Omega} m\phi^2 = 1$. By (4.13) we may replace the middle term in (4.15) by $-\int_{\Omega} m\phi^2$; if we then rearrange terms and multiply by λ_1 , we obtain

$$(4.16) \quad 1 = \lambda_1 \int_{\Omega} m\phi^2 = -2\lambda_1^2 \int_{\Omega} Mm\phi^2 + 2\lambda_1 \int_{\Omega} Md|\nabla \phi|^2.$$

Since

$$\nabla \cdot \mathbf{b} \leq 0, \quad 0 < \int_{\Omega} d|\nabla \phi|^2 \leq \lambda_1 \int_{\Omega} m\phi^2 = 1;$$

also,

$$\int_{\Omega} \phi^2 \leq \frac{1}{\lambda_1(1, 0, 1)d_1} \int_{\Omega} d|\nabla \phi|^2.$$

If we estimate the two integrals on the right of (4.16), we obtain

$$\int_{\Omega} d|\nabla \phi|^2 \leq 1 \leq 2M_2\lambda_1^2 \int_{\Omega} \phi^2 + 2M_1\lambda_1 \int_{\Omega} d|\nabla \phi|^2.$$

If $M_2 \leq 0$, we have $1 \leq 2M_1\lambda_1$. If $M_2 > 0$, then we have

$$1 \leq (2M_2/\lambda_1(1, 0, 1)d_1)\lambda_1^2 + 2M_1\lambda_1.$$

The bounds on λ_1 follow immediately.

Example. Let $\Omega = (0, \pi)$, $d \equiv 1$, $\mathbf{b} \equiv b_0$, and $M = \sin nx$. Then (4.13) becomes $M'' + bM' = \sin nx$, which has a solution

$$M = -[b_0/n(n^2 + b_0^2)] \cos nx - [1/(n^2 + b_0^2)] \sin nx.$$

We may use $M_1 = 1/n(n^2 + b_0^2)^{1/2}$ and $M_2 = (n + b_0)/n(n^2 + b_0^2)$. Theorem 4.3 then yields

$$(4.17) \quad \lambda_1(1, b_0, \sin nx) \geq \frac{1}{2} \left[\frac{-(n^2 + b_0^2)^{1/2}}{n + b_0} + \left(\frac{n^2 + b_0^2}{(n + b_0)^2} + \frac{2n(n^2 + b_0^2)}{n + b_0} \right)^{1/2} \right],$$

which implies that $\lambda_1(1, b_0, \sin nx) \rightarrow \infty$ with order n as $n \rightarrow \infty$ and with order $\sqrt{b_0}$ as $b_0 \rightarrow \infty$.

4.1. Biological interpretation. While the results of this section are technical in appearance in the sense that they represent extensions of existing results, they are potentially the most relevant for studying the effects of environmental factors on population dynamics. In previous sections we established that the size of the eigenvalue $\lambda_1(d, \mathbf{b}, m)$ gives a criterion for persistence, namely, $\lambda_1(d, \mathbf{b}, m) < 1$, so that $\lambda_1(d, \mathbf{b}, m)$ serves as a reasonable measure of the overall suitability of an environment. In the next section we shall strengthen the case for using λ_1 as such a measure by deriving a population estimate in terms of λ_1 . The results of this section give some information on how $\lambda_1(d, \mathbf{b}, m)$ is affected by the aspects of the environment described by the diffusion rate, drift, and local growth rate. Thus, they provide a means of using our models to infer the likely effects of certain environmental changes. The first two major results are qualitative, in that they describe the general behavior of λ_1 when the environment is perturbed in certain ways. The third is quantitative and allows a comparison of the relative impact of different effects, at least in simple cases. Our biological conclusions are somewhat tentative because of the enormous complexity of the problems they address, but they provide a starting point and direction for further work. We undertake a much more detailed analysis of some specific situations in [7].

Theorem 4.1 is a generalization of a result in [6]. Its main significance, we believe, is that it allows us to gain some insight into the effects of habitat fragmentation via reaction-diffusion models. The problem of understanding habitat fragmentation on populations is one of the most important topics in conservation biology. The theory

of island biogeography has been used to a considerable extent in the theoretical work on this problem, and it generally suggests that a few large regions of favorable habitat can be expected to sustain more species than a great many very small regions of the same total area. Theorem 4.1 allows us to consider the question at the species level rather than the community level, but leads to conclusions which are similar in spirit. Specifically, if we consider an environment in which the average habitat quality (as measured by the integral of the growth rate $m(x)$) is zero and vary the spatial distribution of favorable habitat so that it becomes more and more fragmented and more closely interspersed with unfavorable regions, then λ_1 will eventually tend to infinity so that our model predicts extinction.

As a simple example, if we consider a one-dimensional environment with fixed diffusion and drift coefficients and take $m_j(x) = \sin(jx)$, then $\lambda_1(d, b, \sin(jx)) \rightarrow \infty$ as $j \rightarrow \infty$. Whenever j is large enough that $\lambda_1(d, b, \sin(jx)) > 1$, the population cannot be expected to persist. It is important to keep in mind the asymptotic nature of this result; some of our work in [7] indicates that under certain conditions a few medium-sized favorable regions may provide a more suitable overall environment than a single large one. In some cases, we can obtain more precise quantitative information from Theorem 4.3. We have given an example immediately prior to this discussion. For more details on the connections between our work, island biogeography theory, and conservation biology, along with some references, see [6].

Theorem 4.2 gives some information on the effects of drift on the population. It is well known that (in the presence of a hostile exterior) increasing the diffusion rate tends to cause a more rapid loss of population across the boundary of the environment. Under certain conditions the effects of drift can produce the same results, and the theorem described some of those conditions. The case of constant growth and diffusion rates was treated by Murray and Sperr [22], and our results can be viewed as an extension of theirs to the case of variable diffusion. In realistic models we should expect $\nabla \cdot \mathbf{b}$ to change sign unless \mathbf{b} is constant, since otherwise the drift term itself acts as a source or a sink. The condition $\mathbf{b} = -d\nabla B$ with B satisfying $(\nabla \cdot d\nabla B/2) + (d|\nabla B|^2/4) \geq 0$ says roughly that the drift acts to augment the effects of diffusion. This condition can be checked via standard techniques from vector calculus. It was shown in [22] that for constant diffusion and growth rates, constant drift always makes the environment less suitable for the population under the assumption of a hostile exterior. Our results show that the same conclusion holds in the case of variable growth and diffusion rates. In both situations, the effect is due essentially to the drift pushing the population toward the hostile exterior region in one direction, while contributing no inward flux from the other since there will be no population in the hostile exterior region.

The qualitative results of Theorems 4.1 and 4.2 are augmented by the quantitative bounds on λ_1 given by Theorem 4.3. The example following the proof of that theorem shows how it can be used to draw conclusions about the persistence of a population from data on the diffusion, drift, and growth coefficients in a specific case. If the lower bound given in (4.17) is larger than 1, our model predicts extinction for the population. Other situations could be treated in a similar way. Of course, more complicated situations will require more effort in the analysis, but the estimate is based on the well-developed theory of linear differential equations. The specific bound (4.17) is already of some interest biologically since it gives an indication of the relative significance of drift and environmental heterogeneity. If we consider a one-dimensional environment, the estimate increases with the same order as the number of fragments of equal size into which the regions of favorable and unfavorable habitat are divided. It increases with the order of the square root of the coefficient describing the drift.

5. Population estimates. In the situations covered by Corollary 3.2 (density dependent diffusion in divergence form) and Corollary 3.3 (density independent diffusion not necessarily in divergence form), we are able to estimate the total size $\int_{\Omega} u \, dx$ of the positive steady states to (2.1) in a manner analogous to that in Theorem 4.1 of [6]. Since the results for these two cases are different from each other, we include them in this paper for the sake of completeness. We begin with the case of density independent diffusion.

THEOREM 5.1. *Suppose that u is the positive solution to*

$$(5.1) \quad \begin{aligned} -\nabla \cdot (d(x)\nabla u) + \mathbf{b}(x) \cdot \nabla u &= \lambda[m(x)u - u^2] && \text{in } \Omega, \\ u &= 0 && \text{on } \partial\Omega \end{aligned}$$

where $\lambda > \lambda_1(d, \mathbf{b}, m)$. Suppose that the differential operator satisfies the coercivity condition (4.1) and that $\tilde{\lambda} > 0$ is the principal eigenvalue for

$$\begin{aligned} -d_0\Delta z &= \mu mz && \text{in } \Omega, \\ z &= 0 && \text{on } \partial\Omega. \end{aligned}$$

Then $\tilde{\lambda} \leq \lambda_1(d, \mathbf{b}, m)$ and

$$\|u\|_1 \leq \left(1 - \frac{\tilde{\lambda}}{\lambda}\right) \|m_+\|_3 |\Omega|^{2/3}.$$

Proof. Suppose that $w > 0$ on Ω and satisfies

$$\begin{aligned} -\nabla \cdot (d(x)\nabla w) + \mathbf{b}(x) \cdot \nabla w &= \lambda_1(d, \mathbf{b}, m)m(x)w && \text{in } \Omega, \\ w &= 0 && \text{on } \partial\Omega. \end{aligned}$$

Then

$$\lambda_1(d, \mathbf{b}, m) \int_{\Omega} m(x)w^2 = \int_{\Omega} w(-\nabla \cdot (d(x)\nabla w) + \mathbf{b}(x) \cdot \nabla w) \geq d_0 \int_{\Omega} |\nabla w|^2.$$

Consequently, $\int_{\Omega} m(x)w^2 > 0$ and $d_0 \int_{\Omega} |\nabla w|^2 \geq \tilde{\lambda} \int_{\Omega} m(x)w^2$ by the variational characterization of $\tilde{\lambda}$ [21]. Hence $\tilde{\lambda} \leq \lambda_1(d, \mathbf{b}, m)$. Multiplying (5.1) by u and integrating gives

$$\begin{aligned} \int_{\Omega} u^3 &= \int_{\Omega} m(x)u^2 - \int_{\Omega} u \left[\frac{-\nabla \cdot (d(x)\nabla u) + \mathbf{b}(x) \cdot \nabla u}{\lambda} \right] \\ &\leq \int_{\Omega} m(x)u^2 - \frac{d_0}{\lambda} \int_{\Omega} |\nabla u|^2 \\ &\leq \left(1 - \frac{\tilde{\lambda}}{\lambda}\right) \int_{\Omega} m(x)u^2, \end{aligned}$$

since $\int_{\Omega} m(x)u^2 > 0$ by (4.1). Since $\int_{\Omega} mu^2 \leq \int_{\Omega} m_+ u^2 \leq \|m_+\|_3 \|u\|_3^2$ and $\|u\|_1 \leq \|u\|_3 |\Omega|^{2/3}$, the result follows.

Two comments are in order at this point. The first is that the reader will recall that § 4 contains a discussion of conditions under which the coercivity condition (4.1) obtains. The second is that Theorem 5.1 does not provide an estimate of the rate at which $\|u\|_1$ approaches zero as $\lambda \rightarrow \lambda_1(d, \mathbf{b}, m)$ which we know must be the case by the results of §§ 2 and 3. This limitation is due to the presence of the drift term. However, Theorem 5.1 does provide the useful global estimate $\|u\|_1 \leq \|m_+\|_3 |\Omega|^{2/3}$. In the density dependent case in divergence form, we can obtain the same global estimate

as well as estimate the rate at which $\|u\|_1$ tends to zero as $\lambda \rightarrow \lambda_1(d(x, 0), 0, m)$ as the next result shows.

THEOREM 5.2. *Suppose that u is the positive solution to*

$$\begin{aligned} -\nabla \cdot (d(x, u)\nabla u) &= \lambda[m(x)u - u^2] && \text{in } \Omega, \\ u &= 0 && \text{on } \partial\Omega, \end{aligned}$$

where $\lambda > \lambda_1(d(x, 0), 0, m)$ and we assume that $\partial d/\partial u \geq 0$. Then

$$\|u\|_1 \leq \left(1 - \frac{\lambda_1(d(x, 0), 0, m)}{\lambda}\right) \|m_+\|_3 |\Omega|^{2/3}.$$

Proof.

$$0 < \int_{\Omega} \frac{d(x, u)|\nabla u|^2}{\lambda} + \int_{\Omega} u^3 = \int_{\Omega} mu^2.$$

So $\int_{\Omega} mu^2 > 0$, and hence

$$\begin{aligned} \int_{\Omega} u^3 &= \int_{\Omega} mu^2 - \int_{\Omega} \frac{d(x, u)}{\lambda} |\nabla u|^2 \\ &\leq \int_{\Omega} mu^2 - \int_{\Omega} \frac{d(x, 0)}{\lambda} |\nabla u|^2 \\ &\leq \left(1 - \frac{\lambda_1(d(x, 0), 0, m)}{\lambda}\right) \int_{\Omega} mu^2 \end{aligned}$$

by the positivity of $\int_{\Omega} mu^2$ and the variational characterization of $\lambda_1(d(x, 0), 0, m)$. The remainder of the proof follows as in the proof of Theorem 5.1.

Finally, we note that in both these situations, we can obtain estimates on the rate of decay of solutions to (2.1) which are analogous to the result of Theorem 4.7 in [6]. The modifications needed to obtain these results from Theorem 4.7 of [6] are similar to those needed to obtain Theorems 5.1 and 5.2 above from Theorem 4.1 of [6]. Consequently, we omit them from this paper.

5.1. Biological interpretation. The immediate biological interpretation of the results of this section is clear. They yield bounds on the total population which our models predict a given environment can sustain. Theorem 5.1 is less sharp than Theorem 5.2, but for regions with simple geometry $\bar{\lambda}$ may be easier to compute than λ_1 . A deeper interpretation of Theorem 5.2 is that $\lambda_1(d, \mathbf{b}, m)$ is, in fact, an appropriate measure of environmental suitability, for in the original form of our models with $\lambda = 1$, Theorem 5.2 gives a bound on the population in which $1 - \lambda_1(d, \mathbf{b}, m)$ appears as a factor. Thus, if we vary d , \mathbf{b} , and m so that $\lambda_1(d, \mathbf{b}, m)$ approaches 1, the bound on the population goes to zero. (We have considered only the case where the carrying capacity is taken to be 1, but that can always be achieved by a rescaling if the carrying capacity is a constant.)

6. Conclusions. Reaction-diffusion models have been widely used to model population dynamics (see [4]–[7], [9], [10], [19], [20], [24], [27], [28]). We consider a class of such models which incorporate environmental variation, drift, and density dependent diffusion. We establish that in many cases the eigenvalue $\lambda_1(d, \mathbf{b}, m)$ for an associated linear problem is a reasonable measure of environmental suitability by showing that the condition $\lambda_1(d, \mathbf{b}, m) < 1$ implies persistence and obtaining upper bounds for the population in which $1 - \lambda_1(d, \mathbf{b}, m)$ appears as a factor. The significance of this

observation is that $\lambda_1(d, \mathbf{b}, m)$ is a quantity which depends directly on the diffusion, drift, and growth rates for the population and which can be computed by using well-known (although sometimes fairly sophisticated) mathematical techniques. In some cases we can calculate $\lambda_1(d, \mathbf{b}, m)$ fairly easily, but what is perhaps more important is that we can make qualitative inferences about the effects of changing various aspects of the environment on its overall suitability for a population as measured by λ_1 . Specifically, our models predict that a high degree of fragmentation of favorable habitat increases λ_1 and thus decreases environmental suitability, and that the presence of drift may either increase or decrease environmental suitability. (It turns out that under the assumption of a hostile exterior region that constant drift always decreases the overall environmental suitability, but a spatially varying drift term may actually increase it.) Similar conclusions have been drawn in other ways, but largely on the basis of either heuristic arguments or different modeling viewpoints. A conclusion that does not rely on properties of λ_1 is that the presence of density dependent diffusion can lead to multiple equilibria. A similar effect has been observed for models with constant diffusion but compensatory growth rate, but the observation that multiple equilibria can occur with a logistic growth term and density dependent diffusion is apparently new.

REFERENCES

- [1] H. AMANN, *Existence and regularity for semilinear parabolic evolution equations*, Ann. Scuola Norm. Sup. Pisa Cl. Sci. (4), 11 (1984), pp. 576–593.
- [2] ———, *Quasilinear evolution equations and parabolic systems*, Trans. Amer. Math. Soc., 293 (1986), pp. 191–227.
- [3] J. BELL AND C. COSNER, *Threshold behavior and propagation for nonlinear differential-difference systems motivated by modelling myelinated nerves*, Quart. Appl. Math., 17 (1984), pp. 1–14.
- [4] ———, *Wavelike solutions to reaction-diffusion equations on a cylinder: dependence on cylinder width*, SIAM J. Appl. Math., 47 (1987), pp. 534–543.
- [5] R. S. CANTRELL AND C. COSNER, *On the uniqueness and stability of positive solutions in the Lotka-Volterra competition model with diffusion*, Houston J. Math., 15 (1989), pp. 15–34.
- [6] ———, *Diffusive logistic equations with indefinite weights: population models in disrupted environments*, Proc. Roy. Soc. Edinburgh Sect. A, 112 (1989), pp. 293–318.
- [7] ———, *The effects of spatial heterogeneity in population dynamics*, J. Math. Biology, to appear.
- [8] R. S. CANTRELL AND K. SCHMITT, *On the eigenvalue problem for coupled elliptic systems*, SIAM J. Math. Anal., 17 (1986), pp. 850–862.
- [9] C. COSNER, *Eigenvalue problems with indefinite weights and reaction-diffusion models in population dynamics*, preprint.
- [10] P. C. FIFE, *Mathematical Aspects of Reacting and Diffusing Systems*, Lecture Notes in Biomath. 28, Springer-Verlag, Berlin, 1979.
- [11] D. GILBARG AND N. W. TRUDINGER, *Elliptic Partial Differential Equations of Second Order*, Springer-Verlag, Berlin, 1977.
- [12] J. P. GOSSEZ AND E. LAMI DOZO, *On the principal eigenvalue of a second order elliptic problem*, Arch. Rational Mech. Anal., 89 (1985), pp. 169–175.
- [13] P. HESS, *On positive solutions of semilinear periodic-parabolic problems*, in Infinite-Dimensional Systems, Lecture Notes in Math. 1076, Springer-Verlag, Berlin, New York, 1984, pp. 101–114.
- [14] ———, *On the relative completeness of the generalized eigenvectors of elliptic eigenvalue problems with indefinite weight functions*, Math. Ann., 270 (1985), pp. 467–475.
- [15] P. HESS AND T. KATO, *On some linear and nonlinear eigenvalue problems with an indefinite weight function*, Comm. Partial Differential Equations, 5 (1980), pp. 999–1030.
- [16] M. HIRSCH, *Stability and convergence in strongly monotone dynamical systems*, J. Reine Angew. Math., 383 (1988), pp. 1–53.
- [17] C. J. HOLLAND, *A minimum principle for the principal eigenvalue for second-order linear elliptic equations with natural boundary conditions*, Comm. Pure Appl. Math., 31 (1978), pp. 509–519.
- [18] O. A. LADYZHENSKAYA AND N. N. URAL'TSEVA, *Linear and Quasilinear Elliptic Equations*, Academic Press, New York, 1968.

- [19] S. LEVIN, *Population models and community structure in heterogeneous environments*, in *Mathematical Ecology*, T. G. Hallam and S. Levin, eds., Biomathematics 17, Springer-Verlag, Berlin, 1986.
- [20] D. LUDWIG, D. G. ARONSON, AND H. F. WEINBERGER, *Spatial patterning of the spruce budworm*, *J. Math. Biol.*, 8 (1979), pp. 217-258.
- [21] A. MANES AND A. M. MICHELETTI, *Un'estensione della teoria variazionale classica degli autovalori per operatori ellittici del secondo ordine*, *Boll. Un. Mat. Ital.* (6), 7 (1973), pp. 285-301.
- [22] J. D. MURRAY AND R. P. SPERB, *Minimum domains for spatial patterns in a class of reaction-diffusion equations*, *J. Math. Biol.*, 18 (1983), pp. 169-184.
- [23] R. NUSSBAUM, *Periodic solutions of some nonlinear integral equations*, in *Proc. Internat. Symposium on Dynamical Systems*, A. R. Bednarek and L. Cesari, eds., Gainesville, FL, 1976.
- [24] A. OKUBO, *Diffusion and Ecological Problems: Mathematical Models*, Biomathematics 10, Springer-Verlag, Berlin, 1980.
- [25] P. H. RABINOWITZ, *Some aspects of nonlinear eigenvalue problems*, *Rocky Mountain J. Math.*, 3 (1973), pp. 161-202.
- [26] H. SENO, *Effect of a singular patch on population persistence in a multi-patch system*, *Ecological Modelling*, 43 (1988), pp. 271-286.
- [27] J. G. SKELLAM, *Random dispersal in theoretical populations*, *Biometrika*, 38 (1951), pp. 196-218.
- [28] J. SMOLLER, *Shock Waves and Reaction-Diffusion Equations*, Springer-Verlag, Berlin, 1983.
- [29] H. F. WEINBERGER, *Variational Methods for Eigenvalue Approximation*, Society for Industrial and Applied Mathematics, Philadelphia, PA, 1974.