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ORIGINAL ARTICLE

Density Dependent Behavior at Habitat Boundaries and the Allee Effect

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Abstract Habitat edges can have a number of effects on populations, including modifying their patterns of dispersal. Dispersal patterns can influence population dynamics. In this paper, we explore the possible effects of a pattern of dispersal where the response of organisms to the boundary of a habitat patch depends on their local density. We model a population of organisms diffusing and growing logistically inside a patch, but with the likelihood of an individual crossing the patch boundary to leave the patch decreasing as the local density of conspecifics within the patch increases. Such behavior at patch boundaries has been observed among Glanville fritillary butterflies, and has been proposed as a mechanism for generating an Allee effect at the patch level. Our models predict that the behavior can indeed induce an Allee effect at the patch level even though there is no such effect built into the local population dynamics inside the patch. The models are relatively simple and are not intended to give a complete description of any particular population, but only to verify the idea that the mechanism of density-dependent dispersal behavior at a patch boundary is capable of altering population dynamics within the patch.

Keywords Reaction–diffusion · Logistic equation · Allee effect · Edge-mediated effects · Nonlinear boundary conditions · Population dynamics

1. Introduction

1.1. Background and motivation

Habitat edges can have a number of effects on populations. Those include modifying their patterns of dispersal; see Fagan et al. (1999). The dynamics of populations and the structure of communities can be influenced by dispersal patterns; see Cantrell and Cosner (2003). In this paper, we explore the possible effects of a particular type of response to the boundary of a habitat patch. We construct and analyze a simple diffusion model for

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a population growing logistically inside a patch with boundary conditions corresponding to a situation where the likelihood of an individual crossing the patch boundary to leave the patch is a decreasing function of the density of conspecifics at the point where the individual encounters the patch boundary. It turns out that such behavior at the patch boundary can induce a version of bistable population dynamics (i.e., something similar to an Allee effect) at the patch level even though there is no such effect present in the local population dynamics at locations within the patch. Our interest in the possibility of such a phenomenon arises partly from the observations of Kuussaari et al. (1998) of Glanville fritillary butterflies on habitat patches. They observed that the butterflies were less likely to leave a patch when conspecifics were present, and that populations within patches showed an Allee effect. They speculated that the Allee effect might arise from the behavior of individuals at the patch boundary. The model we will study is not intended to be a detailed or precise description of the system studied by Kuussaari et al. (1998). Rather, it is intended to be a simple caricature, designed to test the concept that such behavior at a patch boundary might induce an Allee effect at the patch level. We chose to use a model where the tendency of organisms to cross the patch boundary at a given point depends on the density of conspecifics at that point because that seems to be the simplest type of model that can support the effect of interest. An alternate approach might be to assume that the tendency of an organism to cross the patch boundary depends on the average density of conspecifics within some distance or within the entire patch. Such an assumption would lead to a model similar to (1) but with α depending on the integral of u over part or all of Ω. Such a model should display behavior similar to (1) but the nonlocal nature of the boundary conditions would complicate the analysis. In any case, our goal is just to show that density-dependent dispersal at a patch boundary can induce “bistability” or an “Allee effect” at the patch level even if it is not present in the local population dynamics within the patch. For that purpose, a simple model is adequate.

In a previous paper (Cantrell and Cosner, 2002), we showed that a type of nonlinear diffusion proposed by Turchin (1989) as a mechanism for aggregation can induce a version of bistability or an Allee effect at the patch level even if those are not present in the local population dynamics at locations within the patch. An important difference between the mechanism studied previously by Cantrell and Cosner (2002) and the one treated here is that in (Cantrell and Cosner, 2002), it was assumed that there is density-dependent dispersal within the patch but the boundary conditions are not density dependent, while here the dispersal inside the patch is not density-dependent but the boundary conditions are. Thus, although there may be some relationships or similarities between the mechanisms, they are based on different assumptions about individual dispersal behavior. This suggests that the phenomenon of density-dependent dispersal inducing Allee effects or bistability when such effects would not otherwise be present might occur in a variety of models, perhaps including more realistic models for the system studied by Kuussaari et al. (1998).

1.2. Model formulation

The model we will study is a diffusive logistic equation with density-dependent boundary conditions. Only the boundary conditions are novel; otherwise, the model is of a type widely used in ecology (Cantrell and Cosner, 2003). In the model $u(x, t)$ represents the density of a population on a patch Ω, normalized so that the carrying capacity is equal to one. The patch Ω is a bounded region in $\mathbb{R}^n$, with $n = 1, 2$, or 3. The boundary of Ω is denoted by $\partial\Omega$. The variable x represents the spatial location within Ω. The model is

$$\begin{aligned} &u_t = d\nabla^2 u + ru(1-u) \quad \text{in } \Omega \times (0, \infty), \\ &\alpha(u)\frac{\partial u}{\partial n} + \bigl(1-\alpha(u)\bigr)u = 0 \quad \text{on } \partial\Omega \times (0, \infty). \end{aligned} \tag{1}$$

The term $\partial u/\partial n$ in the boundary condition is the normal derivative of u. The parameter d is the diffusion rate for the population, which is equal to half the mean square distance traveled by an individual in unit time. The parameter r is the intrinsic local growth rate of the population at low density. Both r and d are always positive. The function $\alpha(u)$ in the boundary condition is related to the fraction of individuals that remain in patch if they reach its boundary. If $\alpha(u) \equiv 0$ then the boundary is absorbing, that is, all individuals that encounter it leave the patch. If $\alpha(u) \equiv 1$, then the boundary is reflecting, that is, no individuals leave the patch. For $\alpha(u) \equiv \alpha_0$ with $0 < \alpha_0 < 1$, the boundary conditions describe a situation where some individuals leave the patch when they encounter the boundary and some do not. It is tempting but not necessarily accurate to interpret α_0 as the fraction of individuals that remain in the patch after reaching its boundary. The detailed interpretation of α_0 in the case where $\alpha(u) = \alpha_0 \in (0, 1)$ depends on the derivation used to obtain the boundary conditions and the parameters and scalings used in that derivation. This point is discussed in detail in Appendix A. However, under any reasonable interpretation of α_0, we can view α_0 as increasing with the fraction of individuals that remain in the patch upon reaching the boundary. In the model (1) we will take $\alpha(u)$ to be a nondecreasing function of u such that $\alpha(0) = \alpha_0$ with $0 < \alpha_0 < 1$ and $\alpha(1) = 1$. Thus, as the local density u increases, the fraction of individuals that remain the patch upon reaching the boundary also increases. We will require that $\alpha_0 > 0$ because if $\alpha_0 = 0$ then we would have $\alpha(u) = u\beta(u)$ for some function $\beta(u)$, so that the boundary condition would factor as

$$u\left[\beta(u)\frac{\partial u}{\partial n} + 1 - \alpha(u)\right] = 0.$$

That condition could be satisfied by having either u or the expression in brackets equal to zero, which leads to an ill-posed problem. This issue does not arise if $\alpha_0 > 0$. We will always assume that the patch Ω is bounded. For technical reasons we will assume $\partial\Omega$ and $\alpha(u)$ are smooth. The model (1) describes the density u of a theoretical population on the patch Ω. At any given site within the patch, the local dynamics of the population, without regard to dispersal, are given by the logistic term $ru(1-u)$. The patch Ω could be a part of a collection of patches supporting a metapopulation. Although the model (1) operates on the scale of a patch, we would need to consider both the within-patch and metapopulation scales to adequately discuss the sense in which the nonlinear boundary conditions describing the dependence of individual behavior at the patch boundary on the local population density can induce bistability or Allee effects. Note that at a scale smaller than that of a single patch the local population growth rate in (1) is logistic and thus the model does not reflect an Allee effect at that scale. Typically nonspatial models for population dynamics with Allee effects take the form

$$\frac{du}{dt} = f(u), \tag{2}$$

where u is a population density and $f(u)$ is a bistable nonlinearity, that is, where (2) has stable equilibria $u = 0$ and $u = K > 0$ and an unstable equilibrium $u = a$ with $0 < a < K$. A typical choice for $f(u)$ is

$$f(u) = ru(u - a)(1 - u/K), \tag{3}$$

but various other choices have been used; see for example Boukal and Berec (2002). A model with such a reaction term would describe a situation where the population dynamics at a scale smaller than that of a single patch already display an Allee effect.

1.3. Structure of the paper

In Section 2 we perform a linear stability analysis of the equilibria $u \equiv 0$ and $u \equiv 1$ of (1). The analysis at $u \equiv 1$ leads to eigenvalue problems with a nonstandard form of linear boundary conditions, which we reduce to a standard form by making a change of variables. In Section 3 we analyze the dynamics of the model by using upper and lower solutions, and discuss a specific example where our theoretical results apply. In Section 4 we discuss how the phenomenon modeled here fits into the broader subject of Allee effects in general and describe some possible extensions or variations on the modeling and analysis. In Appendix A we give derivations of linear boundary conditions with $\alpha(u) \equiv \alpha^* \in [0, 1]$ in the context of population models and a discussion of what such conditions mean biologically.

Remarks on notation:

Ω	represents a bounded habitat patch.
$\partial\Omega$	represents the boundary of Ω.
u	represents a population density on Ω.
r	represents the local population growth rate in Ω.
d	represents the diffusion rate of the population.
$1 - \alpha$	describes the rate at which individuals leave the patch Ω if they encounter the boundary $\partial\Omega$. Specifically, if $1 - \alpha = 0$ then no individuals leave the patch but if $1 - \alpha = 1$ then all individuals that reach the boundary leave the patch. In general, we will allow α to depend on u but in some cases we will set α equal to a constant. (In the models α appears as a coefficient in the boundary conditions.)
$\lambda_1(\alpha^*)$	is the principal eigenvalue of the negative Laplace operator on Ω under the boundary conditions that would arise if $\alpha \equiv \alpha^*$ for some constant α^*. (This eigenvalue synthesizes the geometry of Ω with the boundary conditions determined by α^*. It measures the rate at which a population with no births or deaths and with diffusion rate $d = 1$ would diffuse out of Ω under the boundary conditions defined by α. It is formally defined in Lemma 1 of Section 2.)

In general we will use σ to denote eigenvalues of operators arising in our analysis, and ψ and ϕ to denote eigenfunctions. We will sometimes distinguish particular cases of variables by subscripts, superscripts, etc. so that $u, \tilde{u}, \bar{u}$, and u_{α^*} might all be used to represent population densities of some sort, and similarly for other variables.

2. Linearized stability analysis

In this section we will perform a linearized stability analysis of some of the equilibria of (1). We will find conditions under which the equilibrium $u \equiv 0$ is locally stable but where $u \equiv 1$ is also a positive equilibrium which is locally stable, so that (1) is bistable, i.e., (1) has an Allee effect in the sense described in Section 1. The equilibria of (1) satisfy

$$\begin{aligned} &d\nabla^2 u + ru(1-u) = 0 \quad \text{in } \Omega, \\ &\alpha(u)\frac{\partial u}{\partial n} + \big(1-\alpha(u)\big)u = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{4}$$

Recall that α is related to the fraction of individuals that leave Ω when they encounter the boundary $\partial\Omega$. If $\alpha \equiv 0$, all individuals encountering $\partial\Omega$ leave Ω. If $\alpha \equiv 1$, then no individuals leave Ω. We will assume that $0 \le \alpha(u) \le 1$ for $0 \le u \le 1$. We will also assume that $\alpha'(u) \ge 0$, which reflects the idea that individuals become less likely to leave Ω as the density u increases. Finally, we assume that $\alpha(1) = 1$, so that when the population is at carrying capacity no individuals leave Ω. Under that assumption $u \equiv 0$ and $u \equiv 1$ are equilibria of (1) for any d and r. Linearizing the equilibrium Eq. (4) at $u \equiv 0$ yields the eigenvalue problem

$$\begin{aligned} &d\nabla^2 \psi + r\psi = \sigma\psi \quad \text{in } \Omega, \\ &\alpha(0)\frac{\partial \psi}{\partial n} + \big(1-\alpha(0)\big)\psi = 0. \end{aligned} \tag{5}$$

Linearizing (4) at $u \equiv 1$ yields

$$\begin{aligned} &d\nabla^2 \psi - r\psi = \sigma\psi \quad \text{in } \Omega, \\ &\frac{\partial \psi}{\partial n} - \alpha'(1)\psi = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{6}$$

The boundary condition in (5) is classical because $\alpha(0)$ and $1-\alpha(0)$ are both nonnegative and at least one is positive, so the standard theory applies to (5). The boundary condition in (6) is generally nonclassical because the coefficients of $\partial\psi/\partial n$ and ψ have opposite signs, but we will show that (6) can be made classical by a change of variables. It turns out that both (5) and (6) admit principal eigenvalues, which are the largest eigenvalues of (5) and (6) respectively, and which are characterized by having positive eigenfunctions. If the principal eigenvalue for (5) is negative then $u \equiv 0$ is linearly stable; if that eigenvalue is positive then $u \equiv 0$ is unstable. Similarly, $u \equiv 1$ is linearly stable or unstable if the principal eigenvalue of (6) is negative or positive, respectively.

For any $\alpha(0) \in [0, 1]$ the eigenvalue problem (5) is classical. The sign of the principal eigenvalue for (5) is related to the size of the principal eigenvalue of the negative Laplace operator $-\nabla^2$ on Ω under the boundary conditions of (5). For any fixed $\alpha^* \in [0, 1]$ consider the eigenvalue problem

$$\begin{aligned} &-\nabla^2 \phi = \lambda\phi \quad \text{in } \Omega, \\ &\alpha^*\frac{\partial \phi}{\partial n} + (1-\alpha^*)\phi = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{7}$$

We have the following (see Cantrell and Cosner, 2003, Section 2.2):

Lemma 1. *The eigenvalues of* (5) *and* (7) *are real. For each fixed* $\alpha^* \in [0,1]$ *the problem* (7) *has a principal eigenvalue* $\lambda_1(\alpha^*)$ *which is the smallest eigenvalue of* (7) *and which is characterized by having a positive eigenfunction* ϕ_1. *We have* $\lambda_1(1) = 0$ *and* $\lambda_1(\alpha^*) > 0$ *for* $\alpha^* \in [0,1)$. *The problem* (5) *has a principal eigenvalue* σ_1 *characterized by having a positive eigenfunction. We have* $\sigma_1 = r - d\lambda_1(\alpha(0))$. *Thus, the principal eigenvalue of* (5) *is negative so that* $u \equiv 0$ *is linearly stable in* (1) *provided that*

$$r/d < \lambda_1\bigl(\alpha(0)\bigr). \tag{8}$$

Discussion. The existence of principal eigenvalues (characterized by positive eigenfunctions) is classical; see for example the discussion in Cantrell and Cosner (2003). If $\phi_1 > 0$ is the eigenfunction corresponding to $\lambda_1(\alpha(0))$ then we may use $\psi = \phi_1 > 0$ to conclude that $\sigma_1 = r - d\lambda_1(\alpha(0))$ is the principal eigenvalue for (5). The interpretation of (8) is that $\sigma_1 < 0$, so that $u \equiv 0$ is linearly stable, if the local growth rate r is too small or the diffusion rate d is too large relative to the principal eigenvalue $\lambda_1(\alpha(0))$ of the negative Laplace operator with boundary conditions determined by $\alpha(0)$. The eigenvalue $\lambda_1(\alpha(0))$ in effect synthesizes the geometric features of the patch Ω with the boundary condition determined by $\alpha(0)$ to describe the rate at which individuals would diffuse out of Ω for a population with no births or deaths, with $\alpha(u) \equiv \alpha(0)$, and with diffusion rate $d = 1$. Thus, (8) relates the demographic parameters r and d to the boundary conditions when $u = 0$ and to the geometry of Ω. In particular, for any fixed value of $\alpha(0) \in (0,1]$, the eigenvalue $\lambda_1(\alpha(0))$ will decrease if the size of the domain Ω is increased without changing its shape. Thus, the condition (8) can be used to determine the minimum size that a patch of a given shape must have to be able to support a population with a given diffusion rate and tendency to disperse across the patch boundary. This observation was the basis for the pioneering work of Skellam (1951) and Kierstead and Slobodkin (1953) on minimal patch size; see Cantrell and Cosner (2003), Chap. 2, for further discussion.

As we noted previously, the eigenvalue problem (6) is not classical unless $\alpha'(1) = 0$ because the coefficients of ψ and $\partial\psi/\partial n$ in the boundary condition are of opposite signs. If $\alpha'(1) = 0$, the boundary condition in (6) becomes an ordinary no-flux (i.e., Neumann) condition, so the eigenfunction ψ_1 corresponding to the principal eigenvalue σ_1 of (6) may be chosen as $\psi_1(x) \equiv 1$, which yields $\sigma_1 = -r < 0$. Thus, we immediately obtain the following:

Lemma 2. *If* $\alpha'(1) = 0$ *and* (8) *holds then the equilibria* $u \equiv 0$ *and* $u \equiv 1$ *of* (1) *are both linearly stable.*

It turns out that in general the equilibrium $u \equiv 1$ is linearly stable if $\alpha'(1) \geq 0$ is sufficiently small, but to obtain a specific condition on $\alpha'(1)$ for stability we must construct an auxiliary function depending on Ω. Thus, we state the following lemma in terms of requiring $\alpha'(1)$ to be sufficiently small, but the proof of the lemma gives a way of quantifying how small $\alpha'(1)$ needs to be. We will return to this point in the discussion following the proof.

Lemma 3. *If* $\alpha'(1) \geq 0$ *is sufficiently small and* (8) *holds then the equilibria* $u \equiv 0$ *and* $u \equiv 1$ *of* (1) *are both linearly stable.*

Biological Interpretation. Lemmas 2 and 3 show that a version of bistability or an Allee effect at the patch level can indeed be induced by density dependent dispersal behavior at the patch boundary. Specifically, they give conditions under which the equilibria $u \equiv 0$ and $u \equiv 1$ of (1) are both stable in some sense. The condition for $u \equiv 0$ to be stable is for the local growth rate r to be relatively small compared to the rate $d\lambda_1(\alpha(0))$ at which individuals would disperse out of the patch in the absence of conspecifics. (Recall that d is the diffusion rate, $\alpha(0)$ describes the response individuals would have to the patch boundary if no conspecifics were present, and $\lambda_1(\alpha(0))$ is the principal eigenvalue for the Laplace operator under boundary conditions defined by $\alpha(0)$.) The condition for $u \equiv 1$ to be stable means that no individuals leave the patch when the population is at carrying capacity, i.e., $\alpha(1) = 1$, and that the tendency of individuals to leave the patch (as measured by $1 - \alpha(u)$) is small relative to r/d when the population is near carrying capacity. (Recall that if $\alpha(1) = 1$ and $\alpha'(1)$ is small then $\alpha(u) \approx 1$ when $u \approx 1$.)

Proof of Lemma 3: To convert (6) to a classical form we will rewrite it in terms of a new function $\rho = \psi/h$ where $h > 0$ is a function related to the patch Ω. It is easy to see that for any smooth function h we have

$$\begin{aligned} \nabla\psi &= h\nabla\rho + \rho\nabla h, \\ \nabla^2\psi &= h\nabla^2\rho + 2\nabla\rho\cdot\nabla h + \rho\nabla^2 h. \end{aligned} \tag{9}$$

From (6) and (9) we readily obtain

$$\begin{aligned} &d\nabla\cdot h^2\nabla\rho + \left(dh\nabla^2 h - rh^2\right)\rho = \sigma h^2\rho \quad \text{in } \Omega, \\ &\frac{\partial\rho}{\partial n} + \left[\frac{1}{h}\frac{\partial h}{\partial n} - \alpha'(1)\right]\rho = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{10}$$

To define h, choose w to be a function so that $\partial w/\partial n = 1$ on $\partial\Omega$ then let $h = e^{\alpha'(1)w}$. (If the geometry of Ω is simple then it may be possible to explicitly construct w. It is always possible to construct w by solving the equation $\nabla^2 w - w = 0$ subject to the boundary condition $\partial w/\partial n = 1$ on $\partial\Omega$.) We then have $\partial h/\partial n = \alpha'(1)h$ on $\partial\Omega$ so the boundary condition in (10) becomes

$$\frac{\partial\rho}{\partial n} = 0. \tag{11}$$

Thus, the change of variables converts (6) into a classical eigenvalue problem. Multiplying (10) by ρ, integrating by parts via the divergence theorem and using (11) yields

$$\begin{aligned} \sigma\int_\Omega h^2\rho^2\,dx &= -\int_\Omega dh^2\,|\nabla\rho|^2\,dx + \int_\Omega \left(dh\,\nabla^2 h - rh^2\right)\rho^2\,dx \\ &\le d\int_\Omega \left[\left(\frac{\nabla^2 h}{h} - \frac{r}{d}\right)\right] h^2\rho^2\,dx. \end{aligned} \tag{12}$$

Since $\nabla^2 h = (\alpha'(1)\nabla^2 w + \alpha'(1)^2|\nabla w|^2)h$ it follows from (12) that $\sigma < 0$ provided

$$\alpha'(1)\nabla^2 w + \alpha'(1)^2|\nabla w|^2 < (r/d) \quad \text{on } \Omega. \tag{13}$$

□

Discussion and Example. Since the function w depends on Ω but not on $\alpha'(1)$, the condition (13) will be satisfied if $\alpha'(1)$ is sufficiently small. Suppose that Ω is the unit disc $x_1^2 + x_2^2 < 1$ in $\mathbb{R}^2$. Let $w = (x_1^2 + x_2^2)/2$. Then, $\nabla w = (x_1, x_2)$ so $\partial w/\partial n = 1$ on $\partial\Omega$, $|\nabla w|^2 \leq 1$ on Ω, and $\nabla^2 w = 2$. Thus, we may use w in (13) to see that (13) would hold if

$$2\alpha'(1) + \alpha'(1)^2 < r/d. \tag{14}$$

We can combine the proof of Lemma 3 with Lemma 1 to obtain the following:

Theorem 1. *If there is a function w satisfying $\partial w/\partial n = 1$ on $\partial\Omega$ such that*

$$\alpha'(1)\sup_{\bar{\Omega}}\nabla^2 w + \alpha'(1)^2\sup_{\bar{\Omega}}|\nabla w|^2 < \frac{r}{d} < \lambda_1\big(\alpha(0)\big) \tag{15}$$

holds, where $\lambda_1(\alpha(0))$ is the principal eigenvalue of (7) with $\alpha^* = \alpha(0)$, then the equilibria $u \equiv 0$ and $u \equiv 1$ of (1) are both linearly stable.

Proof: If (15) holds then both (8) and (13) hold so the hypotheses of Lemmas 1 and 3 are met. □

Discussion. Condition (15) will hold for some values of the ratio r/d if $\alpha'(1) \geq 0$ is sufficiently small, but how small $\alpha'(1)$ has to be depends on Ω. When (15) holds, it says that the local population growth rate r inside the patch is large enough to compensate for the rate of loss of individuals across $\partial\Omega$ scaled by the diffusion rate d when the population density is near carrying capacity, but not large enough to compensate when the population density is low.

3. Analysis of dynamics

In this section, we will examine the dynamics of solutions to (1). Specifically, under suitable hypotheses on the terms $d, r,$ and $\alpha(u)$ in (1), we will find conditions on the initial population density $u(x, 0)$ which imply $u(x, t) \to 0$ as $t \to \infty$ and other conditions which imply $u(x, t) \to 1$ as $t \to \infty$. The general type of conditions we will impose on $u(x, 0)$ to conclude that $u(x, t) \to 0$ (respectively $u(x, t) \to 1$) as $t \to \infty$ are that $u(x, 0)$ be sufficiently small (respectively large) on all of Ω. The analysis will be based on upper and lower solutions. We will first consider a simple special case, then a more general case, and conclude with an example.

To perform the analysis we first need to recall some basic facts regarding the model

$$\begin{aligned} &u_t = d\nabla^2 u + ru(1-u) \quad \text{in } \Omega \times (0,\infty), \\ &\alpha^* \frac{\partial u}{\partial n} + (1-\alpha^*)u = 0 \quad \text{on } \partial\Omega \times (0,\infty), \end{aligned} \tag{16}$$

which is the case of (1) where $\alpha(u) \equiv \alpha^*$. Let $\lambda_1(\alpha^*)$ be the principal eigenvalue for (7) and let $\sigma_1(\alpha^*)$ be the corresponding eigenvalue for (5), so that $\sigma_1(\alpha^*) = r - d\lambda_1(\alpha^*)$.

Lemma 4. *If the inequality*

$$r/d \le \lambda_1(\alpha^*) \tag{17}$$

is satisfied then $u \equiv 0$ *is a global attractor for nonnegative nontrivial solutions of* (16). *If*

$$r/d > \lambda_1(\alpha^*) \tag{18}$$

then (16) *has a unique positive equilibrium* u_{α^*} *which is a global attractor for nonnegative nontrivial solutions of* (16).

Discussion. This is a standard result; see Cantrell and Cosner (2003, Chap. 3). Note that the strict inequality corresponding to (17) is the inequality (8) with $\alpha(0) = \alpha^*$, which implies the linear stability of $u \equiv 0$.

Theorem 2. *Suppose that* (17) *holds for some* $r, d > 0$ *and* $\alpha_0 \in (0, 1)$. *Suppose that there are numbers* u_1, u_2 *with* $0 < u_1 < u_2 < 1$ *such that*

$$\alpha(u) = \alpha_0 \quad \textit{for } u \le u_1, \qquad \textit{while } \alpha(u) = 1 \quad \textit{for } u \ge u_2. \tag{19}$$

Let $\psi_1 > 0$ *be the eigenfunction corresponding to* σ_1 *in* (5), *normalized so that* $\max_{\bar{\Omega}} \psi_1 = 1$. (*Note that* $\alpha(0) = \alpha_0$ *by* (19).) *If* $u(x, t)$ *is a solution of* (1) *with* $u(x, 0) < u_1\psi_1(x)$ *then* $u(x, t) \to 0$ *as* $t \to \infty$. *If* $u(x, t)$ *is a solution to* (1) *with* $u(x, 0) > u_2$ *then* $u(x, t) \to 1$ *as* $t \to \infty$.

Remark. A sketch of a function $\alpha(u)$ satisfying (19) is shown in Fig. 1.

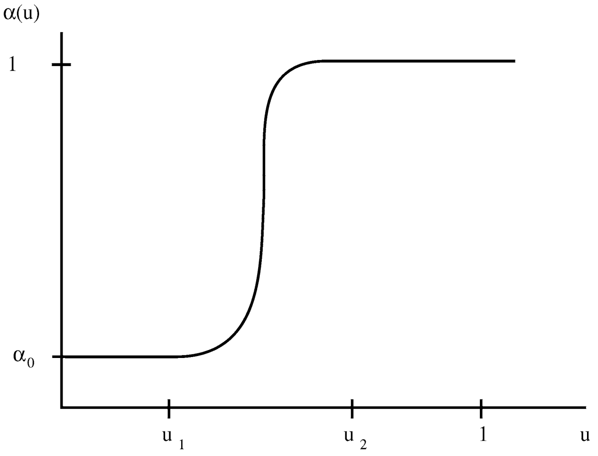

Fig. 1 This figure shows the graph of an example of a function $\alpha(u)$ satisfying (19).

Proof: By Lemma 1, (17) implies $\sigma_1 < 0$. For $\epsilon > 0$ we have

$$\begin{aligned} d\nabla^2(\epsilon\psi_1) + r(\epsilon\psi_1)(1-\epsilon\psi_1) &= \epsilon\big[d\nabla^2\psi_1 + r\psi_1 - r\epsilon\psi_1^2\big] \\ &= \epsilon\psi_1\big[\sigma_1(\alpha_0) - r\epsilon\psi_1\big] < 0 \end{aligned} \tag{20}$$

on $\bar{\Omega}$, so that $\epsilon\psi_1$ is an upper solution of the equilibrium Eq. (16) with $\alpha^* = \alpha_0$. Consequently, as in Aronson and Weinberger (1975, 1978) it follows that for any $\varepsilon > 0$ the solution $\bar{u}(x,t)$ of (16) with $\bar{u}(x,0) = \epsilon\psi_1$ is decreasing in t and converges to the equilibrium solution $u \equiv 0$ as $t \to \infty$. Suppose that $\tilde{u}$ is a solution of (1) with $\tilde{u}(x,0) < u_1\psi_1$. Then for some $t_0 > 0$ we have $\tilde{u}(x,t) < u_1\psi_1 \le u_1$ on $\bar{\Omega}$ for $t \in (0,t_0]$. Consequently, $\alpha(\tilde{u}) = \alpha_0$ for $t \in (0,t_0]$ so that $\tilde{u}$ is a solution of (16) for $t \in (0,t_0]$ with $\tilde{u}(x,0) < u_1\psi_1$. It follows that $\tilde{u} \le \bar{u} \le u_1\psi_1$ for $t \in (0,t_0]$. Iterating this argument gives $\tilde{u}(x,t) \le \bar{u}(x,t)$ for all $t > 0$, so $\tilde{u}(x,t) \to 0$ as $t \to \infty$.

For $\alpha^* = 1$, we have $\sigma_1(1) = r > 0$ and we may choose $\psi_1 \equiv 1$. For any constant $k \in (0,1)$ we have

$$d\nabla^2 k + rk(1-k) > 0 \tag{21}$$

so $u \equiv k$ is a lower solution to the equilibrium problem for (16) with $\alpha^* = 1$. Consequently, the solution $\underline{u}(x,t)$ of (16) with $\alpha^* = 1$ and $\underline{u}(x,0) = k$ is increasing in t and converges to the unique positive equilibrium $u \equiv 1$.

Suppose now that $k > u_2$ and that $\hat{u} = \hat{u}(x,t)$ is a solution to (1) with $\hat{u}(x,0) \ge k$. Then for some $t_1 > 0$, $\hat{u}(x,t) > u_2$ on $\bar{\Omega}$ for $t \in (0,t_1]$. Hence $\alpha(\hat{u}(x,t)) = 1$ for $t \in (0,t_1]$, so that $\hat{u}$ is a solution to (16) (with $\alpha^* = 1$) on $\Omega \times (0,t_1)$ and $\hat{u}(x,0) \ge k$. As a result $\hat{u}(x,t) \ge \underline{u}(x,t) \ge k$ for $t \in [0,t_1]$. Again, by iterating this argument, we establish that $\hat{u}(x,t) \ge \underline{u}(x,t)$ for all $t > 0$, so that $\hat{u} \to 1$ as $t \to \infty$. ☐

Discussion. Theorem 2 gives estimates for the basins of attraction for the equilibria $u \equiv 0$ and $u \equiv 1$ of (1). The condition (19) is simple but it requires that $\alpha(u)$ be constant when $u \approx 0$ or $u \approx 1$. In particular, it is stronger than the conditions for linear stability derived in Section 2. (If $\alpha(u) \equiv 1$ for $u_2 \le u \le 1$ then $\alpha'(1) = 0$, but $u \equiv 1$ is linearly stable in (1) even if $\alpha'(1) > 0$ provided $\alpha'(1)$ is sufficiently small.) However, it does establish that the model (1) can support an Allee effect in the dynamic sense as well as in the sense of linear stability. Specifically, it gives conditions under which populations with uniformly small densities will decline toward zero but populations with densities uniformly close to carrying capacity will approach carrying capacity. A schematic of this is shown in Fig. 2.

The hypothesis (19) of Theorem 2 is easy to state and interpret, but the requirement that $\alpha(u)$ must be constant for $u \approx 0$ and $u \approx 1$ is admittedly rather specialized. We now derive an analogous result under more general hypotheses. The hypotheses are a bit more subtle than (19) but they are related to those needed for the linear stability analysis in Theorem 1. We will discuss that point and provide an example where the hypotheses can be verified after the proof of the next result. Recall that we always assume $\alpha'(u) \ge 0$. The proof of our next result uses the assumption for $u \approx 0$ and $u \approx 1$ but it could be relaxed for intermediate values of u. Recall also that for $\alpha^* \in [0,1]$ with $\lambda_1(\alpha^*) < r/d$ we denote the unique positive equilibrium of (16) by u_{α^*}. Finally, for any $\alpha^* \in [0,1]$ denote by $\sigma_1(\alpha^*)$

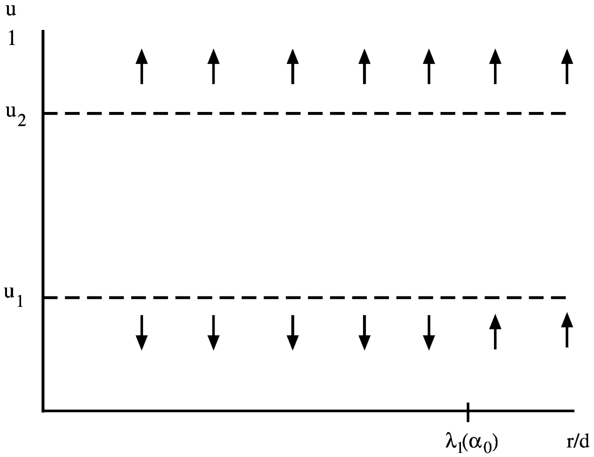

Fig. 2 For $0 < r/d < \lambda_1(\alpha_0)$, solutions to (1) with initial conditions less than u_1 decay to 0 over time. Solutions to (1) with initial conditions greater than u_2 converge over time to 1. This shows the Allee effect in (1) under assumption (19).

the principal eigenvalue of

$$\begin{aligned} &d\nabla^2\psi + r\psi = \sigma\psi \quad \text{in } \Omega, \\ &\alpha^* \frac{\partial\psi}{\partial n} + (1-\alpha^*)\psi = 0 \quad \text{on } \partial\Omega \end{aligned} \tag{22}$$

and denote by $\psi_1 > 0$ the corresponding eigenfunction.

Theorem 3. *Suppose that there are numbers* α_1, α_2 *and* δ *with* $0 < \alpha_1 < \alpha_2 < 1$ *and* $\delta > 0$ *such that*

$$\lambda_1(\alpha_1) > r/d > \lambda_1(\alpha_2), \tag{23}$$

$$\alpha(\delta) < \alpha_1 \tag{24}$$

and

$$\alpha\Big(\min_{\bar{\Omega}}(u_{\alpha_2})\Big) > \alpha_2. \tag{25}$$

If u *is a solution to* (1) *with* $u(x,0) > u_{\alpha_2}(x)$ *on* $\bar{\Omega}$ *then*

$$u(x,t) > u_{\alpha_2}(x) \tag{26}$$

on $\bar{\Omega}$ *for all* $t > 0$. *Let* $\psi_1 > 0$ *denote the eigenfunction corresponding to* $\sigma_1(\alpha_1)$ *in* (22), *normalized by* $\max_{\bar{\Omega}}\psi_1 = 1$. *If* $u(x,0) < \delta\psi_1(x)$ *on* $\bar{\Omega}$ *then* $u(x,t) \to 0$ *as* $t \to \infty$.

Discussion. In this case we do not require that $\alpha(1) = 1$, so we do not necessarily have $u(x,t) \to 1$ as $t \to \infty$ even if $u(x,0)$ is large. The graph of a function $\alpha(u)$ satisfying (24) and (25) is shown in Fig. 3.

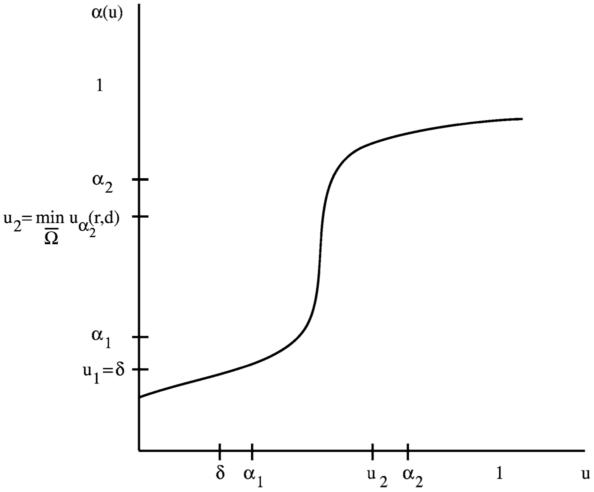

Fig. 3 This figure shows the graph of a function $\alpha(u)$ satisfying (24) and (25).

Proof: Suppose $u(x,t)$ is a solution of (1) with $u(x,0) > u_{\alpha_2}(x)$. Then there exists $t_0 > 0$ so that $u(x,t) > \min_{\bar{\Omega}} u_{\alpha_2}$ on $\bar{\Omega}$ for $0 < t < t_0$. Since $\alpha(u)$ is nondecreasing, we have $\alpha(u(x,t)) > \alpha(\min_{\bar{\Omega}} u_{\alpha_2}) > \alpha_2$ for $x \in \partial\Omega$ and $t \in (0,t_0)$. It follows that $u(x,t)$ is a strict upper solution to (16) with $\alpha^* = \alpha_2$ for $t \in (0,t_0)$. Since u_{α_2} is an equilibrium solution of (16) it follows from the method of upper and lower solutions that $u(x,t) > u_{\alpha_2}$ on $t \in [0,t_0]$. Iteration of this argument allows us to conclude that in fact (26) holds for all $x \in \bar{\Omega}$ and $t > 0$.

Since $r/d < \lambda_1(\alpha_1)$, any positive solution of (16) with $\alpha^* = \alpha_1$ will approach zero as $t \to \infty$ by Lemma 4. As in the proof of Theorem 2, $\delta\psi_1$ can be seen to be a strict upper solution to the equilibrium problem for (16) with $\alpha^* = \alpha_1$. If $\tilde{u}(x,t)$ is the solution to (16) with $\alpha^* = \alpha_1$ and $\tilde{u}(x,0) = \delta\psi_1$ then $\tilde{u}(x,t)$ decreases to zero as $t \to \infty$ by the properties of upper and lower solutions, as in Aronson and Weinberger (1975, 1978). On the other hand, if $u(x,0) < \delta\psi_1(x)$ on $\bar{\Omega}$ then there exists $t_1 > 0$ such that $u(x,t) < \delta$ on $\bar{\Omega}$ for $t \in (0,t_1)$. Thus, $\alpha(u(x,t)) < \alpha_1$ for $t \in (0,t_1)$ and hence $u(x,t)$ is a strict lower solution to (16) with $\alpha^* = \alpha_1$, so $u(x,t) \le \tilde{u}(x,t) < \delta\psi_1(x)$ on $\bar{\Omega}$ for $t \in (0,t_1)$. In particular $u(x,t_1) \le \tilde{u}(x,t_1) < \delta$ so the argument can be iterated to show that $u(x,t) \le \tilde{u}(x,t)$ for $t > 0$. Since $\tilde{u}(x,t) \to 0$ as $t \to \infty$ the conclusion that $u(x,t) \to 0$ as $t \to \infty$ follows. □

Discussion. The hypotheses of Theorem 3 are related to the hypotheses needed for the linear stability of $u \equiv 0$ and $u \equiv 1$ in Theorem 1. It follows from the variational characterization of eigenvalues (see, for example, Cantrell and Cosner, 2003, Chap. 2) that $\lambda_1(\alpha^*)$ depends continuously on α^* for $\alpha^* > 0$ in (7). Thus, if $r/d < \lambda_1(\alpha(0))$ as in (15), then $r/d < \lambda_1(\alpha^*)$ for $\alpha^* \in (\alpha(0), \alpha_3)$ for some $\alpha_3 > \alpha(0)$. Since $\alpha(u)$ is smooth there will be a $\delta > 0$ such that $\alpha(0) \le \alpha(\delta) < \alpha_3$. For any $\alpha_1 \in (\alpha(\delta), \alpha_3)$ inequality (24) and the first inequality in (23) will hold. Suppose now that $\alpha(1) = 1$ so that $u \equiv 1$ is an equilibrium of (1). Since $\lambda_1(\alpha^*) \to 0$ as $\alpha^* \to 1$, the second inequality in (23) will hold if α_2 is sufficiently close to 1. It can be shown that as long as (16) has a positive equilibrium u_{α^*}, that equilibrium depends smoothly on α^* in $C^1(\bar{\Omega})$. (See Cantrell et al., 1998.) In particular,

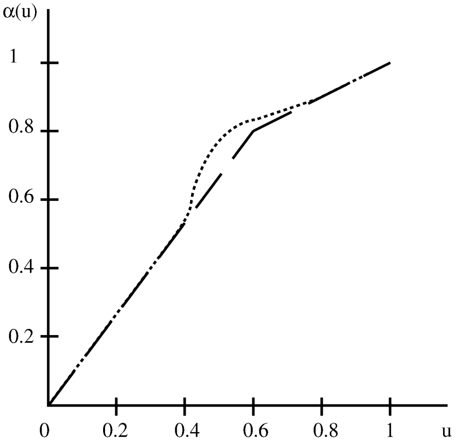

Fig. 4 This figure shows the graphs of $\alpha(u)$ and $\tilde{\alpha}(u)$ as described in the example for the case $\Omega = (-1, 1)$. The graph of $\alpha(u)$ is shown with short dashes while that of $\tilde{\alpha}(u)$ is shown with long dashes. The graphs coincide when u is near 0 or 1.

if $M(\alpha^*) = \min_{\bar{\Omega}} u_{\alpha^*}$ then $M(\alpha^*)$ depends smoothly on α^* for $\alpha^* < 1$, $\alpha^* \approx 1$. Consider $g(\alpha^*) = \alpha^* - \alpha(M(\alpha^*))$. We have $g(1) = 0$ since $u_{\alpha^*} = 1$ when $\alpha^* = 1$ and we are assuming $\alpha(1) = 1$. We have $g'(\alpha^*) = 1 - \alpha'(M(\alpha^*))M'(\alpha^*)$ so $g'(1) = 1 - \alpha'(1)M'(1) > 0$ if $\alpha'(1)$ is sufficiently small. Thus, $g(\alpha^*) < 0$ if $\alpha^* < 1$, $\alpha^* \approx 1$. It follows that if $\alpha'(1)$ is sufficiently small then (25) will hold for all $\alpha_2 \in (\alpha_4, 1)$ for some α_4. Thus, if $\alpha(1) = 1$ and $\alpha'(1)$ is sufficiently small then the second inequality in (23) and inequality (25) will hold, as well as the hypotheses for the linear stability of $u \equiv 1$ in Theorem 1. Thus, although the hypotheses of Theorems 1 and 3 are not the same, they are compatible in the sense that both can be satisfied if $\alpha(1) = 1$, $\lambda_1(\alpha(0)) > r/d$, and $\alpha'(1)$ is sufficiently small.

We believe that it is beneficial to illustrate our results further via a concrete example. We will construct the example by choosing Ω to be the one dimensional habitat $(-1, 1)$ and taking $\alpha(u)$ to be linear for $u \approx 0$ and $u \approx 1$ but with different slopes for $u \approx 0$ and $u \approx 1$. For our results to apply $\alpha(u)$ must be smooth, so instead of taking $\alpha(u)$ to be piecewise linear and using it directly in our example, we construct a piecewise linear function $\tilde{\alpha}(u)$ with the correct behavior when $u \approx 0$ and $u \approx 1$ and then replace $\tilde{\alpha}(u)$ with a function $\alpha(u)$ such that $\alpha(u) = \tilde{\alpha}(u)$ when $u \approx 0$ or $u \approx 1$ but with $\alpha(u)$ smooth for $u \in [0, 1]$. An illustration of how $\alpha(u)$ would be related to $\tilde{\alpha}(u)$ is given in Fig. 4. To construct our example we will take Ω to be the one dimensional habitat $(-1, 1)$. Then for $\alpha^* \in [0, 1]$, if

$$b = \sqrt{\lambda_1(\alpha^*)} \tag{27}$$

then $b \in [0, \pi/2]$. It follows from the method of upper and lower solutions, (7), (16), and (22) that for general Ω if $r/d > \lambda_1(\alpha^*)$, then

$$u_{\alpha^*} > \left(1 - \frac{d\lambda_1(\alpha^*)}{r}\right)\psi_1, \tag{28}$$

where ψ_1 is the principal eigenfunction for (22) normalized so that $\max_{\bar{\Omega}} \psi_1 = 1$. In the case $\Omega = (-1, 1)$,

$$\psi_1(x) = \cos bx. \tag{29}$$

It follows from (27–29) that when $\Omega = (-1, 1)$ and $r/d > \lambda_1(\alpha^*)$, then

$$\min_{\bar{\Omega}} u_{\alpha^*} > \left(1 - \frac{db^2}{r}\right) \cos b. \tag{30}$$

Furthermore, we have from (22) that in this case

$$\alpha^* \psi_1'(1) + (1 - \alpha^*)\psi_1(1) = 0,$$

so that

$$\alpha^* = \frac{\cos b}{b \sin b + \cos b} \tag{31}$$

for $b \in [0, \pi/2]$. (Note that α^* decreases from 1 to 0 as b increases from 0 to $\pi/2$.) Combining (30) and (31), we have that $\alpha(\min_{\bar{\Omega}} u_{\alpha^*}) > \alpha^*$ provided that

$$\alpha\left(\left(1 - \frac{db^2}{r}\right) \cos b\right) > \frac{\cos b}{b \sin b + \cos b}. \tag{32}$$

Now suppose for the sake of illustration that we choose $b_1 = \frac{\pi}{3}$ and $b_2 = \frac{\pi}{6}$. Here $b_1 = \sqrt{\lambda_1(\alpha_1)}$ and $b_2 = \sqrt{\lambda_1(\alpha_2)}$, where by (31) $\alpha_1 = \frac{\sqrt{3}}{\pi+\sqrt{3}}$ ($\approx .3554$) and $\alpha_2 = \frac{6\sqrt{3}}{\pi+6\sqrt{3}}$ ($\approx .7679$). Our analysis shows that (1) exhibits an Allee effect for a particular choice of $\alpha(u)$ and values of $\frac{r}{d}$ in the interval $[\frac{r_0}{d_0}, \frac{\pi^2}{9}]$ where $\frac{r_0}{d_0} \in (\frac{\pi^2}{36}, \frac{\pi^2}{9})$ provided

$$\alpha(0) < \frac{\sqrt{3}}{\pi + \sqrt{3}} = \alpha_1 \tag{33}$$

and

$$\alpha\left(\left(1 - \frac{d_0\pi^2}{36r_0}\right) \frac{\sqrt{3}}{2}\right) > \frac{6\sqrt{3}}{\pi + 6\sqrt{3}}. \tag{34}$$

(There can be such a value of $\frac{r_0}{d_0}$ if and only if (34) holds when $\frac{r_0}{d_0} = \frac{\pi^2}{9}$; i.e., $\alpha(\frac{3\sqrt{3}}{8}) > \frac{6\sqrt{3}}{\pi+6\sqrt{3}}$.) Since $\frac{3\sqrt{3}}{8} \approx .6495$, a way in which to choose a smooth, nondecreasing $\alpha(u)$ so that (1) exhibits an Allee effect for all $r > 0$, $d > 0$ with $\frac{r}{d} \in [\frac{r_0}{d_0}, \frac{\pi^2}{9}]$ would be to take the piecewise linear function

$$\tilde{\alpha}(u) = \begin{cases} (4/3)u, & u \in [0, 3/5], \\ (1/2)u + 1/2, & u \in (3/5, 1], \end{cases}$$

which will satisfy the conditions needed for an Allee effect when $u \approx 0$ and $u \approx 1$, and modify it by smoothing out the corner at $u = 3/5$ without changing it for $u \approx 0$ and $u \approx 1$ to obtain $\alpha(u)$ as in Fig. 4.

4. Discussion

The most common model for density-dependent population dynamics is the logistic equation, which embodies the assumption that the net growth rate of the population decreases with population density. For some populations that assumption is not valid, and the net population growth rate increases with population density. That phenomenon was noted by Allee (1931,1938) and is sometimes called an Allee effect. There has been considerable discussion of the nature and causes of Allee effects in the biological literature. In the case of a sufficiently strong Allee effect it may happen that small populations can be expected to decline while larger populations can be expected to persist. That phenomenon is sometimes called bistability in the context of mathematical models because it corresponds to a situation where a model has both zero population density and some positive population density as stable equilibria. There are various social mechanisms that have been proposed for Allee effects. Recently Kuussaari et al. (1998) have employed an empirical study of the Glanville fritillary butterfly to identify mechanisms which might produce Allee effects. One of the possible mechanisms they uncovered was a lowering of the rate of emigration from habitat patches as the density of butterflies increases near patch edges. The observations of Kuussaari et al. (1998) suggest that Allee effects may arise from edge-mediated alteration of species' movement patterns. In a previous paper (Cantrell and Cosner, 2002) we showed that density-dependent aggregative movement within a patch can sometimes induce an Allee effect in mathematical models where the term describing population dynamics without dispersal is logistic. In the present paper we showed that a similar phenomenon can arise from density-dependent behavior at patch boundaries. The common feature of the two mechanisms is that in both cases the density-dependence in dispersal behavior could be interpreted as a tendency to aggregate with conspecifics. In both papers we used generalizations of reaction–diffusion equations to construct the models.

Roughly speaking, a population is said to exhibit an Allee effect if, at low densities, its per capita rate of growth declines as density declines, or equivalently its per capita rate of growth increases as density increases. Allee (1931, 1938) discussed this effect in the context of social behavior of animals. Generally Allee effects have been accounted for in the ecological literature as resulting from social and behavioral traits such as less efficient feeding at low densities (Way and Banks, 1967; Way and Cammell, 1970) or reduced effectiveness of antipredator defenses (Kruuk, 1964; Kenward, 1978), or from difficulty in finding mates (Stephens and Sutherland, 1999; Boukal and Berec, 2002). Although the general idea of Allee effects is widely known, the question "What is the Allee effect?" remains sufficiently interesting that Stephens et al. (1999) have used it as the title of a paper. The definition they give is "A positive relationship between any component of individual fitness and either numbers or density of conspecifics" (Stephens et al., 1999, p. 186). Stephens et al. (1999) also distinguish between "component Allee effects" which act on some component of fitness and "demographic Allee effects" which act on total fitness and hence influence population dynamics. Finally, Stephens et al. (1999) point out that whether or not a particular type of behavior can induce an Allee effect may depend on the spatial scale on which the focal population is being considered. We have been concerned with what Stephens et al. (1999) called demographic Allee effects at the scale of a patch. (Kuussaari et al., 1998 used the term "Allee effect" to describe the phenomenon they observed at the scale of a patch.) It is possible to consider Allee effects at the metapopulation level; see, for example, Amarasekare (1998). It is not clear how "Allee effects" at the patch level might influence metapopulation dynamics. That topic is certainly worthy of study but it is beyond the scope of this article.

Reaction-diffusion equations provide a modeling framework for studying population dynamics that is well-suited to the examination of edge-mediated effects (Fagan et al., 1999). In particular, a reaction–diffusion model for the density of some species in a bounded patch of habitat requires both an equation that tracks the propagation and dispersal of the species within the patch and an equation describing the behavior of the species at the interface between the patch and the environs surrounding it, i.e., a boundary condition. Frequently, this second equation prescribes a balance between a tendency of the species to be lost through the boundary of the patch to its surroundings and a tendency of the species to remain within the patch, and takes the form

$$\alpha\frac{\partial u}{\partial n} + (1-\alpha)u = 0 \tag{35}$$

with $\alpha \in [0, 1]$. As α increases, the tendency of the species to remain within the patch becomes more and more dominant.

In this article we analyzed a reaction–diffusion model for the density of a species in a focal patch of habitat with a density-dependent boundary condition of the form (35) where the coefficient α increases with the density u. We made that assumption in order to account for an edge-mediated reduction in the tendency of the species to be lost through the patch boundary. Within the patch we assumed that population growth was governed by a logistic equation with diffusion, so that no Allee effect was built into the local population dynamics. Our analysis of the model showed that it can exhibit an Allee effect for appropriate ranges of model parameter values provided that α is sufficiently small when the population density is low and sufficiently large at higher density levels, as shown in Fig. 1. Since an increase in α would correspond to a decrease in the tendency of a species to be lost through the patch boundary, our analytical results complement the empirical results of (Kuussaari et al., 1998). Our analysis was based on comparison principles for elliptic and parabolic partial differential equations and did not require a terribly precise determination of the asymptotics of the model. Further insight into when the model admits Allee effects can be gained through a more detailed mathematical analysis of its longterm behavior. Such a mathematical analysis is the subject of a separate article (Cantrell and Cosner, 2006). In previous work (Cantrell and Cosner, 2002), we showed that a similar phenomenon could occur in models of the form

$$\begin{aligned}&\frac{\partial u}{\partial t} = \nabla\cdot d(u)\nabla u + ru(1-u) \quad \text{in } \Omega\times(0,\infty),\\&u = 0 \quad \text{on } \partial\Omega\times(0,\infty),\end{aligned} \tag{36}$$

provided $d'(0)$ is negative and $|d'(0)|$ is sufficiently large. In (36) there is density dependence in the way organisms move within the patch but not in their behavior at the patch boundary. The assumption that $d(u)$ is decreasing at low densities in (36) reflects the idea that organisms reduce their movement rate in the presence of conspecifics, which induces a form of aggregation (Turchin, 1989). What the models (1) and (36) have in common is that in both cases inverse density dependence in some sort of movement rate can induce bistability or Allee type effects at the patch level even if population dynamics within the patch are logistic. This suggests that there may be other related mechanisms that can do the same thing, or perhaps that the mechanisms leading to bistability or Allee type effects in (1) and (36) are special cases of some more general principle.

Reaction–diffusion equations with bistability built into the reaction terms have been studied in a variety of contexts, including ecology (see Lewis and Kareiva, 1993; Cantrell et al., 1996.) Typically such models use reaction terms of the form

$$f(u) = ru(u-a)(1-u/K)$$

shown in (3). When diffusion is combined with such reaction terms the resulting model may or may not remain bistable. If the underlying spatial domain for the model is nonconvex the model may support multiple stable spatially varying equilibria (Matano, 1979). (This can occur only if the underlying spatial domain has dimension greater than one.) Thus, saying that such a model is bistable or has an Allee effect may not necessarily give a complete and accurate description of its dynamics. Such models do often have the feature that solutions whose initial density $u(x,0)$ is uniformly small on Ω will tend toward zero as $t \to \infty$ while if $u(x,0)$ is uniformly large then solutions will tend toward some positive equilibrium; see, for example, Cantrell et al. (1996). In some cases, it is possible to show that some initial densities that are not uniformly large will still tend toward a positive equilibrium by using Lyapunov functions or constructing lower solutions. Such results are obtained in Aronson and Weinberger (1975, 1978) and Cantrell et al. (1996). However, those methods yield conditions on initial data that are more complicated or subtle to verify and interpret than the simple hypothesis that the initial data are uniformly large. It is conceivable that models such as (1) could support these or other phenomena that are known to occur in models with bistable reaction terms, but we did not address that question in this paper.

Appendix A

There are a number of ways that Robin boundary conditions have been presented in the literature on heat transfer and diffusion. In the case of the heat equation, where $u(x,t)$ represents the temperature inside an object, many standard texts on partial differential equations derive Robin boundary conditions by using Newton's law of cooling to conclude that the heat flux across the boundary of an object is proportional to the difference between the temperature of the object and the ambient temperature u_0. The heat flux into the object across the boundary is proportional to the normal derivative $\nabla u \cdot n$, so one obtains $a\nabla u \cdot n = b(u_0 - u)$ where a and b are positive constants. For diffusion equations arising as population models, a derivation in the equilibrium case in one space dimension is given by Ludwig et al. (1979). The idea there is to assume that outside a habitat patch a population experiences a linear death rate, disperses via diffusion, but has a population density that decays to zero at infinity. That leads to a model

$$\frac{\partial w}{\partial t} = D_0 \frac{\partial^2 w}{\partial x^2} - s_0 w$$

for the population outside the patch. The equilibrium solution which is bounded as $x \to \infty$ is $ce^{-\sqrt{s_0/D_0}x}$; the one which is bounded as $x \to -\infty$ is $ce^{\sqrt{s_0/D_0}x}$, where c is a constant. If the population inside the patch is described by

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + f(u)$$

then matching fluxes and densities across the patch boundary leads to a Robin condition. Specifically, suppose the patch is the interval $(0, L)$. Matching densities at $x = 0$ gives $u(0,t) = w(0,t)$; matching fluxes gives $D\partial u/\partial x = D_0 \partial w/\partial x$ at $x = 0$. For $x < 0$, $w = ce^{\sqrt{s_0/D_0}x}$ so matching across $x = 0$ yields

$$-D\partial u/\partial x = -D_0(\sqrt{s_0/D_0})c, \quad u = c, \tag{A.1}$$

from which one obtains $-D\partial u/\partial x + \sqrt{s_0 D_0}u = 0$ at $x = 0$. (See Ludwig et al., 1979.)

The derivation given by Ludwig et al. assumes that individuals do not respond to the patch boundary but diffuse freely across it. Models for movement across interface with a preferred direction have been proposed in more recent work by Cantrell and Cosner (1999) and Ovaskainen and Cornell (2003). Those models do not address the issue of boundary conditions per se (as opposed to conditions at an interior interface), but they could be used to modify the process of matching densities and fluxes across the patch boundary which was introduced by Ludwig et al. (1979). The conditions used by Cantrell and Cosner (1999) involve terms other than just the density and flux except in special situations, so in general those would lead to nonclassical forms of boundary conditions. Those used by Ovaskainen and Cornell (2003) introduce a constant into the matching condition for the density at the patch boundary which describes the preference of individuals at the patch boundary to move into or out of the patch. Suppose for simplicity that the diffusion process describing dispersal arises as the continuum limit of a random walk where the step size and the rate at which steps are taken are the same inside and outside of the patch. Suppose also that the probability of an individual moving left or right are both $1/2$ for $x \neq 0, L$ but that at $x = 0, L$ the probability of moving to the right is different than the probability of moving to the left. Specifically, suppose that at $x = 0$ the probability that an individual moves to the left (leaving the patch) is $(1 - z)/2$ for some $z \in [-1, 1]$ while the probability of moving to the right is $(1 + z)/2$. Then in the matching procedure used by Ludwig et al. (1979), the equation $u = c$ when $x = 0$ would be replaced by

$$(1 - z)u = (1 + z)c \tag{A.2}$$

(see Ovaskainen and Cornell, 2003, Eq. (2.2)). The other equation in (A.1) would remain as it stands. The boundary condition obtained by using (A.2) and the first equation in (A.1) would be

$$-D(1 + z)(\partial u/\partial x) + \sqrt{s_0 D_0}(1 - z)u = 0. \tag{A.3}$$

If $z = -1$, so all individuals that reach $x = 0$ leave the patch, (A.3) becomes the Dirichlet condition $u = 0$. If $z = 1$, so that no individuals leave the patch, then (A.3) becomes the Neumann or no-flux condition $\partial u/\partial x = 0$. For intermediate values of z, (A.3) is a Robin condition. To capture the situation where the probability of leaving the patch depends on the density at the patch boundary, we would let z depend on u. If $z = z(u)$ we can rewrite (A.3) as

$$-\alpha(u)\frac{\partial u}{\partial x} + \bigl(1 - \alpha(u)\bigr)u = 0 \quad \text{at } x = 0 \tag{A.4}$$

by taking $\alpha(u) = D(1 + z(u))/[D(1 + z(u)) + \sqrt{s_0 D_0}(1 - z(u))]$. The condition (A.4) is the special case of the boundary condition (2) at the left endpoint of a one-dimensional patch Ω. If all individuals that reach the boundary $x = 0$ cross it when the density at the boundary is less than or equal to u_1, then $z(u) = -1$ and hence $\alpha(u) = 0$ for $0 \le u \le u_1$. If no individuals cross the boundary when the density is greater than or equal to u_2 then $z(u) = 1$ so $\alpha(u) = 1$ when $u_2 \le u \le 1$. If the fraction of individuals that leave the patch decreases with respect to the density at the boundary then we have $0 \le \alpha(0) < \alpha(1) \le 1$, which is the type of situation addressed in Section 3.

The preceding derivation explains how a density-dependent Robin condition can be obtained by combining the approach of Ludwig et al. (1979) based on matching solutions inside a patch with an equilibrium solution outside with the model of Ovaskainen and Cornell (2003) for the effects of biased movement at an interface, and then assuming that the bias depends on population density at the patch boundary. The model of Ovaskainen and Cornell (2003) is derived from a consideration of random walks but the matching approach of Ludwig et al. (1979) is not, and it requires that we make some fairly specific assumptions about population dynamics and dispersal in the matrix habitat surrounding the patch. It is also possible to derive Robin conditions directly from a random walk model under appropriate scaling, without any reference to population dynamics outside the patch. We will present such a derivation, partly to avoid assumptions about population dynamics outside the patch, and partly for the additional insight it may provide into the mechanisms that produce the boundary conditions. The derivation is similar both in concept and in terms of the type of scalings that are needed in the derivation of diffusion equations with advection given by Okubo (1980, Section 5.3), although the details of our presentation differ somewhat from Okubo's. A similar but less detailed derivation of boundary conditions in reaction–diffusion models is given by Van Kirk and Lewis (1999).

Let $p(x,t)$ denote the probability that an individual is at location $x \in (0, L)$ at time t. Discretize $(0, L) \times (0, \infty)$ with time step Δt and space step Δx. Thus, $p(x,t) = p(j\Delta x, k\Delta t)$. For points in the interior of the spatial domain, i.e. for $j \ge 1$, assume that at each time step the individual moves one (space) step to the left with probability $1/2$ or moves one step to the right with probability $1/2$. Suppose also that if the individual is at $x = 0$ it moves one step to the right with probability $1/2$, leaves the patch with probability $\delta/2$ and stays at $x = 0$ with probability $(1 - \delta)/2$. It will turn out that δ must be scaled appropriately to obtain Robin boundary conditions in the continuum limit. For $j \ge 1$, $p(x,t) = p(j\Delta x,\ k\Delta t)$ will satisfy $p(x, t + \Delta t) = (1/2)p(x - \Delta x, t) + (1/2)p(x + \Delta x, t)$ so that

$$p(x, t + \Delta t) - p(x, t) = (1/2)\bigl[p(x - \Delta x, t) - 2p(x, t) + p(x + \Delta x, t)\bigr]. \tag{A.5}$$

If we divide both sides of (A.5) by Δt and introduce the scale factor $D = (\Delta x)^2/2\Delta t$, then taking the limit of (A.5) as $\Delta x \to 0$, $\Delta t \to 0$ so that the scaling $D = (\Delta x)^2/2\Delta t$ is preserved yields the diffusion equation

$$\frac{\partial p}{\partial t} = D\frac{\partial^2 p}{\partial x^2}.$$

At $x = 0$ there is also the parameter δ which must be considered. The cases where $\delta = 0$ or $\delta = 1$ will yield no-flux and Dirichlet boundary conditions respectively. The case $0 < \delta < 1$ leads to Robin conditions if δ is scaled correctly. Note that δ is independent of D. We have

$$p(0, t + \Delta t) = (1/2)p(\Delta x, t) + \big[(1-\delta)/2\big]p(0, t). \tag{A.6}$$

Suppose $\delta = 0$, so that no individuals leave the patch. We may rewrite (A.6) as

$$\left(\frac{p(0, t + \Delta t) - p(0, t)}{\Delta t}\right) = \frac{D}{(\Delta x)^2}\big(p(\Delta x, t) - p(0, t)\big) \tag{A.7}$$

(since $D\Delta t/(\Delta x)^2 = 1/2$) so that

$$(\Delta x)\left(\frac{p(0, t + \Delta t) - p(0, t)}{\Delta t}\right) = D\left(\frac{p(\Delta x, t) - p(0, t)}{\Delta x}\right).$$

Letting $\Delta x,\ \Delta t \to 0$ we obtain

$$0 = (0)\left(\frac{\partial p}{\partial t}(0, t)\right) = D\frac{\partial p}{\partial x}(0, t)$$

so that $D\partial p/\partial x = 0$ at $x = 0$, which is in the no-flux condition. Suppose $\delta = 1$, so that no individuals remain at $x = 0$; i.e. any individual that does not move to $x = \Delta x$ leaves the patch. We then have

$$\begin{aligned} p(0, t + \Delta t) - p(0, t) &= (1/2)p(\Delta x, t) - p(0, t) \\ &= (1/2)\big[p(\Delta x, t) - p(0, t)\big] - (1/2)p(0, t) \end{aligned}$$

so that we obtain

$$p(0, t + \Delta t) - p(0, t) = \frac{D\Delta t}{(\Delta x)^2}\big[\big(p(\Delta x, t) - p(0, t)\big) - p(0, t)\big]$$

so that

$$p(0, t + \Delta t) - p(0, t) = \frac{D\Delta t}{(\Delta x)^2}\big[\big(p(\Delta x, t) - p(0, t)\big) - p(0, t)\big] \tag{A.8}$$

which can be written as

$$(\Delta x)^2\left(\frac{p(0, t + \Delta t) - p(0, t)}{\Delta t}\right) = D\big[p(\Delta x, t) - p(0, t)\big] - Dp(0, t).$$

Letting Δx, $\Delta t \to 0$ yields

$$0 = (0)\frac{\partial p}{\partial t}(0,t) = D(0) - Dp(0,t)$$

so that $p(0,t) = 0$, a Dirichlet condition. Finally, suppose that $0 < \delta < 1$. In that case (A.6) can be written as

$$p(0,t+\Delta t) - p(0,t) = \frac{D\Delta t}{(\Delta x)^2}\big[p(\Delta x,t) - p(0,t)\big] - \frac{D\delta\Delta t}{(\Delta x)^2}p(0,t), \tag{A.9}$$

which yields

$$\Delta x\left(\frac{p(0,t+\Delta t) - p(0,t)}{\Delta t}\right) = D\left(\frac{p(\Delta x,t) - p(0,t)}{\Delta x}\right) - \frac{D\delta}{\Delta x}p(0,t). \tag{A.10}$$

If we scale δ as $\delta = E\Delta x$, so that $D\delta/\Delta x = DE$, then letting Δx, $\Delta t \to 0$ in (A.10) yields

$$0 = (0)\frac{\partial p}{\partial t}(0,t) = De\frac{\partial p}{\partial x}(0,t) - DEp(0,t),$$

so that

$$-D(\partial p/\partial x) + DEp = 0 \quad \text{at } x = 0, \tag{A.11}$$

which is a Robin condition. (Note that $DE = \delta\Delta x/2\Delta t$ is in units of velocity. The scaling used here is analogous to the scaling for the drift or advection terms in the derivation of advection-diffusion equations by Okubo, 1980, Section 5.3.) An equation for the density of a dispersing population can be obtained by multiplying $p(x,t)$ by the total population to obtain a population density. The boundary conditions will carry over from those for p. To obtain a formulation such as the boundary condition in (1) we would allow E, the rescaled term corresponding to the probability an individual at $x = 0$ leaves the patch in a given time step, to depend on the density u in such a way that $E(u)$ is small when u is large but large when u is small. If the boundary condition (A.11) is divided by $D(1 + E(u))$ we obtain the condition in (1) with $\alpha(u) = 1/(1 + E(u))$. (If $E(u)$ is decreasing, which is consistent with the scenario we want to model, then $\alpha(u)$ is increasing.)

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