

# Diffusion Models for Population Dynamics Incorporating Individual Behavior at Boundaries: Applications to Refuge Design

R. S. Cantrell and C. Cosner<sup>1, 2</sup>

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

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**We construct models for dispersal of a population which incorporate the response of individuals to interfaces between habitat types. The models are based on random walks where there may be a bias in the direction an individual moves when it encounters an interface. This sort of dispersal process is called skew Brownian motion. Our models take the form of diffusion equations with matching conditions across the interface between regions for population densities and fluxes. We combine the dispersal models with linear population growth models which assume that the population growth rate differs between regions of different habitat types. We use those models to study issues of refuge design. We specifically consider how the effectiveness of buffer zones depends on their size, quality, and the population's response to the interface between the buffer zone and the refuge.** © 1999 Academic Press

## 1. INTRODUCTION

Populations inhabit landscapes, and landscapes consist of mosaics of patches of different habitat types. Often patches of habitat favorable to a given species are surrounded by regions of less favorable habitat. The fragmentation of landscapes is increased by the effects of human development. In some cases the fragmentation is premeditated and the fragments are designated as nature reserves, buffer zones, agricultural areas, suburbs, and so forth. To understand how populations interact with fragmented landscapes it is desirable to have spatially explicit models that can account for environmental heterogeneity and the behavior of individuals at patch boundaries; see, for example, the discussion in the survey articles by Dunning *et al.* (1995) and Wiens *et al.* (1993).

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One modeling approach which has proven quite useful in studying spatial effects in homogeneous environments is based on partial differential equations, especially reaction–diffusion equations; see Okubo (1980), Kareiva (1990) and Holmes *et al.* (1994). The goals of the present article are to show how the behavior of individuals at patch boundaries can be incorporated into reaction–diffusion models and to use the resulting models to study some questions about the design for nature reserves.

There have been a number of empirical studies which indicate that the dispersal behavior of individuals is influenced by boundaries between different types of habitat and that the details of behavior at a boundary often depend on what is on the other side. Some of those studies are Goszczynski (1979a, b), Wegner and Merriam (1979), Yahner (1983), Bach (1984), and Kareiva (1985). We incorporate behavior at a patch boundary into diffusion models by using what is known as skew Brownian motion (Walsh, 1978; Harrison and Shepp, 1981). Skew Brownian motion assumes that individuals move according

to ordinary diffusion (so that movement in any direction is equally likely) unless they encounter a boundary, but at a boundary the probability that an individual will move into the region on one side of the boundary may be different than the probability it will move into the region on the other side. If the probability of crossing the boundary in either direction is  $\frac{1}{2}$ , then the boundary is invisible to the population and the model for dispersal reduces to ordinary diffusion. If the probability of crossing the boundary in one direction is zero, the boundary acts as a perfectly reflecting barrier. If the probability of moving from the boundary into the region on one side is different from the probability of moving into the region on the other side then individuals display a preference for dispersing into one region rather than the other. We consider only the simplest case of a one-dimensional environment, but the essential ideas would make sense in more general settings.

Since our goal is to study the effects of spatial heterogeneity and behavior at interfaces between regions of different habitat types on the dynamics of populations we must make some hypotheses about the rate at which the population grows or declines. We assume that the population grows or declines at a fixed rate on each type of habitat but that the rates differ between different types of habitat. In other words, we use density-independent models for population growth, so we are led to projections of either exponential growth or exponential decay for the population. We could consider density-dependent models, e.g., logistic models, but the predictions of such models about persistence or extinction are often determined by the predictions of associated linear models; see, for example, Cantrell and Cosner (1989, 1991a, b, 1993). In particular the ability of a population to increase its numbers when introduced at low densities, which can often be determined from models without density dependence, typically implies some form of persistence or coexistence in the corresponding density-dependent model. This principle is sometimes stated as "invasibility implies persistence." It is asserted informally in Pacala and Roughgarden (1982) and mathematically rigorous formulations of the principle are given in Cantrell and Cosner (1989, 1991a, b, 1993) and Cantrell *et al.* (1993, 1996). Thus, although simple models without density dependence are limited in their range of applicability, they can provide criteria for the behavior of more complex density-dependent models. Furthermore, models without density dependence can be reasonably accurate descriptions of populations at low densities, and in conservation and refuge design such populations are a common focus of interest. We study the effects of spatial heterogeneity and behavior at patch boundaries on population dynamics

by observing how the average population growth rate in an environment varies when parameters describing patch size and dispersal behavior are varied. The average population growth rate is computed as the principal eigenvalue of a type of differential operator. It is analogous to the principal eigenvalue of a Leslie matrix model for an age-structured population. The analysis is similar to that used in Cantrell and Cosner (1991a), where some of the effects of spatial heterogeneity are considered but the issue of behavior at patch boundaries is not addressed.

The spatial structure upon which we focus our attention consists of a favorable region surrounded by a less favorable region which is in turn surrounded by an immediately lethal boundary. This arrangement is a caricature of a nature reserve surrounded by a buffer zone which is in turn surrounded by developed or cultivated regions. We assume that the arrangement is one dimensional and symmetric. Our analysis then examines how the overall population growth rate depends on the size of the refuge and buffer zone, the quality of habitat in the two regions, and the behavior of the population at the interface or boundary between them. We also consider one case where some of these factors are related, namely where the tendency of the population to remain in the refuge increases as the habitat quality in the buffer zone decreases. The question of how buffer zones affect the population which the refuge is designed to preserve is suggested by the work of Janzen (1983, 1986). One of Janzen's suggestions was that buffer zones may sometimes be most useful when the population in the refuge has as little interaction as possible with the buffer zone, even if the trade-off is that the habitat quality in the buffer zone must be decreased in order to reduce the level of interaction. Our models support Janzen's suggestion in some cases. We drew similar conclusions in Cantrell and Cosner (1993) but in the context of competition between species without any habitat preference for dispersal. The mechanism producing the effect there was a shift in competitive advantage. The mechanism producing the effect in the scenarios considered here is habitat preference.

There are many additional topics which could be treated using diffusion models incorporating habitat preference into behavior at patch boundaries. Many of those have already been addressed in the framework of diffusion models with spatial heterogeneity but no habitat preference. These include the effects of the shape and arrangement of favorable and unfavorable regions (Cantrell and Cosner, 1989, 1991a, b); density dependence in single-species models (Ludwig, *et al.*, 1979; Cantrell and Cosner, 1989, 1991b; Freedman and Krisztin, 1992; Freedman and Wu, 1992); competition (Pacala and

Roughgarden, 1982; Cantrell and Cosner, 1993); predator-prey interactions (Benson *et al.*, 1993); and propagation of waves of invasion (Shigesada *et al.*, 1986). There are also a number of different modeling approaches that could be used. Those include computer simulations as in Stamps *et al.* (1987a, b) and Abramsky and Van Dyne (1980) and analytic models based on patch dynamics, cellular automata, or various other ideas. For discussions of modeling approaches and other topics related to environmental heterogeneity, habitat fragmentation, and dispersal with habitat preferences and realistic behavior at patch boundaries see the reviews by Dunning *et al.* (1995) and Wiens *et al.* (1993).

This paper is organized as follows: the construction of the models is discussed in Section 2; the methods of analysis and some simple conclusions about parameter dependence are discussed in Section 3; the effects of changing the size and quality of the buffer zone and the size of the refuge are discussed in Section 4; and the effects of behavioral sensitivity to differences in habitat quality across patch boundaries are discussed in Section 5. Section 6 describes our conclusions in relatively non-mathematical terms. Some of the detailed calculations and more complicated formulas are shown in the Appendix.

## 2. CONSTRUCTION OF DIFFUSION MODELS INCORPORATING EDGE PERMEABILITY

### Formulation of the General Model

Diffusion models represent one of the standard approaches to modeling population dynamics with dispersal in spatially continuous environments. Such models were introduced to population biology by Skellam (1951) and Kierstead and Slobodkin (1953). They are discussed in detail in Okubo (1980), and reviews of the recent literature on diffusion models are given in Kareiva (1990) and Holmes *et al.* (1994). Our goal is to construct a diffusion model describing the density of population inhabiting an environment consisting of a region or patch of favorable habitat which is separated from a region of less favorable habitat by a more or less permeable edge. To justify the model formulation, however, we will need to briefly review the derivation of the standard diffusion model for dispersal in a spatially uniform environment. For more details see Okubo (1980) or Taira (1988).

Simple diffusion or Brownian motion is based on the assumption that individuals move via unbiased random

walks with a specified average distance traveled per unit time. Skew Brownian motion is a diffusion process which is the same as ordinary one-dimensional Brownian motion except at a distinguished point, where the probability of an individual moving to the left is different than the probability of moving to the right. We shall denote the probability of moving to the right at the distinguished point by  $\alpha$ , so that the probability of moving to the left is  $1 - \alpha$ .

A crucial property of Brownian motion (i.e., standard diffusion) which is shared by much more general diffusion processes is the **semi-group** property; see Taira (1988). To explain this property, let  $(T_t u_0)(x)$  represent the expected population density at time  $t$  given an initial population density  $u_0(x)$  of individuals dispersing under a diffusion process. The semi-group property can be stated as the fact that for  $s, t \geq 0$  we have

$$(T_{t+s} u_0)(x) = (T_s(T_t u_0))(x). \quad (2.1)$$

In other words, the population density which is expected to develop from the initial density  $u_0(x)$  after time  $t + s$  would also be attained if the process ran for time  $t$ , was re-initialized using the expected density at time  $t$ , and then ran for time  $s$ . Two key mathematical features of the semi-group  $\{T_t: t \geq 0\}$  corresponding to Brownian motion or a more general diffusion process are that  $T_0 u_0(x) = u_0(x)$  and that the semi-group has an **infinitesimal generator** defined by

$$(A u_0)(x) = \lim_{t \downarrow 0} \frac{(T_t u_0)(x) - u_0(x)}{t}. \quad (2.2)$$

In the case of standard diffusion, we obtain  $A = D\partial^2/\partial x^2$ . The connection between  $A$  and  $T_t$  is that if  $u(x, t) = (T_t u_0)(x)$  then

$$\frac{\partial u}{\partial t} = A u \quad \text{for } t > 0 \quad (2.3)$$

$$u(x, 0) = u_0(x).$$

Thus, for the standard process of dispersal by simple diffusion we obtain the diffusion equation

$$\frac{\partial u}{\partial t} = \frac{D\partial^2 u}{\partial x^2} \quad \text{for } -\infty < x < \infty, \quad t > 0, \quad (2.4)$$

with the initial density specified by  $u(x, 0) = u_0(x)$ . (For a detailed discussion of the ideas described above see Taira (1988). A more comprehensive but less accessible treatment is given in Ito and McKean (1965).) To justify

the connection between Eq. (2.3) and the process defined by  $T_t$  which it should describe, the class of densities  $w(x)$  to which  $A$  is applied must be restricted. That some sort of restriction is required is clear from the example (2.4) of standard diffusion, since  $D\partial^2 w/\partial x^2$  does not make sense for arbitrary  $w(x)$ . The class of densities to which  $A$  can be applied is called the **domain** of  $A$ . Beyond the obvious requirement that  $Au$  must make sense there is a more subtle restriction which will be crucial in our construction of models for dispersal in habitat patches with more or less permeable edges. If the dispersal process does not allow individuals to become stuck at any fixed location and does not allow any impenetrable barriers to dispersal, then the domain of the infinitesimal generator  $A$  of the semi-group  $\{T_t; t \geq 0\}$  must be restricted to functions  $w(x)$  for which  $(Aw)(x)$  is continuous. (A rigorous but almost impenetrable mathematical treatment of this point is given in Ito and McKean (1965, pp. 83–100).) In the case of standard diffusion with no population growth or decline this restriction means simply that we must consider only population densities with continuous second derivatives in the space variable. In the case we seek to model, however, this restriction will lead to a crucial matching condition across the interface at the patch boundary.

There are a number of possible constructions which lead to equivalent forms of skew Brownian motion; see Ito and McKean (1965, Problem 1, Sect. 4.2), Walsh (1978), and Harrison and Shepp (1981). We shall adapt the treatment given in Walsh (1978), which yields a version of (2.3) analogous to the form (2.4) corresponding to ordinary diffusion. For the parameter values used by Walsh (1978) we find that the semi-group generator  $A$  is defined by

$$(Au)(x) = \frac{1}{2} \frac{\partial^2 u}{\partial x^2} \quad \text{for } x \neq 0 \quad (2.5)$$

with the domain of  $A$  specified so that  $(Aw)(x)$  is continuous at  $x = 0$  for  $w \in \text{dom } A$ , i.e.,

$$\begin{aligned} \frac{\partial^2 w}{\partial x^2} & \text{ is continuous for } x \neq 0; \\ \frac{\partial^2 w}{\partial x^2}(0+) & = \frac{\partial^2 w}{\partial x^2}(0-) \end{aligned} \quad (2.6)$$

together with the matching condition

$$\alpha \frac{\partial w}{\partial x}(0+) = (1 - \alpha) \frac{\partial w}{\partial x}(0-). \quad (2.7)$$

Recall that  $\alpha$  represents the probability of an individual moving to the right at  $x = 0$ ; in general  $\alpha \neq \frac{1}{2}$ .

Condition (2.7) describes the behavior of the process at the interface  $x = 0$ . Condition (2.6) is simply the requirement that the domain of the infinitesimal generator  $A$  should consist of functions  $w(x)$  for which  $(Aw)(x)$  is continuous. If we were satisfied to consider only situations with no growth or decline in total population and the same diffusion rate on either side of the interface we could simply use the matching conditions given in (2.6) and (2.7). However, we want to allow for population growth and differing diffusion rates, and we also want to restrict our spatial region to a finite interval.

For our present purposes we are satisfied to assume that on each side of the interface at  $x = 0$  we have dispersal via standard diffusion combined with linear growth. The infinitesimal generator for such a process is  $D\partial^2/\partial x^2 + r$ ; so we will want a generator  $A$  of the form

$$(Aw)(x) = \begin{cases} D_1 \frac{\partial^2 w}{\partial x^2} + sw, & x < 0 \\ D_2 \frac{\partial^2 w}{\partial x^2} + rw, & x > 0. \end{cases} \quad (2.8)$$

The condition that  $\partial^2 w/\partial x^2$  be continuous for  $x \neq 0$  is unchanged; the matching condition in Eq. (2.6) becomes

$$\left( D_2 \frac{\partial^2 w}{\partial x^2} + rw \right)(0+) = \left( D_1 \frac{\partial^2 w}{\partial x^2} + sw \right)(0-), \quad (2.9)$$

i.e.,  $\lim_{x \rightarrow 0+} [D_2 \partial^2 w/\partial x^2 + rw] = \lim_{x \rightarrow 0-} [D_1 \partial^2 w/\partial x^2 + sw]$ .

The appropriate modification of (2.7) is

$$\alpha D_2 \frac{\partial w}{\partial x}(0+) = (1 - \alpha) D_1 \frac{\partial w}{\partial x}(0-). \quad (2.10)$$

The reason for the modification of (2.7) into (2.10) can be understood by noting that if  $\alpha = \frac{1}{2}$  then the point  $x = 0$  behaves in exactly the same way as any other point, so that unbiased diffusion across  $x = 0$  should lead to continuity of flux. This is exactly the content of (2.10) when  $\alpha = \frac{1}{2}$ ; see Okubo (1980) or Ludwig *et al.* (1979). The possible discontinuity of flux across  $x = 0$  in (2.10) or even (2.7) seems paradoxical, but it can be resolved by the observation in Walsh (1978) that the so-called ‘‘local time’’ of the process with  $\alpha \neq \frac{1}{2}$  is discontinuous across the point  $x = 0$  even in the case with no population growth and the same diffusion rate for  $x > 0$  and  $x < 0$ . (‘‘Local time’’ is not a time scale in the usual sense; it describes the average time an individual remains in the vicinity of a

point.) In general (2.9) does not imply continuity of the density itself across  $x = 0$ ; however, for processes where the population density has a fixed spatial profile and is growing, declining, or at equilibrium in time the condition (2.9) is compatible with continuity of density across  $x = 0$ . Thus, in the case where there is no preferred direction across the interface and where the system is at equilibrium the matching conditions (2.9) and (2.10) are consistent with those imposed, for example, in Ludwig *et al.* (1979), namely that the density and flux of the population be continuous across the interface.

To complete the formulation of our model we restrict the overall spatial domain and impose an absorbing boundary condition (i.e., a condition which implies that any individual that reaches the boundary is permanently removed) at the edge of the overall environment. The situation we have in mind is that of a refuge surrounded by a buffer zone, with the buffer zone surrounded by regions of completely hostile habitat. We could treat situations where the boundary condition at the outside boundary of the overall spatial domain is taken to be reflecting rather than absorbing, or where some fraction of individuals reaching the boundary are reflected and the remainder are absorbed. Our general methods would still apply, but the detailed predictions of the model would probably change. This issue is discussed in the context of ordinary Brownian motion in a heterogeneous environment in Cantrell and Cosner (1991a). To describe that situation we assume that the overall habitat consists of an interval  $(-l, 0)$  of less favorable habitat with diffusion rate  $D_1$  and growth (or decay) rate  $s$ , an interval  $(0, 2L)$  of more favorable habitat with diffusion rate  $D_2$  and growth rate  $r$ , and another interval  $(2L, 2L + l)$  of less favorable habitat. The region outside  $(-l, 2L + l)$  is assumed to be completely hostile. Under these assumptions we can describe the expected population density  $u(x, t)$  at point  $x$  and time  $t$  in terms of the sort of infinitesimal generator  $A$  described in (2.8)–(2.10) as follows:

$$\begin{aligned} \frac{\partial u}{\partial t} &= D_1 \frac{\partial^2 u}{\partial x^2} + su \\ \text{for } -l < x < 0, \\ 2L < x < 2L + l, \quad t > 0 \end{aligned} \tag{2.11}$$

$$\begin{aligned} \frac{\partial u}{\partial t} &= D_2 \frac{\partial^2 u}{\partial x^2} + ru \\ \text{for } 0 < x < 2L, \quad t > 0 \end{aligned}$$

$$\begin{aligned} (1 - \alpha) D_1 \frac{\partial u}{\partial x} \Big|_{x=0-} &= \alpha D_2 \frac{\partial u}{\partial x} \Big|_{x=0+}, \\ \alpha D_2 \frac{\partial u}{\partial x} \Big|_{x=2L-} &= (1 - \alpha) D_1 \frac{\partial u}{\partial x} \Big|_{x=2L+} \end{aligned} \tag{2.12}$$

$$\begin{aligned} \left( D_1 \frac{\partial^2 u}{\partial x^2} + su \right) \Big|_{x=0-} &= \left( D_2 \frac{\partial^2 u}{\partial x^2} + ru \right) \Big|_{x=0+}, \\ \left( D_2 \frac{\partial^2 u}{\partial x^2} + ru \right) \Big|_{x=2L-} &= \left( D_1 \frac{\partial^2 u}{\partial x^2} + su \right) \Big|_{x=2L+} \end{aligned} \tag{2.13}$$

$$u(-l, t) = u(2L + l, t) = 0. \tag{2.14}$$

As always, there would be some specified initial density  $u(x, 0) = u_0(x)$  for  $-l < x < 2L + l$ . We have intentionally built a high degree of symmetry into the model (2.11)–(2.14) to simplify the analysis, but it would certainly be possible to examine less symmetric arrangements of favorable and unfavorable habitats as in Cantrell and Cosner (1991a).

### Reducing the General Model to an Average Growth Rate

The full time-dependent model (2.11)–(2.14) would be quite complicated to analyze completely. However, we can assess the effect of the various parameters in the model on the suitability of the overall environment by determining the average rate of population growth or decline predicted by the model. The full model can be written in condensed form as in (2.3), where  $A$  is the infinitesimal generator of the dispersal and growth process. If we can find a positive function  $\phi(x)$  in the domain of  $A$  such that

$$A\phi = \sigma\phi \tag{2.15}$$

for a constant  $\sigma$  then (2.3) will have solutions  $u = \phi(x) e^{\sigma t}$  which either grow or decline exponentially with rate  $\sigma$ . Equation (2.15) is a type of eigenvalue problem. Eigenvalue problems such as (2.15) have proven useful in many studies of spatial effects via diffusion models; see, for example, Cantrell and Cosner (1989, 1991a, b, 1993, 1994); Cosner (1990), Murray and Sperry (1983), and Pacala and Roughgarden (1982). A fortunate simplification of the matching condition (2.13) occurs for the eigenvalue problem (2.15). In that problem the equations in (2.11) give

$$D_1 \frac{d^2\phi}{dx^2} + s\phi = \sigma\phi \quad \text{for } -l < x < 0$$

$$\text{and } 2L < x < 2L + l \quad (2.16)$$

$$D_2 \frac{d^2\phi}{dx^2} + r\phi = \sigma\phi \quad \text{for } 0 < x < 2L.$$

Using (2.16) the matching condition (2.13) becomes equivalent to matching  $\sigma\phi(x)$  across the interfaces at  $x = 0$  and  $x = 2L$ , i.e.,

$$\phi(0-) = \phi(0+), \quad \phi(2L-) = \phi(2L+). \quad (2.17)$$

(In the case  $\sigma = 0$  notice that  $A\phi = 0$  so if  $v = e^t\phi$  then  $\partial v/\partial t = v = (A + I)v$ , where  $I$  is the identity operator. But then the function  $\phi$  turns out to be an eigenfunction for  $A + I$  since  $(A + I)\phi = \phi$ . Thus,  $\phi$  is also an eigenfunction for a semi-group generator with  $\sigma = 1 \neq 0$  so (2.17) must hold.) An additional simplification in the analysis can be made by noting that the problem is completely symmetric around  $x = L$ , so that the solution  $\phi(x)$  can be constructed by solving the problem on the interval  $-l < x < L$  with condition  $d\phi/dx = 0$  at  $x = L$  and then reflecting  $\phi(x)$  about  $x = L$  to obtain the solution for  $L < x < 2L + l$ . The resulting simplified problem can be stated as

$$D_1 \frac{d^2\phi}{dx^2} + s\phi = \sigma\phi \quad \text{for } -l < x < 0,$$

$$D_2 \frac{d^2\phi}{dx^2} + r\phi = \sigma\phi \quad \text{for } 0 < x < L \quad (2.18)$$

$$\phi(-l) = 0, \quad \frac{d\phi}{dx}(L) = 0 \quad (2.19)$$

$$\alpha D_2 \frac{d\phi}{dx}(0+) = (1 - \alpha) D_1 \frac{d\phi}{dx}(0-) \quad (2.20)$$

$$\phi(0+) = \phi(0-). \quad (2.21)$$

Let  $\sigma_0$  be the value of  $\sigma$  such that there exists  $\phi(x) > 0$  satisfying (2.18)–(2.21); that is, let  $\sigma_0$  be the principal eigenvalue for the problem. We will assume  $s < r$  and will allow  $s < 0$  so that  $s$  may actually represent a death rate. In general  $\alpha$  may depend on  $r$  and  $s$  if individuals can sense and respond to environmental quality. The positive function  $\phi(x)$  associated with  $\sigma_0$  can be viewed as a stable spatial distribution of the population, in analogy with the stable age distribution for a matrix model of an age-structured population. Thus, the population density will behave like  $Ce^{\sigma_0 t}\phi(x)$  after transient effects due to the initial population distribution have become negligible.

### 3. THE BASIC ANALYSIS OF THE MODEL

#### Graphical Determination of the Average Growth Rate

In this section we shall describe how the eigenvalue  $\sigma_0$  describing the average growth rate of the population modeled in (2.18)–(2.21) can be analyzed for its dependence on the intrinsic local growth rates  $r$  and  $s$  in the intervals of favorable and less favorable or unfavorable habitat, the respective lengths  $L$  and  $l$  of those intervals, and the edge permeability  $\alpha$  at the interface between the intervals. The essential idea is that we can solve Eq. (2.18) describing  $\phi$  on  $(-l, 0)$  and  $(0, L)$  subject to the boundary conditions (2.19) and then use the matching conditions in (2.20) and (2.21) to obtain an equation that implicitly determines  $\sigma_0$  in terms of the other parameters. The implicit relation determining  $\sigma_0$  can be analyzed graphically to determine the qualitative effects of changes in parameter values or numerically to obtain quantitative information.

Our first observation about  $\sigma_0$  is that for  $0 < \alpha < 1$  we must have  $\sigma_0 < r$ . This is because the local growth rate  $s$  is assumed to be less than  $r$  and there is some loss of population at the lethal boundary  $x = -l$ . (If  $\alpha = 1$  then the favorable interval  $(0, L)$  is a closed environment since individuals never enter the interval  $(-l, 0)$  and hence  $\sigma_0 = r$  in that case.) In solving (2.18) for  $0 < x < L$  we may thus assume that  $r - \sigma > 0$  so that to satisfy (2.18) and (2.19) with  $\phi(x) > 0$  on  $(0, L)$  we must have

$$\phi(x) = \beta \cos(\sqrt{r - \sigma/D_2}(x - L))$$

$$\text{for } 0 < x < L \quad (3.1)$$

with  $\beta > 0$ . From (3.1) we see that we must have  $\sigma > r - \pi^2 D_2/4L^2$  to prevent  $\phi(x)$  from becoming negative on  $(0, L)$ . Thus, independently of  $s$ ,  $l$ , or  $\alpha$ , we have  $r - \pi^2 D_2/4L^2 < \sigma_0 < r$ .

The relation between  $\sigma_0$  and  $s$  is less obvious. In particular it is not clear whether  $\sigma_0 < s$ ,  $\sigma_0 = s$ , or  $\sigma_0 > s$ . (It will turn out that all three cases can occur.) Allowing each of the possibilities we can solve (2.18) and (2.19) on  $(-l, 0)$  to obtain

$$\phi(x) = \begin{cases} C \sinh(\sqrt{(\sigma - s)/D_1}(x + l)) & \text{if } \sigma > s \\ C(x + l) & \text{if } \sigma = s \\ C \sin(\sqrt{(s - \sigma)/D_1}(x + l)) & \text{if } \sigma < s \end{cases} \quad (3.2)$$

for  $-l < x < 0$ .

Again we need  $C > 0$  to have  $\phi(x) > 0$ .

To determine  $\sigma_0$  we compute  $(d\phi/dx)(0 \pm)$  and  $\phi(0 \pm)$  and then apply some algebra to (2.20) and (2.21) to deduce an implicit equation for  $\sigma_0$ , namely

$$\left(\frac{(1-\alpha)D_1}{\alpha D_2}\right) f(\sigma, r, L, D_2) = g(\sigma, s, l, D_1), \quad (3.3)$$

where

$$f(\sigma, r, L, D_2) = \frac{\cot(\sqrt{(r-\sigma)/D_2} L)}{\sqrt{(r-\sigma)/D_2}} \quad (3.4)$$

and

$$g(\sigma, s, l, D_1) = \begin{cases} \frac{\tan(\sqrt{s-\sigma}/D_1) l}{\sqrt{(s-\sigma)/D_1}} & \text{if } \sigma < s \\ l & \text{if } \sigma = s \\ \frac{\tanh(\sqrt{\sigma-s}/D_1) l}{\sqrt{(\sigma-s)/D_1}} & \text{if } \sigma > s. \end{cases} \quad (3.5)$$

To make the matching conditions feasible, so that there is a meaningful solution  $\sigma_0$  to (3.3), we must have  $(d\phi/dx)(0-) > 0$ . (Recall that we must have  $r > \sigma_0$ , so that for  $\sigma = \sigma_0$  we have  $D_2(d^2\phi/dx^2) = (\sigma - r)\phi < 0$  on  $(0, L)$ ; also,  $(d\phi/dx)(L) = 0$ . Thus, if  $d\phi(0-)/dx < 0$  then we must have  $(d\phi/dx)(0+) < 0$  which implies  $(d\phi/dx)(L) < 0$ , in violation of the condition  $(d\phi/dx)(L) = 0$ .) The requirement that  $(d\phi/dx)(0-) > 0$  imposes the restriction that  $\sigma > s - \pi^2 D_1 / 4L^2$ . In the limiting case as  $L \rightarrow 0$  we have  $d\phi(0+)/dx \rightarrow 0$  so that  $\sigma_0 = s - \pi^2 D_1 / 4L^2$  would be the value attained if  $L = 0$ . (This is exactly the eigenvalue for a model with growth rate  $s$  on an interval of length  $2l$  with a lethal boundary.) To determine  $\sigma_0$ , we solve (3.3) for  $\sigma$  with  $f$  defined for  $r - \pi^2 D_2 / 4L^2 < \sigma < r$  and  $g$  defined for  $s - \pi^2 D_1 / 4L^2 < \sigma$ . It turns out that on those intervals  $f$  is increasing in  $\sigma$  with a vertical asymptote at  $\sigma = r$  and  $f = 0$  at  $\sigma = r - \pi^2 D_2 / 4L^2$ , and  $g$  is continuous and decreasing in  $\sigma$  with a vertical asymptote at  $s - \pi^2 D_1 / 4L^2$ . The graphs are shown in Fig. 3.1. It is clear that  $\partial f / \partial \sigma$  is continuous on the domain of  $f$ . It turns out that  $\partial g / \partial \sigma$  is continuous as well.

We shall explore the qualitative dependence of  $\sigma_0$  on the parameters by noting that since  $[(1-\alpha)D_1/\alpha D_2]f$  is increasing in  $\sigma$  but  $g$  is decreasing in  $\sigma$ , any change that raises the graph of  $[(1-\alpha)D_1/\alpha D_2]f$  but leaves the graph of  $g$  fixed will lower  $\sigma_0$ , and any change that leaves  $[(1-\alpha)D_1/\alpha D_2]f$  fixed but lowers  $g$  will lower  $\sigma_0$  (see Fig. 3.1). Conversely, lowering  $[(1-\alpha)D_1/\alpha D_2]f$  or

raising  $g$  will raise  $\sigma_0$ . Since the expression  $[(1-\alpha)D_1/\alpha D_2]f - g$  is monotone in  $\sigma$  and has a continuous derivative with respect to  $\sigma$  the value of  $\sigma_0$  is unique and can readily be computed numerically from (3.3) via Newton's method for any fixed set of parameters. (Notice that since  $l = g(s, s, l, D_1)$  the intersection of  $g(\sigma, s, l, D_1)$  and  $[(1-\alpha)D_1/\alpha D_2]f(\sigma, r, L, D_2)$  must occur for  $\sigma_0 < s$  if  $l < [(1-\alpha)D_1/\alpha D_2]f(s, r, L, D_2)$  and for  $\sigma_0 > s$  if  $l > [(1-\alpha)D_1/\alpha D_2]f(s, r, L, D_2)$ ; see Fig. 3.1. This observation provides a simple way of deciding which formula from (3.5) should be used for  $g(\sigma, s, l, D_1)$ .)

A number of biological conclusions about the effects of various parameters on the average population growth rate  $\sigma_0$  can be drawn immediately from the graphs in Fig. 3.1. One immediate conclusion is that  $\sigma_0$  is increasing with respect to  $L$ . This follows from the observation that increasing  $L$  decreases the value of  $[(1-\alpha)D_1/\alpha D_2]f(\sigma, r, L, D_2)$  and thus lowers that graph but does not affect  $g(\sigma, s, l, D_1)$ . Similarly obvious conclusions are that if all other factors including  $\alpha$  are fixed, then increasing  $r$  or  $s$  will increase  $\sigma_0$ . This assumes that the degree of preference  $\alpha$  for the favorable habitat does not depend on the degree of variability there or in the less favorable surroundings. If the population can sense and respond to environmental quality that complicates matters; we shall address that point later. Furthermore, some caution is required in applying these last conclusions, because the model treats only a single species. For competing species increases in the growth rates of both competitors in a buffer zone may shift the balance of competition and cause the extinction of one or the other in the refuge; see Cantrell and Cosner (1993). Another fairly obvious conclusion is that since increasing  $l$  (the size of the buffer zone) increases  $g(\sigma, s, l, D_1)$  it thus increases  $\sigma_0$ . It turns out that there are strict limits to the beneficial effects of a buffer zone, however, and we shall return to treat that point in detail in the next subsection.

A specific goal of this paper is to consider the effects of edge permeability on the predictions of diffusion models. A conclusion can be drawn immediately from (3.3) via Fig. 3.1, namely that if all other factors remain fixed then increasing  $\alpha$ , the tendency to remain in the favorable patch or refuge, will decrease  $[(1-\alpha)D_1/\alpha D_2]f(\sigma, r, L, D_2)$  and thus will increase  $\sigma_0$ . The conclusion is not surprising, but it must be used with care. This is because  $\sigma_0$  represents the average population growth rate. Clearly it is beneficial, even necessary for survival, to have  $\sigma_0 > 0$ . On the other hand, achieving a given positive value for the growth rate of a population restricted to a small region might be less desirable from the viewpoint of conservation than achieving a slightly smaller but still solidly positive growth rate for a population distributed over a much

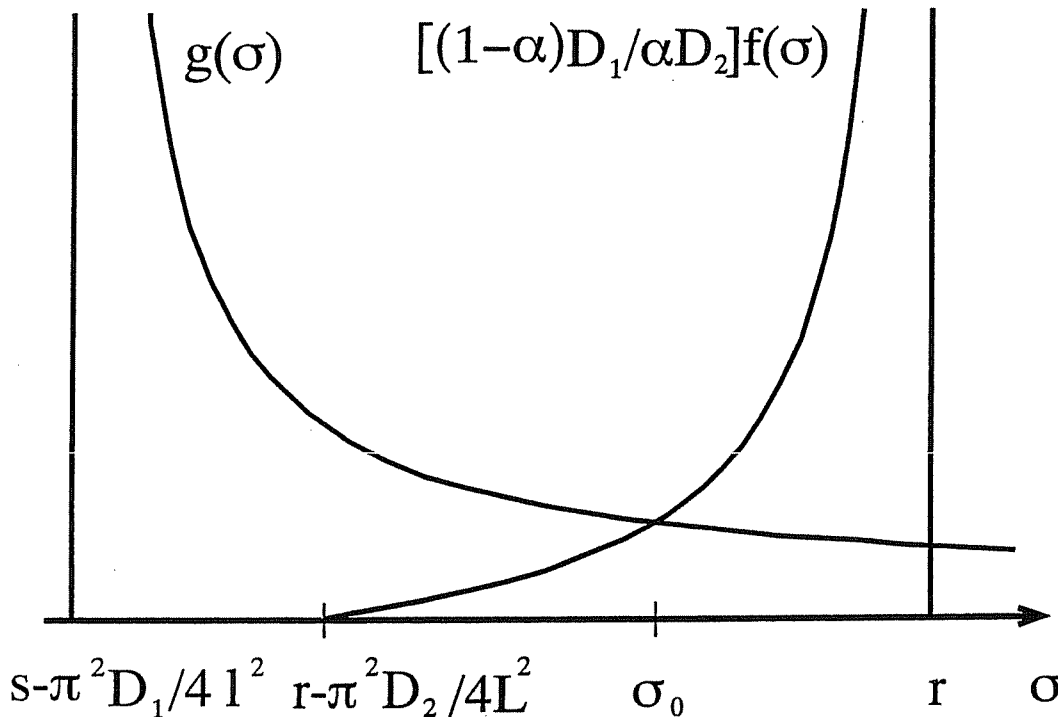


FIG. 3.1. The graphs of  $[(1-\alpha)D_1/\alpha D_2]f(\sigma, r, L, D_2)$  and  $g(\sigma, s, l, D_1)$ . We always have  $r > s$ , but the relationships between  $r - (\pi^2 D_2/4L^2)$  and  $s$ ,  $r - (\pi^2 D_2/4L^2)$  and  $s - (\pi^2 D_1/4l^2)$ , and  $s$  and  $\sigma_0$  depend on the parameters. Observe that if the graph of  $g$  is shifted upward or that of  $[(1-\alpha)D_1/\alpha D_2]f$  is shifted downward then the point of intersection moves to the right; i.e.,  $\sigma_0$  increases. Similarly, if  $g$  decreases or  $[(1-\alpha)D_1/\alpha D_2]f$  increases, the intersection moves to the left and  $\sigma_0$  decreases.

larger region. This sort of point is addressed in the source-sink dynamics of Pulliam (1988). At the level of our linear growth models the utility of increasing  $\alpha$  will depend on the size of  $\sigma_0$  and the sensitivity of  $\sigma_0$  to  $\alpha$ . The case where increasing  $\alpha$  would appear to be most beneficial would be when  $\sigma_0 < 0$  for  $\alpha = \frac{1}{2}$  since  $[(1-\alpha)D_1/\alpha D_2]f \rightarrow 0$  as  $\alpha \rightarrow 1$  except at  $\sigma = r$ , so that  $\sigma_0 \rightarrow r$  as  $\alpha \rightarrow 1$ . The point is that in such a situation there would be a negative average growth rate (i.e., a net death rate) if the population could disperse freely out of the refuge but a positive growth rate if the permeability of the boundary were decreased sufficiently.

**Boundary Conditions and Bounds on Benefits from Big Buffers**

To understand what happens as the size  $l$  of the buffer zone or unfavorable region surrounding the refuge or habitat patch becomes very large, we observe that the function  $g(\sigma, s, l, D_1)$  used in (3.3) to determine  $\sigma_0$  has the properties that for  $\sigma = s$ ,  $g(s, s, l, D_1) = l$  and that as  $l \rightarrow \infty$  the asymptote at  $s - \pi^2 D_1/4l^2$  moves toward  $s$ . As  $l \rightarrow \infty$  the value of  $\sigma_0$  as determined by the intersection point of  $g$  and  $[(1-\alpha)D_1/\alpha D_2]f$  as in Fig. 3.1 must

eventually lie to the right of  $\sigma = s$ . This follows because  $g = l$  when  $\sigma = s$  but  $[(1-\alpha)D_1/\alpha D_2]f$  at  $\sigma = s$  does not depend on  $l$ , so as  $l$  is increased eventually  $g > [(1-\alpha)D_1/\alpha D_2]f$  at  $\sigma = s$ . (See Fig. 3.2.) For  $\sigma > s$  we have  $g(\sigma, s, l, D_1) \leq \sqrt{D_1/(\sigma-s)}$  and  $\lim_{l \rightarrow \infty} g(\sigma, s, l, D_1) = \sqrt{D_1/(\sigma-s)}$ . Since  $g(\sigma, s, l, D_1)$  is increasing with respect to  $l$ , it follows that as  $l \rightarrow \infty$ ,  $\sigma_0 \rightarrow \sigma^* > s$ , where  $\sigma^*$  is determined by

$$\frac{(1-\alpha)D_1}{\alpha D_2} f(\sigma, r, L, D_2) = \sqrt{D_1/(\sigma-s)}. \quad (3.6)$$

Furthermore,  $\sigma_0 < \sigma^*$  for any finite  $l$ , and since  $f(\sigma, r, L, D_2) \rightarrow \infty$  as  $\sigma \rightarrow r$ , we have  $\sigma^* < r$ . (See Fig. 3.2.) Since  $\sigma_0 < \sigma^* < r$ , the effective growth rate of a population with  $\alpha < 1$  will always be less than what it would be in a completely favorable region. Furthermore, since  $\sigma_0$  increases monotonically toward  $\sigma^*$  as  $l \rightarrow \infty$ , we must have the sensitivity  $\partial \sigma_0 / \partial l \rightarrow 0$  as  $l \rightarrow \infty$ . **Thus there is ultimately a diminishing benefit of increasing the size of buffer zones, and the size of the buffer zone can never completely compensate for its lower quality.** In Ludwig *et al.* (1979) a situation corresponding to  $l = \infty$  was analyzed



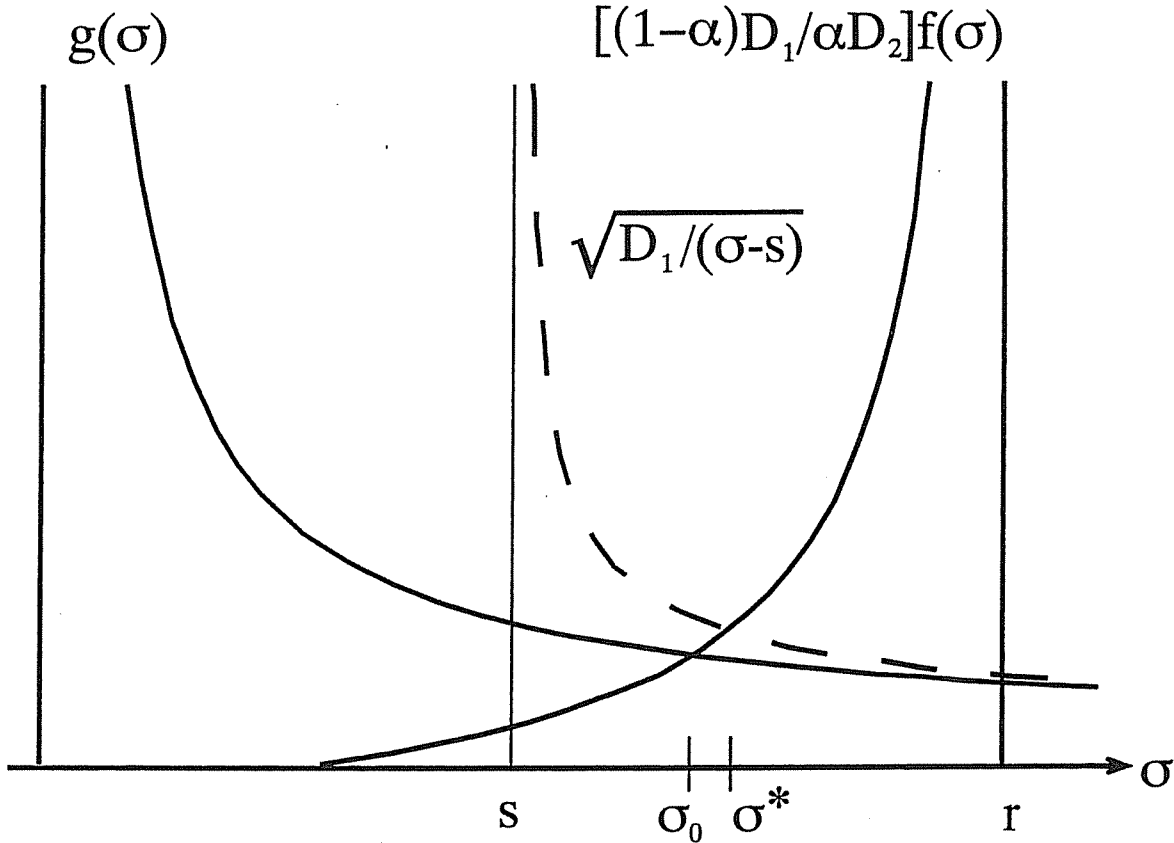


FIG. 3.2. This figure shows the graphs of  $[(1-\alpha) D_1/\alpha D_2] f(\sigma, r, L, D_2)$  and  $g(\sigma, s, l, D_1)$  as solid lines and shows the graph of

$$\sqrt{D_1/(\sigma-s)} = \lim_{l \rightarrow \infty} g(\sigma, s, l, D_1)$$

as a broken line. As  $l \uparrow \infty$ ,  $\sigma_0 \uparrow \sigma^* < r$ . It follows that there is a limit to the beneficial effects of a buffer zone, even if it can be made arbitrarily large.

by using matching conditions (2.20) and (2.21) with  $\alpha = \frac{1}{2}$  to set up boundary conditions at  $x = 0, x = 2L$ . At  $x = 0$  the conditions took the form

$$\frac{-d\phi}{dx}(0+) + c\phi(0+) = 0. \tag{3.7}$$

These are a classical type of boundary conditions known as Robin or third-kind boundary conditions; see Strauss (1992). In the cases treated by Ludwig *et al.* (1979) the population density was assumed to be at a static equilibrium, which in our scenario would correspond to  $\sigma_0 = 0$ . In that case our modeling approach yields exactly the same boundary conditions as those derived in Ludwig *et al.* (1979) for  $l = \infty$  provided that  $\alpha = \frac{1}{2}$ . For  $\alpha \neq \frac{1}{2}$  and a static population we obtain a slightly different Robin condition with  $c$  replaced by  $c(1-\alpha)/\alpha$ . Thus, our boundary conditions are equivalent to a type of Robin

boundary condition in the case of static populations and  $l = \infty$ , which is the only case where the derivation of the Robin conditions in Ludwig *et al.* (1979) makes sense.

#### 4. EFFECTS OF BUFFER ZONES

##### **Determining Growth Rates via Buffer Zone Design**

In the context of refuge design for conservation it is of interest to determine whether it is useful to create buffer zones around a refuge and what size and quality of buffer zone is needed to achieve a specified goal. In the present article we consider only the average rate of population growth predicted by a density-independent (i.e., linear) single-species model, and ask what sort of buffer zone is needed to achieve a given growth rate. This approach

must be used with caution in any practical situation because density-dependent interactions can produce qualitatively different effects. However, even with density dependence, we must have a positive average growth rate  $\sigma_0$  to avoid extinction. More generally we may wish to achieve an average growth rate which is some given fraction  $\gamma$  of the local growth rate  $r$  which would be attained in the optimal habitat inside the refuge. The reason for wanting  $\sigma_0 = \gamma r$  for some  $\gamma > 0$  rather than simply wanting  $\sigma_0 > 0$  is to allow for factors such as demographic and environmental stochasticity.

We shall assume that the size  $l$  and quality  $s$  of the buffer zone can be manipulated more easily than the remaining parameters and ask what choices of  $l$  and  $s$  are required to achieve an average growth rate that is equal to some specified fraction of the optimal growth rate  $r$ , i.e.,  $\sigma_0 = \gamma r$  for some  $\gamma$  with  $0 \leq \gamma < 1$ . The question is only relevant if  $\gamma r > r - \pi^2 D_2 / 4L^2$  because the average growth rate  $\sigma_0$  is always larger than  $r - \pi^2 D_2 / 4L^2$ . Hence, we shall suppose that  $L$  is fixed and that  $\gamma r > r - \pi^2 D_2 / 4L^2$ .

The first observation is that if the size  $l$  of the buffer zone is allowed to increase but all other parameters are fixed then there is a number  $\sigma^* < r$  such that the growth rate  $\sigma_0$  satisfies  $\sigma_0 < \sigma^*$  for any finite  $l$  and  $\sigma_0 \rightarrow \sigma^*$  as  $l \rightarrow \infty$ . The quantity  $\sigma^*$  is defined by (3.6); see Fig. 3.2. Thus, it is possible to achieve  $\sigma_0 = \gamma r$  by taking  $l$  to be sufficiently large if and only if  $\sigma^* > \gamma r$ . Since  $\sigma^* > s$  (see Fig. 3.2) we can always achieve  $\sigma_0 = \gamma r$  by choosing  $l$  to be large enough provided that  $s \geq \gamma r$ . It follows that the smallest value  $s_\gamma$  of  $s$  for which  $\sigma^* \geq \gamma r$  must satisfy  $s_\gamma < \gamma r$ . We can determine  $s_\gamma$  by substituting  $\sigma = \gamma r$  into (3.6) and using (3.4). We have

$$s_\gamma = r \left[ \gamma - \frac{\alpha^2 D_2 (1 - \gamma)}{(1 - \alpha)^2 D_2} \tan^2(\sqrt{(1 - \gamma) r / D_2} L) \right] < \gamma r. \tag{4.1}$$

If  $s \leq s_\gamma$ , as given in (4.1) then it is not possible to achieve an average growth rate  $\sigma_0 \geq \gamma r$  no matter how large the buffer zone is made. If  $s > s_\gamma$  then we can achieve  $\sigma_0 = \gamma r$  by taking  $l$  to be sufficiently large. To determine how large  $l$  must be we substitute  $\sigma = \gamma r$  into (3.3) and solve for  $l$ . If  $s < \gamma r$  we have

$$l = \frac{\sqrt{D_1}}{\sqrt{\gamma r - s}} \tanh^{-1} \left\{ \frac{(1 - \alpha)}{\alpha} \sqrt{\frac{D_1}{D_2}} \frac{\sqrt{\gamma r - s}}{\sqrt{(1 - \gamma) r}} \times \cot \left[ \sqrt{\frac{(1 - \gamma) r}{D_2}} L \right] \right\}, \tag{4.2}$$

if  $s = \gamma r$  then

$$l = \frac{1 - \alpha}{\alpha} \frac{D_1}{\sqrt{D_2}} \frac{1}{\sqrt{(1 - \gamma) r}} \cot \left[ \sqrt{\frac{(1 - \alpha) r}{D_1}} L \right], \tag{4.3}$$

and if  $s > \gamma r$

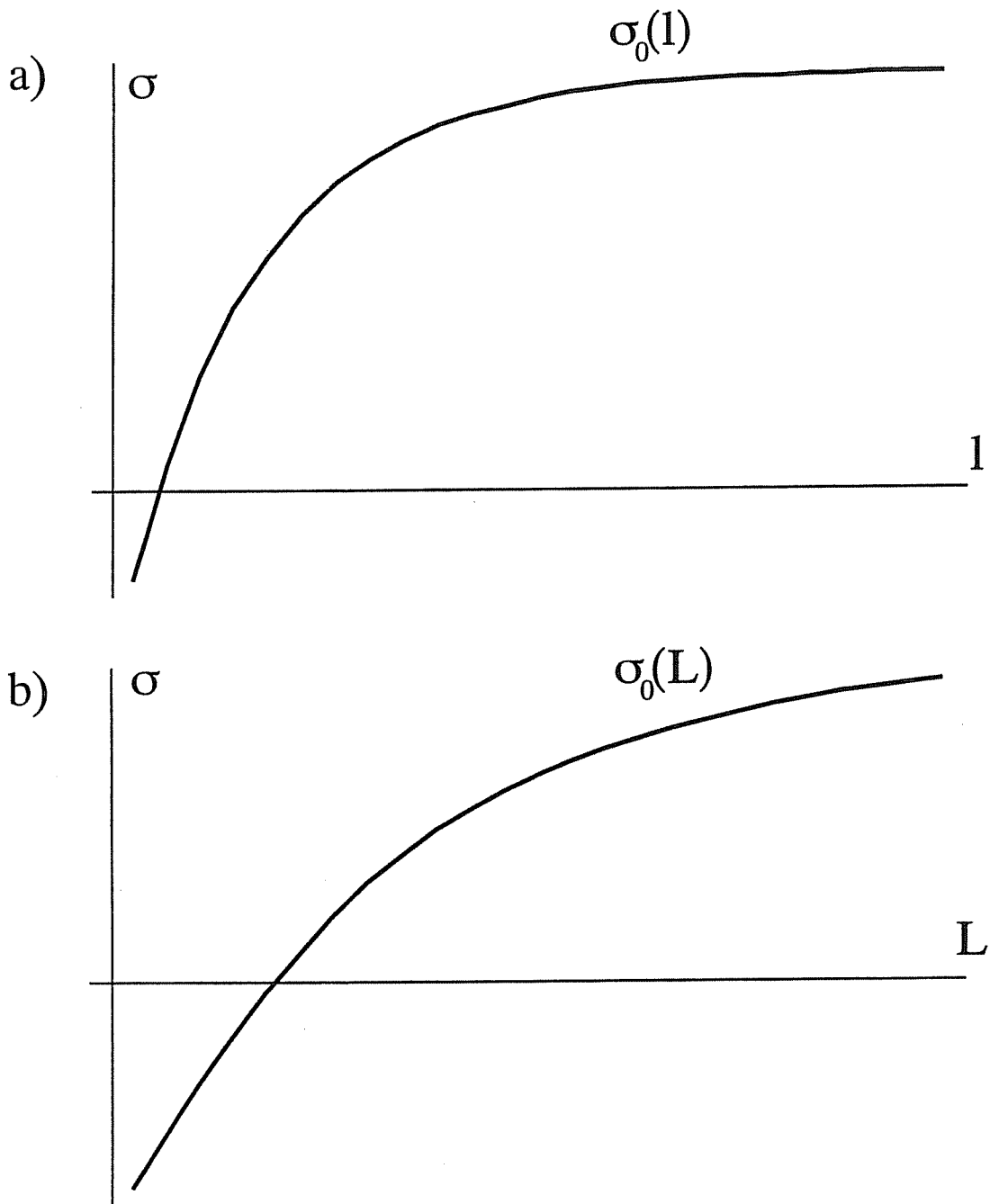
$$l = \frac{\sqrt{D_1}}{\sqrt{s - \gamma r}} \tan^{-1} \left\{ \frac{(1 - \alpha)}{\alpha} \sqrt{\frac{D_1}{D_2}} \frac{\sqrt{s - \gamma r}}{\sqrt{(1 - \gamma) r}} \times \cot \left[ \sqrt{\frac{(1 - \gamma) r}{D_2}} L \right] \right\}. \tag{4.4}$$

Note that if  $s$  decreases toward the value  $s_\gamma$  shown in (4.1) the appropriate formula for  $l$  is (4.2) and since the expression inside the  $\tanh^{-1}$  approaches 1 as  $s \rightarrow s_\gamma$ , we have  $l \rightarrow \infty$ . On the other hand if  $s > \gamma r$  so that (4.4) holds we have  $l < \pi \sqrt{D_1} / 2 \sqrt{s - \gamma r}$ . This is not surprising since if  $s > \gamma r$  we could take  $L = 0$  and still achieve a growth rate of  $\sigma_0 = \gamma r$  on the interval  $(-l, l)$  for  $l = \pi \sqrt{D_1} / 2 \sqrt{s - \gamma r}$ . If  $s = r$ ,  $D_1 = D_2$ , and  $\alpha = \frac{1}{2}$  then the model describes a single uniform region of length  $2l + 2L$ . In that case (4.4) reduces to  $\gamma r = r - \pi^2 D_2 / 4(L + l)^2$ , which is exactly the growth rate expected on a uniformly favorable habitat of length  $2l + 2L$  with local growth rate  $r$ , diffusion rate  $D_2$ , and a lethal boundary.

Note that if the other parameters are fixed the value of  $l$  necessary to sustain a given growth rate is decreasing in  $\alpha$ , and that as  $\alpha \rightarrow 1$ ,  $l \rightarrow 0$ . However, this conclusion should be used with some caution since  $\sigma_0 \rightarrow r$  as  $\alpha \rightarrow 1$  independently of the size  $2L$  of the refuge in this modeling approach. This assumes that the refuge is effectively large enough to sustain an optimal growth rate if it were completely enclosed. Generally this means that the refuge would need to be large enough that demographic stochasticity is not a major problem.

**Sensitivity of growth Rates to Refuge and Buffer Size**

It is of interest from the viewpoint of refuge design to ask how changes in the quantities  $L$  and  $l$  describing the size of a refuge and buffer zone respectively will affect the average growth rate  $\sigma_0$ . The general behavior of  $\sigma_0$  as a function of  $l$  and  $L$  is shown in Fig. 4.1. Generally, the increase in  $\sigma_0$  relative to a given increase in  $L$  or  $l$  appears to be largest for small values of  $L$  and  $l$  and to decrease as  $L$  and  $l$  become larger. We can make this more precise by examining the partial derivatives  $\partial \sigma_0 / \partial L$  and  $\partial \sigma_0 / \partial l$ . These measure the sensitivity of  $\sigma_0$  to changes in  $L$  and  $l$ , respectively. To determine  $\partial \sigma_0 / \partial L$  and  $\partial \sigma_0 / \partial l$  we can



**FIG. 4.1.** These graphs show  $\sigma_0$  as a function of  $l$  and of  $L$ , respectively, with the other parameters held fixed. The graphs show that the effect of increasing either  $l$  or  $L$  becomes smaller as the value of the variable becomes larger. However, the effect of increasing  $l$  becomes small (i.e., the graph of  $\sigma_0$  as a function of  $l$  becomes flat) much sooner than does the effect of increasing  $L$ . This supports the view that most of the beneficial effects of a buffer zone are already realized with a small buffer. The benefits of increasing the size of the reserve continue to be significant even if the reserve is fairly large.

differentiate (3.3) implicitly and solve. For  $\partial\sigma_0/\partial L$  we obtain

$$\frac{\partial\sigma_0}{\partial L} = \frac{-[(1-\alpha)/\alpha] D_1(\partial f/\partial L)}{[(1-\alpha)/\alpha] D_1(\partial f/\partial\sigma) - D_2(\partial g/\partial\sigma)} \Big|_{\sigma=\sigma_0}, \quad (4.5)$$

where  $f$  and  $g$  are defined by (3.4) and (3.5) and  $\sigma_0$  is determined by (3.3). By explicitly evaluating the expression in (4.5) we can produce a somewhat complicated formula for  $\partial\sigma_0/\partial L$ ; see the Appendix. Here we shall be concerned primarily with examining the behavior of  $\partial\sigma_0/\partial L$  and  $\partial\sigma_0/\partial l$  as  $L$  or  $l$  becomes large or small.

As  $l \rightarrow \infty$  for  $L$  fixed it turns out that  $\partial\sigma_0/\partial l \rightarrow 0$  but  $\partial\sigma_0/\partial L$  converges to a positive value which depends on the remaining parameters in a somewhat complicated way (see the Appendix). As  $L \rightarrow \infty$  with  $l$  fixed,  $\partial\sigma_0/\partial l \rightarrow 0$  and  $\partial\sigma_0/\partial L \rightarrow 0$  but

$$\lim_{L \rightarrow \infty} \frac{(\partial\sigma_0/\partial l)}{(\partial\sigma_0/\partial L)} = \frac{\alpha D_2}{(1-\alpha) D_1} \operatorname{sech}^2[(r-s)^{1/2} D_1^{-1/2} l].$$

Since  $\operatorname{sech} x \rightarrow 0$  as  $x \rightarrow \infty$ , it follows from the above observations that as the buffer zone becomes large the benefits of further increasing the size of the buffer diminish and become negligible relative to the benefits of increasing the size of the refuge.

For intermediate sizes of  $l$  and  $L$  we have

$$\frac{(\partial\sigma_0/\partial l)}{(\partial\sigma_0/\partial L)} \leq \frac{\alpha D_2}{(1-\alpha) D_1}$$

as long as  $s < \sigma_0$ . In any case, independent of whether  $s > \sigma_0$  or  $s < \sigma_0$ , it turns out that we have

$$\lim_{l \rightarrow 0} \frac{(\partial\sigma_0/\partial l)}{(\partial\sigma_0/\partial L)} = \frac{\alpha D_2}{(1-\alpha) D_1}. \quad (4.6)$$

(See the Appendix.) The conclusion here is that when  $l$  is small it may be more advantageous in some cases to increase  $l$  than to increase  $L$ , but **only** if  $\alpha D_2 > (1-\alpha) D_1$ . The requirement  $\alpha D_2 > (1-\alpha) D_1$  implies that either the population prefers to remain inside the refuge or disperses more slowly in the buffer than in the refuge or both. Hence, for a small buffer or a buffer of relatively low quality ( $s < r - \pi^2 D_2 / 4L^2$ ) to be worthwhile, it must act as a partial barrier to dispersal out of the refuge.

If  $s > r - \pi^2 D_2 / 4L^2$  (i.e., the refuge is small or the buffer is of high quality) and  $l$  is small then  $s > \sigma_0$  so the formula for  $g$  and hence for  $\partial\sigma_0/\partial l$  and  $\partial\sigma_0/\partial L$  would be

different than when  $s < \sigma_0$ . In fact we always have  $s > \sigma_0$  as  $L \rightarrow 0$ . We have

$$\lim_{L \rightarrow 0} \frac{(\partial\sigma_0/\partial l)}{(\partial\sigma_0/\partial L)} = \left( \frac{1-\alpha}{\alpha} \right) \frac{(\pi^2 D_1 / 4L^2)}{[r-s + (\pi^2 D_1 / 4L^2)]}. \quad (4.7)$$

Since  $\alpha \geq \frac{1}{2}$  and  $r > s$ , it follows from (4.7) that  $(\partial\sigma_0/\partial l)/(\partial\sigma_0/\partial L) < 1$  for  $L$  small. The implication is that when the refuge is small it is always more beneficial to increase the size of the refuge than to increase the size of the buffer.

The general conclusion about refuge design is that the only situation in which increasing the size of the buffer is highly beneficial is if the refuge is at least moderately large, the buffer is relatively small, and the buffer acts as an impediment to dispersal of the population. An important way that the buffer can impede dispersal is by being unattractive to the population, i.e., having a relatively large value of  $\alpha$ . If the population responds to environmental quality then large values of  $\alpha$  may be associated with buffers of low quality (i.e., small  $s$ ), so there may be a trade-off between having a relatively high growth rate (or relatively low death rate) in the buffer and having the buffer act as a dispersal barrier. We shall explore that point in the next section.

## 5. POPULATIONS THAT DISPERSE IN RESPONSE TO HABITAT QUALITY

In this section we consider how the average population growth rate is affected by the sensitivity of the population to the difference in habitat quality across interfaces between favorable and unfavorable habitats. In this scenario we suppose that the percentage  $\alpha$  of individuals which return to the favorable region when they reach the boundary depends on the relative quality of the favorable and unfavorable regions. In terms of the local population growth rates  $r$  and  $s$  on the favorable and unfavorable regions, respectively, it is reasonable to assume that if  $\alpha$  depends on  $r$  and  $s$  then  $\alpha = \alpha(r, s)$  with  $\alpha(r, r) = \frac{1}{2}$  (so there is no preference if the two regions have the same quality of habitat) and with  $\alpha(r, s)$  increasing as  $r-s$  increases (so that  $\alpha$  increases as the difference in habitat quality increases.)

### Models for Habitat-Sensitive Behavior at an Interface

A simple way to model how  $\alpha$  might depend on  $r$  and  $s$  is to take  $\alpha(r, s) = \alpha_0(r-s)$ , where  $\alpha_0(0) = \frac{1}{2}$  and  $\alpha_0(x)$  is a nondecreasing function. Since  $\frac{1}{2} \leq \alpha < 1$  we must have

$\alpha_0(x) \rightarrow \bar{\alpha} \leq 1$  as  $x \rightarrow \infty$ , so  $\alpha(r, s) \rightarrow \bar{\alpha}$  as  $r - s \rightarrow \infty$ . The interpretation of  $\bar{\alpha}$  is that  $1 - \bar{\alpha}$  is the percentage of individuals that are willing to cross from a region of more favorable habitat into a region of less favorable habitat no matter how much difference there is in habitat quality. Thus, if  $\bar{\alpha} < 1$  there will always be some individuals crossing into the less favorable region, while if  $\bar{\alpha} = 1$  the percentage that cross into the less favorable region will tend to zero as the habitat quality becomes sufficiently bad, i.e., as the local growth rate  $s \rightarrow -\infty$ . Whether  $\bar{\alpha} < 1$  or  $\bar{\alpha} = 1$  may have significance for the behavior of the average growth rate  $\sigma_0$  as  $s \rightarrow -\infty$ , depending on the functional form of  $\alpha_0(x)$ . If we assume any particular functional form for  $\alpha_0$  we can introduce another parameter  $\delta > 0$  as a scale factor on the difference  $r - s$  of local growth rates so that  $\alpha(r, s) = \alpha_0(\delta(r - s))$ . This parameter scales the intensity of response to any given value of  $r - s$ . If  $\alpha_0(x)$  is an increasing function then for any  $r - s > 0$  an increase in  $\delta$  will increase  $\alpha$ , so increasing  $\delta$  will increase  $\sigma_0$ . Some examples of possible functions  $\alpha_0$  include

$$\alpha_0(x) = \bar{\alpha} e^x / [(2\bar{\alpha} - 1) + e^x] \quad (5.1)$$

and

$$\alpha_0(x) = \bar{\alpha}(1 + x^p) / (2\bar{\alpha} + x^p) \quad \text{for some } p > 0. \quad (5.2)$$

The significance of the forms (5.1) and (5.2) is that if  $\alpha_0$  has form (5.1) then  $\alpha_0(\delta x) \rightarrow \bar{\alpha}$  exponentially as  $x \rightarrow \infty$  since  $\bar{\alpha} - \alpha_0(\delta x) = \bar{\alpha}(2\bar{\alpha} - 1) / [(2\bar{\alpha} - 1) + e^{\delta x}]$ , and similarly  $\alpha_0(\delta x) \rightarrow \bar{\alpha}$  with order  $x^{-p}$  as  $x \rightarrow \infty$  if  $\alpha_0$  has the form (5.2). We shall see that when  $\bar{\alpha} = 1$ , the rate at which  $\alpha_0(\delta x)$  approaches  $\bar{\alpha}$  determines what happens as the local growth rate  $s$  in the less favorable region approaches  $-\infty$ .

### Effects of Habitat-Sensitive Behavior on the Average Growth Rate

We now consider the effect of sensitivity to habitat quality on the behavior of the average growth rate  $\sigma_0$  as the quality of habitat in the more favorable or less favorable region (measured by local growth rates  $r$  and  $s$ , respectively) is varied. *A specific issue that we address is the extent to which sensitivity to differences in habitat quality can compensate for decreases in the habitat quality in the less favorable region or buffer zone.* To analyze the situation where  $\alpha$  depends on  $r - s$ , recall that the average

growth rate  $\sigma_0$  is determined by (3.3), which we reproduce here:

$$\frac{(1 - \alpha) D_1}{\alpha D_2} f(\sigma, r, L, D_2) = g(\sigma, s, l, D_1). \quad (5.3)$$

Recall that increasing the expression on the left of (5.3) or decreasing the expression on the right decreases  $\sigma_0$ , and vice versa. (See Fig. 3.1.) The function  $f$  is decreasing in  $r$  and the function  $g$  is increasing in  $s$ , so if  $\alpha$  is fixed then  $\sigma_0$  increases if either  $r$  or  $s$  is increased. If  $\alpha = \alpha_0(\delta(r - s))$  then holding  $s$  fixed and increasing  $r$  causes  $\alpha$  to increase so that  $(1 - \alpha)/\alpha = (1/\alpha) - 1$  decreases; also,  $f(\sigma, r, L, D_2)$  decreases, so the left side of (5.3) decreases and  $\sigma_0$  increases. Thus, increasing  $r$  is even more beneficial (and decreasing  $r$  more detrimental) than if  $\alpha$  were fixed, because the way that  $\alpha$  changes with  $r$  augments the way that  $f(\sigma, r, L, D_2)$  changes with  $r$ . On the other hand, if we rewrite (5.3) as

$$f(\sigma, r, L, D_2) = \frac{\alpha D_2}{(1 - \alpha) D_1} g(\sigma, s, l, D_1) \quad (5.4)$$

and  $\alpha = \alpha_0(\delta(r - s))$  is decreasing in  $s$ , then since  $\alpha/(1 - \alpha)$  is an increasing function of  $\alpha$ , the expression  $\alpha_0(\delta(r - s)) / [1 - \alpha_0(\delta(r - s))]$  is decreasing in  $s$  while  $g(\sigma, s, l, D_1)$  is increasing in  $s$ . Whether the product is increasing or decreasing with respect to  $s$  will depend on the form of  $\alpha_0$  and the various parameters in the problem. *The reason why the average growth rate might decrease with increasing  $s$  or increase with decreasing  $s$  is that the aversion of the population to unfavorable habitat might compensate for the deleterious effects of declining habitat quality in the less favorable region.* It turns out that this effect can actually occur under certain conditions. As an example, suppose that  $\alpha_0$  has the form (5.1) with  $\bar{\alpha} = 1$ . Then  $\alpha/(1 - \alpha) = e^{\delta(r - s)}$  and (5.4) becomes

$$f(\sigma, r, L, D_2) = [e^{\delta(r - s)} D_2 / D_1] g(\sigma, s, l, D_1). \quad (5.5)$$

For fixed values of the parameters the expressions in (5.5) have the same dependence on  $\sigma$  as in (3.3). It follows that  $r - \pi^2 D_2 / 4L^2 < \sigma_0 < r$  for any  $s$ . If  $\sigma > s$  then using (3.5) we see that  $g(\sigma, s, l, D_1)$  is bounded and has the form

$$g(\sigma, s, l, D_1) = (\sigma - s)^{-1/2} D_1^{1/2} \tanh [(\sigma - s)^{1/2} D_1^{-1/2} l] \quad (\text{for } s < \sigma). \quad (5.6)$$

Suppose that  $s < r - \pi^2 D_2 / 4L^2$  so that  $s < \sigma$  and (5.6) holds. Computing the partial derivative with respect to  $s$  of the expression on the right in (5.5) yields

$$\begin{aligned} & \frac{\partial}{\partial s} ([e^{\delta(r-s)} D_2 / D_1] g) \\ &= (D_2 / D_1) e^{\delta(r-s)} \left[ -\delta g + \frac{\partial g}{\partial s} \right]. \end{aligned} \quad (5.7)$$

Thus, by (5.7), if  $\delta$  is large enough then  $-\delta g + (\partial g / \partial s) < 0$  so the expression on the right in (5.6) will be decreasing as  $s$  increases. In other words, if the strength of aversion to less favorable habitats (as measured by  $\delta$ ) is sufficiently strong, a decrease in the quality of the less favorable habitat might actually increase the average population growth rate. The rate at which the strength of aversion increases relative to decreases in habitat quality will depend on the parameters  $\delta$  and  $\bar{\alpha}$  and the functional form of  $\alpha_0$ . We next examine the behavior of the average growth rate  $\sigma_0$  as  $s \rightarrow -\infty$ .

To understand how  $\sigma_0$  behaves when  $\alpha = \alpha_0(\delta(r-s))$  and  $s \rightarrow -\infty$  we return to (5.4). Recall that increasing the right side of (5.4) increases  $\sigma_0$ . If  $\bar{\alpha} < 1$  then since  $\alpha \leq \bar{\alpha}$  independent of  $r, s$ , and  $\delta$  it follows that for any given  $s$  we have  $\sigma_0 \leq \bar{\sigma}_0$ , where  $\bar{\sigma}_0$  is the value determined by

$$f(\sigma, r, L, D_2) = \frac{\bar{\alpha} D_2}{(1 - \bar{\alpha}) D_1} g(\sigma, s, l, D_1). \quad (5.8)$$

If  $s \rightarrow -\infty$  then eventually  $s < r - \pi^2 D_2 / 4L^2 \leq \bar{\sigma}_0$  so that  $g$  is given by (5.6) and thus  $g(\sigma, s, l, D_1) \rightarrow 0$  as  $s \rightarrow -\infty$  within the range of values of  $\sigma$  where  $f > 0$ . It follows that  $\bar{\sigma}_0$  converges to the point where  $f(\sigma, r, L, D_2) = 0$ , namely  $\bar{\sigma}_0 = r - \pi^2 D_2 / 4L^2$ . Since  $r - \pi^2 D_2 / 4L^2 < \sigma_0 \leq \bar{\sigma}_0$  for any finite  $s$  we have  $\sigma_0 \rightarrow r - \pi^2 D_2 / 4L^2$  as  $s \rightarrow -\infty$ . Since  $f(\sigma, r, L, D_2)$  is defined and is nonnegative only for  $r - \pi^2 D_2 / 4L^2 \leq \sigma \leq r$ , the value  $r - \pi^2 D_2 / 4L^2$  is the lowest possible for the average growth rate  $\sigma_0$  no matter what the specific parameters occurring in  $[\alpha D_2 / (1 - \alpha) D_1] g(\sigma, s, l, D_1)$  may be. The conclusion is that if  $\bar{\alpha} < 1$  then the growth rate  $\sigma_0$  has the same behavior as  $s \rightarrow -\infty$  as it would if  $\alpha$  were fixed. If  $\bar{\alpha} = 1$  then the behavior of  $\sigma_0$  as  $s \rightarrow -\infty$  depends on the details of how rapidly  $\alpha(r, s) \rightarrow 1$  as  $r - s \rightarrow \infty$ ; that is, it depends on the form of  $\alpha_0$ . For some choices of  $\alpha_0$ ,  $\sigma_0 \rightarrow r - \pi^2 D_2 / 4L^2$  as  $s \rightarrow -\infty$  but for others  $\sigma_0 \rightarrow r$  as  $s \rightarrow -\infty$ . If the expression on the right in (5.4) approaches zero as  $s \rightarrow -\infty$  for  $\sigma$  between  $r - \pi^2 D_2 / 4L^2$  and  $r$  then  $\sigma_0 \rightarrow r - \pi^2 D_2 / 4L^2$  since  $r - \pi^2 D_2 / 4L^2$  is the value of  $\sigma$  for which  $f(\sigma, r, L, D_2) = 0$ . On the other hand if the right side of (5.4) approaches infinity as  $s \rightarrow -\infty$  then  $\sigma_0 \rightarrow r$  as  $s \rightarrow -\infty$

since  $r$  is the value of  $\sigma$  for which  $f(\sigma, r, L, D_2)$  becomes infinite. Suppose that  $\alpha_0$  has the form (5.2) with  $\bar{\alpha} = 1$ , so that  $\alpha(r, s) = (1 + (\delta(r-s))^p) / [2 + (\delta(r-s))^p]$ . Then  $\alpha / (1 - \alpha) = [1 + (\delta(r-s))^p]$ . As  $s \rightarrow -\infty$  we must have  $s < r - \pi^2 D_2 / 4L^2$  eventually and so  $g(\sigma, s, l, D_1)$  will be given by (5.6) so that

$$\begin{aligned} & \frac{\alpha D_2}{(1 - \alpha) D_1} g(\sigma, s, l, D_1) \\ &= D_2 D_1^{-1/2} [1 + \delta^p (r-s)^p] (\sigma - s)^{-1/2} \\ & \quad \times \tanh [(\sigma - s)^{1/2} D_1^{-1/2} l]. \end{aligned} \quad (5.9)$$

If  $\sigma$  and the remaining parameters are fixed then  $\tanh [(\sigma - s)^{1/2} D_1^{-1/2} l] \rightarrow 1$  as  $s \rightarrow -\infty$  while  $[1 + \delta^p (r-s)^p] (\sigma - s)^{-1/2} \rightarrow 0$  if  $p < \frac{1}{2}$  but  $[1 + \delta^p (r-s)^p] (\sigma - s)^{-1/2} \rightarrow \infty$  if  $p > \frac{1}{2}$ . Thus, if  $p < \frac{1}{2}$  then  $\sigma_0 \rightarrow r - \pi^2 D_2 / 4L^2$  as  $s \rightarrow -\infty$  but if  $p > \frac{1}{2}$  then  $\sigma_0 \rightarrow r$  as  $s \rightarrow -\infty$ . The parameter  $p$  describes the rate at which  $\alpha_0(x) \rightarrow 1$  as  $x \rightarrow \infty$ , with a larger value of  $p$  corresponding to a more rapid approach to the limiting value. (If  $\alpha_0$  has the form (5.1) with  $\bar{\alpha} = 1$  then  $\alpha_0(x) \rightarrow 1$  even more rapidly as  $x \rightarrow \infty$  so again  $\sigma_0 \rightarrow r$  as  $s \rightarrow -\infty$ .) The interpretation is that sometimes making the habitat quality in the less favorable region as bad as possible can actually have a beneficial effect on the average growth rate of the population in the overall environment if the degree of aversion to the unfavorable habitat increases rapidly enough as habitat quality decreases. Specifically, this will be the case if  $1 - \alpha(x) \rightarrow 0$  exponentially or with order  $x^{-p}$ ,  $p > \frac{1}{2}$ , as  $x \rightarrow \infty$ . The key factor is again how effective a barrier the unfavorable region or buffer zone is to the dispersal of the population. The idea that buffer zones of lower quality might sometimes be more effective in isolating a refuge from its exterior was suggested by Janzen (1983, 1986) and explored in the context of competition between two species in Cantrell and Cosner (1993). **The most important implication of those works and the above analysis is that the quality of habitat in a buffer zone is not the only factor in determining the benefits or absence thereof to be expected from the buffer zone. The effects of the buffer zone on dispersal and competition (and probably on other things as well) may also be relevant to the effectiveness of a buffer zone.**

## 6. DISCUSSIONS AND CONCLUSIONS

### Conclusions about Mathematical Models

Our basic conclusion about modeling is that it is feasible to incorporate the behavior of individuals at a

patch boundary or an interface between habitat types into diffusion models for population dynamics with dispersal. To do so requires only one additional parameter  $\alpha$  which measures the extent to which individuals are willing to cross the patch boundary or interface. The remaining parameters in our models are diffusion rates and local population growth rates. The parameters related to dispersal could be measured by direct observation of individuals and/or mark and recapture experiments. (Diffusion coefficients are proportional to the mean square distance moved by an individual in unit time, with the constant of proportionality depending on the number of space dimensions.) Local population growth rates correspond to the parameter  $r$  in the logistic equation. They can be estimated from data on reproductive and mortality rates, for example, via construction and evaluation of a Leslie matrix. Diffusion and population growth rates are calculated from demographic data in Andow *et al.* (1990); see also Skellam (1951), Okubo *et al.* (1989), and Okubo (1980). Empirical studies on rates of emigration from (or dispersal between) habitat patches and their surrounding regions include Goszczynski (1979a, b), Wegner and Merriam (1979), Yahner (1983), Bach (1984), and Kareiva (1985). Once the parameters in our models are specified, the analysis can be performed in more or less the same manner as for an ordinary diffusion model with discontinuities in growth or diffusion rates. The point is that our models are feasible in the sense that their calibration and analysis are within the range of existing experimental and analytic techniques.

### **Conclusions about Ecology and Reserve Design**

Some of the conclusions from our models are intuitively obvious. The growth rate  $\sigma_0$  will always increase at least to some extent with increases in the size of either the refuge or the buffer zone or with an increase in the habitat quality inside the refuge. The growth rate  $\sigma_0$  will also increase with an increase in the preference of the population to remain in the refuge. However, this observation should be used with caution in refuge design because it does not take into account the total population. It may be that in some situations dispersal into less favorable regions may decrease the population growth rate but increase the total population; see, for example, the discussion of source-sink dynamics in Pulliam (1988). If the preference of the population to remain in the refuge does not depend on the habitat quality in the buffer zone then increasing the habitat quality in the buffer zone will increase the growth rate. **However, if the preference of the population to remain in the refuge**

**depends on the habitat quality in the buffer zone, then increasing the habitat quality in the buffer zone may either increase or decrease the overall population growth rate.** The situations where the growth rate varies inversely with the habitat quality in the buffer zone are those where the habitat in the buffer zone is of relatively low quality and the behavior of the population at a habitat interface is highly sensitive to habitat quality. The mechanism in this situation is that the aversion of the population to entering the buffer zone may increase more rapidly than do the detrimental effects of low habitat quality in the buffer. Thus, decreasing the habitat quality in the buffer zone may cause it to be a more effective barrier between the refuge and the completely inhospitable regions outside the buffer zone. That such a phenomenon can sometimes occur is one of the suggestions of Janzen (1983, 1986). The situations where the growth rate increases with habitat quality in the buffer zone are those where the population is relatively insensitive to habitat quality in its dispersal patterns and/or the habitat quality in the buffer is relatively high.

Although there is always some increase in the population growth rate corresponding to an increase in the size of the buffer zone, the benefits of increasing the size of the buffer zone are limited in two important ways. First, for a refuge of any fixed size and quality and a buffer zone of any fixed quality there is an upper limit on the possible growth rate that can be achieved by increasing the size of the buffer zone, and that upper bound is lower than the growth rate which could be obtained in a sufficiently large refuge. Second, the relative benefits of increasing the size of the buffer to those of increasing the size of the refuge decrease as the buffer and/or refuge get larger. Thus, from the viewpoint of the population growth rate, **there is generally little point in making buffer zones extremely large, unless their quality is so high that they should really be regarded as refuges.** The situation where increasing the size of the buffer zone is most beneficial is where the refuge and buffer zone are relatively small and where either the preference for remaining in the refuge is strong or the dispersal rate in the buffer zone is low. Thus, **a buffer zone of low to moderate habitat quality is most valuable when it acts as a barrier to dispersal out of a relatively small refuge,** and this effect can often be achieved with buffer zones of moderate size. Again, this result is in philosophical agreement with one of the points raised in Janzen (1983, 1986), namely that the effectiveness of a reserve depends substantially on the extent to which it is insulated from the external environment and that buffer zones can sometimes be most useful when they are good insulators.

In summary, our models predict that buffer zones can be beneficial but there are limits on the extent of those benefits; that the relative benefits of buffer zones decrease as the size of the refuge or buffer zone increases; and that buffer zones of low habitat quality are most effective when they act as barriers to dispersal out of the refuge, e.g., by inducing an aversion to leaving the refuge.

## APPENDIX

In this appendix we shall give some additional details on the computations of  $\partial\sigma_0/\partial L$  and  $\partial\sigma_0/\partial l$  in Section 4. Since the formula used to determine  $\sigma_0$  is different when  $s < \sigma_0$  than it is when  $s > \sigma_0$ , we must consider these cases separately. (See (3.3)–(3.5).) Recall that  $\sigma_0$  is implicitly defined in (3.3) and implicit differentiation yields (as in (4.5))

$$\frac{\partial\sigma_0}{\partial L} = \frac{-[(1-\alpha)/\alpha] D_1(\partial f/\partial L)}{[(1-\alpha)/\alpha] D_1(\partial f/\partial\sigma) - D_2(\partial g/\partial\sigma)} \Big|_{\sigma=\sigma_0} \quad (\text{A.1})$$

$$\frac{\partial\sigma_0}{\partial l} = \frac{D_2(\partial g/\partial l)}{[(1-\alpha)/\alpha] D_1(\partial f/\partial\sigma) - D_2(\partial g/\partial\sigma)} \Big|_{\sigma=\sigma_0} \quad (\text{A.2})$$

and hence

$$\frac{(\partial\sigma_0/\partial l)}{(\partial\sigma_0/\partial L)} = \frac{\alpha D_2}{(1-\alpha) D_1} \left( \frac{(\partial g/\partial l)}{(\partial f/\partial L)} \right) \Big|_{\sigma=\sigma_0}. \quad (\text{A.3})$$

*Case 1:  $s < \sigma_0$ .* Note that this is the relevant case if either  $l$  or  $L$  is large. Since by hypothesis  $s < r$ , we have  $s < r - \pi^2 D_2/4L^2 < \sigma_0$  for  $L$  large (see Fig. 3.1). Similarly as  $l \rightarrow \infty$  we have  $\sigma_0 \rightarrow \sigma^* > s$  (see Fig. 3.2). When  $s < \sigma_0$  (A.1) becomes

$$\begin{aligned} \frac{\partial\sigma_0}{\partial L} &= [2[(1-\alpha)/\alpha] D_1 \csc^2((r-\sigma_0)^{1/2} D_2^{-1/2} L)] \\ &\div \left[ \begin{aligned} &[(1-\alpha)/\alpha] D_1 D_2^{1/2} (r-\sigma_0)^{-3/2} \cot((r-\sigma_0)^{1/2} D_2^{-1/2} L) \\ &+ [(1-\alpha)/\alpha] D_1 L (r-\sigma_0)^{-1} \csc^2((r-\sigma_0)^{1/2} D_2^{-1/2} L) \\ &+ D_2 D_1^{1/2} (\sigma_0-s)^{-3/2} \tanh((\sigma_0-s)^{1/2} D_1^{-1/2} l) \\ &- D_2 l (\sigma_0-s)^{-1} \operatorname{sech}^2((\sigma_0-s)^{1/2} D_1^{-1/2} l) \end{aligned} \right]. \end{aligned} \quad (\text{A.4})$$

Similarly (A.2) becomes

$$\begin{aligned} \frac{\partial\sigma_0}{\partial l} &= [2D_2 \operatorname{sech}^2((\sigma_0-s)^{1/2} D_1^{-1/2} l)] \\ &\div \left[ \begin{aligned} &[(1-\alpha)/\alpha] D_1 D_2^{1/2} (r-\sigma_0)^{-3/2} \cot((r-\sigma_0)^{1/2} D_2^{-1/2} L) \\ &+ [(1-\alpha)/\alpha] D_1 L (r-\sigma_0)^{-1} \csc^2((r-\sigma_0)^{1/2} D_2^{-1/2} L) \\ &+ D_2 D_1^{1/2} (\sigma_0-s)^{-3/2} \tanh((\sigma_0-s)^{1/2} D_1^{-1/2} l) \\ &- D_2 l (\sigma_0-s)^{-1} \operatorname{sech}^2((\sigma_0-s)^{1/2} D_1^{-1/2} l) \end{aligned} \right], \end{aligned} \quad (\text{A.5})$$

and (A.3) becomes

$$\frac{(\partial\sigma_0/\partial l)}{(\partial\sigma_0/\partial L)} = \frac{\alpha D_2 \operatorname{sech}^2((\sigma_0-s)^{1/2} D_1^{-1/2} l)}{(1-\alpha) D_1 \csc^2((r-\sigma_0)^{1/2} D_2^{-1/2} L)}. \quad (\text{A.6})$$

To understand the behavior of the expressions in (A.4) and (A.5) as  $l \rightarrow \infty$  or  $L \rightarrow \infty$  and to compare the numerator and denominator in (A.6) it is convenient to use the matching condition (3.3), which becomes

$$\begin{aligned} &\frac{\cot((r-\sigma)^{1/2} D_2^{-1/2} L)}{(r-\sigma)^{1/2}} \\ &= \frac{\alpha D_2^{1/2}}{(1-\alpha) D_1^{1/2}} \frac{\tanh((\sigma-s)^{1/2} D_1^{-1/2} l)}{(\sigma-s)^{1/2}}. \end{aligned} \quad (\text{A.7})$$

Letting  $T = \tanh((\sigma_0-s)^{1/2} D_1^{-1/2} l)$ ,  $Q = (1-\alpha)/\alpha$ , and applying the appropriate trigonometric and hyperbolic identities we may write (A.4) as

$$\begin{aligned} \frac{\partial\sigma_0}{\partial L} &= 2[QD_1 + QD_2^{-1}(r-\sigma_0)(\sigma_0-s)^{-1} T^2] \\ &\div \left[ \begin{aligned} &\{D_1 Q L (r-\sigma_0)^{-1} - D_2 (\sigma_0-s)^{-1} l\} \\ &+ \{D_1^{1/2} D_2 (r-\sigma_0)^{-1} (\sigma_0-s)^{-1/2} + D_1^{1/2} D_2 (\sigma_0-s)^{-3/2}\} T \\ &+ \{D_2 (\sigma_0-s)^{-1} l + D_2 Q^{-1} (\sigma_0-s)^{-1} L\} T^2 \end{aligned} \right]. \end{aligned} \quad (\text{A.8})$$

Now, by the discussion in the beginning of Section 3, we have  $r - \pi^2 D_2/4L^2 < \sigma_0 < r$ , so as  $L \rightarrow \infty$  we must have  $\sigma_0 \rightarrow r$ . It follows that as  $L \rightarrow \infty$ ,  $T \rightarrow \tanh((r-s) D_1^{-1/2} l)$ . Examining (A.8) we see that as  $L \rightarrow \infty$ , the numerator is bounded while the denominator approaches infinity. Thus, we have  $\lim_{L \rightarrow \infty} (\partial\sigma_0/\partial L) = 0$ . A similar analysis



shows that  $\lim_{L \rightarrow \infty} (\partial\sigma_0/\partial l) = 0$ . Finally, we may rewrite (A.6) as

$$\frac{(\partial\sigma_0/\partial l)}{(\partial\sigma_0/\partial L)} = \frac{D_2(1-T^2)}{(QD_1 + Q^{-1}D_2(r-\sigma)(\sigma-s)^{-1}T^2)}. \quad (\text{A.9})$$

We observe that  $(\partial\sigma_0/\partial l)/(\partial\sigma_0/\partial L) \leq D_2/QD_1 = (\alpha D_2)/(1-\alpha)D_1$  for  $s < \sigma$ . As  $L \rightarrow \infty$ , we have

$$\lim_{L \rightarrow \infty} \frac{(\partial\sigma_0/\partial l)}{(\partial\sigma_0/\partial L)} = \frac{\alpha D_2}{(1-\alpha)D_1} \operatorname{sech}^2[(r-s)^{1/2} D_1^{-1/2} l]. \quad (\text{A.10})$$

The behavior of  $\partial\sigma_0/\partial l$  and  $\partial\sigma_0/\partial L$  as  $l \rightarrow \infty$  can be analyzed similarly using the fact that as  $l \rightarrow \infty$ ,  $\sigma_0 \rightarrow \sigma_* \in (s, r)$  as in (3.6) (see Fig. 3.2). Since  $s < \sigma_* < r$  we have  $\lim_{l \rightarrow \infty} T = \lim_{l \rightarrow \infty} \tanh((\sigma_0 - s)^{1/2} D_1^{-1/2} l) = 1$  as the argument of the hyperbolic tangent approaches infinity.

Thus, by (A.9),

$$\lim_{l \rightarrow \infty} \frac{(\partial\sigma_0/\partial l)}{(\partial\sigma_0/\partial L)} = 0. \quad (\text{A.11})$$

The analysis of  $\partial\sigma_0/\partial L$  and  $\partial\sigma_0/\partial l$  as  $l \rightarrow \infty$  is complicated slightly by the fact that the terms in the denominator of (A.8) and the corresponding formula for  $\partial\sigma_0/\partial l$  which contain factors of  $l$  are of opposite signs. However, those terms may be written as

$$\begin{aligned} & D_2(\sigma_0 - s)^{-1} l [\tanh^2((\sigma_0 - s)^{1/2} D_1^{-1/2} l) - 1] \\ &= -D_2(\sigma_0 - s)^{-1} l [\operatorname{sech}^2((\sigma_0 - s)^{1/2} D_1^{-1/2} l)] \end{aligned}$$

which approaches zero as  $l \rightarrow \infty$  since  $\sigma_0 \rightarrow \sigma_* > s$  and  $\operatorname{sech}$  decays exponentially at infinity. Since  $T \rightarrow 1$  as  $l \rightarrow \infty$  all the other terms in the denominator of (A.8) have finite limits as  $l \rightarrow \infty$ , so

$$\begin{aligned} & \lim_{l \rightarrow \infty} \frac{\partial\sigma_0}{\partial L} \\ &= 2[QD_1 + Q^{-1}D_2(r-\sigma^*)(\sigma^*-s)^{-1}] \\ & \quad \div \left[ D_1QL(r-\sigma^*)^{-1} + D_1^{1/2}D_2(r-\sigma^*)^{-1}(\sigma^*-s)^{-1/2} \right. \\ & \quad \left. + D_1^{1/2}D_2(\sigma^*-s)^{-3/2} + D_2Q^{-1}L(\sigma^*-s)^{-1} \right]. \end{aligned}$$

In the corresponding formula for  $\partial\sigma_0/\partial l$  the numerator contains a factor of  $1-T^2$  which approaches zero as  $l \rightarrow \infty$  while the denominator is the same as for  $\partial\sigma_0/\partial L$ , so we have

$$\lim_{l \rightarrow \infty} \frac{\partial\sigma_0}{\partial l} = 0. \quad (\text{A.12})$$

In the case where  $s < r - \pi^2 D_2 / 4L^2$  the relation  $s < \sigma$  will be maintained as  $l \rightarrow 0$ . In that situation as  $l \rightarrow 0$  we have  $\sigma_0 \rightarrow r - \pi^2 D_2 / 4L^2$  so that  $T = \tanh((\sigma - s)^{1/2} D_1^{-1/2} l) \rightarrow 0$  as  $l \rightarrow 0$ . Thus, if  $s < r - \pi^2 D_2 / 4L^2$  we have

$$\lim_{l \rightarrow 0} \frac{\partial\sigma_0}{\partial L} = \frac{\pi^2 D_2}{2L^3} \quad (\text{A.13})$$

by (A.8); and by (4.9)

$$\lim_{l \rightarrow 0} \frac{\partial\sigma_0/\partial l}{\partial\sigma_0/\partial L} = \frac{\alpha D_2}{(1-\alpha)D_1}. \quad (\text{A.14})$$

Finally we have

$$\lim_{l \rightarrow 0} \frac{\partial\sigma_0}{\partial l} = \frac{\alpha\pi^2 D_2^2}{2(1-\alpha)D_1 L^3}. \quad (\text{A.15})$$

*Case 2:  $s > \sigma_0$ .* The analysis in Section 3 as illustrated by Fig. 3.1 indicates that  $\sigma_0 < s$  if  $s > r - \pi^2 D_2 / 4L^2$  and  $l$  is relatively small. Thus, when  $l$  and  $L$  are both small we must use the formula  $g(\sigma, s, l, D_1) = (s - \sigma)^{-1/2} D_1^{1/2} \tan((s - \sigma)^{1/2} D_1^{-1/2} l)$ . The formulas (A.1)–(A.3) remain valid, but the expressions in (A.4)–(A.6) will change. The expressions correspond to (A.4) is

$$\begin{aligned} & \frac{\partial\sigma_0}{\partial L} \\ &= [2[(1-\alpha)/\alpha] D_1 \csc^2((r-\sigma_0)^{1/2} D_2^{-1/2} L)] \\ & \quad + \left[ \begin{aligned} & [(1-\alpha)/\alpha] D_1 D_2^{1/2} (r-\sigma_0)^{-3/2} \cot((r-\sigma_0)^{1/2} D_2^{-1/2} L) \\ & + [(1-\alpha)/\alpha] D_1 L (r-\sigma_0)^{-1} \csc^2((r-\sigma_0)^{1/2} D_2^{-1/2} L) \\ & - D_2 D_1^{1/2} (s-\sigma_0)^{-3/2} \tan((s-\sigma_0)^{1/2} D_2^{-1/2} l) \\ & + (s-\sigma_0)^{-1} l \sec^2((s-\sigma_0)^{1/2} D_2^{-1/2} l) \end{aligned} \right]. \end{aligned} \quad (\text{A.16})$$

Similarly, corresponding to (A.5) and (A.6) we have

$$\begin{aligned} & \frac{\partial\sigma_0}{\partial l} \\ &= [2D_2 \sec^2((s-\sigma_0)^{1/2} D_1^{-1/2} l)] \\ & \quad + \left[ \begin{aligned} & [(1-\alpha)/\alpha] D_1 D_2^{1/2} (r-\sigma_0)^{-3/2} \cot((r-\sigma_0)^{1/2} D_2^{-1/2} L) \\ & + [(1-\alpha)/\alpha] D_1 L (r-\sigma_0)^{-1} \csc^2((r-\sigma_0)^{1/2} D_2^{-1/2} L) \\ & - D_2 D_1^{1/2} (s-\sigma_0)^{-3/2} \tan((s-\sigma_0)^{1/2} D_1^{-1/2} l) \\ & + (s-\sigma_0)^{-1} l \sec^2((s-\sigma_0)^{1/2} D_2^{-1/2} l) \end{aligned} \right]. \end{aligned} \quad (\text{A.17})$$

and

$$\frac{(\partial\sigma_0/\partial l)}{(\partial\sigma_0/\partial L)} = \frac{\alpha D_2 \sec^2((s-\sigma_0)^{1/2} D_1^{-1/2} l)}{(1-\alpha) D_1 \csc^2((r-\sigma_0)^{1/2} D_2^{-1/2} L)}. \quad (\text{A.18})$$

The behavior of these expressions as  $l \rightarrow 0$  or  $L \rightarrow 0$  may be analyzed as in the case  $s > \sigma_0$  by writing the various terms as expressions in  $\tilde{T} = \tan((s-\sigma_0)^{1/2} D_1^{-1/2} l)$ . (Again, the matching condition (3.3) must be used for some terms.) Note that as  $l \rightarrow 0$  we have  $\tilde{T} \rightarrow 0$  and  $\sigma_0 \rightarrow r - \pi^2 D_2 / 4L^2$ . It turns out that as  $l \rightarrow 0$  the relations (A.13)–(A.15) still hold for  $s > \sigma_0$ . As  $L \rightarrow 0$  we have for  $s > \sigma_0$

$$\lim_{L \rightarrow 0} \frac{\partial\sigma_0}{\partial L} = \frac{2\alpha(r-s + \pi^2 D_1 / 4L^2)}{(1-\alpha)l} \quad (\text{A.19})$$

$$\lim_{L \rightarrow 0} \frac{\partial\sigma_0}{\partial l} = \frac{\pi^2 D_1}{2l^3}, \quad (\text{A.20})$$

so that

$$\lim_{L \rightarrow 0} \frac{(\partial\sigma_0/\partial l)}{(\partial\sigma_0/\partial L)} = \frac{\pi^2 D_1 (1-\alpha)}{4l^2 \alpha (r-s + \pi^2 D_1 / 4L^2)}. \quad (\text{A.21})$$

If  $\alpha \geq \frac{1}{2}$  then  $(1-\alpha)/\alpha \leq 1$ , and since  $r-s > 0$  we must have the right side in (A.21) less than one in that case. The implication of having the right side in (A.21) less than one is that when the refuge is small it is more useful to increase the size of the refuge than the size of the buffer zone.

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## REFERENCES

- Abramsky, Z., and van Dyne, G. M. 1980. Field studies and a simulation model of small mammals inhabiting a patchy environment, *Oikos* **35**, 80–92.
- Andow, D. A., Kareiva, P. M., Levin, S. A., and Okubo, A. 1990. Spread of invading organisms, *Landscape Ecol.* **4**, 177–188.
- Bach, C. E. 1984. Plant spatial pattern and herbivore population dynamics: Plant factors affecting the movement patterns of a tropical cucurbit specialist (*Acalymma Innubum*), *Ecology* **65**, 175–190.
- Benson, D. L., Sherratt, J. A., and Maini, P. K. 1993. Diffusion driven instability in an inhomogeneous domain, *Bull. Math. Biol.* **55**, 365–384.
- Cantrell, R. S., and Cosner, C. 1989. Diffusive logistic equations with indefinite weights: Population models in disrupted environments, *Proc. R. Soc. Edinburgh Sect. A* **112**, 293–318.
- Cantrell, R. S., and Cosner, C. 1991a. The effects of spatial heterogeneity in population dynamics, *J. Math. Biol.* **29**, 315–338.
- Cantrell, R. S., and Cosner, C. 1991b. Diffusive logistic equations with indefinite weights: Population models in disrupted environments II, *SIAM J. Math. Anal.* **22**, 1043–1064.
- Cantrell, R. S., and Cosner, C. 1993. Should a park be an island? *SIAM J. Appl. Math.* **53**, 219–252.
- Cantrell, R. S., and Cosner, C. 1994. Insular biogeographic theory and diffusion models in population dynamics, *Theor. Popul. Biol.* **45**, 177–202.
- Cantrell, R. S., Cosner, C., and Hutson, V. 1993. Permanence in ecological systems with spatial heterogeneity, *Proc. R. Soc. Edinburgh Sect. A* **123**, 533–559.
- Cantrell, R. S., Cosner, C., and Hutson, V. 1996. Ecological models, permanence, and spatial heterogeneity, *Rocky Mountain J. Math.* **26**, 1–36.
- Cosner, C. 1990. Eigenvalue problems with indefinite weights and reaction–diffusion models in population dynamics, in “Reaction–Diffusion Equations” (K. J. Brown and A. A. Lacey, Eds.), pp. 47–137, Clarendon Press, Oxford.
- Dunning, J. B., Jr., Stewart, D. J., Danielson, B. J., Noon, B. R., Root, T. L., Lamerson, R. H., and Stevens, E. E. 1995. Spatially explicit population models: Current forms and future uses, *Ecol. Appl.* **5**, 3–11.
- Freedman, H., and Krisztin, T. 1992. Global stability in models of population dynamics with diffusion in patchy environments, *Proc. R. Soc. Edinburgh Sect. A* **122**, 69–84.
- Freedman, H., and Wu, J. 1992. Steady-state analysis in a model for population diffusion in a multipatch environment, *Nonlinear Anal. T.M.A.* **18**, 517–542.
- Goszczyński, J. 1979a. Density estimation for an urban population of the field mouse, *Acta Theor. Biol.* **24**, 417–419.
- Goszczyński, J. 1979b. Penetration of mammals over urban green spaces in Warsaw, *Acta Theor. Biol.* **24**, 419–423.
- Harrison, J. M., and Shepp, L. A. 1981. On skew Brownian motion, *Ann. Probab.* **9**, 309–313.
- Holmes, E. E., Lewis, M. A., Banks, J. E., and Veit, R. R. 1994. Partial differential equations in ecology: Spatial interactions and population dynamics, *Ecology* **75**, 17–29.
- Ito, K., and McKean, H. P., Jr. 1965. “Diffusion Processes and Their Sample Paths,” Springer-Verlag, New York.
- Janzen, D. H. 1983. No park is an island: Increase in interference from outside as park size decreases, *Oikos* **41**, 402–410.
- Janzen, D. H. 1986. The eternal external threat, in “Conservation Biology: The Science of Scarcity and Diversity” (M. E. Soulé, Ed.), Sinauer, Sunderland, MA.
- Kareiva, P. 1985. Finding and losing host plants by Phyllostreta: Patch size and surrounding habitat, *Ecology* **66**, 1809–1816.
- Kareiva, P. 1990. Population dynamics in spatially complex environments: Theory and data, *Philos. Trans. R. Soc. London Ser. B* **330**, 175–190.
- Kierstead, H., and Slobodkin, L. B. 1953. The size of water masses containing plankton bloom, *J. Mar. Res.* **12**, 141–147.
- Ludwig, D., Aronson, D. G., and Weinberger, H. F. 1979. Spatial patterning of the spruce budworm, *J. Math. Biol.* **8**, 217–258.
- Murray, J. D., and Sperr, R. P. 1983. Minimum domains for spatial patterns in a class of reaction–diffusion equations, *J. Math. Biol.* **18**, 169–184.

- Okubo, A. 1980. "Diffusion and Ecological Problems: Mathematical Models," Springer-Verlag, Berlin.
- Okubo, A., Maini, P. K., Williamson, M. H., and Murray, J. D. 1989. On the spatial spread of the grey squirrel in Britain, *Proc. R. Soc. London Ser. B* **238**, 113-125.
- Pacala, S., and Roughgarden, J. 1982. Spatial heterogeneity and inter-specific competition, *Theor. Popul. Biol.* **21**, 92-113.
- Pulliam, R. 1988. Sources, sinks, and population regulation, *Am. Natur.* **132**, 652-661.
- Shigesada, N., Kawasaki, K., and Teramoto, E. 1986. Travelling periodic waves in heterogeneous environments, *Theor. Popul. Biol.* **30**, 143-160.
- Skellam, J. G. 1951. Random dispersal in theoretical populations, *Biometrika* **38**, 196-218.
- Stamps, J. A., Buechner, M., and Krishnan, V. V. 1987a. The effects of edge permeability and habitat geometry on emigration from patches of habitat, *Am. Natur.* **129**, 533-552.
- Stamps, J. A., Buechner, M., and Krishnan, V. V. 1987b. The effects of habitat geometry on territorial defense costs: Intruder pressure in bounded habitats, *Am. Zool.* **27**, 307-325.
- Strauss, W. 1992. "Partial Differential Equations: An Introduction," Wiley, New York.
- Taira, K. 1988. "Diffusion Processes and Partial Differential Equations," Harcourt Brace Jovanovich, New York.
- Walsh, J. B. 1978. A diffusion with discontinuous local time, *Astérisque* **52-53**, 37-45.
- Wegner, J. F., and Merriam, G. 1979. Movements by birds and small mammals between a wood and adjoining farmland habitats, *J. Appl. Ecol.* **16**, 349-357.
- Wiens, J. A., Stenseth, N. C., van Horne, B., and Ims, R. A. 1993. Ecological mechanisms and landscape ecology, *Oikos* **66**, 369-380.
- Yahner, R. H. 1983. Population dynamics of small mammals in farmstead shelterbelts, *J. Mammal.* **64**, 380-386.

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