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The effects of spatial heterogeneity in population dynamics*

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Abstract. The dynamics of a population inhabiting a heterogeneous environment are modelled by a diffusive logistic equation with spatially varying growth rate. The overall suitability of an environment is characterized by the principal eigenvalue of the corresponding linearized equation. The dependence of the eigenvalue on the spatial arrangement of regions of favorable and unfavorable habitat and on boundary conditions is analyzed in a number of cases.

Key words: Population dynamics – Spatial heterogeneity – Reaction-diffusion equations – Eigenvalue problems – Environmental quality

0. Introduction, modelling, and interpretation

One of the major problems in mathematical ecology is that of describing the effects of spatial dispersal and environmental heterogeneity on the dynamics of populations. A particular aspect of the problem which is of practical importance in refuge design, pest control, and environmental planning is that of determining how the spatial arrangement of favorable and unfavorable habitats affects the overall suitability of an environment for a given population. Our objectives in this article are to use mathematical models to examine which arrangements are most or least favorable in a number of specific situations and then to draw some general conclusions about the significance of various environmental factors by comparing or contrasting different concrete situations. Our models for population dynamics are reaction-diffusion equations with spatially varying coefficients. Such models and their discrete analogues form one of the main classes of models for spatial effects in population dynamics; the other main class consists of models based on island biogeography theory. The advantages of using reaction-diffusion equations as our models are that they can be tailored to fit vairous biological hypotheses via relatively minor adjustments of the coefficients or boundary conditions, and that they operate at the species rather than community level. We

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draw our specific conclusions in a number of special cases by observing how small adjustments affect the predictions of the model. A typical question we address is whether it is better for a population inhabiting an environment containing regions of favorable habitat and regions of unfavorable habitat to have the favorable regions located near the boundary of the environment or far away from the boundary. The answer turns out to depend on the modelling assumptions in a fairly delicate way. We draw our general conclusions by taking an overview of the various special cases. The most striking of the general conclusions is that relatively small changes in the modelling assumptions can have a dramatic effect on the predictions of the model. The practical biological conclusion is that efforts toward refuge design or pest control must be based on a detailed knowledge of the biology of the populations being considered, and that no single approach can be expected to be effective in all situations. Such conclusions have been drawn before, but not on the basis of the type of models we consider here.

The approach we take to modelling the growth and spread of populations is based on ideas introduced in the pioneering work of Skellam [12]. Skellam assumed that the population would disperse through a region Ω via random walks or Brownian motion and would grow according to a linear or logistic growth law with coefficients that might vary with location. The most general sort of models he considered took the form

$$u_t = d\,\Delta u + m(x)u - c(x)u^2 \quad \text{in} \quad \Omega \times (0, \infty), \tag{0.1}$$

supplemented with boundary conditions on $\partial\Omega \times (0, \infty)$ with $d > 0$ representing the rate of diffusion, $m(x)$ the intrinsic rate of population growth or decay at the point x, $c(x) > 0$ the carrying capacity at x, and u the density of the population. Typical boundary conditions would be $u = 0$ on $\partial\Omega$, corresponding to a completely hostile exterior region, $\partial u/\partial n = 0$ on $\partial\Omega$, corresponding to the boundary acting as a perfect barrier to the population, or $\beta u + \partial u/\partial n = 0$ on $\partial\Omega$ for some $\beta > 0$, corresponding to a situation where some members of the population that reached the boundary of Ω would die and others would turn back. (A slightly different modelling approach leading to equivalent boundary conditions, at least for steady state solutions, is given in [5].) Models similar to (0.1) have been widely used in population dynamics; for further discussion and references, see [4, 10]. Because of the limitations of the analytical techniques available to Skellam when he considered models such as (0.1) in 1951, he was only able to treat certain special cases where the coefficients were constants and the domain Ω had simple geometry. A typical result of [12] is that the simple model

$$\begin{aligned} &u_t = d\,\Delta u + mu && \text{on } \{(x, y) \colon x^2 + y^2 < R^2\} \times (0, \infty), \\ &u = 0 && \text{on } \{(x, y) \colon x^2 + y^2 = R^2\} \times (0, \infty), \end{aligned} \tag{0.2}$$

predicts growth of the population if $d < m/\lambda_1$, and decay if $d > m/\lambda_1$, where λ_1 is the first eigenvalue for the problem

$$\begin{aligned} -\Delta\phi &= \lambda\phi && \text{on } \{(x, y) \colon x^2 + y^2 < R^2\}, \\ \phi &= 0 && \text{on } \{(x, y) \colon x^2 + y^2 = R^2\}, \end{aligned}$$

that is, $\lambda_1 = j_1^2/R^2$ where j_1 is the first zero of the Bessel function $J_0(r)$. A similar but distinct point of view was taken by Ludwig et al. [5] in their study of the minimal domain size needed to sustain a refuge or an outbreak for the spruce budworm. They considered a model of the form

$$u_t = du_{xx} + f(u) \quad \text{on } (0, l) \times (0, \infty),$$

with boundary conditions as described above, where $f(u) = u - u^2/Q - u^2/R(1+u^2)$ for some constants Q and R. They also gave a discussion of diffusive logistic equations. Their analysis was based on determining the existence or nonexistence of nonzero steady states for their models. Their conditions for existence of a small (refuge) nonzero steady state for the spruce budworm or any nonzero steady state for the diffusive logistic equation were similar to those given in [12] in that they required d to be smaller than the reciprocal of the first eigenvalue of the operator $-d^2/dx^2$ subject to the given boundary conditions. Since the size of that eigenvalue depends on the length of the spatial interval $(0, l)$, their results gave information on the minimum size of regions that could sustain nonzero populations. Murray and Sperb [8] extended some of the results of [5] to cases where the domain was two dimensional and where the population was subject to drift due to winds or currents rather than dispersing via pure diffusion. Many of their results were essentially estimates of the first eigenvalues of the elliptic operators describing the dispersal of the populations under consideration. Our modelling approach follows the general lines of those in [5, 8, 12], but we focus our attention more closely on the effects of variations in habitat quality as described by $m(x)$ and on the interaction of variations in $m(x)$ with boundary effects.

We use models of the form (0.1) to describe the dynamics of our populations. We have shown in [2] that such models predict persistence if $d < 1/\lambda_1(m)$ and extinction if $d \geqslant 1/\lambda_1(m)$, where $\lambda_1(m)$ is the principal eigenvalue of the problem

$$-\Delta\phi = \lambda m(x)\phi \quad \text{in } \Omega, \tag{0.3}$$

subject to the same boundary conditions that are imposed on the population density. Our models differ from those of [5, 8] in that we allow $m(x)$ to change sign in Ω. (That a problem such as (0.3) admits a principal eigenvalue even when $m(x)$ may change sign is not obvious, but can be derived from variational principles under appropriate hypotheses; see [1, 2, 3, 7].) We introduce the spatial variation in $m(x)$ because we wish to study how the arrangement of favorable ($m(x) > 0$) and unfavorable ($m(x) < 0$) habitats affects the dynamics of a population. Following [5, 8, 12] we use the principal eigenvalue $\lambda_1(m)$ of (0.3) as a measure of overall environmental suitability for the population. The larger the value of $\lambda_1(m)$, the smaller the diffusion coefficient d must be to allow persistence; in fact, in [2] we obtained estimates in terms of the quantity $-d + 1/\lambda_1(m)$ on the size of steady state populations when (0.1) admits steady states and on the rate of decrease of the population in situations where (0.1) predicts extinction. Similar sorts of results in different contexts are also given in [5, 8, 12]; in view of those, the use of $\lambda_1(m)$ as a measure of environmental suitability seems reasonable.

In the present article we closely examine a number of situations where the spatial domain for the population is one dimensional and where the local growth rate of the population is piecewise constant, that is, $m(x) = m_1 > 0$ on part of the domain and $m(x) \equiv -m_2 < 0$ on the remainder. We derive estimates which suggest the following conclusions: generally, it is better for the population to have a few large regions of favorable habitat than a great many small ones closely intermingled with unfavorable regions; however, the location of the favorable and unfavorable regions relative to the boundary also has a significant effect on the suitability of the overall environment, and the nature of the arrangements relative to the boundary which are best for the population varies with the type of boundary conditions the population is assumed to satisfy. Since we shall find that changing the assumptions on the boundary can change the most favorable arrangement in a given class to the least favorable, it is clear that a great deal of attention must be given to details of the underlying biology if we wish to obtain accurate environmental assessments from mathematical models. The importance of detailed biological information has been discussed at length in the biological literature on conservation; see for example [13]. One of the objectives of this article is to show how some of that complex dependence on fine details is reflected even in relatively simple mathematical models.

We note that our conclusions are spiritually similar to those in Seno [11]. Seno studied the persistence of a population distributed over patches in a one dimensional environment. He assumed there was precisely one patch (which he called a singular patch) within which emigration and growth rates were different from the corresponding rates within the other patches. He modelled the dynamics of the population by a first-order system of linear ordinary differential equations of the form

$$\begin{bmatrix} x_1(t) \\ \vdots \\ x_n(t) \end{bmatrix} = M \begin{bmatrix} x_1(t) \\ \vdots \\ x_n(t) \end{bmatrix},$$

where n is the number of patches in the system, M is a constant $n \times n$ matrix, and $x_i(t)$ is the population density of the ith patch of time t. In this context, the population becomes extinct if all the eigenvalues of the matrix M have negative real parts and grows infinitely otherwise. Consequently, Seno determined persistence or extinction of the population in question from the sign of the maximum real part of the eigenvalues of M and investigated the dependence of this quantity on the location of the singular patch, the degree of difference between the growth and extinction rates in the singular patch and the corresponding rates in the other patches, and the total number of patches. Such models may be viewed as discrete analogues to the linearization of the models considered in this paper in the case of zero Dirichlet boundary conditions. Moreover, in [11] and this paper, an eigenvalue is used to quantify the notion of environmental suitability, and the dependence of this quantity on various environmental factors is illustrated via particular examples. For instance, Seno noted that a region of especially favorable or unfavorable habitat has a greater impact on the overall suitability of the environment if it is centrally located than it does if it is near a boundary. This conclusion is similar to those we draw in Sect. 1 of this paper. In [11], Seno did not treat the case corresponding to Neumann boundary conditions, as that case introduces additional technical details in the analysis of discrete models, but remarked that consideration of the nature of the boundary or edge effects may sometimes be biologically significant. Our results in Sect. 2 give some insight into the sensitivity of continuous models to the nature of boundary conditions.

Another modelling approach which has been widely used to describe the effects of habitat size and location on populations is based on the theory of island biogeography. A fundamental work on that topic is [6]; see also [4]. In its simplest form, island biogeography theory predicts that the number of species, denoted by S, on an island of area A in a hypothetical archipelago will be related to A by the formula $S = CA^z$ for some positive constants C and z, with $z \approx 0.27$.

The theoretical predictions are supported by data from various island chains, with values of z typically ranging between 0.20 and 0.35; see [6]. Such results and observations suggest that at the community level, one large preserve may be a better refuge than several smaller preserves of the same habitat type. Some empirical support for that viewpoint is given in [9], but it has also been criticized on various grounds as being oversimplified or sometimes inappropriate; see [13] for a discussion and references to the ecological literature. The models we discuss describe populations rather than communities, but they partially support the sort of conclusions which have been drawn from island biogeography. However, our models also suggest that sometimes a few smaller preserves may form a more effective refuge than a single larger preserve, depending on location, boundary effects, or other environmental details. An advantage of our modelling approach is that we can "fine tune" our models to some extent to explore the interactions of geographical effects. A disadvantage to both our viewpoint and that of island biogeography is that while the populations involved may be viewed as dynamic, the environment must generally be regarded as static. Thus, neither approach is really suitable for describing "fugitive species" which typically inhabit transitional environments; again, see [13] for a biological discussion. Probably some new modelling and analysis will be needed to treat situations where both spatial and temporal variation in the environment are important.

We shall now state and interpret our mathematical results. Some of these are taken from [2], which includes a fairly complete analysis of the theoretical aspects of models such as (0.1). The remainder are derived in the later sections of the present article. The analysis in [2] is moderately technical, but that used here is elementary, being based primarily on applications of calculus and the properties of trigonometric and hyperbolic functions. We shall sometimes need to refer to the spaces $L^p(\Omega)$ of functions on Ω whose pth powers are integrable; for $u \in L^p(\Omega)$, we denote the norm of u in $L^p(\Omega)$ by $\|u\|_p = (\int_\Omega |u|^p\,dx)^{1/p}$ for $1 \leqslant p < \infty$, with $\|u\|_\infty$ being the essential supremum of $|u|$. (If $u \geqslant 0$ represents a population density, $\|u\|_1$ represents the total population and $\|u\|_\infty$ represents the maximum density if such a maximum exists.)

Result. Suppose that Ω is a bounded region in 1, 2, or 3 dimensional space, c and d are positive constants, and $m(x)$ is a bounded measurable function with $m(x) > 0$ on a set of positive measure. (We will primarily be concerned with the case where Ω is an interval and $m(x)$ is piecewise constant with $m(x) > 0$ on a subinterval.) Let Δ denote the operator d^2/dx^2 in one dimension or the Laplacian in two or more dimensions. The model (0.1) with boundary condition $u = 0$ on $\partial\Omega \times (0, \infty)$ has a positive steady state which is a global attractor for nontrivial nonnegative solutions if and only if $d < 1/\lambda_1(m)$, and $\|u\|_1 \to 0$ exponentially with rate proportional to $-d + 1/\lambda_1(m)$ as $t \to \infty$ for any nonnegative solution of (0.1) if $d > 1/\lambda_1(m)$, where $\lambda_1(m)$ is the smallest positive eigenvalue of the linear problem (0.3) with boundary condition $\phi = 0$ on $\partial\Omega$.

Remarks. The results on (0.1) are proved in [2], where it is also shown that the steady states determine the dynamics. The existence of positive eigenvalues for (0.3) under homogeneous Dirichlet boundary conditions follows from results of [3, 7]. The first positive eigenvalue of (0.3) is characterized by its possession of a positive eigenfunction; that can be deduced from the variational formulation of the problem as in the classical case. An analysis similar to that of [2, 3, 7] could be given for mixed boundary conditions of the type $\beta u + \partial u/\partial n = 0$ on $\partial\Omega \times (0, \infty)$ with $\beta > 0$. The case of the Neumann or no-flux boundary condition $\partial u/\partial n = 0$ is somewhat different. In that case, (0.3) does not admit a positive eigenvalue with positive eigenfunction unless $m(x)$ changes sign in Ω and $\int_\Omega m(x)\,dx < 0$; see [1]. If $\int_\Omega m(x)\,dx < 0$ but $m(x) > 0$ on a set of positive measure then the conclusions stated above for (0.1) under the boundary condition $u = 0$ on $\partial\Omega \times (0, \infty)$ could be extended to the case $\partial u/\partial n = 0$ on $\partial\Omega \times (0, \infty)$. The specific form of density dependence shown in (0.1) is not crucial; many results in [2] are given for growth terms of the form $f(x, u)u$ where $f(x, 0)$ changes sign in Ω and $f(x, u)$ is decreasing with respect to u. If $f(x, u)$ admits depensation, that is, if $f(x, u)$ increases in u for some ranges of u and/or x, then the derivations in [2] are no longer valid; however, the sign of $-d + 1/\lambda_1(m)$ still determines the local stability or instability of the extinction state.

Interpretation. The quantity $-d + 1/\lambda_1(m)$ is crucial in deciding the predictions of (0.1), and in particular the model predicts persistence for the population if $-d + 1/\lambda_1(m) > 0$ and extinction if $-d + 1/\lambda_1(m) < 0$. On that basis it is reasonable to use $-d + 1/\lambda_1(m)$ as a measure of overall environmental suitability. Since $-d + 1/\lambda_1(m)$ depends inversely on $\lambda_1(m)$ for fixed d, large values of $\lambda_1(m)$ correspond to relatively unsuitable environments for the population modelled in (0.1) while a small value of $\lambda_1(m)$ correspond to more suitable arrangements. (The steady states of (0.1) determine the dynamics of the model, so our population need not be near equilibrium for the analysis to be valid; however, the environment must be in equilibrium. The results of [2] could probably be extended to some time periodic models, but not to models for more general time dependent environments.)

Result. Suppose that $\{m_j(x)\}$ is a sequence of bounded measurable functions on Ω with $m_j(x) > 0$ on a set of positive measure for each j and with $|m_j(x)| \leqslant M$ for some constant M and all j. If $\lambda_1(m_j)$ is the principal eigenvalue for (0.3) with growth rate $m_j(x)$, then $\lambda_1(m_j) \to \infty$ as $j \to \infty$ if and only if $\limsup_{j\to\infty} \int_\Omega m_j(x)\psi(x)\,dx \leqslant 0$ for all nonnegative integrable functions $\psi(x)$ on Ω.

Remarks. This is Theorem 3.1 of [2]; we derive a number of related results in that article.

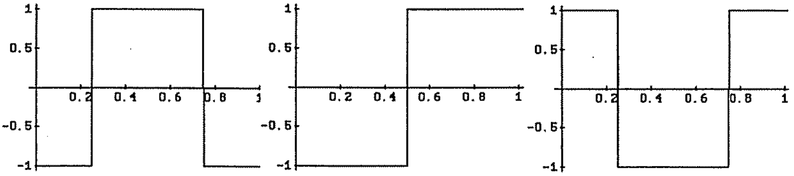
Interpretation. The condition $\limsup_{j\to\infty} \int m_j(x)\psi(x)\,dx \leqslant 0$ for all $\psi \geqslant 0$ says essentially that the average value of the functions m_j over any subset of Ω goes to zero or becomes negative for j taken sufficiently large. Clearly this can occur if the growth rates m_j decrease toward zero uniformly on Ω so that there is eventually nowhere that the population can grow. It can also occur if the functions $m_j(x)$ maintain large positive values at some points but have corresponding negative values at others, with the positive and negative regions closely intermingled. For example, $\int_0^\pi \sin(jx)\psi(x)\,dx \to 0$ as $j \to \infty$ for any integrable $\psi(x)$. Although $\sin(jx) = 1$ at some points of $[0, \pi]$ for all j, the *average* of $\sin(jx)$ on any subinterval goes to zero as $j \to \infty$ and $\sin(jx)$ becomes more highly oscillatory. The biological significance of such a result is that even if some fixed percentage of a region is maintained as favorable habitat for some population modelled by (0.1), the model will still predict extinction if the favorable regions are too small and too close to unfavorable regions. Thus, it is not only the amount of favorable habitat but also its arrangement that determines the overall suitability of the environment. This interpretation tends to support the viewpoint that a few large reserves may be more effective for conservation than a great many small ones; however, the size at which reserves will lose their effectiveness may be very small. Numerical experiments indicate that several medium sized preserves may sometimes represent a better refuge (as measured by $\lambda_1(m)$ and related quantities) than a single large preserve. One reason for this, noted in the next results, is the presence of boundary effects in the model. Since boundary effects are likely to be present in real situations, it is important to consider them in our models.

Results. Let Ω be the one dimensional interval $(0, 1)$. First suppose that $m(x) \equiv m_1 > 0$ on a single subinterval of length T and $m(x) \equiv -m_2 < 0$ on the remainder of $(0, 1)$. Under the boundary condition $\phi = 0$ at $x = 0, 1$, the smallest value of $\lambda_1(m(x))$ with $m(x)$ so restricted occurs when the subinterval where m is positive is at the center of the interval $(0, 1)$ and the largest value of $\lambda_1(m)$ occurs when this subinterval is at one of the ends of the larger interval. Next, suppose that the region where $m(x) \equiv -m_2 < 0$ is a single subinterval of length $1 - T$, with $m(x) \equiv m_1 > 0$ elsewhere. Under the same boundary conditions on ϕ, the smallest value for $\lambda_1(m(x))$ with $m(x)$ now restricted in that way occurs when the subinterval where $m(x)$ is negative is at one of the ends of the larger interval $(0, 1)$.

Remarks. These results are derived in Sect. 1 of this article. The derivations give some additional mathematical detail. (In the derivation we assume that m_2 has been rescaled to the value 1; there is no loss of generality with such a rescaling.)

Interpretation. The above results indicate that under boundary conditions associated with a completely hostile exterior region a single favorable region in the center is more suitable than a single favorable region of the same size near the boundary, and that in turn is more suitable than a pair of favorable regions of the same total size with both favorable regions at the boundary. A graphical description is given in Fig. 1. It is not too surprising that centering the favorable interval gives a more suitable environment than locating it at a boundary, since the unfavorable interior regions can insulate the population somewhat from the completely hostile exterior if the favorable region is far from the boundary. Similarly, a single favorable region in contact with the boundary is better than two separate favorable regions both in contact with the boundary. We shall see that if we replace the assumption of a lethal boundary with that of a boundary acting as a barrier, the conclusions change radically.

Result. Again let Ω be the interval $(0, 1)$ and suppose that $m(x) \equiv m_1 > 0$ on a single subinterval of length T and $m(x) \equiv -m_2 < 0$ on the remainder of the interval, with $m_1 T - m_2(1 - T) < 0$. Under the boundary condition $\partial\phi/\partial n = 0$



Most favorable Intermediate Less favorable

Fig. 1. Comparison of the overall suitabilities of environments with different spatial arrangements of the regions of good and bad habitat, assuming a lethal boundary

(i.e. $\phi'(x) = 0$) at $x = 0, 1$, the smallest value of $\lambda_1(m(x))$ with $m(x)$ so restricted occurs when the subinterval where $m(x)$ is positive is at one of the ends of the interval (0, 1) and the largest value occurs when the subinterval of positivity is in the center of the larger interval. If we restrict $m(x)$ so that $m(x) \equiv -m_2 < 0$ on a single subinterval of length $1 - T$ and $m(x) \equiv m_1 > 0$ on the remainder of (0, 1), then under the same boundary conditions the smallest value for $\lambda_1(m(x))$ occurs when the subinterval where m is negative is at one of the ends of (0, 1).

Remarks. These results are derived in Sect. 2. The requirement $m_1 T - m_2(1 - T) < 0$ is imposed so that $\int_0^1 m(x)\,dx < 0$ and hence $\lambda_1(m(x))$ exists; see [1]. Again, in the derivation, we have rescaled $m(x)$ so that $m_2 = 1$.

Interpretation. Under boundary conditions describing a boundary that acts as a perfect barrier, a single favorable region near the boundary provides a more suitable overall environment than either a single favorable region far from the boundary or a pair of favorable regions of the same total size lying near the boundary but separated by an unfavorable region. A graphical description is given in Fig. 2. An especially interesting observation is that in the situation where there is a single favorable interval, the arrangement best for the population under the assumption of a deadly boundary is the worst arrangement under the assumption that the boundary acts as a barrier. The obvious question of deciding what happens in intermediate cases is addressed in the next result.

Result. Suppose that $m(x) \equiv 1$ on a subinterval of length T of (0, 1) and $m(x) \equiv -1$ elsewhere. Suppose that $\lambda_1(m)$ is the principal eigenvalue for (0.3) under the boundary condition $\beta\phi + \partial\phi/\partial n = 0$ on $\partial\Omega$ (i.e. $\beta\phi - \phi' = 0$ at $x = 0$ and $\beta\phi + \phi' = 0$ at $x = 1$) for some $\beta > 0$. If $0 < \beta < \pi/2T$ then the largest value for $\lambda_1(m)$ occurs when the interval where m is positive is in the center of the larger interval and the smallest value occurs when this interval is at one of the ends. If $\beta > \pi/2T$ then the smallest value of $\lambda_1(m)$ occurs when the subinterval where m is positive is in the center and the largest value when it is at one of the ends. If $\beta = \pi/2T$ then the location of the positive subinterval does not affect $\lambda_1(m)$, which in that case is $\pi^2/4T^2$.

Remarks. This result is proved in Sect. 2.

Interpretation. This result indicates that for a relatively hostile exterior (β large) the behavior of the model is similar to that corresponding to a completely inhospitable exterior, while for a relatively benign exterior or a boundary that acts as a moderately effective barrier, the behavior is similar to that correspond-

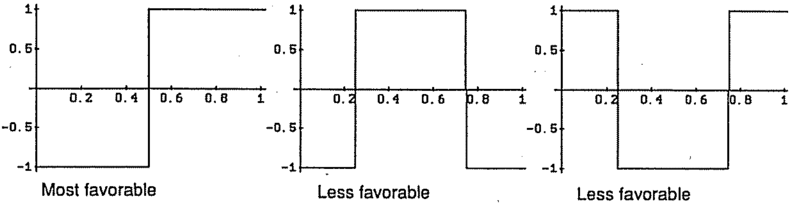


Fig. 2. Comparison of the overall suitabilities of environments with different spatial arrangements of the regions of good and bad habitat, assuming a boundary that acts as a barrier

ing to a boundary which acts as a perfect barrier. The difference between the cases occurs because the detrimental effects of the unfavorable region inside (0, 1) as measured by $m(x)$ may be stronger or weaker than those produced by the boundary effects, as measured by β. If the level of hostility on the interior unfavorable region is the same as that of the exterior, the location of the favorable region becomes irrelevant, and that is reflected in the transitional case corresponding to $\beta = \pi/2T$.

We shall draw some general conclusions from the above results, but first we state one more result of a slightly different nature:

Result. Suppose that $m(x)$ has the form $m(x) = -1$ on $(0, (1-T)/2)$ and on $((1+T)/2, 1)$ and $m(x) = k$ on $((1-T)/2, (1+T)/2)$ where k and T are related in such a way that $\int_0^1 m(x)\,dx = q$ for some fixed constant $q < 1$, and that the boundary condition for (1.3) is $\phi = 0$ on $\partial\Omega$. If k is allowed to range between q and 1 (so that T ranges from 1 to $(1+q)/2$) then the largest value for $\lambda_1(m)$ occurs when $k = q$ and the smallest when $k = 1$.

Remarks. This is proved in Sect. 1.

Interpretation. This result indicates that in the case of a spatially heterogeneous environment surrounded by a hostile exterior region, there are distributions of favorable and unfavorable habitats wherein a small preserve of high quality habitat may provide for a more suitable overall environment than a larger preserve of favorable but lower quality habitat. Such may be due in part to the fact that expanding the favorable region moves its edges close to the boundary. The situation for the case of a boundary acting as a barrier is similar in a sense but more extreme. In that case, we can only use the analysis based on $\lambda_1(m)$ when $\int_0^1 m(x)\,dx < 0$, so that if we increase the length of the more favorable interval but decrease the favorability so that $\int_0^1 m(x)\,ds$ remains constant we must eventually have $m(x) < 0$ everywhere so that no growth is possible.

We now draw some more general conclusions by surveying and synthesizing the results described above. The first observation is that these simple models display enough different effects and sensitivity to modelling assumptions to describe some of the complexities of the underlying biology, and that they permit analysis which provides both support and criticism for conclusions made from other viewpoints. To briefly summarize the analysis, these models predict that a preserve of moderate size and high quality can be expected to provide a better refuge than a great many very small preserves and can sometimes provide a better refuge than a larger preserve of lower quality; however, the location of preserves also plays a role in the predictions of the models so that a single large preserve in a relatively poor location may be less desirable than several smaller ones in better locations, and which locations are better depends on the nature of the boundary and exterior of the total environment being considered. Some of these conclusions can be drawn from different modelling approaches such as island biogeography theory (see [9]). Others have been discussed and debated to a considerable extent from nonmathematical viewpoints (see [13] and the references therein). Our results suggest that there is no simple criterion which permits evaluation of a broad range of situations, but rather that several different sorts of biological effects must be considered if we wish to make reasonable projections. That leads us to our second observation, which echoes a common theme in the nonmathematical literature on environmental heterogeneity and refuge design; namely, that accurate assessment of environmental suitability requires a knowledge of specific details of the biology and geography involved. Our final conclusion is that simple reaction-diffusion models can capture enough biological detail that further investigation of such models can be expected to provide additional insight into the effects of spatial dispersal and heterogeneity in population ecology.

1. Homogeneous Dirichlet boundary data

We begin by supposing that $T \in (0, 1)$ is fixed and that for $a \in [0, 1-T]$,

$$m_a(x) = \begin{cases} -1 & \text{on } [0, a) \\ k & \text{on } [a, a+T], \\ -1 & \text{on } (a+T, 1] \end{cases}$$

where k is an arbitrary positive constant. As the map $a \to m_a$ is a continuous function from $[0, 1-T]$ into $L^p[0, 1]$, $1 \leqslant p < \infty$, we know that $\lambda_1(m_a)$ is a continuous real valued function of a, where $\lambda_1(m_a)$ denotes the unique positive eigenvalue of

$$\begin{aligned} -u'' &= \lambda m_a u \quad \text{in } (0, 1), \\ u(0) &= 0 = u(1), \end{aligned} \tag{1.1}$$

for which (1.1) admits a solution $u(x)$ such that $u(x) > 0$ for $x \in (0, 1)$, $u'(0) > 0$ and $u'(1) < 0$.

Moreover, we also know that according to our modelling (see Sect. 0) the smaller the number $\lambda_1(m_a)$ the more advantageous the situation for the species in question. The question we now pose is, for which value(s) of $a \in [0, 1]$ does $\lambda_1(m_a)$ obtain its minimum? Notice that we may take as eigenfunction for (1.1) $u_a(x)$, where

$$u_a(x) = \begin{cases} \sinh \alpha\lambda, & 0 \leqslant x \leqslant a \\ A \cos \alpha\sqrt{k}(x-c), & a \leqslant x \leqslant a+T \\ B \sinh \alpha(1-x), & a+T \leqslant x \leqslant 1, \end{cases}$$

where $\alpha = \sqrt{\lambda(m_a)}$, $c \in (a, a+T)$, and $A, B > 0$. Matching $u_a(x)$ and $u_a'(x)$ across the interfaces at a and at $a+T$ yields

$$\begin{aligned} \sinh \alpha a &= A \cos \alpha\sqrt{k}(a-c), \\ \alpha \cosh \alpha a &= -\alpha A\sqrt{k} \sin \alpha\sqrt{k}(a-c) \end{aligned}$$

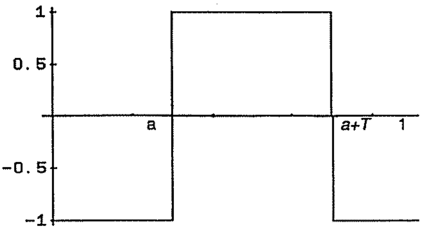


Fig. 3. An example of a spatially varying growth rate showing regions of good and bad habitat

and

$$A\cos\alpha\sqrt{k}(a+T-c)=B\sinh\alpha(1-(a+T)),$$
$$-\alpha A\sqrt{k}\sin\alpha\sqrt{k}(a+T-c)=-\alpha B\cosh\alpha(1-(a+T)).$$

These equations reduce to

$$\tanh\alpha a=-\frac{1}{\sqrt{k}}\cot\alpha\sqrt{k}(a-c)$$

and (1.2)

$$\frac{1}{\sqrt{k}}\cot\alpha\sqrt{k}(a+T-c)=\tanh\alpha(1-(a+T)).$$

From (1.2) it follows that

$$\begin{aligned}\cot\alpha\sqrt{k}T&=\cot(\alpha\sqrt{k}(a+T-c)-\alpha\sqrt{k}(a-c)) \qquad (1.3)\\ &=\frac{\cot(\alpha\sqrt{k}(a+T-c))\cot(\alpha\sqrt{k}(a-c))+1}{\cot(a\sqrt{k}(a-c))-\cot(\alpha\sqrt{k}(a+T-c))}\\ &=\frac{k\tanh[\alpha(1-a-T)]\tanh\alpha a-1}{\sqrt{k}(\tanh\alpha a+\tanh\alpha(1-a-T))}\\ &=f(a,\alpha).\end{aligned}$$

We know from the positivity of u_a on $(0, 1)$ that $\alpha\in(0,\pi/\sqrt{kT})$. It is of course well known that $\cot(\alpha\sqrt{kT})$ is a strictly decreasing function on $(0,\pi/\sqrt{kT})$ with $\lim_{\alpha\to0+}\cot(\alpha\sqrt{kT})=+\infty$ and $\lim_{\alpha\to\pi/\sqrt{kT}-}\cot(\alpha\sqrt{kT})=-\infty$. If we now fix $a\in[0,1-T]$, then it is evident that $\lim_{\alpha\to0+}f(a,\alpha)=-\infty$, and moreover, calculation shows that $\partial f/\partial\alpha(a,\alpha)>0$ for all $\alpha>0$. Consequently, for $a\in[0,1-T]$ fixed, there is a unique $\alpha\in(0,\pi/\sqrt{kT})$ for which (1.3) holds. This value is $\sqrt{\lambda_1(m_a)}$ and the curves $y=\cot\alpha\sqrt{kT}$ and $y=f(a,\alpha)$ intersect as indicated in Fig. 4. It is evident from Fig. 4 that if the graph of the curve $y=f(a,\alpha)$ moves up corresponding to a change in the parameter a, then the α-coordinate of the point of intersection of $y=\cot\alpha\sqrt{kT}$ and $y=f(a,\alpha)$ moves

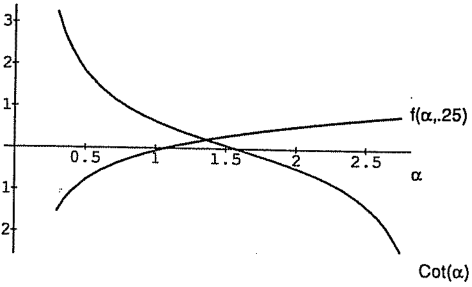


Fig. 4. Graphical determination of α in the case of a single region of good habitat and a lethal boundary

to the left. Hence if $\partial f/\partial a(a, \alpha) > 0$ for $\alpha \in (0, \pi/\sqrt{k}T)$ and $a \in I$, a subinterval of $[0, 1-T]$, $\lambda_1(m_a)$ decreases on I. From the quotient rule, it follows that for any $\alpha > 0$ and $a \in (0, 1-T)$, the sign of $\partial f/\partial a(a, \alpha)$ is determined by

$$\begin{aligned} R(a, \alpha) &= (\operatorname{sech}^2 \alpha a)(1 + k \tanh^2 \alpha(1-a-T)) \\ &\quad - (\operatorname{sech}^2 \alpha(1-a-T))(1 + k \tanh^2 \alpha a). \end{aligned}$$

A simple calculation reveals that the auxiliary function

$$H(x) = \frac{1 + k \tanh^2 x}{\operatorname{sech}^2 x}$$

is one-to-one on $(0, \infty)$. Then $R(a, \alpha) = 0$ implies

$$\frac{1 + k \tanh^2 \alpha(1-a-T)}{\operatorname{sech}^2 \alpha(1-a-T)} = \frac{1 + k \tanh^2 \alpha a}{\operatorname{sech}^2 \alpha a}.$$

Since H is one-to-one, $1 - a - T = a$ or $a = (1-T)/2$. Moreover, it is easy to see that

$$\lim_{a \to 0+} R(a, \alpha) = 1 + k \tanh^2 \alpha(1-T) - \operatorname{sech}^2 \alpha(1-T) > 0$$

and

$$\lim_{a \to (1-T)-} R(a, \alpha) = \operatorname{sech}^2 \alpha(1-T) - 1 - k \tanh^2 \alpha(1-T) < 0,$$

for $\alpha > 0$ fixed. So $\partial f/\partial a(a, \alpha) > 0$ for $a \in (0, (1-T)/2)$ and $\alpha > 0$ and $\partial f/\partial a(a, \alpha) < 0$ for $a \in ((1-T)/2, 1-T)$ and $\alpha > 0$. Consequently, $f(a, \alpha)$ increases on $(0, (1-T)/2)$ and decreases on $((1-T)/2, 1-T)$ for all $\alpha > 0$. It follows that $\lambda_1(m_a)$ decreases steadily as a approaches the centering value $(1-T)/2$.

One may conclude that for the models

$$\begin{aligned} &u_t = du_{xx} + m_a u - cu^2 && \text{in } (0, 1) \times (0, \infty), \\ &u(x, 0) \geqslant 0 && \text{in } (0, 1), \\ &u(0, t) = 0 = u(1, t) && \text{in } [0, \infty) \end{aligned}$$

the situation for the population becomes progressively better as a approaches $(1-T)/2$. Since $a = (1-T)/2$ corresponds to a centering of the region where the growth rate is 1, these results suggest that such a strategy is the optimal approach for preservation of a population in a habitat surrounded by a completely inhospitable region (as indicated by homogeneous Dirichlet boundary data), independent of the relative strength of the positive and negative parts of the intrinsic growth rate.

So far in this section, we have dealt with the situation where the intrinsic growth rate is positive and constant on a subinterval of $[0, 1]$ having length T and is equal to -1 on the remainder of $[0, 1]$. A complementary situation occurs if there is a single subinterval upon which the intrinsic growth rate $m = -1$ and if the intrinsic growth rate is a positive constant on the complement in $[0, 1]$ of this subinterval. In particular, if the regions on which the intrinsic growth rate is positive have total length T, we may write

$$m_a(x) = \begin{cases} k & \text{on } [0, a) \\ -1 & \text{on } [a, a+1-T] \\ k & \text{on } (a+1-T, 1], \end{cases}$$

where $k > 0$ is fixed and $a \in [0, T]$. Then there is an eigenfunction $u_a(x)$ of (1.2) of the form

$$u_a(x) = \begin{cases} \sin(\alpha\sqrt{k}x), & x \in [0, a] \\ \gamma_1 \cosh \alpha x + \gamma_2 \sinh \alpha x, & x \in [a, a+1-T] \\ C \sin(\alpha\sqrt{k}(x-1)), & x \in [a+1-T, 1], \end{cases}$$

where γ_1, γ_2 and C are constants determined by the normalization $u_a(x) = \sin(\alpha\sqrt{k}x)$ on $[0, a]$ and $C < 0$. Since $u_a \in C^1[0, 1]$, the values of γ_1 and γ_2 can be determined by matching across the interface at a or at $a + 1 - T$. This process produces two sets of equations for γ_1 and γ_2. Using these equations, we may derive that α must satisfy

$$\begin{aligned}&\sqrt{k}\cosh(\alpha(1-T))\sin(\alpha\sqrt{k}T) \\ &= \frac{\sinh(\alpha(1-T))}{2}\{(1-k)\cos(\alpha\sqrt{k}T) - (1+k)\cos(\alpha\sqrt{k}(2a-T))\}.\end{aligned} \tag{1.4}$$

We now make the change of variables $s = 2a - T$. Then $s \in [-T, T]$ and $s = 0$ corresponds to having the negative part of the intrinsic growth rate centered in $(0, 1)$. Since $m_{(s+T)/2}(x) = m_{(-s+T)/2}(1-x)$ for all $x \in [0, 1]$ and $s \in [0, T]$, $\lambda_1(m_{(s+T)/2}) = \lambda_1(m_{(-s+T)/2})$. We shall therefore concern ourselves only with $s \in [0, T]$.

We know from the previous example that if $s = T$, $\sqrt{\lambda_1(m_T)} < \pi/\sqrt{k}T$. If $\alpha < \pi/\sqrt{k}T$, (1.4) is equivalent to

$$\sqrt{k}\coth(\alpha(1-T)) = \frac{1}{2}\left\{\frac{(1-k)\cos(\alpha\sqrt{k}T) - (1+k)\cos(\alpha\sqrt{k}s)}{\sin(\alpha\sqrt{k}T)}\right\}. \tag{1.5}$$

If $s = T$, (1.5) reduces to

$$\coth(\alpha(1-T)) = -\sqrt{k}\cot\alpha\sqrt{k}T. \tag{1.6}$$

Since the left hand side of (1.6) is decreasing on $(0, \pi/\sqrt{k}T)$ while the right hand side is increasing on that interval, there can be at most one $\alpha^* \in (0, \pi/\sqrt{k}T)$ satisfying (1.6). Clearly $\alpha^* = \sqrt{\lambda_1(m_T)}$.

Suppose now that there is an $s \in [0, T)$, and an $\alpha \in (0, \alpha^*)$ such that (1.4) is met. Then we have

$$\begin{cases} \sqrt{k}\coth(\alpha(1-T)) = \dfrac{1}{2}\left\{\dfrac{(1-k)\cos(\alpha\sqrt{k}T) - (1+k)\cos(\alpha\sqrt{k}s)}{\sin(\alpha\sqrt{k}T)}\right\} \\ \text{and} \\ \sqrt{k}\coth(\alpha^*(1-T)) = \dfrac{1}{2}\left\{\dfrac{(1-k)\cos(\alpha^*\sqrt{k}T) - (1+k)\cos(\alpha^*\sqrt{k}T)}{\sin(\alpha^*\sqrt{k}T)}\right\}. \end{cases} \tag{1.7}$$

Of course, the right hand side of the second equation of (1.7) reduces to (1.6). However, it is to our advantage to express it in the given form. Since $\alpha < \alpha^*$,

$$\sqrt{k}\coth(\alpha(1-T)) > \sqrt{k}\coth(\alpha^*(1-T)).$$

Hence,

$$\frac{(1-k)\cos(\alpha\sqrt{k}T)-(1+k)\cos(\alpha\sqrt{k}s)}{\sin(\alpha\sqrt{k}T)} > \frac{(1-k)\cos(\alpha^*\sqrt{k}T)-(1+k)\cos(\alpha^*\sqrt{k}T)}{\sin(\alpha^*\sqrt{k}T)},$$

which, since $\alpha < \alpha^* < \pi/\sqrt{k}T$, implies

$$\begin{aligned}&(1-k)\{\sin(\alpha^*\sqrt{k}T)\cos(\alpha\sqrt{k}T)-\sin(\alpha\sqrt{k}T)\cos(\alpha^*\sqrt{k}T)\}\\ &\quad >(1+k)\{\sin(\alpha^*\sqrt{k}T)\cos(\alpha\sqrt{k}s)-\sin(\alpha\sqrt{k}T)\cos(\alpha^*\sqrt{k}T)\}.\end{aligned}$$

Since

$$\alpha\sqrt{k}s < \alpha\sqrt{k}T < \pi, \qquad \cos(\alpha\sqrt{k}s) > \cos(\alpha\sqrt{k}T).$$

So

$$(1+k)\sin(\alpha^*\sqrt{k}T)\cos(\alpha\sqrt{k}s) > (1+k)\sin(\alpha^*\sqrt{k}T)\cos(\alpha\sqrt{k}T).$$

It follows that

$$(1-k)\sin((\alpha^*-\alpha)\sqrt{k}T) > (1+k)\sin((\alpha^*-\alpha)\sqrt{k}T),$$

a contradiction. We conclude that if $s \in [0, T)$ any solution α of (1.4) is at least as large as $\sqrt{\lambda_1(m_T)}$. A slightly closer examination will show that in fact $\alpha > \sqrt{\lambda_1(m_T)}$. Hence, $\lambda_1(m_T) = \lambda_1(m_0) < \lambda_1(m_a)$ for all $a \in (0, T)$.

The ramification for the model in case the intrinsic growth rate has value -1 on a subinterval of $[0, 1]$ of length $1-T$ and has the value $k>0$ on the complement of this subinterval is that the best situation for the population occurs when the subinterval on which the intrinsic growth rate is -1 is at either end of $[0, 1]$. In the preceding example, where the intrinsic growth rate had value $k > 0$ on a single subinteval of $[0, 1]$ of length T and value -1 on its complement, the situations

$$\begin{array}{llll} k & \text{on } [0, T], & -1 & \text{on } (T, 1] \\ -1 & \text{on } [0, 1-T), & k & \text{on } [1-T, 1] \end{array}$$

were the *least* advantageous for the population. This last fact allows us to make a comparison which is a principal observation of this section on our model. Recall that a population following

$$\begin{cases} u_t = du_{xx} + m(x)u - cu^2 & \text{in } (0, 1) \times (0, \infty) \\ u(x, 0) \geqslant 0 & \text{in } (0, 1) \\ u(0, t) = 0 = u(1, t), & \text{in } [0, \infty) \end{cases} \tag{1.8}$$

can be expected to persist for all time if $d < [\lambda_1(m)]^{-1}$ and to become extinct as t becomes large if $d > [\lambda_1(m)]^{-1}$, where $\lambda_1(m)$ is the principal positive eigenvalue of

$$\begin{aligned} -u_{xx} &= \lambda m(x)u \quad \text{in } (0, 1), \\ u(0) &= 0 = u(1). \end{aligned}$$

Observation 1.1. Suppose we consider the model (1.8) for $m_1(x)$ and $m_2(x)$, with

$$m_1(x)=\begin{cases}-1 & \text{on } [0,a)\\ k & \text{on } [a,a+T]\\ -1 & \text{on } (a+T,1]\end{cases}$$

and

$$m_2(x)=\begin{cases}k & \text{on } [0,b)\\ -1 & \text{on } [b,b+1-T]\\ k & \text{on } (b+1-T,1],\end{cases}$$

for $k>0$, $0\leqslant a\leqslant 1-T$, $0\leqslant b\leqslant T$, $0<T<1$. Then for any $a\in(0,1-T)$ and $b\in(0,T)$, $\lambda_1(m_1)<\lambda_1(m_2)$. Consequently, *having the positive part of the intrinsic growth rate in one piece is always more advantageous to the population than having the positive part occur in two pieces* (*of the same total length*) *which meet* 0 *and* 1, *respectively, provided homogeneous Dirichlet boundary data are imposed* (i.e. our one-dimensional environment is surrounded by a completely hostile exterior).

We have just seen that for a species inhabiting a one-dimensional environment with completely hostile exterior, the optimal location for a single refuge of any given size is in the center of the environment. If the size of this centered refuge is increased and its quality (as measured by the positive part of the intrinsic growth rate $m(x)$) is maintained, then certainly we expect a more advantageous situation for the population, and in fact, the model concurs. The reason such is the case is that the intrinsic growth rate m for the smaller refuge is less than or equal to the rate $\tilde{m}$ for the larger refuge (it is well known [2, 3, 7] that then $\lambda_1(\tilde{m})<\lambda_1(m)$). It is more interesting to speculate about what happens if we now compare the case of a small refuge in which the environmental quality (as measured by $m(x)$) is very high with that of a larger one where the environmental quality is only moderately high. To be specific, suppose that $m(x)$ has the form

$$m(x)=\begin{cases}-1 & \text{on } [0,(1-T)/2)\\ k & \text{on } [(1-T)/2,(1+T)/2]\\ -1 & \text{on } ((1+T)/2,1],\end{cases}\tag{1.9}$$

where k and T are positive numbers with $k\leqslant 1$ chosen so that $\int_0^1 m(x)\,dx\equiv kT-(1-T)=q$ for some fixed $q<1$. The idea is to model a situation where we could either preserve a small region at its original quality (so $k=1$ and $T=(q+1)/2$) or a larger region at lower quality ($0<k<1$ and $T=(q+1)/(k+1)$). Here q represents the average quality of the environment for $0<x<1$ and we shall assume that it remains constant, forcing a trade-off between k and T. Expressing k in terms of T, we have $k=k(T)=(q+1-T)/T$. We want to have $k\leqslant 1$, since $k=1$ corresponds to completely undamaged habitat in this version of the model, so we require $(q+1)/2\leqslant T$. If we express $m(x)$ from (1.9) in terms of q and T, we have

$$m_T(x)=\begin{cases}-1 & \text{on } [0,(1-T)/2)\\ (q+1-T)/T & \text{on } [(1-T)/2,(1+T)/2]\\ -1 & \text{on } ((1+T)/2,1].\end{cases}$$

Constructing the eigenfunction $u_T(x)$ for

$$-u'' = \alpha^2 m_T(x) u \quad \text{in } (0, 1), \qquad (1.10)$$
$$u(0) = 0 = u(1),$$

it follows from the symmetry of $m_T(x)$, the boundary conditions, and the fact that the eigenvalues for problems such as (1.10) are simple, that for $(q+1)/2 \leqslant T < 1$ we may choose

$$u_T(x) = \begin{cases} \sinh \alpha x & \text{on } [0, (1-T)/2) \\ \beta \cos[\alpha\sqrt{(q+1-T)/T}(x-\frac{1}{2})] & \text{on } [(1-T)/2, (1+T)/2] \\ \sinh \alpha(1-x) & \text{on } ((1+T)/2, 1] \end{cases}$$

If we match u_T and u_T' across $x = (1 \pm T)/2$ we obtain

$$\sinh \alpha(1-T)/2 = \beta \cos[\alpha\sqrt{(q+1-T)/T}(T/2)]$$

and

$$\cosh \alpha(1-T)/2 = \beta\sqrt{(q+1-T)/T} \sin[\alpha\sqrt{(q+1-T)/T}(T/2)],$$

so that for $(q+1)/2 \leqslant T < 1$ we have

$$\coth \alpha(1-T)/2 = \sqrt{(q+1-T)/T} \tan[\alpha\sqrt{(q+1-T)T}/2]. \qquad (1.11)$$

If $T = 1$ we have $k(T) = q$ and we may take $u = \sin \alpha\sqrt{q}x$; then we must have $\alpha\sqrt{q} = \pi$ to satisfy the boundary conditions, so $\alpha = \pi/\sqrt{q}$. Returning to (1.11), we observe that if q and T are fixed and $T < 1$, there will always be a unique solution between zero and the first vertical asymptote of $\tan(\alpha\sqrt{q+1-T)T/2})$, which occurs at

$$\alpha = \frac{\pi}{2} \div (\sqrt{(q+1-T)T}/2) = \frac{\pi}{\sqrt{(q+1-T)T}}.$$

(See Fig. 5.) Moreover, the form of u_T implies that $\sqrt{\lambda_1(m_T(x))}$ is this unique

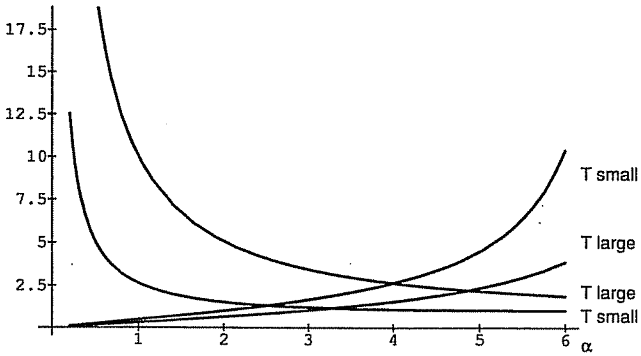


Fig. 5. Graphical determination of α comparing a small region of good habitat (T small) with a larger region of fair habitat (T large). The increasing functions are multiples of tangents; the decreasing functions are hyperbolic cotangents

solution. Hence $\lambda_1(m_T(x)) < \pi^2/((q+1-T)T)$. It follows immediately that for fixed q and for $m_T(x)$ of the form (1.12), the case $T=1$ yields the highest value for α and hence for $\lambda_1(m_T(x)) = \alpha^2$. (Observe that $d/dT((q+1-T)T) = q+1-2T<0$ if $(q+1)/2 < T < 1$, so for the admissible values of $T, q < (q+1-T)T$ and

$$\lambda_1(m_T(x)) < \frac{\pi^2}{(q+1-T)T} < \frac{\pi^2}{q} = \lambda_1(m_1(x)).$$

In fact, we can say more by carefully examining what increasing T does to the graphs in Fig. 5. Note that $d[(q+1-T)/T]/dT = -(q+1)/T^2 < 0$, so increasing T between $(q+1)/2$ and 1 decreases both $(q+1-T)T$ and $(q+1-T)/T$, and hence lowers the graph of the function on the right side of (1.11). However, since the function $\coth z$ is decreasing, any increase in T decreases $1-T$ and hence raises the graph of the function on the left side of (1.11). The overall effect is to increase the value of α where the curves intersect; so we may conclude that $\lambda_1(m_T(x)) = \alpha^2$ increases as we increase T from $(q+1)/2$ to 1 while maintaining a constant average quality q. The biological conclusion is that a smaller favorable region of high quality makes a better refuge under our modelling assumptions than a larger favorable region of lower quality.

2. Neumann and mixed boundary conditions

We now consider the situation where the region inhabited by our population is not surrounded by a completely inhospitable region, but rather by a barrier or by a region which is only somewhat inhospitable. The standard approach to modelling such situations is to use Neumann (i.e. no-flux) boundary conditions in the case of a barrier and to use mixed boundary conditions for the case of a somewhat inhospitable exterior. (The modelling for the second case is discussed in some detail in [5].) The case in which the boundary acts as a barrier is somewhat special. Specifically, if the average environmental quality $\int_0^1 m(x)\,dx$ is positive, then under the assumption that the boundary acts as a barrier, our models predict persistence for the population for *any* diffusion rate. In that situation there is no eigenvalue corresponding to λ_1. However, if $\int_0^1 m(x)\,dx < 0$ then there is an eigenvalue $\lambda_1(m(x))$, which measures the overall suitability of the environment as in the case of a completely hostile exterior region. (These results are derived in [1].) In the case where the exterior region is somewhat inhospitable, there will always be an eigenvalue $\lambda_1(m(x))$ as in the case of a toally inhospitable exterior. We shall see that even when $\int_0^1 m(x)\,dx < 0$, the way in which $\lambda_1(m(x))$ depends on $m(x)$ is different in the case where the boundary is a barrier than in the case where the boundary is deadly (that is, the exterior is totally inhospitable), and that the behavior of $\lambda_1(m(x))$ in the intermediate case of a somewhat inhospitable exterior region may be similar to either of the extreme cases depending on the degree of inhospitability of the exterior.

Let us first consider the problem

$$-u'' = \lambda m_a(x)u \quad \text{on } (0,1), \tag{2.1}$$
$$u'(0) = 0 = u'(1),$$

where

$$m_a(x) = \begin{cases} -1 & x \in [0, a) \\ k & x \in [a, a+T] \\ -1 & x \in (a+T, 1], \end{cases}$$

for some $T \in (0, 1/(k+1))$ (so that $\int_0^1 m_a(x)\,dx < 0$) and $a \in [0, 1-T]$. Again, we set $\alpha = \sqrt{\lambda_1(m_a)}$, and for $a \neq 0, 1-T$ we have an eigenfunction of the form

$$u_a(x) = \begin{cases} \cosh \alpha x & x \in [0, a] \\ A \cos \alpha\sqrt{k}(x-c) & x \in [a, a+T] \\ B \cosh \alpha(1-x) & x \in [a+T, 1], \end{cases}$$

for some $c \in (a, a+T)$. Matching u_a and u_a' across the interfaces and reducing yields

$$\cot \alpha\sqrt{k}(a-c) = -\sqrt{k} \coth \alpha a$$

and

$$\cot \alpha\sqrt{k}(a+T-c) = \sqrt{k} \coth \alpha(1-a-T).$$

Using the identity for the cotangent of a difference and simplifying, we obtain

$$\begin{aligned} \cot \alpha\sqrt{k}T &= \frac{k \cosh \alpha a \cosh \alpha(1-a-T) - \sinh \alpha a \sinh \alpha(1-a-T)}{\sqrt{k} \sinh \alpha(1-T)} \\ &= g(a, \alpha). \end{aligned} \tag{2.2}$$

If $a=0$ or $a=1-T$, we will have only one interface, and matching across it yields the relation $\cot \alpha\sqrt{k}T = \sqrt{k} \coth \alpha(1-T)$, which is in fact the case of (2.2) with $a=0$ or $a=1-T$; thus, (2.2) defines α for all $a \in [0, 1-T]$. Next, we observe that as $\alpha \to 0+$ we have that the expressions in (2.2) approach $+\infty$ with orders of growth $\cot \alpha\sqrt{k}T \sim 1/\alpha\sqrt{k}T$ and $g(a, \alpha) \sim \sqrt{k}/\alpha(1-T)$ respectively. Since we assumed $0 < T < 1/(k+1)$, we have $1/T\sqrt{k} > \sqrt{k}/(1-T)$, so that $\cot \alpha\sqrt{k}T \to +\infty$ more rapidly than $g(a, \alpha)$ as $\alpha \downarrow 0$. Also, we may use the identities for products of hyperbolic sines and cosines to obtain

$$g(a, \alpha) = \frac{(k-1) \cosh \alpha(1-T) + (k+1) \cosh \alpha(1-2a-T)}{2\sqrt{k} \sinh \alpha(1-T)}.$$

If we now compute $\partial g(a, \alpha)/\partial\alpha$, we find that the numerator reduces to

$$\begin{aligned} &\{-(k-1)(1-T) + (k+1)(1-2a-T) \sinh \alpha(1-T) \sinh \alpha(1-2a-T) \\ &\quad - (k+1)(1-T) \cosh \alpha(1-T) \cosh \alpha(1-2a-T)\} \\ &= \{-(k-1)(1-T) - (k+1)(1-T) \cosh 2\alpha a \\ &\quad - (k+1)a[\cosh 2\alpha(1-a-T) - \cosh 2\alpha a]\} \\ &= \{-(k-1)(1-T) - (k+1)(1-a-T) \cosh 2\alpha a \\ &\quad - (k+1)a \cosh 2\alpha(1-a-T)\} \leqslant 0 \end{aligned}$$

since $1-a-T \geqslant 0$ and $\cosh x \geqslant 1$ for all x, where we have used various hyperbolic identities in the reduction. Since the numerator of the derivative of a

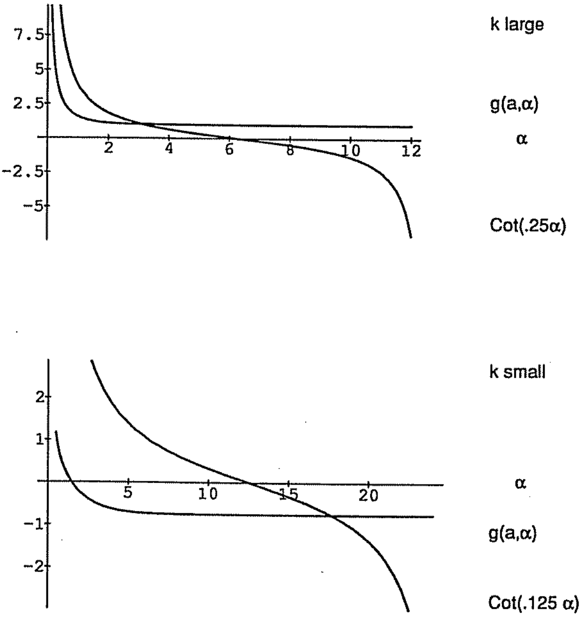


Fig. 6. Graphical determination of α in the case of a boundary that acts as a barrier. The parameter k measures the quality of the good habitat

quotient determines the sign, we have $\partial g/\partial\alpha \leqslant 0$. Thus, since $\cot \alpha\sqrt{kT} \to -\infty$ as $\alpha \uparrow \pi/\sqrt{kT}$ and $g(a, \alpha)$ is defined for all nonzero α, we have the situation shown in Fig. 6 with (2.2) satisfied for some $\alpha \in (0, \pi/\sqrt{kT})$. Finally, if we calculate $\partial g/\partial a$, we obtain the numerator $-2\alpha(k+1)\sinh\alpha(1-2a-T)$, which is negative for $a \in [0, (1-T)/2)$ and positive for $a \in ((1-T)/2, 1-T)$, so that the graph of $g(a, \alpha)$ with respect to α is lowest for $a = (1-T)/2$ and highest for $a = 0$ or $a = 1-T$, increasing monotonically for each fixed α as a moves away from $(1-T)/2$.

As we raise the graph of $g(a, \alpha)$ we also raise the point where it intersects the graph of $\cot \alpha\sqrt{kT}$, and thereby decrease the value of α where the intersection occurs. The conclusion is that moving the region where m_a is positive away from the center of the interval decreases $\lambda_1(m_a) = \alpha^2$ monotonically until the favorable region is at one of the ends, with one of its boundaries coinciding with either 0 or 1. Since the boundary points $x = 0$ and $x = 1$ are assumed to represent perfect barriers, the conclusion is not surprising biologically, although it is the reverse of what we observed in the case of a completely hostile exterior.

We may also consider the Neuman problem (2.1) under the assumption that the intrinsic growth rate is equal to -1 on a single subinterval of $[0, 1]$ of length $1-T$ and equal to $k > 0$ on the remainder of $[0, 1]$ and ask how the principal positive eigenvalue for (2.1) varies as the subinterval is moved across $[0, 1]$. As in the preceding example we need $T < 1/(k+1)$ in order to have a principal positive eigenvalue in the first place. If we make this assumption, we may consider (2.1) with m_a given by

$$m_a(x) = \begin{cases} k, & x \in [0, a) \\ -1, & x \in [a, a+1-T] \\ k, & x \in (a+1-T, 1] \end{cases}$$

and ask how $\lambda_1(m_a)$ varies as a ranges over $[0, T]$. We may take as eigenfunction $u_a(x)$ given by

$$u_a(x) = \begin{cases} \cos \alpha\sqrt{k}x, & x \in [0, a] \\ \gamma_1 \cosh \alpha x + \gamma_2 \sinh \alpha x, & x \in [a, a+1-T] \\ \beta \cos \alpha\sqrt{k}(x-1), & x \in [a+1-T, 1], \end{cases}$$

where γ_1, γ_2, and β are uniquely determined by our choice of normalization.

By matching appropriately across the interfaces at a and at $a+1-T$, we may conclude that $\alpha = \sqrt{\lambda_1(m_a)}$ must satisfy

$$\frac{\sinh \alpha(1-T)}{2}\{(1-k)\cos \alpha\sqrt{k}T + (1+k)\cos \alpha\sqrt{k}(2a-T)\}$$

$$= \sqrt{k} \cosh \alpha(1-T) \sin \alpha\sqrt{k}T. \tag{2.3}$$

Let $s = 2a - T$. Then $a \in [0, T]$ implies that $s \in [-T, T]$. Notice that $m_{T-a}(x) = m_a(1-x)$ for $a \in [0, T]$ and $x \in [0, 1]$. Consequently $\lambda_1(m_{T-a}) = \lambda_1(m_a)$ for all $a \in [0, T]$, and so we need only consider (2.3) for $s \in [0, T]$. In case $s = T$, (2.3) yields

$$\sqrt{k} \coth \alpha(1-T) = \cot \alpha\sqrt{k}T. \tag{2.4}$$

Observe that as (2.4) is the exceptional case of (2.2) as well as (2.3), we may appeal to Fig 6 to see that $\alpha^* = \sqrt{\lambda_1(m_T)}$ is the unique solution to (2.4) in the interval $(0, \pi/\sqrt{k}T)$ and that if $\alpha \in (0, \alpha^*)$,

$$\sqrt{k} \coth \alpha(1-T) < \cot \alpha\sqrt{k}T.$$

Suppose now that $s \in [0, T)$ and $\alpha \in (0, \alpha^*]$. Then

$$(1-k)\cos \alpha\sqrt{k}T + (1+k)\cos \alpha\sqrt{k}s > (1-k)\cos \alpha\sqrt{k}T + (1+k)\cos \alpha\sqrt{k}T$$
$$= 2\cos \alpha\sqrt{k}T.$$

Since $\alpha^* < \pi/\sqrt{k}T$,

$$\frac{(1-k)\cos \alpha\sqrt{k}T + (1+k)\cos \alpha\sqrt{k}s}{2 \sin \alpha\sqrt{k}T} > \cot \alpha\sqrt{k}T.$$

Since $\sqrt{k} \coth \alpha(1-T) < \cot \alpha\sqrt{k}T$ for $\alpha \in (0, \alpha^*)$, we may conclude that (2.3) has no roots in $(0, \alpha^*]$ if $s \in [0, T)$. We conclude that $\lambda_1(m_T) < \lambda_1(m_{(s+T)/2})$ for $s \in [0, T)$, or equivalently, $\lambda_1(m_T) < \lambda_1(m_a)$ for $a \in [T/2, T)$.

We learn from these observations that the optimal situation for the preservation of the population in the model subject to Neumann conditions is quite different from that in the case of a completely hostile exterior. Namely, we learn that whether we think of varying a single subinterval of [0, 1] of length T upon which the intrinsic growth rate is positive or think of varying a single subinterval of length $1 - T$ upon which the intrinsic growth rate is negative, it is best for the preservation of the population to have a single refuge against one of the boundary points. In this case, if in (2.1)

$$m_1(x) = \begin{cases} -1 & \text{on } [0, a) \\ k & \text{on } [a, a+T] \\ -1 & \text{on } (a+T, 1] \end{cases}$$

and

$$m_2(x) = \begin{cases} k & \text{on } [0, b) \\ -1 & \text{on } [b, b+1-T] \\ k & \text{on } (b+1-T, 1], \end{cases}$$

for $a \in (0, 1-T)$ and $b \in (0, T)$, we cannot immediately say which of $\lambda_1(m_1)$ and $\lambda_1(m_2)$ is the smaller. In the case of a completely hostile exterior, being near the boundary is detrimental to the population and so it is not so surprising that $\lambda_1(m_1) < \lambda_1(m_2)$ in that situation. But once Neumann conditions are imposed, being near the boundary is no longer a detriment. Hence deciding which of $\lambda_1(m_1)$ and $\lambda_1(m_2)$ is smaller is tantamount to deciding the outcome of a competition between a refuge which is in one piece but is surrounded by "negative" regions and a refuge in two pieces each of which has a "negative" region only on one side.

In Sect. 1 and in the preceding part of this section, we have considered cases corresponding to a boundary that is deadly (any individual reaching the boundary dies) or acts as a barrier (any individual reaching the boundary returns to the interior). In many situations, it is more realistic to suppose that the exterior region is hostile but not necessarily immediately lethal, so that some individuals crossing the boundary may be expected to die and other to return. A reasonable way of modelling such a situation is to use mixed or Robin boundary conditions, that is, to require some combination of the solution and its normal derivative to be zero. Such conditions are discussed, for example, in [5]. The corresponding eigenvalue problem is

$$-u'' = \lambda m(x)u, \quad x \in (0, 1),$$
$$\beta y(0) - y'(0) = 0 = \beta y(1) + y'(1), \quad \text{some } \beta > 0,$$

where β measures the hostility of the exterior environment. As $\beta \to 0$, we recover the conditions corresponding to an impassable boundary, while as $\beta \to \infty$, we approach the conditions corresponding to a deadly boundary. If we consider the situation where

$$m_a(x) = \begin{cases} -1 & x \in [0, a) \\ 1 & x \in [a, a+T] \\ -1 & x \in (a+T, 1] \end{cases} \tag{2.5}$$

and let $\alpha = \sqrt{\lambda_1(m_a(x))}$ then we may seek an eigenfunction of the form

$$u(x) = \begin{cases} \cosh \alpha x + \gamma \sinh \alpha x & x \in [0, a] \\ A \cos \alpha(x - c) & x \in [a, a + T] \\ B(\cosh \alpha(1 - x) + \delta \sinh \alpha(1 - x)) & x \in [a + T, 1], \end{cases}$$

for some $c \in (a, a + T)$. To satisfy the boundary conditions at $x = 0$ and $x = 1$ we must have $\gamma = \delta = \beta/\alpha$. If we match at $x = a$ and $x = a + T$ we obtain

$$\cot \alpha(a - c) = -\left(\frac{\alpha \cosh \alpha a + \beta \sinh \alpha a}{\alpha \sinh \alpha a + \beta \cosh \alpha a}\right),$$

$$\cot \alpha(a + T - c) = \frac{\alpha \cosh \alpha(1 - a - T) + \beta \sinh \alpha(1 - a - T)}{\alpha \sinh \alpha(1 - a - T) + \beta \cosh \alpha(1 - a - T)}.$$

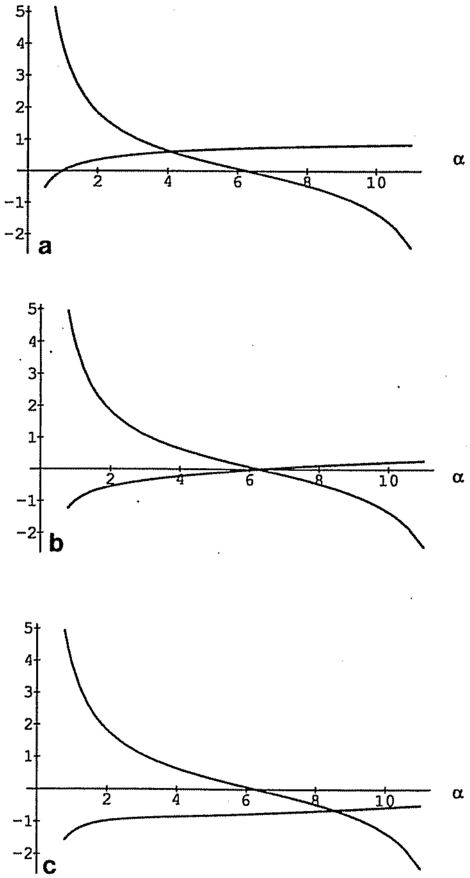


Fig. 7. Graphical determination of α comparing different boundary conditions (**a** $\beta = 1$; **b** $\beta = 2\pi$; **c** $\beta = 20$). The case of a boundary that acts as a barrier corresponds to $\beta = 0$, and the boundary becomes lethal as β approaches infinity. The decreasing function is $\cot(\alpha/4)$; the increasing function is $h(0, \alpha, \beta)$

Using the formula for the cotangent of a difference and simplifying via identities for hyperbolic functions yields

$$\begin{aligned}\cot \alpha T &= \frac{(\alpha^2-\beta^2)\cosh \alpha(1-2a-T)}{(\alpha^2+\beta^2)\sinh \alpha(1-T)+2\alpha\beta\cosh \alpha(1-T)}\\ &= h(a,\alpha,\beta).\end{aligned} \tag{2.6}$$

Observe that $h(a, \alpha, \beta) \to -\infty$ as $\alpha \downarrow 0$ and that $h(a, \alpha, \beta) < 0$ for $\alpha < \beta$, $h(a, \alpha, \beta) > 0$ for $\alpha > \beta$. There are essentially three different cases of (2.6), depending on whether $\beta < \pi/2T$, $\beta = \pi/2T$, or $\beta > \pi/2T$, which are shown schematically in Fig. 7 (a), (b) and (c), respectively.

If we have $\beta = \pi/2T$ then (2.6) is first satisfied for $\alpha = \pi/2T = \beta$, with no dependence whatsoever on a. The biological interpretation is that the degree of hostility of the exterior region as measured by the boundary condition is equivalent to that of the unfavorable interior region, so the location of the favorable interior region is irrelevant. If we move a away from $a = (1-T)/2$ toward 0 or $1-T$, the numerator of $h(a, \alpha, \beta)$ increases in absolute value for all $\alpha \neq \beta$. If $\beta < \pi/2T$, the first intersection of $\cot \alpha T$ and $h(a, \alpha, \beta)$ must occur for $\alpha > \beta$, where $h(a, \alpha, \beta)$ is necessarily positive. Thus, increasing the absolute value of the numerator of h increases h: so as a moves toward 0 or $1-T$, the value of α where the first intersection occurs must decrease (since $\cot \alpha T$ is decreasing) so that $\lambda_1(m_a(x))$ decreases. On the other hand, if $\beta > \pi/2T$ then the first intersection must occur for $\alpha < \beta$, where h is negative. In that case increasing the absolute value of the numerator decreases h and increases the value of α where the intersection occurs, hence increasing $\lambda_1(m_a(x))$. We may draw the following conclusions: for $m_a(x)$ of the form (2.5), moving the favorable region from the center to either end of the interval increases $\lambda_1(m_a(x))$ if the exterior is relatively hostile ($\beta > \pi/2T$) and decreases $\lambda_1(m_a(x))$ if the exterior is relatively benign so that many individuals that leave the environment will ultimately return ($\beta < \pi/2T$). In mathematical terminology, the problem with mixed boundary conditions shows the same behavior as the Dirichlet problem when β is large and as the Neumann problem when β is small.

References

1. Brown, K. J., Lin, C. C.: On the existence of positive eigenfunctions for an eigenvalue with an indefinite weight function. J. Math. Anal. Appl. **75**, 112–120 (1980)
2. Cantrell, R. S., Cosner, C.: Diffusive logistic equations with indefinite weights: population models in disrupted environments. Proc. Roy. Soc. Edinb. **112**, 293–318 (1989)
3. Figueiredo, de D. G.: Positive solutions of semilinear elliptic problems. In: Figueiredo, D. G. de, Honig, C. S. (eds.) (Lect. Notes Maths., vol. 957, pp. 34–88). Berlin Heidelberg New York: Springer 1982
4. Levin, S.: Population models and community structure in heterogeneous environments. In: Hallam, T. G., Levin, S. (eds.) Mathematical ecology (Lect. Notes Biomath., vol. 17). Berlin Heidelberg New York: Springer 1986
5. Ludwig, D., Aronson, D. G., Weinberger, H. F.: Spatial patterning of the spruce budworm. J. Math. Biology **8**, 217–258 (1979)
6. MacArthur, R. H., Wilson, E. O.: The theory of island biogeography. Princeton: Princeton University Press, 1967
7. Manes, A., Micheletti, A. M.: Un' estensione della teoria variazionale classica degli autovalori per operatori ellitici del secondo ordine. Boll. U.M.I. 7, 285–301 (1973)

8. Murray, J. D., Sperb, R. P.: Minimum domains for spatial patterns in a class of reaction-diffusion equations. J. Math. Biology **18**, 169–184 (1983)
9. Newmark, W. D.: Species-area relationship and its determinants for mammals in western North American national parks. Biol. J. Linnean Soc. **28**, 83–98 (1986)
10. Okubo, A.: Diffusion and ecological problems: mathematical models. Berlin Heidelberg New York: Springer 1980
11. Seno, H.: Effect of a singular patch on population persistence in a multi-patch system. Ecol. Modell. **43**, 271–286 (1988)
12. Skellam, J. G.: Random dispersal in theoretical populations. Biometrika **38**, 196–218 (1951)
13. Soule, M. E., Wilcox, B. A. (eds.): Conservation biology: an evolutionary-ecological perspective. Sunderland, Mass.: Sinauer 1980