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# Habitat edges and predator–prey interactions: effects on critical patch size

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## Abstract

We use partial differential equation models to examine the effects of cross-edge incursions by a predator on the persistence or extinction of a patch-resident prey species. For each of two predator-incursion profiles (namely, a constant incursion distance and a constant loss rate for predators during incursions), we examine the conditions under which the predator can (and cannot) influence the critical patch size of a prey species. © 2002 Published by Elsevier Science Inc.

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## 1. Introduction

Increasing attention among ecologists to spatial aspects of population and community dynamics (e.g. [1]) has included a specific focus on the ways in which habitat edges can change species interactions [2,3]. Differential effects of habitat edges on species' growth, mortality, or movement can affect the strength and outcome of many kinds of species interactions, including pollination [4], herbivory [5,6], predation [7,8], and parasitism [9,10]. Previous theoretical treatments have examined the roles habitat edges play in interspecific competition [11,12], disease

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transmission [13], and outbreak dynamics [14]. However, generally lacking from such theoretical studies has been an explicit examination of how habitat edges (through their effects on species' movement and survival) can influence predator–prey dynamics.

In contrast, a variety of field studies of edge-mediated predator–prey interactions already exist, and these motivate our theoretical examinations. Perhaps the most widely studied category of effects involves bird nest predation near edges, particularly in landscapes featuring a mix of forest and rural habitats [7,15,16]. In many such cases, the predators are generalist foragers (e.g., foxes, crows, domestic animals) for whom the habitat edge may form a travel corridor [17]. Patch residents in contrast are often much more specialized in their habitat requirements [18]. When placed in a spatial context, this specialist–generalist dichotomy raises the interesting point that cross-edge foraging, which may be a strong mortality source from the prey's perspective, may have only weak or incidental benefits for the predator (e.g., [16,19]).

Several studies have characterized predator density profiles across habitat edges, either directly, through movement or sighting records of the predators themselves [17], or indirectly, with predator activity densities inferred from patterns of depredation on natural or artificial bird nests distributed across the edge (e.g., [7,15,20–22]). Various attributes of edge structure (e.g., edge permeability or edge contrast) and the composition of local predator assemblages influence patterns of predator incursion [23,24]. Such factors can govern both how deeply foraging predators penetrate into the patch and the degree of mortality they exert on patch residents [16]. For example, patches with edges that are relatively impermeable to foraging predators (e.g., freeway-bounded forest tracts as in Ref. [19]) can feature elevated population growth rates for resident species compared with more accessible patches.

Here we use partial differential equation models to examine the effects of cross-edge incursions by a predator on the persistence or extinction of a patch-resident prey species. For each of two predator-incursion profiles (namely, a constant incursion distance and a constant loss rate for predators during incursions), we examine the conditions under which the predator can (and cannot) influence the critical patch size of a prey species.

## 2. Modeling and general analysis of models

### 2.1. Modeling set-up

We envision a situation in which a distinguished species (the prey) inhabits a patch $\Omega$ of some preferred habitat. The patch $\Omega$ is surrounded by matrix habitat populated by a second species (the predator) which can feed upon the prey species in $\Omega$. In our scenario, the prey is significantly vulnerable within $\Omega$ to predator incursions from the surrounding matrix. However, we assume the predator is generalist having sufficient resources outside $\Omega$ so as to maintain a fixed population density in the matrix surrounding $\Omega$. Consequently, while the predator may have a substantial effect on the population dynamics of the prey in $\Omega$, the contribution of the prey in $\Omega$ to the overall diet of the predator is negligible, thus mirroring the biological examples in Ref. [16,19].

Our fundamental aim in considering the preceding set-up is to ask whether a model for such a predator–prey interaction can predict the extinction of the prey in $\Omega$ and if so what are the dominant features in the model determining the extinction. We model the predator–prey interaction within the habitat patch $\Omega$ as follows. First we postulate that the prey density $v$ is governed by the diffusive logistic model with predation

$$\begin{aligned} &\frac{\partial v}{\partial t} = D\nabla^2 v + r\left(1 - \frac{v}{K}\right)v - g(v,p)p \quad \text{in } \Omega \times (0,\infty), \\ &\beta v + (1-\beta)\frac{\partial v}{\partial \eta} = 0 \quad \text{on } \partial\Omega \times (0,\infty), \end{aligned} \tag{2.1}$$

where $\beta \in [0,1]$ and $\partial v/\partial\eta = \nabla v \cdot \eta$ is the outer normal derivative of $v$ in the $\eta$ direction along the boundary $\partial\Omega$ of the patch $\Omega$. The value of $\beta$ in the boundary condition indicates the balance between the tendency of the prey to remain in the patch when it approaches the boundary and the tendency of the prey to be lost from the patch through the boundary. When $\beta = 0$, the patch is completely insulating, whereas when $\beta = 1$, the boundary may be regarded as immediately lethal. In (2.1),

$$\nabla^2 v = \frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2}$$

represents random movement of the prey through $\Omega$ by diffusion. $D$ is the diffusion coefficient. The local population dynamics for the prey are assumed to be of the logistic form $r(1 - (v/K))v$, where $r$ is the intrinsic growth rate for the prey and $K$ is its carrying capacity. The predation term in the equation is $g(v,p)p$, where $p$ denotes the predator density and $g(v,p)$ the predator's functional response to the prey.

We choose the logistic form for the local population growth term so that the predictions of model (2.1) in the absence of a predation term are clear cut and well understood. So doing provides an established starting point from which we can elucidate the effects of predator incursion into the patch $\Omega$. (This particular choice is not crucial, however; see below.) It is well-known (see, for example, [25]) that in the absence of predation, (2.1) predicts persistence of the prey when $r/D > \lambda_1(\beta)$ and extinction when $r/D \leqslant \lambda_1(\beta)$, where $\lambda_1(\beta)$ is the principal eigenvalue of the negative Laplacian $-\nabla^2$ on $\Omega$ for the given boundary condition, i.e., the unique necessarily non-negative number for which

$$\begin{aligned} &-\nabla^2 w = \lambda w \quad \text{in } \Omega, \\ &\beta w + (1-\beta)\frac{\partial w}{\partial \eta} = 0 \quad \text{on } \partial\Omega, \end{aligned} \tag{2.2}$$

admits a solution $w$ with the property that $w > 0$ in $\Omega$. Note that the condition $r/D > \lambda_1(\beta)$ is equivalent to having $\sigma > 0$ where $\sigma$ is the unique real value for which

$$\begin{aligned} &D\nabla^2 w + rw = \sigma\omega \quad \text{in } \Omega, \\ &\beta w + (1-\beta)\frac{\partial w}{\partial \eta} = 0 \quad \text{on } \partial\Omega, \end{aligned} \tag{2.3}$$

admits a solution $\omega$ which is positive in $\Omega$. The logistic form is by no means the only choice for local population growth that would result in this sharp dichotomy between persistence and extinction in the absence of predation. Indeed, if the logistic term is replaced with a term $f(v)v$ with the properties that $f(0) > 0$, $f(0) > f(v)$ for $v$ positive and $f(v) < 0$ for $v$ large, the corresponding model without predation would predict persistence if $f(0)/D > \lambda_1(\beta)$ and extinction if $f(0)/D \leqslant \lambda_1(\beta)$. Moreover, if in addition, $f'(v) < 0$ for $v > 0$, the prediction of persistence is a result of having a globally attracting positive equilibrium, as is the case with a logistic growth term (see, for example, [25]).

Now consider the issue of persistence versus extinction in the predictions of model (2.1) with the predation term $g(v,p)p$ included. Note first that any reasonable functional response term has the property that $g(0,p) = 0$ for all $p > 0$ and frequently has $g(v,p)$ is non-decreasing in $v$. Hence the predation term in (2.1) is expressible in the form

$$g(v,p)p = \frac{\partial g}{\partial v}(0,p)vp + \tilde{g}(v,p)p,$$

where $\tilde{g}(v,p)$ is higher order in $v$. Second, we have postulated that the prey in $\Omega$ makes a negligible contribution to the overall diet of the predator and that the predator maintains a fixed population density $p_0$ in the matrix habitat surrounding $\Omega$. As a result, we employ a dispersal equation *independent of the prey density v* to track the values of $p$ in $\Omega$ over time. (We shall examine some specific possible scenarios shortly.) Solutions to such equations evolve to equilibria (possibly spatially dependent) over time. Let $p(x)$ denote a representative example of an equilibrium distribution of the predator density in $\Omega$. Then arguing as in Ref. [26,27], we may assert that the prey is predicted to persist in $\Omega$ if $\sigma > 0$ when

$$\begin{aligned} &D\nabla^2 w + rw - \frac{\partial g}{\partial v}(0,p(x))p(x)w = \sigma w \quad \text{in } \Omega, \\ &\beta w + (1-\beta)\frac{\partial w}{\partial \eta} = 0 \quad \text{on } \partial\Omega, \end{aligned} \tag{2.4}$$

admits a positive solution and that the prey is predicted to go extinct if $\sigma < 0$ when (2.4) admits a positive solution. Notice that if $\frac{\partial g}{\partial v}(0,p) = 0$, the linearized problem (2.4) is identical to (2.3). In such a case, the predictions of model (2.1) *as regards persistence versus extinction of the prey* are unchanged from the case of no predatory incursion into $\Omega$. However, such does not mean that predator incursion has no effect on the prey. Indeed, the asymptotic values of the prey density $v$ may be significantly reduced by virtue of the predation. (It is perhaps instructive to think of this reduction as analogous to a reduced prey carrying capacity.) It is entirely possible that such predator incursions could have consequences which are undesirable for the prey species. For instance, the lowered prey densities could facilitate the invasion of an exotic which competes with the prey into $\Omega$ which would otherwise not be possible. We shall not pursue this possibility further in this paper, but we do plan to address this issue in subsequent work. The reader should note that there are widely used functional responses of both types, i.e., with $\frac{\partial g}{\partial v}(0,p) = 0$ and with $\frac{\partial g}{\partial v}(0,p) \neq 0$. Indeed, among the most familiar of all functional responses, Lotka–Volterra and Holling Type II functional responses have $\frac{\partial g}{\partial v}(0,p) \neq 0$ while Holling Type III functional responses satisfy $\frac{\partial g}{\partial v}(0,p) = 0$.

Since the focus of this paper is the effect of predator incursion into $\Omega$ on the persistence of the prey species, we are motivated by the preceding discussion to postulate for the remainder of this paper that $\frac{\partial g}{\partial v}(0,p) \neq 0$ for $p > 0$. The question remains as to how to arrive at $p(x)$ for (2.4). We offer two scenarios. The first possibility is that the predators disperse into $\Omega$ by simple diffusion some distance $\delta$ whereupon they encounter a 'virtual interface' where they (i) turn around, (ii) die or

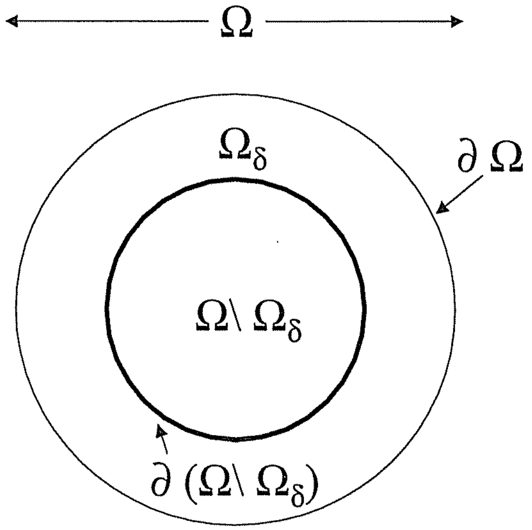

Fig. 1. Schematic diagram clarifying different components of a theoretical patch, shown here for the two-dimensional case. The entire patch is denoted $\Omega$, the portion into which the predator intrudes is $\Omega_\delta$ and the predator-free core is denoted by $\Omega\backslash\Omega_\delta$. The patch edge and the interface between the predator-free and predator-occupied areas are denoted using $\partial$. As used in the text, single bars enclosing the above symbols, such as $|\Omega|$ or $|\partial\Omega|$, denote the area or length (respectively) of the region or boundary in question.

(iii) do one or the other of (i) or (ii) with some probability. Let $\Omega_\delta$ denote the set of points in $\Omega$ of distance $\leqslant \delta$ from $\partial\Omega$ (see Fig. 1). Then the predator density is 0 in $\Omega\backslash\overline{\Omega}_\delta$, and is governed in $\Omega_\delta$ by

$$\begin{aligned} &p_t = d\nabla^2 p \quad \text{in } \Omega_\delta, \\ &p = p_0 \quad \text{on } \partial\Omega, \\ &\gamma p + (1-\gamma)\frac{\partial p}{\partial \eta} = 0 \quad \text{on } \partial\Omega_\delta\backslash\partial\Omega, \end{aligned} \tag{2.5}$$

where $\gamma \in [0,1]$ (if $\gamma = 0$, case (i) above holds; if $\gamma = 1$, case (ii); if $\gamma \in (0,1)$, case (iii)). Then $p(x) = 0$ in $\Omega\backslash\overline{\Omega}_\delta$ and is the equilibrium to (2.5) in $\overline{\Omega}_\delta$ (the closure of $\Omega_\delta$). Notice that if the predators simply turn around at the interface ($\gamma = 0$), the constant value $p_0$ must be the equilibrium to (2.5) and hence $p(x)$ is the step function given by

$$p(x) = \begin{cases} p_0 & x \in \overline{\Omega}_\delta, \\ 0 & x \in \Omega\backslash\overline{\Omega}_\delta. \end{cases}$$

In cases (ii) or (iii), the equilibrium to (2.5) depends in general on the geometry of $\Omega$. However, if we specialize to one space dimension, we can give a precise formula for $p(x)$. To this end, let $\Omega = (-\ell, \ell)$, so that $\Omega_\delta = (-\ell, -\ell+\delta) \cup (\ell-\delta, \ell)$ and $p(x)$ is symmetric about 0. Since $\nabla^2 p = p_{xx}$ in this case, equilibria to (2.5) are necessarily linear in $\Omega_\delta$. So let $p = mx + b$. In case (ii), $\gamma = 1$ so that $p = 0$ at $-\ell+\delta$ and $\ell-\delta$. Then

$$p(x) = \begin{cases} p_0\left(\frac{-x-\ell}{\delta} + 1\right) & \text{on } [-\ell, -\ell+\delta], \\ 0 & \text{on } [-\ell+\delta, \ell-\delta], \\ p_0\left(\frac{x-\ell}{\delta} + 1\right) & \text{on } [\ell-\delta, \ell]. \end{cases}$$

In case (iii), $\gamma p-(1-\gamma)p'=0$ at $\ell-\delta$, $\gamma p+(1-\gamma)p'=0$ at $-\ell+\delta$ and $p'=m$. It follows that

$$p(x)=\begin{cases}\frac{p_0}{\gamma\delta+1-\gamma}\{-\gamma x+\gamma(\delta-\ell)+1-\gamma\} & \text{on } [-\ell,-\ell+\delta],\\ 0 & \text{on } (-\ell+\delta,\ell-\delta),\\ \frac{p_o}{\gamma\delta+1-\gamma}\{\gamma x+\gamma(\delta-\ell)+1-\gamma\} & \text{on } [\ell-\delta,\ell].\end{cases}$$

The other possible scenario for predator incursion into $\Omega$ we consider is to eliminate the 'virtual interface' and instead assume a net death rate $\mu$ for the predators as they move into $\Omega$. In this case, the predator density in $\Omega$ is governed by

$$\begin{aligned}&\frac{\partial p}{\partial t}=d\nabla^2 p-\mu p \quad \text{in } \Omega\times(0,\infty),\\ &p=p_0 \quad \text{on } \partial\Omega\times(0,\infty).\end{aligned} \tag{2.6}$$

In this scenario, $p(x)$ is the equilibrium solution to (2.6). If $\Omega$ is the one dimensional interval $(-\ell,\ell)$, $p(x)$ is given by the formula

$$p(x)=p_0\frac{\cosh(\sqrt{\mu/d}x)}{\cosh(\sqrt{\mu/d}\ell)}$$

for $x\in[-\ell,\ell]$.

### 2.2. General analytic observations

As noted in the preceding section, the value of $\sigma$ in (2.4) for which (2.4) admits a solution which is positive in $\Omega$ is the crucial factor in determining whether model (2.1) predicts persistence or extinction of the prey species in $\Omega$. If $\sigma>0$, the prediction is that the prey species will persist, whereas if $\sigma<0$, the model predicts extinction of the prey species. Having $\sigma=0$ in (2.4) when (2.4) admits a solution which is positive in $\Omega$ suggests that the combination of parameters $D$, $r$, $p(x)$, $\frac{\partial g}{\partial v}(0,p(x))$, $\beta$ and $\Omega$ in the model is critical in the sense that a small change in any one of these factors may result in a reversal of the prediction of the model, either from persistence to extinction or vice versa. A particularly useful line of inquiry of this sort that we shall pursue in a number of different regimes is to view $\sigma=0$ as corresponding to $\Omega$ being of 'critical patch size' (see [28,29]). Before proceeding to analyses of critical patch size for $\Omega$, however, there are several general observations we need to make.

First of all, note that (2.4) has variational structure. Consequently, $\sigma$ can be expressed as the supremum of a collection of Rayleigh quotients as in [30]. For $\beta\in[0,1)$, the representation for $\sigma$ takes the form

$$\sigma=\sup_{\substack{\psi\in W^{1,2}(\Omega)\\ \psi\not\equiv 0}}\left[\frac{-D\int_\Omega|\nabla\psi|^2\,\mathrm{d}x+\int_\Omega\left(r-\frac{\partial g}{\partial v}(0,p(x))p(x)\right)\psi^2\,\mathrm{d}x-\frac{D\beta}{1-\beta}\oint_{\partial\Omega}\psi^2\,\mathrm{d}S}{\int_\Omega\psi^2\,\mathrm{d}x}\right], \tag{2.7}$$

where $W^{1,2}(\Omega)$ is the Sobolev space of square integrable functions which are once weakly differentiable in $\Omega$ with square integrable weak derivatives. If $\beta=1$, the last term in the numerator of the Rayleigh quotient in (2.7) is undefined. Recall that $\beta=1$ corresponds to a lethal boundary on the habitat $\Omega$. In this case, we may modify (2.7) by restricting ourselves to the subspace $W_0^{1,2}(\Omega)$ of $W^{1,2}(\Omega)$ consisting of those elements of $W^{1,2}(\Omega)$ which vanish on $\partial\Omega$. We obtain

$$\sigma = \sup_{\substack{\psi \in W_0^{1,2}(\Omega) \\ \psi \not\equiv 0}} \left[ \frac{-D\int_\Omega |\nabla\psi|^2\,\mathrm{d}x + \int_\Omega \left(r - \frac{\partial g}{\partial v}(0,p(x))p(x)\right)\psi^2\,\mathrm{d}x}{\int_\Omega \psi^2\,\mathrm{d}x} \right]. \tag{2.8}$$

The preceding formulations have an immediate consequence. Note that if we do not restrict the distance a predator can penetrate into the patch $\Omega$, it is possible to have $r - \frac{\partial g}{\partial v}(0,p(x))p(x) < 0$ on all of $\Omega$. In this event, we see from (2.7) and (2.8) that $\sigma < 0$ independent of diffusion coefficient or boundary condition, leading to prey extinction in $\Omega$. Such a phenomenon of course would be very likely on a sufficiently small patch $\Omega$ through which predators may roam effectively at will. On the other hand, if we do restrict the predator so that $p(x) > 0$ in $\Omega_\delta$ but $p(x) = 0$ on $\Omega\backslash\Omega_\delta$, the situation for the prey can be no worse than what would occur if the prey were restricted to $\Omega\backslash\Omega_\delta$ by having a lethal boundary $\partial(\Omega\backslash\Omega_\delta)$. Consequently, if $\sigma = \sigma^* > 0$ when

$$\begin{aligned} &D\nabla^2 w + rw = \sigma w \quad \text{in } \Omega\backslash\Omega_\delta, \\ &w = 0 \quad \text{on } \partial(\Omega\backslash\Omega_\delta), \end{aligned} \tag{2.9}$$

admits a solution $w > 0$ in $\Omega\backslash\Omega_\delta$, $\sigma$ in (2.4) should be positive when (2.4) admits a solution which is positive in $\Omega$, independent of the value of $\beta$ in the boundary condition. As a result, if $\sigma^* > 0$ in (2.9), then the portion of the habitat $\Omega$ not subject to predator incursion is larger than it has to be in order for model (2.1) to predict persistence of the prey if the predators can penetrate up to a distance of $\delta$ from $\partial\Omega$ into $\Omega$.

Now consider the special case where the prey is subject to a reflecting boundary. If

$$\int_\Omega \left(r - \frac{\partial g}{\partial v}(0,p(x))p(x)\right)\mathrm{d}x > 0,$$

it can be shown (see, for example, [31]) that $\sigma > 0$ and model (2.1) predicts persistence of the prey species in $\Omega$. In case the functional response $g$ is independent of $p$ and

$$\frac{\partial g}{\partial v}(0,p(x)) = \frac{\mathrm{d}g}{\partial v}(0), \qquad \int_\Omega \left(r - \frac{\partial g}{\partial v}(0,p(x))p(x)\right)\mathrm{d}x > 0$$

is equivalent to

$$r > \frac{\mathrm{d}g}{\partial v}(0)\cdot\left(\frac{1}{|\Omega|}\int_\Omega p(x)\,\mathrm{d}x\right).$$

(As noted in the legend to Fig. 1, $|\Omega|$ denotes the area of $\Omega$.) Thus model (2.1) predicts persistence of the prey in this case when the prey's intrinsic growth rate exceeds the product of the predator's marginal functional response at zero prey density and the average predator density over $\Omega$. If $p(x) \leqslant p_0$ and $p(x) = 0$ on $\Omega\backslash\Omega_\delta$,

$$\int_\Omega p(x)\,\mathrm{d}x = \int_{\Omega_\delta} p(x)\,\mathrm{d}x \leqslant p_0|\Omega_\delta|,$$

so that model (2.1) predicts persistence of the prey species if

$$r > \frac{\mathrm{d}g}{\partial v}(0)\cdot p_0\cdot\frac{|\Omega_\delta|}{|\Omega|}.$$

Finally, note that $\sigma$ is monotonically decreasing with respect to either $p(x)$ or $\beta$. For instance, suppose the parameters $D$, $r$, $g$, $\beta$ and $\Omega$ are fixed in (2.1) and consider two predator penetration densities $p_1(x)$ and $p_2(x)$. If $p_1(x) \leqslant p_2(x)$ in $\Omega$ and $\sigma_1$ and $\sigma_2$ denote the corresponding $\sigma$ values for which (2.4) admits a solution which is positive in $\Omega$, then $\sigma_1 > \sigma_2$. In other words, an increased predator penetration density exerts more pressure on a prey population. Likewise, a more lethal boundary condition on $\Omega$ exerts more pressure on a prey population. While neither of these observations is at all surprising, they are useful in examining different assumptions about $p(x)$ and/or $\beta$ on the basis of comparison with other choices, as we shall note in the following section.

## 3. Predator incursions and minimum patch size of refuge – particular cases

We explore three specific cases. First we investigate the case of a linear habitat into which predators penetrate a fixed distance at a constant density. Second, we extend these results to two-dimensional patches, including a specific treatment of predator incursions reaching a fixed distance into a square block of habitat. Lastly, we return to a one-dimensional habitat to study how prey persistence is affected when we change the pattern of predator incursion from one involving a fixed predation distance to one involving a net death rate for predators.

### 3.1. Predator penetration to a fixed distance within a linear habitat at constant density

In this case, predator penetration is at a constant density $p_0$ a distance of $\delta$ into $\Omega = (-\ell, \ell)$, so that $\Omega_\delta$ is the union of the disjoint intervals $(-\ell, -\ell + \delta)$ and $(\ell - \delta, \ell)$. Symmetry considerations allow us to reduce (2.4) to the following problem on $(0, \ell)$:

$$\begin{aligned}
&D\psi_{xx} + r\psi = \sigma\psi \quad \text{on } (0, \ell - \delta),\\
&D\psi_{xx} + (r - p_0 g_0)\psi = \sigma\psi \quad \text{on } (\ell - \delta, \ell),\\
&\psi_x(0) = 0,\\
&\beta\psi(\ell) + (1 - \beta)\psi_x(\ell) = 0,\\
&\psi > 0 \quad \text{on } (0, \ell).
\end{aligned} \tag{3.1}$$

In (3.1), $g_0 = \frac{\partial g}{\partial v}(0, p_0)$ and the condition $\psi_x(0) = 0$ reflects the symmetry of $\psi$ on $(-\ell, \ell)$.

The discontinuity in the local intrinsic growth rate of the prey species at $\ell - \delta$ induced by the predator incursion means that the eigenfunction $\psi$ of (3.1) cannot be *twice* continuously differentiable at $\ell - \delta$. However, the regularity theory of elliptic partial differential equations [32] does guarantee that $\psi$ is *once* continuously differentiable on $[0, \ell]$. On the subintervals $(0, \ell - \delta)$ and $(\ell - \delta, \ell)$, (3.1) reduces to a constant coefficient second-order ordinary differential equation, the solutions of which are basically linear combinations of either sines and cosines or hyperbolic sines and hyperbolic cosines. The boundary conditions at 0 and $\ell$ plus the fact that $\psi$ and $\psi_x$ must match across the interface at $\ell - \delta$ enable us to obtain $\sigma$ in (3.1) as the $\sigma$-coordinate of the intersection of two appropriate curves $(\sigma, g(\sigma))$ and $(\sigma, f(\sigma))$, as follows.

It should be clear that the 'global' growth rate $\sigma$ for the prey species in $\Omega$ can never exceed its local intrinsic growth rate in the absence of predator incursion (i.e., $\sigma \leqslant r$) and moreover, that

$\sigma = r$ is possible only if $\delta = 0$ or $p_0 = 0$ (i.e., there is no predator penetration into $\Omega$) *and* $\beta = 0$ (no dissipation of the prey occurs across the boundary of $\Omega$). As a consequence, we may assume that $\sigma < r$. Thus the eigenfunction $\psi$ is a linear combination of

$$\sin\left(\sqrt{\frac{r-\sigma}{D}}x\right) \quad \text{and} \quad \cos\left(\sqrt{\frac{r-\sigma}{D}}x\right)$$

on the interval $(0, \ell - \delta)$. The symmetry condition $\psi_x(0) = 0$ forces $\psi$ to have the form

$$\psi(x) = c_1 \cos\left(\sqrt{\frac{r-\sigma}{D}}x\right)$$

on $(0, \ell - \delta)$. The form of $\psi$ on $(\ell - \delta, \ell)$ depends on whether $\sigma + p_0 g_0 - r$ is positive, negative or zero. When $\sigma + p_0 g_0 - r > 0$, $\psi(x)$ takes the form

$$c_3 \cosh\left(\sqrt{\frac{(\sigma + p_0 g_0 - r)}{D}}(x - \ell)\right) + c_4 \sinh\left(\sqrt{\frac{(\sigma + p_0 g_0 - r)}{D}}(x - \ell)\right)$$

on $(\ell - \delta, \ell)$, whereas when $\sigma + p_0 g_0 - r < 0$, $\psi(x)$ takes the form

$$c_5 \cos\left(\sqrt{\frac{(r - p_0 g_0 - \sigma)}{D}}(x - \ell)\right) + c_6 \sin\left(\sqrt{\frac{(r - p_0 g_0 - \sigma)}{D}}(x - \ell)\right)$$

on $(\ell - \delta, \ell)$. In case $\sigma + p_0 g_0 - r = 0$, $\psi(x)$ takes the linear form

$$mx + b$$

on $(\ell - \delta, \ell)$. If there is no dissipation of the prey species across the boundary of $\Omega$ (i.e., $\beta = 0$), $\sigma$ in (3.1) must exceed $r - p_0 g_0$ so that we need only consider the form of $\psi(x)$ on $(\ell - \delta, \ell)$ corresponding to $\sigma + p_0 g_0 - r > 0$. If $\beta > 0$, $\sigma$ in (3.1) may well be less than or equal to $r - p_0 g_0$, so that any one of the three forms for $\psi(x)$ on $(\ell - \delta, \ell)$ is possible.

If we now employ the boundary condition at $\ell$ plus the fact that $\psi$ and $\psi_x$ are continuous on $[0, \ell]$ (and hence, in particular, are continuous at $\ell - \delta$), we find that $\sigma$ in (3.1) is the abcissa of the unique point of intersection of the curves $y = g(\sigma, r, D, \ell, \delta)$ and $y = f(\sigma, r, p_0 g_0, D, \beta, \delta)$. Here

$$g(\sigma, r, D, \ell, \delta) = \sqrt{\frac{D}{r-\sigma}} \cot\left(\sqrt{\frac{r-\sigma}{D}}(\ell - \delta)\right) \tag{3.2}$$

while the form of $f$ depends on whether $\beta > 0$ or not. If $\beta > 0$,

$$f(\sigma, r, p_0 g_0, D, \beta, \delta) = \begin{cases} \dfrac{(1-\beta)\tau \cosh \delta\tau + \beta \sinh \delta\tau}{(1-\beta)\tau^2 \sinh \delta\tau + \beta\tau \cosh \delta\tau} \quad \left(\tau = \sqrt{\dfrac{\sigma + p_0 g_0 - r}{D}}\right) \\ \quad \text{if } \sigma + p_0 g_0 - r > 0, \\ \dfrac{1 + \beta\delta - \beta}{\beta} \quad \text{if } \sigma + p_0 g_0 - r = 0, \\ \dfrac{(1-\beta)\rho \cos \delta\rho + \beta \sin \delta\rho}{\beta\rho \cos \delta\rho - (1-\beta)\rho^2 \sin \delta\rho} \quad \left(\rho = \sqrt{\dfrac{r - p_0 g_0 - \sigma}{D}}\right) \\ \quad \text{if } \sigma + p_0 g_0 - r < 0. \end{cases} \tag{3.3}$$

If $\beta = 0$, only $\sigma + p_0 g_0 - r > 0$ is possible as noted above and hence $f$ simplifies to

$$f(\sigma, r, p_0 g_0, D, 0, \delta) = \sqrt{\frac{D}{\sigma + p_0 g_0 - r}} \coth\left(\delta\sqrt{\frac{\sigma + p_0 g_0 - r}{D}}\right). \tag{3.4}$$

We have averred that $\sigma$ in (3.1) is the abcissa of the unique point of intersection of the two curves. Our ability to make such an assertion comes from our knowledge of the graphs of the curves. It is a simple matter to check that $g$ as defined in (3.2) is continuous and increasing on the interval

$$\left[r - \frac{D\pi^2}{4(\ell - \delta)^2}, r\right)$$

with

$$g\left(r - \frac{D\pi^2}{4(\ell - \delta)^2}, r, D, \ell, \delta\right) = 0 \tag{3.5}$$

and

$$\lim_{\sigma \to r^-} g(\sigma, r, D, \ell, \delta) = +\infty. \tag{3.6}$$

It is a somewhat less simple matter (see [33] for a similar calculation), but one may also check that $f$ in (3.3) is continuous and decreasing on the interval $(r - p_0 g_0 - D\rho_0^2, \infty)$ with

$$\lim_{\sigma \to (r - p_0 g_0 - D\rho_0^2)^+} f(\sigma, r, p_0 g_0, D, \beta, \delta) = +\infty \tag{3.7}$$

and

$$\lim_{\sigma \to +\infty} f(\sigma, r, p_0 g_0, D, \beta, \delta) = 0. \tag{3.8}$$

(The quantity $\rho_0$ in the above arises as the singularity of the expression

$$\frac{(1 - \beta)\rho \cos \delta\rho + \beta \sin \delta\rho}{\beta\rho \cos \delta\rho - (1 - \beta)\rho^2 \sin \delta\rho}$$

from (3.3) in the interval $(0, \pi/2\delta]$; i.e., $\rho_0$ satisfies

$$\cot \delta\rho = \frac{1 - \beta}{\beta}\rho. \tag{3.9}$$

Notice from (3.9) that when $\beta = 1$, $\rho_0 = \pi/2\delta$ while $\lim_{\beta \to 0^+} \rho_0 = 0$. If we take $\rho_0 = 0$ when $\beta = 0$, then $f$ is continuous and decreasing on $(r - p_0 g_0 - D\rho_0^2, \infty)$ and (3.7) and (3.8) hold also in the case when $f$ is defined by (3.4).) Consequently, the two curves have a unique point of intersection corresponding to a value of $\sigma$ with

$$\sigma > \max\left\{r - \frac{D\pi^2}{4(\ell - \delta)^2}, r - p_0 g_0 - D\rho_0^2\right\}. \tag{3.10}$$

An immediate consequence of (3.10) is that when $r - p_0 g_0 < 0$, the right hand side of (3.10) is negative whenever $\delta$ is large enough in comparison to $\ell$ allowing the *possibility* that $\sigma$ may be negative. On the other hand, suppose that $r - p_0g_0 > 0$. If $r - p_0g_0 - D\rho_0^2 < 0$, then $\rho_0 \leqslant \pi/2\delta$ implies

$$r - p_0g_0 - \frac{D\pi^2}{4\delta^2} < 0,$$

which in turn implies

$$\delta < \frac{\pi}{2}\sqrt{\frac{D}{r - p_0g_0}}.$$

If now

$$r - \frac{D\pi^2}{4(\ell - \delta)^2} < 0, \quad \ell - \delta < \sqrt{\frac{D}{r}}\frac{\pi}{2}$$

so that

$$\ell - \sqrt{\frac{D}{r}}\frac{\pi}{2} < \delta.$$

Consequently, to have the right-hand side of (3.10) negative when $r - p_0g_0 > 0$ requires that

$$\ell - \sqrt{\frac{D}{r}}\frac{\pi}{2} < \delta < \frac{\pi}{2}\sqrt{\frac{D}{r - p_0g_0}}. \tag{3.11}$$

Hence if

$$\ell - \sqrt{\frac{D}{r}}\frac{\pi}{2} \geqslant \frac{\pi}{2}\sqrt{\frac{D}{r - p_0g_0}},$$

(3.11) cannot hold and $\sigma$ in (3.1) is positive independent of $\delta \in (0, \ell)$. This last condition can be expressed as

$$\ell \geqslant \sqrt{D}\frac{\pi}{2}\left(\frac{1}{\sqrt{r}} + \frac{1}{\sqrt{r - p_0g_0}}\right) \tag{3.12}$$

and for this particular case, the model always predicts persistence of the prey species regardless of the extent of predator incursion into $\Omega = [-\ell, \ell]$.

Suppose now that $\sigma = 0$ in (3.1). Then the curves $y = g(\sigma, r, D, \ell, \delta)$ and $y = f(\sigma, r, p_0g_0, D, \beta, \delta)$ intersect when $\sigma = 0$. What happens if $\ell$ is increased? The curve $y = f(\sigma, r, p_0g_0, D, \beta, \delta)$ is independent of $\ell$ and hence is unchanged. However,

$$\frac{\partial g}{\partial \ell} = -\sec^2\left(\sqrt{\frac{r - \sigma}{D}}(\ell - \delta)\right) < 0$$

so that the curve $y = g(\sigma, r, D, \ell, \delta)$ moves downward. Consequently, it cannot intersect $y = f(\sigma, r, p_0g_0, D, \beta\delta)$ until $\sigma$ is at some positive value. So if $\sigma = 0$ and the parameter $\ell$ (half-length of the habitat) is increased, $\sigma$ becomes positive and the model predicts persistence of the prey species when subject to the same extent and intensity of predator incursion but within a slightly larger habitat. As a consequence, it is reasonable to regard twice the value of $\ell$ corresponding to $\sigma = 0$

(i.e., $2\ell$) as a 'minimum patch size' necessary for the prey species to persist in the face of this form of predator incursion into $\Omega$.

Let us now denote this critical value of $\ell$ by $\ell^*$. Then $\ell^*$ is a function of $\delta, \beta, D, r$ and the predation-reduced prey intrinsic growth rate $r - p_0 g_0$. As can be anticipated from the form of $f$ in (3.3), when $\beta > 0$, the explicit formula for $\ell^*$ varies as $r - p_0 g_0 < 0$, $r - p_0 g_0 = 0$ or $r - p_0 g_0 > 0$. Indeed, setting $\sigma = 0$ in the formulae for $g$ in (3.2) and $f$ in (3.3) and equating these quantities, we find that $\ell^*$ satisfies the following. Namely,

$$\ell^* = \begin{cases} \delta + \sqrt{\frac{D}{r}}\cot^{-1}\left\{ \dfrac{\sqrt{\frac{r}{D}}\left[(1-\beta)\sqrt{\frac{r-p_0g_0}{D}}\cos\left(\sqrt{\frac{r-p_0g_0}{D}}\delta\right)+\beta\sin\left(\sqrt{\frac{r-p_0g_0}{D}}\delta\right)\right]}{\left[\beta\sqrt{\frac{r-p_0g_0}{D}}\cos\left(\sqrt{\frac{r-p_0g_0}{D}}\delta\right)-(1-\beta)\left(\frac{r-p_0g_0}{D}\right)\sin\left(\sqrt{\frac{r-p_0g_0}{D}}\delta\right)\right]} \right\} \\ \quad \text{if } r - p_0g_0 > 0 = \sigma \\ \delta + \sqrt{\frac{D}{r}}\cot^{-1}\left(\sqrt{\frac{r}{D}}\left(\frac{1+\beta\delta-\beta}{\beta}\right)\right) \\ \quad \text{if } r - p_0g_0 = 0 = \sigma, \\ \delta + \sqrt{\frac{D}{r}}\cot^{-1}\left\{ \dfrac{\sqrt{\frac{r}{D}}\left[(1-\beta)\sqrt{\frac{p_0g_0-r}{D}}\cosh\left(\sqrt{\frac{p_0g_0-r}{D}}\delta\right)+\beta\sinh\left(\sqrt{\frac{p_0g_0-r}{D}}\delta\right)\right]}{\left[(1-\beta)\left(\frac{p_0g_0-r}{D}\right)\sinh\left(\sqrt{\frac{p_0g_0-r}{D}}\delta\right)+\beta\left(\sqrt{\frac{p_0g_0-r}{D}}\right)\cosh\left(\sqrt{\frac{p_0g_0-r}{D}}\delta\right)\right]} \right\} \\ \quad \text{if } r - p_0g_0 < 0 = \sigma, \end{cases} \tag{3.13}$$

when $\beta \in (0, 1]$. If $\beta = 0$, (3.3) reduces to (3.4), and in particular $r - p_0 g_0 < \sigma = 0$ when we calculate for $\ell^*$. In this instance, we obtain

$$\ell^* = \delta + \sqrt{\frac{D}{r}}\cot^{-1}\left(\sqrt{\frac{r}{p_0 g_0 - r}}\coth\left(\sqrt{\frac{p_0 g_0 - r}{D}}\delta\right)\right). \tag{3.14}$$

We noted earlier that when $f$ is given by (3.3), $\sigma > r - p_0 g_0 - D\rho_0^2$, where $\rho_0$ is the root of (3.9) in the interval $(0, \pi/2\delta]$. Consequently, if $\sigma = 0$,

$$\frac{r - p_0 g_0}{D} < \rho_0^2,$$

so that

$$\sqrt{\frac{r - p_0 g_0}{D}} < \rho_0$$

when $r - p_0 g_0 > 0$. It follows that the arguments of the inverse cotangent in both (3.13) and (3.14) are necessarily positive. This observation allows us to make the following basic estimate on the size of $\ell^*$, independent of the value of $\beta \in [0, 1]$.

**Proposition 3.1.** *If* $\ell^*$ *is given by* (3.13) *or* (3.14), *then*

$$\ell^* < \delta + \sqrt{\frac{D}{r}}\left(\frac{\pi}{2}\right). \tag{3.15}$$

Proposition 3.1 has a very important interpretation in this modeling scenario. The quantity $2(\ell - \delta)$ is the size of that portion of $\Omega$ which is free from predator incursion. Proposition 3.1 implies that $\sigma$ in (3.1) is necessarily positive when

$$\ell = \delta + \sqrt{\frac{D}{r}}\left(\frac{\pi}{2}\right).$$

On the other hand, if an undisturbed habitat patch for the same prey species of length $2(\ell - \delta)$ has an immediately lethal boundary, its overall growth rate $\tilde{\sigma}$ in such a patch fragment is determined by

$$\begin{aligned} &D\psi_{xx} + r\psi = \tilde{\sigma}\psi \quad \text{on } (0, \ell - \delta), \\ &\psi_x(0) = 0, \\ &\psi(\ell - \delta) = 0, \\ &\psi > 0 \quad \text{on } (0, \ell - \delta). \end{aligned} \tag{3.16}$$

In this case, $\tilde{\sigma} = 0$ corresponds to

$$\ell - \delta = \sqrt{\frac{D}{r}}\left(\frac{\pi}{2}\right). \tag{3.17}$$

As a consequence of (3.16) and (3.17), we may conclude that in this modeling scenario the size of the habitat patch fragment free from predator incursion that is required to predict persistence of the prey species is always less than the size of undisturbed habitat patch fragment needed to predict persistence of the prey species when the habitat fragment has an immediately lethal boundary.

We may also estimate $\ell^*$ somewhat more closely. Consider first the case in which $r - p_0 g_0 < 0$. In this case, if we let $\sigma = 0$ in the relevant formulae for $f$ in (3.3) and (3.4) and calculate $\partial f / \partial \delta$ for $\delta > 0$, we find that $f$ is increasing as a function on $\delta$ on $(0, \infty)$ when

$$\beta > (1 - \beta)\sqrt{\frac{p_0 g_0 - r}{D}},$$

decreasing as a function of $\delta$ on $(0, \infty)$ when

$$\beta < (1 - \beta)\sqrt{\frac{p_0 g_0 - r}{D}},$$

and a constant in $\delta$ on $(0, \infty)$ when

$$\beta = (1 - \beta)\sqrt{\frac{p_0 g_0 - r}{D}}.$$

(Having

$$\beta > (1 - \beta)\sqrt{\frac{p_0 g_0 - r}{D}}$$

suggests that dissipation from the boundary condition is a stronger effect than the negative effective intrinsic growth rate that results from predation (i.e., from having $r < p_0 g_0$). When

$$\beta < (1 - \beta)\sqrt{\frac{p_0 g_0 - r}{D}},$$

the relative impacts of the two effects are reversed, while if

$$\beta = (1-\beta)\sqrt{\frac{p_0 g_0 - r}{D}},$$

the two effects appear to have some sort of balance.) In any event, if

$$\beta > (1-\beta)\sqrt{\frac{p_0 g_0 - r}{D}},$$

we obtain that

$$\frac{1-\beta}{\beta} = \lim_{\delta \to 0^+} f \leqslant \sqrt{\frac{D}{r}} \cot\left(\sqrt{\frac{r}{D}}(\ell^* - \delta)\right) \leqslant \lim_{\delta\to\infty} f = \sqrt{\frac{D}{p_0 g_0 - r}}. \tag{3.18}$$

It follows from (3.18) that

$$\sqrt{\frac{D}{r}}\left(\cot^{-1}\left(\sqrt{\frac{r}{p_0 g_0 - r}}\right)\right) \leqslant \ell^* - \delta \leqslant \sqrt{\frac{D}{r}}\left(\cot^{-1}\left(\frac{(1-\beta)}{\beta}\sqrt{\frac{r}{D}}\right)\right), \tag{3.19}$$

hence providing both upper and lower bounds on $\ell^*$. Note in particular that the lower bound is insensitive to $\beta$ for

$$\beta > (1-\beta)\sqrt{\frac{p_0 g_0 - r}{D}}$$

and that as $\beta \to 1$,

$$\sqrt{\frac{D}{r}}\left(\cot^{-1}\left(\frac{(1-\beta)}{\beta}\sqrt{\frac{r}{D}}\right)\right) \to \sqrt{\frac{D}{r}}\left(\frac{\pi}{2}\right)$$

recovering the estimate in (3.15). If

$$0 < \beta < (1-\beta)\sqrt{\frac{p_0 g_0 - r}{D}},$$

the inequalities in (3.18) are reversed. This time, however, if $\beta \to 0$, (3.18) merely informs us that $\ell^* > \delta$. In this case, (3.14) more closely tracks $\ell^*$ with respect to $\delta$. When

$$\beta = (1-\beta)\sqrt{\frac{p_0 g_0 - r}{D}},$$

it is easy to see that

$$f \equiv \sqrt{\frac{D}{p_0 g_0 - r}},$$

so that

$$\ell^* - \delta \equiv \sqrt{\frac{D}{r}}\cot^{-1}\left(\sqrt{\frac{r}{p_0 g_0 - r}}\right),$$

as could be anticipated from (3.18).

Now suppose $r - p_0 g_0 > 0$ and consider $\ell^*$. In this case, $\sigma = 0$ is possible only if $\beta > 0$ and hence $f$ is as given in (3.3) when $r - p_0 g_0 > 0 = \sigma$. By calculating $\partial f/\partial\delta$, one finds that $f$ increases from $(1-\beta)/\beta$ to $+\infty$ as $\delta$ ranges from 0 up to

$$\delta^* = \frac{1}{\sqrt{r - (p_0 g_0/D)}}\cot^{-1}\left(\frac{(1-\beta)}{\beta}\sqrt{\frac{r - p_0 g_0}{D}}\right).$$

(Note that for $\delta = \delta^*$ and $\sigma = 0$, $\sqrt{(r - p_0 g_0)/D}$ corresponds to $\rho_0$ in (3.9).) Consequently, $\ell^* - \delta$ satisfies

$$0 < \ell^* - \delta < \sqrt{\frac{D}{r}}\cot^{-1}\left(\sqrt{\frac{r}{D}}\left(\frac{1-\beta}{\beta}\right)\right) \tag{3.20}$$

with

$$\lim_{\delta\to 0^+} \ell^* - \delta = \sqrt{\frac{D}{r}}\cot^{-1}\left(\sqrt{\frac{r}{D}}\left(\frac{1-\beta}{\beta}\right)\right)$$

and $\lim_{\delta\to\delta^{*-}} \ell^* - \delta = 0$. If $\delta = 0$,

$$\frac{1-\beta}{\beta} = \frac{\cos\left(\sqrt{r/D}\,\ell\right)}{\sqrt{r/D}\sin\left(\sqrt{r/D}\,\ell\right)},$$

and $\psi(x)$ in (3.1) is given by $\cos(\sqrt{r/D}\,x)$, as would be expected in a habitat free from predator intrusions. On the other hand, if $\delta = \delta^*$ and $\ell \geqslant \ell^*$, then

$$\phi(x) = c\left(\beta\sin\left(\sqrt{\frac{r - p_0 g_0}{D}}(x-\ell)\right) - (1-\beta)\sqrt{\frac{r - p_0 g_0}{D}}\cos\left(\sqrt{\frac{r - p_0 g_0}{D}}(x-\ell)\right)\right)$$

satisfies

$$\begin{aligned}
&D\phi_{xx} + (r - p_0 g_0)\phi = 0 \quad \text{on } (\ell - \delta^*, \ell),\\
&\phi_x(\ell - \delta^*) = 0,\\
&\beta\phi(\ell) + (1-\beta)\phi_x(\ell) = 0,\\
&\phi > 0 \quad \text{on } (\ell - \delta^*, \ell),
\end{aligned} \tag{3.21}$$

for $c < 0$. $\delta^*$ in (3.21) corresponds to half the size of habitat required for the prey species to persist when its intrinsic growth rate is reduced by predation to the *lower but still positive value* $r - p_0 g_0$ throughout the habitat. Indeed, if $\delta \geqslant \delta^*$ and $\ell > \delta$, then $\sigma$ in (3.1) is necessarily positive. For $\sigma$ satisfies (see [30])

$$\sigma \geqslant \max_{\substack{\psi\in C^1[0,\ell],\ \psi\not\equiv 0\\ \psi'(0)=0,\ \beta\psi(\ell)+(1-\beta)\psi'(\ell)=0}} \frac{-D\int_0^\ell \psi_x^2\,\mathrm{d}x + \int_0^\ell r(x)\psi^2\,\mathrm{d}x}{\int_0^\ell \psi^2\,\mathrm{d}x},$$

where

$$r(x) = \begin{cases} r, & x \in (0, \ell - \delta),\\ r - p_0 g_0, & x \in (\ell - \delta, \ell).\end{cases}$$

Observe that if

$$\tilde{\phi} = \begin{cases} \phi(\ell-\delta^*), & x \in (0, \ell-\delta^*), \\ \phi(x), & x \in (\ell-\delta^*, \ell), \end{cases}$$

$\tilde{\phi}'(\ell-\delta^*) = 0$ so that $\tilde{\phi} \in C^1[0,\ell]$ and meets the boundary conditions of (3.1). So

$$\begin{aligned} \sigma &\geqslant \frac{-D\int_0^\ell \tilde{\phi}_x^2\,\mathrm{d}x + \int_0^\ell r(x)\tilde{\phi}^2\,\mathrm{d}x}{\int_0^\ell \tilde{\phi}^2\,\mathrm{d}x} \\ &= \frac{-D\int_{\ell-\delta^*}^\ell \phi_x^2\,\mathrm{d}x + \int_{\ell-\delta^*}^\ell (r-p_0g_0)\phi^2\,\mathrm{d}x + \int_0^{\ell-\delta} r\phi^2(\ell-\delta^*)\,\mathrm{d}x + \int_{\ell-\delta}^{\ell-\delta^*}(r-p_0g_0)\phi^2(\ell-\delta^*)\,\mathrm{d}x}{\int_0^\ell \tilde{\phi}^2\,\mathrm{d}x} \\ &= \frac{\phi^2(\ell-\delta^*)[r(\ell-\delta) + (r-p_0g_0)(\delta-\delta^*)]}{\int_0^\ell \tilde{\phi}^2\,\mathrm{d}x} > 0. \end{aligned}$$

Finally, suppose $r - p_0g_0 = 0 = \sigma$. Then one may still obtain inequality (3.19), as in the case when $r - p_0g_0 > 0$. However, in this case $\ell^* - \delta$ ranges between the limits

$$\sqrt{\frac{D}{r}}\cot^{-1}\left(\sqrt{\frac{r}{D}}\left(\frac{1-\beta}{\beta}\right)\right)$$

and 0 as $\delta$ ranges between 0 and $\infty$. This change reflects the fact that when $r - p_0g_0 = 0$ predator incursion *may* be a serious detriment to the species no matter how large the prey habitat might be, in contrast to the case when $r - p_0g_0$ remains positive. Such an effect requires dissipation of the prey species from the boundary of the habitat. Indeed, since

$$\ell^* - \delta = \sqrt{\frac{D}{r}}\cot^{-1}\left(\sqrt{\frac{r}{D}}\left(\frac{1+\beta\delta-\delta}{\beta}\right)\right)$$

in this case, for any fixed $\delta > 0$, $\lim_{\beta\to 0^+} \ell^* - \delta = 0$. In particular, when there is no dissipation from the boundary (i.e., when $\beta = 0$) and $r - p_0g_0 = 0$, if $\delta > 0$ is fixed, then $\sigma$ in (3.1) is positive for any choice of $\ell$ with $\ell > \delta$.

### *3.2. Predator penetration to a fixed distance within a planar habitat at constant density*

Notice that $p(x)$ in this example is the same as in sub-section 3.1. The difference is that now $\Omega$ is a general two-dimensional habitat. Consequently, we can no longer specify the general form of $\psi$ on $\Omega_\delta$ and on $\Omega\backslash\Omega_\delta$ and require them to match across the interface to obtain an equation for $\sigma$ in (2.4). However, the variational formulas for $\sigma$ given in (2.7) and (2.8) still hold and may be made somewhat more specific with $p(x)$ identified as it is here. We find that $\sigma$ is given by

$$\sigma = \sup_{\substack{\psi\in W^{1,2}(\Omega) \\ \psi\not\equiv 0}} \left[\frac{-D\int_\Omega |\nabla\psi|^2\,\mathrm{d}x + r\int_\Omega \psi^2\,\mathrm{d}x - p_0g_0\int_{\Omega_\delta}\psi^2\,\mathrm{d}x - \frac{D\beta}{1-\beta}\oint_{\partial\Omega}\psi^2\,\mathrm{d}s}{\int_\Omega \psi^2\,\mathrm{d}x}\right] \tag{3.22}$$

when $0 \leqslant \beta < 1$ and that $\sigma$ is given by

$$\sigma = \sup_{\substack{\psi \in W^{1,2}(\Omega) \\ \psi \not\equiv 0}} \left[ \frac{-D\int_\Omega |\nabla\psi|^2\,\mathrm{d}x + r\int_\Omega \psi^2\,\mathrm{d}x - p_0 g_0 \int_{\Omega_\delta} \psi^2\,\mathrm{d}x}{\int_\Omega \psi^2\,\mathrm{d}x} \right] \tag{3.23}$$

when $\beta = 1$, i.e., when the boundary of $\Omega$ may be regarded as completely lethal.

If we let $\psi$ be the solution to (2.2) with $\beta = 1$, we have by (3.22) and (3.23) that $\sigma(\beta)$ satisfies

$$\sigma(\beta) \geqslant r - \lambda_1(1)D - p_0 g_0 \frac{\int_{\Omega_\delta} \psi^2\,\mathrm{d}x}{\int_\Omega \psi^2\,\mathrm{d}x} \tag{3.24}$$

for any $\beta \in [0, 1]$. On the other hand, if we let $\psi$ be the solution to (2.2) with $\beta = 0$, namely $\psi \equiv$ a constant, we get from (3.22) that $\sigma(\beta)$ satisfies

$$\sigma(\beta) \geqslant r - p_0 g_0 \frac{|\Omega_\delta|}{|\Omega|} - \frac{D\beta}{1-\beta} \frac{|\partial\Omega|}{|\Omega|} \tag{3.25}$$

for any $\beta \in [0, 1)$. Since

$$\lim_{\beta \to 1^-} \frac{\beta}{1-\beta} = +\infty,$$

the right-hand side of (3.25) tends to $-\infty$ as $\beta \to 1^-$. Consequently, when dissipation from the boundary becomes a significant factor in the model (i.e., when $\beta$ is close to 1), (3.24) (which is independent of $\beta$) gives a far more accurate lower bound on $\sigma(\beta)$ than does (3.25). On the other hand, the presence of the term $-\lambda_1(1)D$ in the right-hand side of (3.24) indicates that the situation frequently is just the opposite when dissipation from the boundary is minimal (i.e., when $\beta$ is near 0), i.e., the right-hand side of (3.25) exceeds that of (3.24).

We see from (3.25) that if

$$r > p_0 g_0 \frac{|\Omega_\delta|}{|\Omega|} + \frac{D\beta}{1-\beta} \frac{|\partial\Omega|}{|\Omega|}, \tag{3.26}$$

then the prey species can be expected to persist, (as $\sigma(\beta) > 0$) and, moreover, if $\beta$ is small, such a requirement is rather reasonable as a 'coarse but quick and ready' rule of the thumb in understanding the effect of predator incursions into $\Omega$ under this scenario. When boundary dissipation becomes significant, we may in principle employ (3.24) in a similar manner. Of course, in practice, we are limited by our knowledge of how the quantity $\int_{\Omega_\delta} \psi^2\,\mathrm{d}x / \int_\Omega \psi\,\mathrm{d}x$ depends on $\delta$ and the geometry of $\Omega$. Consequently, to explore (3.24) further in this vein (i.e., set $\sigma(\beta) = 0$), effectively speaking we need to specify $\Omega$ more precisely. Of course, there are choices of $\Omega$ where $\psi$ is explicitly known. For specificity, we take $\Omega$ to be the square $[0, A] \times [0, A]$ so that $\psi$ may be chosen as

$$\sin\frac{\pi x}{A} \sin\frac{\pi y}{A}$$

and

$$\Omega_\delta = ([0, A] \times [0, \delta]) \cup ([0, A] \times [A - \delta, A]) \cup ([0, \delta] \times [0, A]) \cup ([A - \delta, A] \times [0, A]).$$

We find in this instance

$$\frac{\int_{\Omega_\delta}\psi^2\,\mathrm{d}x}{\int_\Omega \psi^2\,\mathrm{d}x} = 1-\left(\frac{1}{\pi}\sin\left(\frac{2\pi\delta}{A}\right)+1-\frac{2\delta}{A}\right)^2. \tag{3.27}$$

Since $\lambda_1(1)=2\pi^2/A^2$ in this case, we have from (3.27) that (3.24) becomes

$$\sigma(\beta)\geqslant r-\frac{2\pi^2 D}{A^2}+p_0g_0\left(\left(\frac{1}{\pi}\sin\left(\frac{2\pi\delta}{A}\right)+1-\frac{2\delta}{A}\right)^2-1\right). \tag{3.28}$$

Using the expansion

$$\sin x = x-\frac{1}{3!}x^3+\frac{1}{5!}x^5+\mathrm{O}(x^7),$$

we have that for $\delta/A$ small that

$$\left(\frac{1}{\pi}\sin\left(\frac{2\pi\delta}{A}\right)+1-\frac{2\delta}{A}\right)^2-1=-\frac{8}{3}\pi^2\left(\frac{\delta}{A}\right)^3+\mathrm{O}\left(\left(\frac{\delta}{A}\right)^5\right),$$

where the $\mathrm{O}((\delta/A)^5)$ term is positive for $\delta/A$ small. It follows from (3.28) that

$$\sigma(\beta)>r-\frac{2\pi^2 D}{A^2}-\frac{8\pi^2 p_0 g_0}{3}\left(\frac{\delta}{A}\right)^3. \tag{3.29}$$

Now suppose that $\sigma(\beta)=0$. Assume also that $r-(2\pi^2D/A^2)>0$ so that $r-\lambda_1(\beta)D>0$ for any $\beta\in[0,1]$. This last ensures that having $\sigma(\beta)$ at its critical threshold is not solely attributable to boundary dissipation. From (3.29) we get that

$$p_0g_0\delta^3>\frac{3(A^3r-2\pi^2DA)}{8\pi^2} \tag{3.30}$$

is a necessary condition for predator incursions to threaten the persistence of the prey species in $\Omega$ for $\delta/A$ small.

### 3.3. *Predator penetration into a linear habitat with exponentially decaying density*

In this example, $p(x)$ is the equilibrium solution

$$p_0\frac{\cosh(\sqrt{\mu/d}\,x)}{\cosh(\sqrt{\mu/d}\,\ell)}$$

to (2.6) when we revert to the one-dimensional habitat $\Omega=(-\ell,\ell)$. The variational formula (2.7) in this case reduces to

$$\sigma(\beta)=\sup_{\substack{\psi\in W^{1,2}(-\ell,\ell)\\ \psi\not\equiv 0}}\left\{\frac{-D\int_{-\ell}^{\ell}(\psi_x)^2\,\mathrm{d}x+\int_{-\ell}^{\ell}(r-g_0p(x))\psi^2\,\mathrm{d}x-\frac{D\beta}{1-\beta}[\psi^2(\ell)+\psi^2(-\ell)]}{\int_{-\ell}^{\ell}\psi^2\,\mathrm{d}x}\right\}. \tag{3.31}$$

If we let $\psi=1$ in (3.31) (i.e., $\psi$ is the eigenfunction for $-\nabla^2$ on $(-\ell,\ell)$ subject to homogeneous Neumann boundary data) and use the fact that $p(x)$ is even, we obtain the estimate

$$
\begin{aligned}
\sigma(\beta) &\geqslant \left\{ \left( 2\ell r - 2g_0p_0 \int_0^{\ell} \frac{\cosh\left(\sqrt{u/d}\,x\right)}{\cosh\left(\sqrt{\mu/d}\,\ell\right)}\,\mathrm{d}x - \frac{2D\beta}{1-\beta} \right) \Big/ 2\ell \right\} \\
&= r - p_0g_0 \frac{\tanh\sqrt{\mu/d}\,\ell}{\sqrt{\mu/d}\,\ell} - \frac{D\beta}{\ell(1-\beta)}. \qquad (3.32)
\end{aligned}
$$

Notice now that if there is no predator intrusion into $\Omega$ (so that we can assume $\rho_0 = 0$), then $\sigma(\beta) = 0$ in (3.32) forces

$$\ell \leqslant \frac{D\beta}{r(1-\beta)}.$$

It follows that if $\ell > D/r$, boundary dissipation alone cannot lead to a loss of persistence in the prey population in $\Omega$ for any $\beta \in [0, 1/2]$. So let us assume $\ell > D/r$ and $\beta \in [0, 1/2]$. We have

$$r - \frac{D\beta}{\ell(1-\beta)} > 0.$$

Moreover,

$$\frac{\tanh\sqrt{\mu/d}\,\ell}{\sqrt{\mu/d}\,\ell}$$

is strictly decreasing in $\ell$ (or, for that matter, in $\mu$) with

$$\lim_{\ell\to 0^+} \frac{\tanh\sqrt{\mu/d}\,\ell}{\sqrt{\mu/d}\,\ell} = 1 \quad \text{and} \quad \lim_{\ell\to\infty} \frac{\tanh\sqrt{\mu/d}\,\ell}{\sqrt{\mu/d}\,\ell} = 0.$$

Clearly,

$$p_0g_0 \frac{\tanh\sqrt{\mu/d}\,\ell}{\sqrt{\mu/d}\,\ell} < r - \frac{D}{\ell}$$

for any $\ell$ above a threshold depending on $p_0g_0$, $\mu/d$ and $D/r$. If we let $\tilde{\ell}$ denote this threshold, then $\ell^* \leqslant \tilde{\ell}$.

As in the previous example, the lower estimate on $\sigma(\beta)$ in (3.32) ceases to be meaningful as $\beta \to 1$ since then

$$-\frac{D\beta}{\ell(1-\beta)} \to -\infty$$

for any fixed $\ell$. Consequently, we make a different choice of $\psi$ in (3.31), as follows. Let $0 < \tilde{\ell} < \ell$, and consider $(-\tilde{\ell}, \tilde{\ell})$. Any function $\tilde{\psi} \in W_0^{1,2}((-\tilde{\ell}, \tilde{\ell}))$ can be extended to a function $\psi \in W^{1,2}((-\ell, \ell))$ by defining

$$\psi(x) = \begin{cases} \psi(x), & x \in (-\tilde{\ell}, \tilde{\ell}), \\ 0 & \text{otherwise.} \end{cases}$$

It follows from (3.31) that

$$\begin{aligned}\sigma(\beta) &\geqslant \sup_{\substack{\tilde\psi\in W_0^{1,2}((-\tilde\ell,\tilde\ell))\\ \tilde\psi\not\equiv 0}} \left\{ \frac{-D\int_{-\tilde\ell}^{\tilde\ell}\tilde\psi_x^2\,\mathrm{d}x+\int_{-\tilde\ell}^{\tilde\ell}(r-p(x)g_0)\tilde\psi^2\,\mathrm{d}x}{\int_{-\tilde\ell}^{\tilde\ell}\tilde\psi^2\,\mathrm{d}x}\right\}\\ &\geqslant \sup_{\substack{\tilde\psi\in W_0^{1,2}((-\tilde\ell,\tilde\ell))\\ \tilde\psi\not\equiv 0}} \left\{ \frac{-D\int_{-\tilde\ell}^{\tilde\ell}\tilde\psi_x^2\,\mathrm{d}x+\int_{-\tilde\ell}^{\tilde\ell}(r-\tilde p)\tilde\psi^2\,\mathrm{d}x}{\int_{-\tilde\ell}^{\tilde\ell}\tilde\psi^2\,\mathrm{d}x}\right\}\end{aligned} \tag{3.33}$$

for any constant

$$\tilde p \geqslant p_0g_0\frac{\cosh\sqrt{\mu/d}\,\tilde\ell}{\cosh\sqrt{\mu/d}\,\ell}.$$

The last term in (3.33) is the principal eigenvalue for the problem

$$\begin{aligned}&D\nabla^2\phi+(r-\tilde p)\phi=\sigma\phi \quad \text{in } (-\tilde\ell,\tilde\ell),\\ &\phi=0 \quad \text{on } \partial((-\tilde\ell,\tilde\ell)),\end{aligned}$$

which has the value

$$-\frac{D\pi^2}{4\tilde\ell^2}+r-\tilde p.$$

Provided

$$r > p_0g_0\frac{\cosh\sqrt{\mu/d}\,\tilde\ell}{\cosh\sqrt{\mu/d}\,\ell},$$

it follows that

$$\sigma(\tilde\beta) \geqslant -\frac{D\pi^2}{4\tilde\ell^2}+r-\frac{p_0g_0\cosh\sqrt{\mu/d}\,\tilde\ell}{\cosh\sqrt{\mu/d}\,\ell}. \tag{3.34}$$

In order for the right-hand side of (3.34) to be positive (and hence guarantee persistence of the prey population), we must have

$$r > \frac{D\pi^2}{4\tilde\ell^2}+p_0g_0\frac{\cosh\sqrt{\mu/d}\,\tilde\ell}{\cosh\sqrt{\mu/d}\,\ell}.$$

As $\tilde\ell$ decreases,

$$p_0g_0\frac{\cosh\sqrt{\mu/d}\,\tilde\ell}{\cosh\sqrt{\mu/d}\,\ell}$$

decreases with

$$\lim_{\tilde\ell\to 0} p_0g_0\frac{\cosh\sqrt{\mu/d}\,\tilde\ell}{\cosh\sqrt{\mu/d}\,\ell}=\frac{p_0g_0}{\cosh\sqrt{\mu/d}\,\ell}.$$

So if

$$r > \frac{p_0 g_0}{\cosh \sqrt{\mu/d}\,\ell}, \quad r > p_0 g_0 \frac{\cosh \sqrt{\mu/d}\,\tilde{\ell}}{\cosh \sqrt{\mu/d}\,\ell}$$

for small enough $\tilde{\ell}$. However, as $\tilde{\ell}$ decreases $D\pi^2/4\tilde{\ell}^2$ increases with

$$\lim_{\tilde{\ell}\to 0} \frac{D\pi^2}{4\tilde{\ell}^2} = +\infty.$$

Consequently, having

$$r > \frac{D\pi^2}{4\tilde{\ell}^2} + p_0 g_0 \frac{\cosh \sqrt{\mu/d}\,\tilde{\ell}}{\cosh \sqrt{\mu/d}\,\ell}$$

for some $\tilde{\ell} \in (0, \ell)$ is a balancing act. The predator density in this case decays exponentially as we move away from the edge of $(-\ell, \ell)$. So by considering a subhabitat $(-\tilde{\ell}, \tilde{\ell})$ the effect of predatory incursion is markedly diminished. However, to estimate $\sigma(\beta)$ from below in this way (i.e., to derive (3.33) from (2.7)), mathematically we needed to view the subhabitat as having a lethal boundary and such a boundary effect becomes decidedly more and more pronounced as the size of the subhabitat shrinks. So, in order for this approach to estimating $\sigma(\beta)$ from below to work (i.e., to guarantee that $\sigma(\beta) > 0$), we want a 'mid-size' subhabitat far enough away from the edge of $(-\ell, \ell)$ to take advantage of the mediation in effects of predator incursion yet not so small that a prey population on the subhabitat would be decimated by a lethal boundary imposed on the subhabitat. Note that in order for the method to imply that $\sigma(\beta) > 0$ it is necessary that

$$r > \frac{p_0 g_0}{\cosh(\sqrt{\mu/d}\,\ell)}. \tag{3.35}$$

Notice that (3.35) is equivalent to

$$\ell > \sqrt{\frac{d}{\mu}} \cosh^{-1}\left(\frac{p_0 g_0}{r}\right)$$

and can arise in several ways:

1. a reduction in the predator density outside $\Omega$ (a lower $p_0$);
2. a reduction in the rate of diffusion of the predators into the habitat (a lower $d$);
3. an increase in the mortality rate of the predator species in $\Omega$ (a larger $\mu$);
4. an increase on the size of $\Omega$ itself (a larger $\ell$); or
5. a reduction in the predator's attack rate on the prey ($a$ lower $g$).

It is possible to maximize the right-hand side of (3.34) with respect to $\tilde{\ell} \in (0, \ell)$ and then to use this information to obtain an upper bound on the minimum patch size ($2\ell^*$) of refuge needed in this case for a prey population to persist in the presence of predator intrusions. However, the result is sufficiently implicit so as not to be particularly informative. Consequently, we use (3.34) as a starting point to obtain a lower estimate of $\sigma(\beta)$ that we can maximize with respect to $\tilde{\ell} \in (0, \ell)$ rather easily and obtain a less sharp but more informative upper bound for $\ell^*$. We begin with the right-hand side of (3.34). It is easy to establish that

$$\cosh\sqrt{\frac{\mu}{d}}\ell \geqslant \left(\cosh\sqrt{\frac{\mu}{d}}(\ell-\tilde{\ell})\right)\cosh\sqrt{\frac{\mu}{d}}\tilde{\ell}$$

so that

$$r-\frac{D\pi^2}{4\tilde{\ell}^2}-p_0g_0\frac{\cosh(\sqrt{\mu/d}\,\tilde{\ell})}{\cosh(\sqrt{\mu/d}\,\ell)} \geqslant r-\frac{D\pi^2}{4\tilde{\ell}^2}-\frac{p_0g_0}{\cosh(\sqrt{\mu/d}\,(\ell-\tilde{\ell}))}.$$

Since

$$\cosh\left(\sqrt{\frac{\mu}{d}}(\ell-\tilde{\ell})\right)=1+\frac{\mu}{2d}(\ell-\tilde{\ell})^2\cosh\left(\sqrt{\frac{\mu}{d}}(z-\tilde{\ell})\right)$$

for some $z\in(\tilde{\ell},\ell)$,

$$\cosh\left(\sqrt{\frac{\mu}{d}}(\ell-\tilde{\ell})\right)\geqslant\frac{\mu}{2d}(\ell-\tilde{\ell})^2$$

so that

$$r-\frac{D\pi^2}{4\tilde{\ell}^2}-\frac{p_0g_0}{\cosh(\sqrt{\mu/d}\,(\ell-\tilde{\ell}))}\geqslant r-\frac{\pi^2D}{4\tilde{\ell}^2}-\frac{2p_0g_0d}{\mu(\ell-\tilde{\ell})^2}.$$

As a consequence, (3.34) implies

$$\sigma(\beta)\geqslant r-\frac{\pi^2D}{4\tilde{\ell}^2}-\frac{2p_0g_0d}{\mu(\ell-\tilde{\ell})^2}. \tag{3.36}$$

Maximizing the right-hand side of (3.36) with respect to $\tilde{\ell}$ leads to

$$\begin{aligned}\tilde{\ell}&=\frac{1}{1+2\left(\frac{p_0g_0d}{\pi^2\mu D}\right)^{1/3}}\ell,\\ \ell-\tilde{\ell}&=\frac{2\left(\frac{p_0g_0d}{\pi^2\mu D}\right)^{1/3}}{1+2\left(\frac{p_0g_0d}{\pi^2\mu D}\right)^{1/3}}\ell.\end{aligned} \tag{3.37}$$

Substituting the values of $\tilde{\ell}$ and $\ell-\tilde{\ell}$ in (3.37) into (3.36) leads to

$$\sigma(\beta)\geqslant r-\left[\frac{D\pi^2}{4}+\frac{1}{2}\left(\frac{p_0g_0d}{\mu}\right)^{1/3}(\pi^2D)^{2/3}\right]\left[\left\{1+2\left(\frac{p_0g_0d}{\pi^2\mu D}\right)^{1/3}\right\}\Big/\ell^2\right]. \tag{3.38}$$

It follows that $\sigma(\beta)>0$ for any $\ell$ large enough to make the right-hand side of (3.38) positive. As a consequence we obtain the upper bound

$$\ell^*\leqslant\left[\frac{1}{r}\left[\frac{D\pi^2}{4}+\frac{1}{2}\left(\frac{p_0g_0d}{\mu}\right)^{1/3}(\pi^2D)^{2/3}\right]\left[1+2\left(\frac{p_0g_0d}{\pi^2\mu D}\right)^{1/3}\right]\right]^{1/2}. \tag{3.39}$$

## 4. Discussion

In the absence of predation, whether the prey persists or not is determined by a balance between population growth rate in the patch and mortality at the patch edge. This balance, including the effects of dispersal rate and boundary conditions on edge mortality, is often interpreted in the context of critical patch size [25,29]. By reducing the prey's effective growth rate, cross edge predation can sensitively affect this balance. Consequently, in our modeling scenarios, as in some real-life cases, predator incursions can pose a threat to the persistence of patch-resident species. Note however that while the above is true for the class of functional responses examined here (which includes those of Lotka–Volterra and Holling Type II forms) it is not true for predators that exhibit prey switching (Holling Type III). We examine this difference, and related features, in Ref. [34].

Because edge-foraging predators present an additional source of mortality for a patch-resident prey species, they serve to increase critical patch size for the prey, regardless of boundary conditions. For example, when predators forage a fixed distance from the edge, the critical patch size for the prey is increased to a level no larger than the sum of the predators' incursion distance and the prey's critical patch size in the absence of cross-predation. This is because the effect of predation can never exceed the effect of an immediately lethal patch edge located at the predator's maximum incursion distance. Note that this result also means that predators can induce a critical patch size for the prey even when none would exist in the absence of predation (i.e., when the prey has reflecting boundary conditions). Predators whose incursion features a constant loss rate rather than fixed foraging distances also increase the critical patch size for the prey. In this scenario, we were able to obtain upper and lower bounds on the magnitude of the critical patch size when predators are present (Eqs. (3.35) and (3.39)). Thus, for both types of predator foraging behaviors explored here, patches in which a prey species could persist in the absence of predation may be too small for the species to survive when predators exact a toll inside the patch.

Historically, ecology has tended to have something of a patch-centric view, in which local dynamics are generally insulated from changes outside the patch. However, this perspective is gradually changing. Increased emphases on spatially subsidized dynamics [35] exemplify increasing recognition of the importance of larger scale processes. Another avenue of change involves increased attention to the quality of the matrix habitat. For example, [36] provides an overview of how the quality of matrix habitat surrounding a patch can influence the rate of successful immigration to that patch. The authors then go on to explore the consequences of such altered immigration patterns for metapopulation persistence, demonstrating an interesting, counterintuitive result that enhancing matrix quality can sometimes increase the risk of global metapopulation extinction. Empirical data are presented in Ref. [37] documenting the impacts of different matrix habitats on dispersal of several butterfly species, emphasizing that matrix quality can determine the 'effective isolation' of individual patches relative to potential sources of colonists. In addition, our own analyses ([34], this paper) make clear that matrix quality, as indexed by the presence of generalist predators capable of intruding into a patch, can also affect extinction processes. Thus, changes in quality of matrix habitat can influence both colonization and extinction components of metapopulation dynamics.

An increased predator incursion distance, an increased density of predators foraging inside the patch, or a combination of both will influence the predation pressure experienced by the prey in a local patch (Eq. (3.25)). Thus efforts to conserve patch-resident species may benefit both from reductions in the densities of edge-foraging predators (e.g., through fencing) and from reductions in how much of the patch is accessible to predators (e.g., through planting of buffer strips). The benefits of such actions may be especially pronounced for remnant patches that are small in comparison with the surrounding matrix. Moreover, for predators that exhibit a fixed incursion distance, the degree to which the prey's effective growth rate is reduced by predation depends upon the ratio of the size of the predator-occupied zone to the size of the patch as a whole. As patch sizes increases, this ratio decreases more slowly than the perimeter to area ratio, to which prey mortality from cross-edge dispersal is proportionate. Consequently, predator incursions (and other edge-mediated interactions with similar geometries) may have pronounced impacts on patch-resident species over a much larger range of fragment sizes than do other kinds of edge effects.

Cross-edge incursions by foraging predators represent a widespread type of ecological change that regularly accompanies habitat fragmentation [2,3]. For us, a key issue has been how deeply such predators penetrate into remnant patches. In many cases, features of the habitat edges themselves may help set the limit on predator penetration distances. For example, habitat edges in nature often involve gradual changes in biological or physical characteristics such as altered vegetation structure or environmental regimes [38]. In tropical forests, recently cut edges sometimes quickly 'seal up' as a result of extensive vegetative growth in response to sunlight, thereby preventing predator access to the patch over the long term [39,40]. Edge effects, whether due to gradients in sunlight, predators, or other features, may extend different distances into a patch, and as a result may influence different species in different ways. The ultimate effect of a habitat edge on an ecological community may thus reflect a mix of factors. Yet, diverse edge-mediated effects share an important commonality. Namely, because habitat fragmentation (and the resulting increased 'edginess' of landscapes) facilitates cross-edge incursions from species in the matrix, the ecological consequences of creating extensive habitat edges may be felt long before the habitat itself is gone.

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