

*Am Nat 158 (2001), 368-375.*

How Predator Incursions Affect Critical Patch Size :

The Role of the Functional Response

Robert Stephen Cantrell,<sup>1,3</sup> Chris Cosner,<sup>1</sup> and William F. Fagan<sup>2,4</sup>

<sup>1</sup>Department of Mathematics

University of Miami, Miami, FL 33124

<sup>2</sup>Department of Biology

Arizona State University, Tempe, AZ 85287-1501

<sup>3</sup>Order of Authorship is alphabetical

<sup>4</sup>Address Correspondence to:

William F. Fagan  
Department of Biology  
Arizona State University,  
Tempe, AZ 85287-1501  
Email: [bfagan@asu.edu](mailto:bfagan@asu.edu)  
FAX: (602) 965-2519  
Phone: (602) 965-8263

Keywords: generalist predators, spatial subsidies, edge effects, habitat fragmentation, metapopulation dynamics, partial differential equations

Running Head: Predator Incursions and Critical Patch Size

## Introduction

Understanding why patterns of species occupancy and diversity vary among landscape patches that differ in size and other characteristics has long been a central focus in ecology (e.g., MacArthur and Wilson 1967). In many cases, ecologists have looked to biotic factors intrinsic to the patches themselves (e.g., productivity, habitat diversity) to explain how many and which species occur there. However, as ecologists have increasingly attended to understanding the species composition and dynamics of fragmented landscapes, interest in extrinsic biotic factors (e.g., allochthonous biomass, aerial deposition of weed seeds) has surged. For example, recent work by the late Gary Polis and colleagues (Polis and Hurd 1996, Polis et al. 1997) demonstrated that extrinsic biotic factors can profoundly influence the local community structure and dynamics of desert islands. In that system, the relative importance of allochthonous resources to local processes was mediated in part by patch size (specifically, by patch perimeter-to-area ratio [Polis and Hurd 1996]). Additional examples of such extrinsic factors include weedy competitors invading habitat patches from surrounding “matrix” habitats (e.g., Janzen 1983, Cantrell and Cosner 1993), generalist predators such as foxes and corvids that forage in both anthropogenic habitats (e.g., farms, suburban areas) and remnant patches of native habitat (e.g., Angelstam 1986), and brood parasites such as cowbirds that can ravage populations of forest bird species nesting along edges (e.g., Brittingham and Temple 1983).

A key commonality among these diverse interactions is that they may be strongly asymmetrical. For example, cross-edge foraging by generalist predators may severely damage populations of patch-resident species despite having only weak or incidental benefits for the predators themselves (e.g., Gates and Gysel 1972, Angelstam 1986, Pasitschniak-Arts and Messier 1995). This is because population sizes for the intruding predator species are often

largely determined by resources available in surrounding matrix habitat, which is typically much larger in size. We find it helpful to characterize such activities as “edge incursions” because the term simultaneously emphasizes that the principal direction of impact is from matrix habitat into local patches and highlights the critical role of patch edges in mediating the interactions.

Perhaps the most widely studied examples of edge incursions are those influencing populations and assemblages of birds and other species in fragmented forest landscapes. Of particular concern is the loss of so-called “forest interior” species such as Ovenbirds, Scarlet Tanagers, and Woodthrushes that require highly specialized habitat conditions for successful reproduction or foraging (e.g., Robinson et al. 1995). Population declines and local extirpations of forest interior species have been linked to increasing forest fragmentation that has made it easier for brood parasites and generalist predators to gain access to previously remote portions of forest habitat (Robinson et al. 1995). Several studies have suggested that “critical patch size” phenomena (Kierstead and Slobodkin 1953, Ludwig et al. 1979) may exist in scenarios in which large remnant forest patches (which may be somewhat buffered from the effects of edge incursions) retain forest interior species while small patches (in which edge-mediated dynamics may dominate) suffer extirpations of patch residents (e.g., Whitcomb et al. 1981, Wilcove 1985; see also Robinson et al. 1995, Helzer and Jelinski 1999). Other studies have attempted to characterize the depths to which various generalist predators forage into forest patches by studying spatial variation in their depredations of artificial and real bird nests located at different distances in from the edge (see Soderstrom et al 1998 for a review, also Brand and George 2000). Figure 1 provides an overview of the kinds of predator edge incursions reported.

Here we provide a brief theoretical perspective on how and when such critical patch size effects may arise through the impacts of predator incursions. Though we save much of the

detailed mathematical analyses for publication elsewhere (Cantrell et al. 2000), we present here a novel result concerning the key role that the functional responses of intruding predators play in determining whether a critical patch size effect is observed.

## Model Formulation

We envision a habitat patch ( $\Omega$ ) separated from surrounding (much larger) matrix habitat by an edge ( $\partial\Omega$ ). A prey species ( $u$ ) inhabits, and is restricted to, the patch. A generalist predator species ( $p$ ) inhabits the matrix but can wander into  $\Omega$  where it can feed upon the prey. Motivated by empirical examples (Gates and Gysel 1972, Angelstam 1986, Pasitschniak-Arts and Messier 1995), we assume that the predator's population size is fixed at an equilibrium that is completely determined by processes in the matrix. Consequently, while the predator may have substantial local effects on the prey species within the focal patch, the contribution of the prey to the size and dynamics of the predator's population is negligible.

To study the interaction between predator and prey in this spatially explicit context, we use the diffusive logistic model with predation:

$$\frac{\partial u}{\partial t} = r u \left(1 - \frac{u}{K}\right) - g(u, p(x, y)) p(x, y) + D \left( \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) \quad \text{in } \Omega \quad (\text{Eq. 1A})$$

$$\beta u + (1 - \beta) \frac{\partial u}{\partial \eta} = 0 \quad \text{on } \partial\Omega \quad (\text{Eq. 1B})$$

where  $r$ ,  $K$ , and  $D$  are the intrinsic rate of increase, carrying capacity, and diffusion coefficient of the prey species (respectively) and  $g(u, p(x, y))$  is the functional response of the predator. Note that  $p(x, y)$  represents the equilibrium density of the predator for spatial coordinates  $x$  and  $y$  inside the patch. Because of our assumptions outlined above,  $p(x, y)$  is determined both by the predator's equilibrium density in the surrounding matrix and by the nature of the predator's

incursion profile into  $\Omega$  (Fig. 1). (For convenience we will hereafter omit explicit dependence of  $p$  on the spatial coordinates.) Equation 1B specifies the boundary conditions of the model, and in it, the parameter  $\beta$  can be interpreted as an edge hostility factor, determining the extent to which the prey species will be lost from the patch during dispersal ( $\beta=1$ ) versus tend to remain in or return to the patch ( $\beta=0$ ). Lastly,  $\eta$  is an outward unit normal vector along the patch edge (used to relate the orientation of the edge to the directions of dispersal).

Reaction diffusion models like Eq. 1 have a long history in ecology as a starting point for understanding general spatial problems (e.g., Skellam 1951, Kierstead and Slobodkin 1953, Ludwig et al. 1979, Pacala and Roughgarden 1982, see Holmes et al. 1994 for an overview). That such models make a minimum of assumptions about the nature of species dispersal is often considered one of their key strengths. In the present context however, we also adopt this formulation because such models are well suited for the study of edge-mediated interactions (Fagan et al. 1999). Readers are referred to Cantrell et al. (2000) for predictions of Eq. 1 when different predator incursion profiles and specific spatial domains are assumed.

### **Model Analysis and Implications**

Perhaps the most basic question to be asked of the model in Equation 1—and one of primary biological interest—is whether the model predicts persistence or extinction of the prey species within the patch. It is now well understood that persistence or extinction in the context of models like Eq. 1 is determined by the average growth rate over  $\Omega$  of the prey species at low densities subject to equilibrium predation pressure (e.g., Cantrell et al. 1993, Cantrell and Cosner 1996). Consequently, this problem of persistence vs. extinction is also tightly connected to the

question of whether the prey species could successfully colonize (i.e., invade) an empty patch that was subject to a particular level of predator incursions.

Expressed mathematically, persistence (or invasion potential) is determined via a linearization of Eq. 1, specifically:

$$D\nabla^2 w + rw - \frac{\partial g(0, p)}{\partial u} w = \sigma w \quad \text{in } \Omega \quad \text{Eq. 2A}$$

$$\beta w + (1 - \beta) \frac{\partial w}{\partial \eta} = 0 \quad \text{on } \Omega \quad \text{Eq. 2B}$$

$$w > 0 \quad \text{in } \Omega \quad \text{Eq. 2C}$$

where  $\underline{w}$  is the linearized prey density and  $\underline{\sigma}$  is the principal eigenvalue. When  $\underline{\sigma} > 0$ , the prey species is predicted to persist in  $\underline{\Omega}$  (though possibly at low densities), whereas when  $\underline{\sigma} < 0$ , the prey species is predicted to go extinct in  $\underline{\Omega}$ . Note that  $\underline{\sigma} > 0$  means that the average rate of growth of the prey species over  $\underline{\Omega}$  would be positive if the prey species colonized the habitat patch with the predator present at its equilibrium. In other words, if  $\underline{\sigma} > 0$  the prey species can invade the habitat patch despite impacts from the intruding predator. Consequently,  $\underline{\sigma} = 0$  identifies a threshold between persistence and extinction for the prey species in  $\underline{\Omega}$ . From another perspective, the above result means that if one fixed the remaining parameters ( $\underline{D}$ ,  $\underline{r}$ ,  $\underline{\beta}$ , and  $\underline{p}$ ) and then varied the size of  $\underline{\Omega}$  to find the particular patch size for which  $\underline{\sigma} = 0$  in Eq. 2, one would be identifying the critical patch size for persistence of the prey species (with the specified traits and subject to the specified edge hostility and in-patch predation pressure).

As a simple example, consider a linear habitat ( $\Omega$ ) with reflecting boundary conditions for the prey ( $\beta=0$ ) into which a predator may intrude to a fixed distance ( $\Omega_\delta$ ) at a fixed density ( $p_0$ ) from the surrounding matrix. In this case, Eq. 1 predicts persistence of the prey species if (Cantrell et al. 2000)

$$|\Omega| > \frac{\partial g(0, p_0)}{\partial u} \frac{|\Omega_\delta| p_0}{r} \quad \text{Eq. 3}$$

which identifies the threshold patch size below which the prey species cannot invade because of the impacts of predators foraging across the patch edge.

We now return to the more general case of Eq. 2 to consider the effect of altering the predator's functional response on the predictions concerning the prey's persistence. The predator's functional response helps determine persistence versus extinction of the prey species

when it enters Eq. 2A in the form  $\frac{\partial g(0, p)}{\partial u}$ , which characterizes the predator's functional

response at very low densities of the prey species. If  $\frac{\partial g(0, p)}{\partial u} = 0$ , then the predator has no

impact on  $\sigma$ , and critical patch size phenomena are determined solely by habitat characteristics

(e.g., patch size, edge hostility) and the balance between the prey species' reproduction and

dispersal. This implies that a patch that is invulnerable by the prey species in the absence of

predation will always be invulnerable regardless of the predator's equilibrium density. In contrast, if

$\frac{\partial g(0, p)}{\partial u} \neq 0$ , then whether or not the prey species can invade from low densities depends not

only upon patch characteristics and the prey species' traits, but also upon the predator's

equilibrium density profile inside the patch (and by extension, upon the nature of the predator's

incursion into the patch and its density in the matrix).

Whether  $\frac{\partial g(0, p)}{\partial u}$  equals zero or not depends upon the shape of the predator's functional response. For example, if the functional response is of either Lotka-Volterra form

$(g(u, p) = \alpha u)$  or of Holling Type II form  $\left( g(u, p) = \frac{\alpha u}{1 + \gamma u} \right)$  then  $\frac{\partial g(0, p)}{\partial u} \neq 0$ , and the

predator population helps determine critical patch size for the prey species. In contrast, if the

functional response is Holling Type III  $\left( g(u, p) = \frac{\alpha u^2}{1 + \gamma u^2} \right)$ , then  $\frac{\partial g(0, p)}{\partial u} = 0$ , and the

incursions of the predator do not influence critical patch size for the prey. Cantrell et al. (2000)

analyzed critical patch size effects in Eq. 1 for the case of  $\frac{\partial g(0, p)}{\partial u} \neq 0$ .

However, when  $\frac{\partial g(0, p)}{\partial u} = 0$ , it does not mean that the prey population suffers no ill effects from the predator's incursions into the habitat patch. Instead it means that predator impacts are negligible at low prey densities, and it is what happens at low prey densities that determine critical patch sizes (i.e., whether the prey can invade). Indeed the predator's impacts may be quite pronounced at higher densities of the prey species, but our analyses do not delineate such effects. This is because having  $\sigma > 0$  in Eq. 2 does not provide information concerning the asymptotic prey density. Consequently, even if the predator does not have an effect on critical patch size phenomena, it may still result in asymptotic prey densities that are unacceptably low either in absolute terms or to compete effectively with other patch-resident species. In addition, predator incursions may complicate substantially the simple diffusive logistic dynamics that otherwise governs the prey species density.

It is important to note that these effects of predator incursions are also present in non-spatial ordinary differential equation models corresponding to the spatial model given in Eq. 1.



Figure 2 illustrates this for cases involving functional responses of Types II and III. The

parameter  $\alpha$  in the terms  $g(u, p) = \frac{\alpha u}{1 + \gamma u}$  (Type II) and  $g(u, p) = \frac{\alpha u^2}{1 + \gamma u^2}$  (Type III) represents a

constant level of predation pressure, as would be the case for the equilibrium density  $p(x, y)$  in the spatial models if the predator diffuses throughout the habitat patch. As  $\alpha$  increases, the effective carrying capacity of the prey is reduced and additional equilibria are created (Fig. 2). For a Type II functional response, the newly created equilibrium demarcates a threshold for persistence of the prey (Fig. 2A). Given further increases in predation pressure, per capita growth rate of the prey can be made negative for all prey densities. In contrast, for a Type III functional response, per capita growth rate of the prey at some very low density will always be positive, regardless of predation pressure (Fig. 2B).

When space is considered, spatial variation in the equilibrium predator density and the spatial extent of the incursion of the predator into the habitat patch play important roles in determining the predator's ultimate effects on the prey. For example, if the predator incursions are restricted to the outermost margins of the patch, the effects of increasing predation pressure demonstrated in Figure 2 may be substantially mitigated. However, if a Type III predator can diffuse freely throughout the patch, then Eq. 1 corresponds to adding a dispersal term to the ordinary differential equation, and we would expect an analysis of Eq. 1 would yield equally dramatic effects on asymptotic prey density. Previous results (Cantrell and Cosner 1989) suggest a mathematical approach to obtain estimates of the effects of predation on equilibrium prey densities.

Lastly, we note that in Ludwig et al. (1979) a minimal patch size for an "outbreak" of the spruce budworm is given and shown to depend on a Holling III type functional response.

Someone may suggest that the "outbreak" results provide a contradiction to our observations.

However, they do not, because in our present discussion of minimal patch sizes, we are speaking of a minimal patch size for invasibility (i.e., persistence of the prey). Even though the critical patch size for invasibility would not be affected by a functional response term with  $\frac{\partial g(0, p)}{\partial u} = 0$ , the model may admit alternative stable states (e.g., outbreak conditions), and the existence of those additional equilibria may well depend on domain size.

## **Discussion**

In Fagan et al. (1999) we outlined four classes of mechanisms through which habitat edges can fundamentally change the nature of species interactions. Edge incursions by foraging predators fall into the broader category of edge-mediated effects involving so-called “cross-boundary subsidies” (Janzen 1986), in which impacts of one species on another inside a patch are subsidized by resources, propagules, etc. from outside the patch. As we have outlined here, not all kinds of predator incursions will influence critical patch size effects for patch resident species. When predators exhibit Type II or Lotka-Volterra type functional responses, they serve to increase critical patch size for the prey, regardless of boundary conditions (Cantrell et al. 2000). Consequently, habitat patches in which prey populations could persist in the absence of predation may be too small for the prey to survive in the face of edge incursions by predators. Furthermore, for predators that exhibit a fixed incursion distance (Fig. 1), the effects of predator incursions on patch-resident species scale as the ratio of the predator-occupied area to the total patch area (Cantrell et al. 2000). As patch size increases, this ratio decreases more slowly than the perimeter to area ratio. 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.

By focusing our attention on the relationship of predator functional responses to critical patch size effects, we have implicitly made our theoretical efforts most relevant to empirical cases in which generalist predators such as foxes, corvids, and domestic animals feed upon forest resident species. However, it is also worth noting that the impacts of brood parasites such as cowbirds can also influence critical patch size effects for patch residents. Although one could quantify the impacts of such brood parasites through a predation term like that in Eq. 1, an alternative approach would be to assume that the parasites engender no mortality within the prey population and instead contribute to a decrease in the apparent  $r$  of the prey. Even in this formulation, brood parasites can influence critical patch size by shifting the balance between population growth and mortality (or other loss) across the edge.

At first glance, our results suggest that predators with “simple” functional responses are capable of inducing critical patch size effects through edge incursions whereas those capable of learning and prey switching (i.e., those with Type III functional responses) are not. This is something of a mismatch with our empirical examples, most of which involve highly generalized predators that one might suspect would exhibit Type III functional responses with respect to specific prey species. However it is important to keep in mind that our modeling framework assumes that the predator foraging is merely incidental to the predator species itself (i.e., the predator population is completely determined through processes extrinsic to the habitat patch in question). Consequently, it is not unreasonable to assume that individual predators may possess similarly expansive ranges for foraging. From this viewpoint, the spatial scale over which an individual predator hones its searching abilities may be vastly larger than the scale of an individual patch.

To the extent that predator incursions can prevent successful recolonization of empty patches by prey, these edge-mediated interactions may also have important implications for metapopulation dynamics. For example, when edge incursions induce critical patch size effects in fragmented landscapes, they may effectively exclude whole suites of patches from meaningful membership in a prey species' metapopulation. In such cases, the true number of patches available for colonization by the prey species (and hence available to offset the effects of local extinctions of occupied patches) may be far lower than the amount of available habitat would indicate. In addition, critical patch size effects of this sort could also affect metapopulation-scale dynamics by "draining" potential colonists into unproductive sink patches (Pulliam 1988). Similar effects would likely be important for efforts in restoration ecology, where researchers and managers may need to give additional consideration to matrix habitat conditions when evaluating the suitability of particular patches for species reestablishment.

In closing, we suggest that increased attention to asymmetrical models of species interactions (like that in Eq. 1.) is warranted as a component of increasing attention to the dynamics of fragmented landscapes (see also Polis et al. 1997). Because such models afford one approach to the scaling up of ecological processes, they may eventually help us understand the ways in which species interactions can interact with chance colonization events to produce patterns of species occupancy across a landscape.

### **Acknowledgments**

We thank Jessamy Rango and Colleen McFadden for comments on the manuscript. NSF grant DMS 9973017 supported efforts of RSC and CC; Arizona State University supported WF's participation.

## References Cited

- Angelstam, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. *Oikos* 47: 365-373.
- Brand, L.A., and T.L. George. 2000. Predation risks for nesting birds in fragmented coast redwood forest. *Journal Of Wildlife Management* 64: 42-51.
- Brittingham, M.C. and S.A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *Bioscience* 33: 31-35.
- Cantrell, R.S. and C. Cosner. 1989. Diffusive logistic equations with indefinite weights: population models in disrupted environments. *Proceedings of the Royal Society of Edinburgh*. 112A: 293-318.
- Cantrell, R.S. and C. Cosner. 1996. Practical persistence in ecological models via comparison methods. *Proceedings of the Royal Society of Edinburgh*. 126A: 247-272.
- Cantrell, R.S., C. Cosner, and V. Hutson. 1993. Permanence in some diffusive Lotka-Volterra models for three interacting species. *Dynamic Systems* 2: 505-530.
- Cantrell, R.S., C. Cosner, and W.F. Fagan. 2000. Habitat edges and predator-prey interactions: effects on critical patch size. *Bulletin of Mathematical Biology*, in review.
- Fagan, W.F., R.S. Cantrell, and C. Cosner. 1999. How habitat edges change species interactions. *American Naturalist*. 153: 165-182.
- Gates, J.E. and L.W. Gysel. 1972. Avian nest dispersion and fledgling success in field-forest ecotones. *Ecology* 59: 871-883.
- Helzer, C. J. and D.E. Jelinski. 1999. The relative importance of patch area and perimeter-area ratio to grassland breeding birds. *Ecological Applications*. 9: 1448-1458.

- Holmes, E.E., M.A. Lewis, J.E. Banks, and R.R. Veit. 1994. Partial differential equations in ecology: spatial interactions and population dynamics. *Ecology* 75: 17-29.
- Janzen, D.H. 1983. No park is an island: increase in interference from outside as park size decreases. *Oikos* 41: 402-410.
- Janzen, D.H. 1986. The eternal external threat. Pp. 286-303 In: *Conservation Biology: The Science of Scarcity and Diversity*, ed. M.E. Soule. Sinauer Associates, Sunderland, Mass.
- Kierstead, H. and L.B. Slobodkin. 1953. The size of water masses containing plankton blooms. *Journal of Marine Resources*. 12: 141-147.
- Ludwig, D., D.G. Aronson, and H.F. Weinberger. 1979. Spatial patterning of the spruce budworm. *Journal of Mathematical Biology* 8: 217-258.
- MacArthur, R. H., and E.O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- Pacala, S.W. and J. Roughgarden. 1982. Spatial heterogeneity and interspecific competition. *Theoretical Population Biology* 21: 92-113.
- Pasitschniak-Arts, M. and F. Messier. 1995. Risk of predation on waterfowl nests in the Canadian prairies: effects of habitat edges and agricultural practices. *Oikos* 73: 347-355.
- Polis, G.A., W.B. Anderson, and R.D Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*. 28: 289-316 1997.
- Polis, G.A. and S.D. Hurd. 1996. Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *American Naturalist*. 147: 396-423.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:642-661.

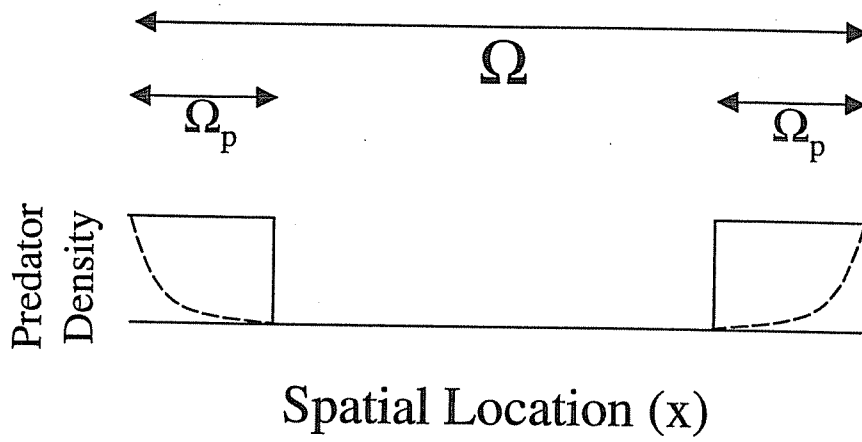
- Robinson, S.K., F.R. Thompson, T.M. Donovan, D.R. Whitehead, and J. Faaborg. 1995. Regional nesting success of migratory birds. *Science* 267: 1987-1990.
- Soderstrom, B., T. Part, and J. Ryden. 1998. Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and a review. *Oecologia*. 117: 108-118.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika*. 38: 196-218.
- Whitcomb, R.F., C.S. Robbins, J.F. Lynch, B.L. Whitcomb, M.K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pp. 125-292 In: R.L. Burgess and D.M. Sharpe, eds. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York.
- Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66: 1211-1214.

## Figure Legends

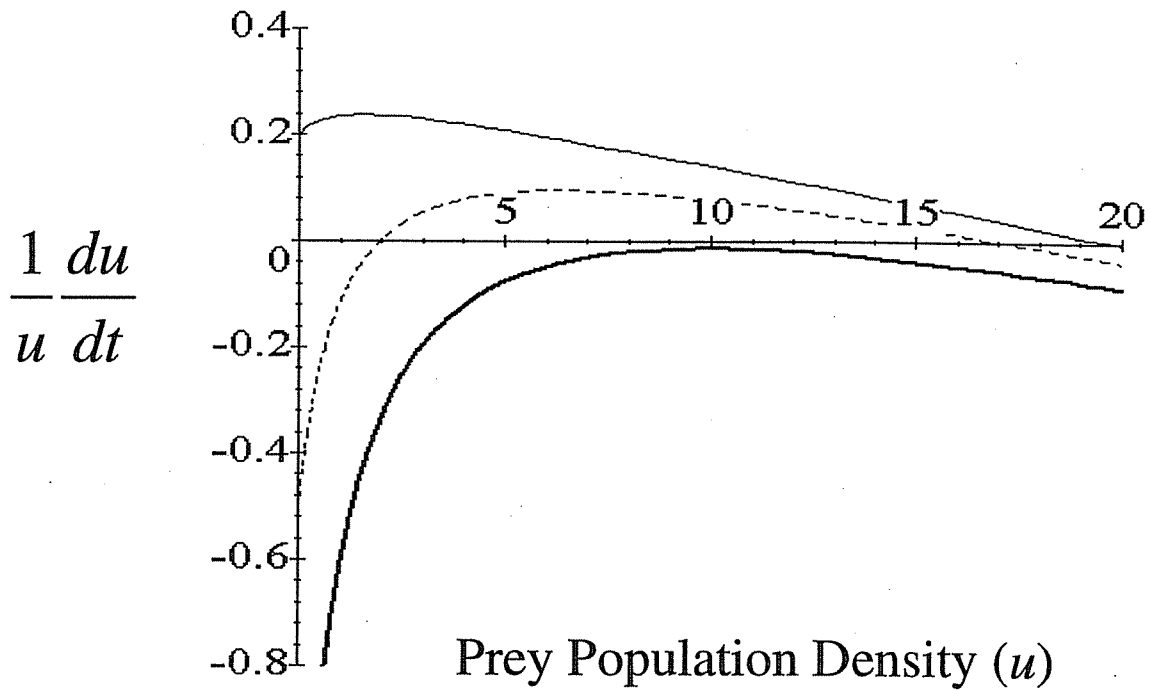
Figure 1. Two different kinds of penetration profiles for edge incursions of generalist predators. In this simple example, the fringes of a one-dimensional habitat patch of size  $\Omega$  are utilized by predators foraging across the patch boundary. Population densities of the predator are determined entirely by processes operating in and resources available in the surrounding matrix habitat. The predator intrudes into the focal patch a distance  $\Omega_p$  on each side either at a fixed density or at a density that attenuates with increasing distance into the patch. These penetration profiles are motivated by empirical examples (Janzen 1983, Angelstam 1986). See Cantrell et al. (2000) for analysis of these and other critical patch size problems involving predator incursions into 1 and n-dimensional patches.

Figure 2. Per capita growth rates for prey populations subjected to externally set predation. In A), we plot the function  $\left( \frac{1}{u} \frac{du}{dt} = r - \frac{ru}{K} - \frac{\alpha}{1 + \gamma u} \right)$  and in B),  $\left( \frac{1}{u} \frac{du}{dt} = r - \frac{ru}{K} - \frac{\alpha u}{1 + \gamma u^2} \right)$ , in both cases with  $r = 0.3$ ,  $K = 20$ , and  $\gamma = 1$ . These panels represent non-spatial counterparts to Eq. 1 with functional responses of Types II and III (A and B, respectively). Different curves plotted in each panel delineate the impacts of increasing predation pressure ( $\alpha=0.1$  [solid line];  $\alpha=0.8$  [dashed line];  $\alpha=1.8$  [bold line]). In A, increasing predation a little makes population growth rates negative at low prey densities, and further increases lead to complete extinction of the prey. In B, increasing predation also gives rise to multiple equilibria, but the prey population can always grow in size at very low densities.





### A) Type II Functional Response



### B) Type III Functional Response

