

## MODELS FOR PREDATOR-PREY SYSTEMS AT MULTIPLE SCALES\*

R. S. CANTRELL<sup>†</sup> AND C. COSNER<sup>†</sup>

**Abstract.** Spatially explicit models are constructed for predator dispersal, predator-prey interactions, and prey dispersal and population dynamics in a system where the appropriate spatial and temporal scales for the predator are different from those for the prey. The models are based on the hypotheses that the predator experiences the environment as a collection of patches and disperses among the patches by immigration and emigration on a time scale much shorter than its reproductive interval, while the prey experiences each patch as a continuum on which it disperses by diffusion while reproducing logistically. The models are motivated by a natural system in which ladybird beetles aggregate at and feed upon colonies of aphids which grow on patches of host plants. Structurally the models are a hybrid of patch models and reaction-diffusion (i.e., KISS) models. The models are studied at equilibrium or pseudoequilibrium via methods derived from reaction-diffusion theory. The behavior of the models under variations in patch size is analyzed, and it is shown that in some cases they predict smaller prey densities on larger patches, or even maximum as well as minimum patch sizes which can sustain a prey population. This last prediction is in contrast with the predictions of reaction-diffusion (KISS) models for the prey alone, in which there is typically a minimum patch size which will sustain a prey population and the prey density increases toward carrying capacity as patch size increases.

**Key words.** predator-prey, patch models, reaction-diffusion, spatial scales, temporal scales

**AMS subject classifications.** 92D40, 92D25, 35K47

**1. Introduction.** Ecological phenomena occur in space and time across a wide range of scales. The scale on which a phenomenon occurs can affect both quantitative and qualitative features of that phenomenon. In some situations the different populations involved in an ecological interaction may experience space and time on very different scales, so that the most appropriate theoretical and mathematical descriptions of their behavior are qualitatively different. There are only a few models or theoretical treatments which incorporate such qualitative differences. More typically, interacting populations are all assumed to experience their spatial environment in the same way—either as a single point, a collection of patches, or a continuum—and at the same rate. In fact, it is common to see models where dispersal, predation and resource consumption, and reproduction all seem to occur on the same time scale for all the populations involved. Our goal in this article is to construct and analyze some models which explicitly consider the qualitative differences in the appropriate population dynamical models for the different interacting species in a system where those species operate on very different spatial and temporal scales. Specifically, we consider a situation where a predator operates on a large spatial scale and experiences its environment as patchy while the prey operates on a small spatial scale and experiences each patch as a continuum. We also assume that the time scale for predator dispersal is very fast, the time scales for prey dispersal and reproduction are moderately fast, but the time scale for predator reproduction is relatively slow. Hence, we will view the predators as immigrating to and emigrating from patches rapidly enough that the predator population on any patch effectively reaches equilibrium almost immediately but the prey population on any patch disperses by diffusion through the patch while growing logistically. We will view the dispersal and reproduction time scale for the prey to be faster enough than the reproductive time scale for the predator for it to be reasonable to study the system in terms of the logistic equilibrium for the prey corresponding to a given population or supply rate for the predator. Returning to the spatial scale of the system, we will then analyze how the prey equilibrium is affected by patch size. Our work is motivated

\*Received by the editors August 12, 1994; accepted for publication (in revised form) July 26, 1995. This research was partially supported by NSF grant DMS-9303708.

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For that reason we have considered only the simplest sort of reaction-diffusion models for the prey, but our results would extend directly to the more complicated models studied in [3, 5] and to arbitrary patch shapes. It would be possible to incorporate patch shape as a variable, e.g., by viewing patches as rectangles and using the length/width ratio as a parameter, but we have not done that.

The ecological background of the models and the modeling procedure are discussed in §2. The mathematical background for analysis of the models is given in §3, and the analysis and interpretation is also performed in that section. The models are divided into cases by the hypotheses, specifically purely geometric vs. aggregative predator immigration/emigration and unlimited predator supply vs. a finite predator population. Finally, some general conclusions and comparisons are drawn in §4. The reader who is primarily interested in the ecological aspects of this work may want to read §§2 and 4 before turning to §3. The mathematically oriented reader will probably find §3 to be the most interesting.

## 2. The models.

**2.1. Ecological background.** Our goal in this section is to construct a class of spatially explicit predator-prey models for situations where the dynamics of dispersal and population growth for the predator and the prey occur on such different scales that the descriptions of spatial effects that are most appropriate for the predator are qualitatively different than those that are most appropriate for the prey. Specifically, we envision a situation in which the scale of dispersal for the prey is small but the rate of reproduction is large relative to those of the predator, and where the environment consists of a number of patches which are large relative to the spatial scale experienced by the prey but small relative to the spatial scale of the predator. Thus, it is most appropriate to describe the spatial dynamics of the predator in terms of a patch model and those of the prey in terms of a collection of spatially continuous models, one for each patch. We shall use simple diffusion models for the prey since those models can easily incorporate patch size but are analytically tractable. Since the population dynamics of the prey are assumed to occur on a faster time scale than those of the predator, we describe the dynamics of the prey populations within the patches in terms of logistic growth with predation and those of the predator in terms of immigration and emigration. We have both theoretical and applied reasons for considering the scenario described above. The theoretical reason is to address the general question of how to connect phenomena at different scales, as discussed in [32] and treated in [26] in the case of a single continuous but heterogeneous environment. Our assumptions are somewhat different from those of [26] because we are interested in studying situations where the effects of scale are qualitative as well as quantitative, specifically where the predator experiences a patchy environment while the prey experiences a collection of continuous environments. The applied reason for considering models with those features is that they may give a rough description of certain real systems. The direct inspiration for the scenario is the work of Kareiva and his colleagues [17, 34] on the fireweed (*Epilobium angustifolium* (*Onagraceae*))/aphid (*Aphis varians*)/ladybird beetle (*Hippodamia convergens* (*Coccinellidae*)) system which emerged near Mt. St. Helens after the eruption of 1980. A specific phenomenon which we address in our models is the observation in [17, p. 185] that sometimes larger patches of fireweed sustained lower densities of aphids than smaller patches, in reverse of the predictions of standard reaction-diffusion theory. *Our models suggest that in certain cases there may be an inverse relation between patch size and prey density due to the presence of predators.*

Much of the background information we considered in constructing our models is from [34]; see also [15] for a discussion of other aphid/coccinellid systems. We shall summarize some of the pertinent observations. The fireweed grows (among other places) in patches in the harsh volcanic regions of the blast zone of Mt. St. Helens [17]. The aphids live on the

by a natural system involving aphids inhabiting patches of host plants and ladybird beetles preying upon the aphids, which was studied by Turchin and Kareiva [34] and is described in [17]. It is noted in [17] that in some cases larger patches of host plants had lower aphid densities, which is the opposite of the predictions of simple spatially explicit models for the aphid population based on classical reaction-diffusion theory. (Such models are sometimes called KISS models.) We shall see that such an effect is sometimes predicted by various models which take predator immigration and emigration into account.

We consider and compare the implications of a number of different hypotheses. Our models are based on the assumption that the predator experiences the spatial domain as a collection of patches while the prey experiences each patch as a continuum. We consider two sorts of predator dispersal: purely geometric, in which the immigration and emigration rates of the predator depend only on the size of the patch; and aggregative, where the predator emigration rate also depends inversely on the average prey density. The inverse dependence on prey density in the emigration rate is a crude model for area-restricted search by the predator. Area-restricted search is known to predict a type of predator aggregation in continuous habitats [18], so it is in that sense that our second type of model may be called aggregative. We also consider two hypotheses about the number of predators: either an unlimited supply, reflecting the presence of a large nearby source population, or a finite population, reflecting a closed system. In the second case we consider the possibility that increasing the size of patches corresponds to an increase in the total size or geographic area of the closed system, and thus corresponds to a proportional increase in the predator population.

Our modeling of the patches as continua is done as simply as possible so that our computations can be made easily and explicitly. In particular, we assume that the patches are square, that the prey disperse through each patch by simple diffusion, and that each patch is spatially homogeneous in the sense that the prey growth rate and carrying capacity are constant. None of these hypotheses is crucial for the qualitative aspects of our results. Those depend on existence theory for stable equilibria of diffusive logistic equations, which depends in turn on the behavior of eigenvalues of certain associated elliptic differential operators. The simplest sort of model would in one space dimension lead to the eigenvalue problem

$$(1.1) \quad \begin{aligned} -D \frac{d^2 \phi}{dx^2} &= \lambda r \phi \quad \text{for } 0 < x < l, \\ \phi(0) &= \phi(l) = 0. \end{aligned}$$

A quite general class of models with spatial heterogeneity in growth and/or diffusion rates and perhaps even density-dependent dispersal was studied in [3, 5] and shown to behave in the same way as simple KISS (i.e., spatially homogeneous reaction-diffusion) models in the sense that the existence of a stable positive equilibrium depends on the principal eigenvalue of a problem of the form

$$(1.2) \quad \begin{aligned} - \left[ \frac{\partial}{\partial x} D_1(x, y) \frac{\partial \phi}{\partial x} + \frac{\partial}{\partial y} D_2(x, y) \frac{\partial \phi}{\partial y} \right] &= \lambda r(x, y) \phi \\ \text{for } (x, y) \in \Omega, \quad \phi(x, y) &= 0 \text{ on } \partial\Omega, \end{aligned}$$

where  $\Omega$  is a bounded region in two-dimensional space. The key point here is that the criterion for existence of a stable positive prey equilibrium depends on the size of the positive principal eigenvalue of (1.1) or (1.2), and that in both (1.1) and (1.2) that principal eigenvalue varies proportionally with  $1/l^2$  if the spatial domain is rescaled by multiplying the linear dimension by a factor  $l$ . Thus, the behavior of the system with respect to changes of the spatial scale of the patches would be the same in the simple case and the more complicated case. The numerical values of certain parameters would change, but the asymptotic behavior as  $l \rightarrow \infty$  would not.

For that reason we have considered only the simplest sort of reaction-diffusion models for the prey, but our results would extend directly to the more complicated models studied in [3, 5] and to arbitrary patch shapes. It would be possible to incorporate patch shape as a variable, e.g., by viewing patches as rectangles and using the length/width ratio as a parameter, but we have not done that.

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fireweed. They disperse slowly, on the order of cm/day, but reproduce rapidly, with up to 10 generations per summer [34]. Ladybird beetles can disperse rapidly, up to 1 km/day (P. Kareiva, personal communication) and aggregate quickly at aphid colonies via immigration, with their numbers reaching a temporary plateau in a few hours. The ladybird beetle population per aphid colony will then typically decrease as the aphids are eaten and the ladybirds emigrate [34]. These are some of the considerations we shall try to incorporate into our models. We note that the phenomena we consider are rather different than those studied in [34]. We shall consider the basic size parameter to be patch size, i.e., the area covered by fireweed plants, rather than aphid colony size, i.e., number of aphids, and we shall not focus especially on aphid aggregation. Also, although it is clear from [15, 18, 34] that it is reasonable to hypothesize that ladybirds aggregate at locations with high aphid densities, we shall also consider as null models situations where aggregation depends only on patch size, rather than prey density.

**2.2. Models.** We shall model patches of fireweed as having a uniform density independent of time or the density of aphids, but having specified areas and perimeter/area ratios. For much of our discussion we shall assume that they are squares so that we can focus on the effects of changing patch size. That assumption is not crucial; any fixed shape would yield qualitatively equivalent results, but squares are convenient. We shall assume that within each patch there is an aphid density  $v(x, y, t)$  satisfying a KISS-type reaction-diffusion model with predation. (See [19, 30] and the discussion in [17, 21, 27]. A particular application of passive diffusion models for herbivorous insects is given in [14].) We assume that in the air above and around the patches is a population of ladybird beetles which immigrate to the patches in search of prey and later emigrate. Since the ladybird beetles can fly relatively long distances we assume that all patches are equally accessible to them; thus, the model for the ladybirds is a type of island model in the terminology of [17]. Some cases of our models include ladybird beetle aggregation on patches with higher aphid densities. (Because of our assumptions about spatial scale we have treated the beetle habitat as patchy (i.e., discrete). Models for aggregation in continuous habitats are discussed in [18, 33].)

To describe a system of  $N$  patches, each a square of side  $l_n$  and area  $A_n = l_n^2$ , we will need  $N$  state variables  $v_n(x, y, t)$  denoting prey densities in the patches,  $N$  more state variables  $P_n(t)$  denoting predator numbers (not densities) in the patches, and another state variable  $P_A(t)$ , the number of predators in the air. The variable  $P_A(t)$  will appear explicitly in only some of our models, but it is needed in their derivation. We will often assume that there is a finite total population  $C$  of predators so that

$$(2.1) \quad C = P_A + \sum_{n=1}^N P_n,$$

but for some purposes it is interesting to consider the scenario where there is an effectively unlimited supply of predators. In such a situation any predator that alights would be immediately replaced in the air by another from somewhere else (possibly outside the system of patches) so that

$$(2.2) \quad P_A = \text{constant}.$$

Our basic models take the form

$$(2.3) \quad \frac{dP_n}{dt} = I_n P_A - E_n P_n,$$

$$\frac{\partial v_n}{\partial t} = D \left( \frac{\partial^2 v_n}{\partial x^2} + \frac{\partial^2 v_n}{\partial y^2} \right) + r \left( 1 - \frac{v_n}{K} \right) v_n - c \left( \frac{P_n}{l_n^2} \right) v_n$$

for  $0 < x < l_n, 0 < y < l_n,$

$$v_n(x, y, t) = 0 \text{ for } x = 0, l_n, y = 0, l_n.$$

(Note that  $l_n^2 = A_n =$  area of the  $n$ th patch.) (Compare the first equation to [16, Eq. (1)] and the second to [26, Eq. (10)]; see also [15, Eqs. 3a and 3b].) The parameters  $I_n$  and  $E_n$  describe the per capita immigration and emigration rates on the  $n$ th patch, and will depend on patch size and geometry. To model predator aggregation we would assume some sort of dependence on prey density as well. If (2.1) holds then  $P_A$  depends on  $C$  and  $P_1, \dots, P_N$ . Much of our work will be devoted to understanding how different hypotheses about the dependence of  $I_n$  and  $E_n$  and about the size and number of patches and total population of ladybirds influence the predictions of the model. We shall assume that the predator aggregation response is so rapid that the predator numbers immediately adjust to prey densities appearing in  $E_n$ . This modeling hypothesis is philosophically similar to that used in [22, 23] to model consumptive competition when the resources have a faster time scale than the consumers; see also the discussion in [36, Chap. 5] or the comments in [29, p. 205].

The choices of hypotheses which are most crucial in determining the qualitative structure and properties of our models are the choice between finite and unlimited predator populations and between dependence on purely geometric factors and dependence on prey densities in the per capita immigration and emigration rates  $I_n$  and  $E_n$ . The simplest case occurs when we consider an unlimited supply of predators (2.2) with immigration and emigration depending only on geometric effects. In that case  $I_n$  and  $E_n$  vary only with  $n$ ,  $P_A$  is constant, and there is no density dependence, so that by the first equation of (2.3) we have  $P_n - (I_n/E_n)P_A$  decaying exponentially. Substituting the equilibrium  $P_n = I_n P_A / E_n$  into the second equation for (2.3) yields

$$(2.4) \quad \frac{\partial v_n}{\partial t} = D \left( \frac{\partial^2 v_n}{\partial x^2} + \frac{\partial^2 v_n}{\partial y^2} \right) + r \left( 1 - \frac{v_n}{K} \right) v_n - \frac{c P_A (I_n / E_n) v_n}{l_n^2}.$$

Notice that in (2.4) there is no coupling between patches and that the effect of predation is to decrease the linear term corresponding to the intrinsic rate of growth at low densities in the logistic equation for the prey. Thus, in this scenario, the number of patches is irrelevant and we need only consider what happens in a single patch. That will depend on our assumptions about how  $I_n$  and  $E_n$  depend on patch size. In all of our models we can make two sorts of hypotheses about the geometric dependence of  $I_n$  and  $E_n$ , which may be called general and specific. The general hypothesis is that  $I_n$  and  $E_n$  depend on powers of  $l_n$ , the linear dimension of the  $n$ th patch. That implies there are constants  $i$  and  $e$  so that

$$(2.5) \quad I_n = i l_n^p, \quad E_n = e l_n^q$$

for some  $p$  and  $q$ . The specific hypothesis is that  $p = 2$  and  $q = -1$  in (2.5). The reason for that specific hypothesis is that we envision the predators landing at random on the habitat patches which sustain the prey. Since the predators are envisioned as essentially falling out of the sky, it is plausible that the number landing in a given patch in unit time might be proportional to the area  $A_n = l_n^2$  of the patch. Once they have landed, we suppose that the predators walk around the patch looking for prey. If we consider only geometric effects it is plausible that the predators might wander until they reach the boundary of the patch and then fly away. In such a scenario it is reasonable to assume that the emigration rate depends on the perimeter/area ratio  $4l_n/A_n = 4/l_n$ . Some related ideas are discussed in [16, p. 1815]. (Remember that we are considering only geometric factors at this point; we have not yet introduced density dependence.) Thus, our specific hypothesis about the geometric dependence of  $I_n$  and  $E_n$  is

$$(2.6) \quad I_n = i l_n^2, \quad E_n = e / l_n.$$

(Changing the patch shape would affect  $i$  and  $e$  but not dependence on  $l_n$ .)

If we assume that there is a finite predator population (2.1) then we obtain a more sophisticated model where there is a relation between patches. Generally we might expect the immigration rate to be proportional to  $P_A$ , the number of predators in the air. If that number remains constant, it can simply be attached to the constant  $i$ . Otherwise, under the geometric hypotheses (2.5) on  $I_n$  and  $E_n$  we have

$$(2.7) \quad I_n P_A = i P_A l_n^p = i \left( C - \sum_{k=1}^N P_k \right) l_n^p,$$

so that our model becomes

$$(2.8) \quad \frac{dP_n}{dt} = i \left( C - \sum_{k=1}^N P_k \right) l_n^p - (e l_n^q) P_n,$$

$$\frac{\partial v_n}{\partial t} = D \left( \frac{\partial^2 v_n}{\partial x^2} + \frac{\partial^2 v_n}{\partial y^2} \right) + r \left( 1 - \frac{v_n}{K} \right) v_n - c \left( \frac{P_n}{l_n^2} \right) v_n$$

for  $0 < x < l_n, 0 < y < l_n,$   
 $v_n(x, y, t) = 0$  for  $x = 0, l_n, y = 0, l_n.$

If we impose (2.6) we have  $p = 2, q = -1$ . This system is coupled in the predator equations, but those are linear and do not involve the prey. Hence we can analyze (2.8) by determining the behavior of the predator equations and substituting the results into the prey equations. That will be an aspect of the analysis in the next section.

The observations in [34] indicate that a realistic model for the fireweed/aphid/ladybird system should involve predator aggregation in response to increases in prey density. A simple and reasonably accurate hypothesis about predator behavior is that the emigration rate decreases with prey density, so that if prey density is high immigrating predators stay in the patch and consume prey but when the prey density is reduced the predators emigrate and search for more prey. (Something of this sort is discussed by Kareiva in [15] in relation to equation (3b) of that article.) Since we are describing the prey in terms of densities and the predators in terms of populations we shall use the average prey density given by  $V_n/A_n = V_n/l_n^2$ , where

$$(2.9) \quad V_n = \int_0^{l_n} \int_0^{l_n} v_n(x, y, t) dx dy$$

= total prey population on patch  $n$  at time  $t$ .

The basic form of the predator equations in the density-dependent model is then

$$(2.10) \quad \frac{dP_n}{dt} = I_n P_A - E_n P_n / (V_n / A_n)$$

$$= I_n P_A - l_n^2 E_n P_n / V_n.$$

As in the predator models without density dependence, if there is an unlimited supply of predators then  $P_A$  is constant and we have  $I_n = i l_n^p, E_n = e l_n^q$ , so there is no coupling between patches. Thus we again need only consider what happens in a single patch. If we assume that predator aggregation occurs at a much faster rate than prey dispersal and dynamics, we can proceed along the lines used by MacArthur [22, 23] and assume further that the population with the faster time scale "tracks" the other closely; that is,  $P_n$  adjusts so quickly to  $V_n$  that the predator population stays at whatever equilibrium would be determined by  $V_n$ . In this case equation (2.10) yields the pseudoequilibrium

$$(2.11) \quad P_n = (I_n P_A / E_n l_n^2) V_n$$

(where  $I_n$  and  $E_n$  also depend on  $l_n$  as in (2.5) or (2.6)). Substituting into the second equation of the basic model (2.3) yields

$$(2.12) \quad \frac{\partial v_n}{\partial t} = D \left( \frac{\partial^2 v_n}{\partial x^2} + \frac{\partial^2 v_n}{\partial y^2} \right) + r \left( 1 - \frac{v_n}{K} \right) v_n - \frac{c I_n P_A}{E_n l_n^4} v_n V_n,$$

where  $V_n$  is the integral of  $v_n$  as in (2.9). Equation (2.12) can be viewed as a diffusive logistic equation with an extra nonlocal term describing something of the nature of a decreased carrying capacity. This is in contrast to the equation (2.4) obtained without the hypothesis of predator aggregation. In that case the most direct effect of predation is on the intrinsic growth rate at low densities. We shall return to this point later.

The most complicated of our models assumes a finite predator population and predator aggregation. The predator equations then become under hypothesis (2.5)

$$(2.13) \quad \frac{dP_n}{dt} = i l_n^p P_A - e l_n^q P_n / (V_n / l_n^2)$$

$$= i l_n^p \left( C - \sum_{k=1}^N P_k \right) - e l_n^{q+2} P_n / V_n.$$

Again, we shall assume that the predators "track" the prey densities so that the predator populations are always at whatever equilibrium is determined by the current prey densities. The equations for the predator populations are then

$$(2.14) \quad 0 = i l_n^p \left( C - \sum_{k=1}^N P_k \right) - e l_n^{q+2} P_n / V_n$$

for  $n = 1, \dots, N$ .

If we solve (2.14) for  $P_n$  in terms of  $V_1, \dots, V_N$  (which we shall do in the next section) and call the result  $P_n^*(V_1, \dots, V_N)$  we can substitute into the second equation of (2.3) and obtain the system

$$(2.15) \quad \frac{\partial v_n}{\partial t} = D \left( \frac{\partial^2 v_n}{\partial x^2} + \frac{\partial^2 v_n}{\partial y^2} \right) + r \left( 1 - \frac{v_n}{K} \right) v_n - \frac{c P_n^*(V_1, \dots, V_N)}{l_n^2} v_n$$

for  $0 < x < l_n, 0 < y < l_n,$   
 $v_n(x, y, t) = 0$  for  $x = 0, l_n, y = 0, l_n,$   
 $n = 1, \dots, N$ .

The system (2.15) is a reaction-diffusion system with equations coupled via the nonlinear nonlocal terms involving  $P_n^*(V_1, \dots, V_N)$ . The analysis of this system is nontrivial and we defer it to the next section. ( $P_n^*$  can and will be computed explicitly.)

### 3. Analysis and interpretation of the models.

**3.1. An overview and listing of cases.** This section is devoted to the analysis and interpretation of the models constructed in the last section. The focus will primarily be on examining the effects of changing the size of patches on the predictions of the models. We shall see that the relationship among patch size, persistence of the prey populations, and prey densities (when populations persist) can be much more delicate and complicated than those obtained from simple KISS-type reaction-diffusion models for the prey alone. As noted in

§2, the models we consider can be classified according to the assumptions about predator numbers and aggregation or the absence thereof. The number of predators might be viewed as unlimited or finite. If it is finite, we could consider cases where the total predator population is fixed or where it depends on the size or number of patches. If we think of both patches and predators as being uniformly (perhaps randomly) distributed throughout a large area, then the numbers of both predators and patches in our models will be proportional to the size of the part of that large region which we choose to consider in the models. In that case the total number of predators will be proportional to the number of patches. If we think of the number of patches as fixed with the patches embedded in a larger environment and rescale the size of the patches and their surrounding environment, an initially uniform distribution of predators would lead to a total number of predators that would be proportional to the overall area of the environment and hence to the area of the patches. Thus, if we consider cases where the total predator population  $C$  is finite but depends on the number of patches, we should assume

$$(3.1) \quad C = C_0 N,$$

where  $N$  is the number of patches, whereas if we consider cases where the number  $N$  of patches is fixed and the total predator population  $C$  is finite but depends on the total area of patches, we should assume

$$(3.2) \quad C = C_0 \left( \sum_{j=1}^N l_j^2 \right),$$

where  $l_j$  describes the linear dimension of the  $j$ th patch.

In all of our models the coupling between patches occurs only in the equations for the predator populations, and those are coupled only in the cases where the total predator population is finite. Thus, in the cases where we assume an effectively unlimited supply of predators in our system (arising perhaps from the presence of a large nearby source population), the patches are independent so we need only consider a single patch. This simplifies the models considerably.

We have four cases of our models to consider. We shall first consider the two cases without aggregation, that is, where the predator per capita immigration rates depend only on geometric factors. We consider the possibility of an unlimited supply of predators and also the possibility of a finite total predator population. In the case of a finite total predator population, we focus primarily on the situation in which (3.2) obtains; i.e., the total predator population is proportional to the total area inhabited by the prey. After that we shall examine the remaining two cases under which we have the assumption (probably more realistic) that predators aggregate in response to prey densities. Again we shall consider the possibility of both an unlimited supply of predators and a finite population, and again when we consider the case of a finite population, focus chiefly on the subcase in which (3.2) holds. In all four cases, we assume  $p$  and  $q$  in (2.5) are such that

$$(3.3) \quad p - q > 2.$$

We make this additional assumption for several reasons. First, notice that in the case of our specific hypothesis (2.6),  $p - q = 2 - (-1) = 3$ , so that (3.3) is satisfied. Second, in each of our four cases, we need (3.3) in order to see that the predation can result in an inverse relation between patch size and mean prey density. Moreover, in each case, the mathematical analysis is essentially the same whether we assume (2.6) specifically or (3.3) more generally. Finally, (3.3) allows for the likelihood that the specific hypothesis (2.6) is only approximately correct. (For instance, it is clear that in the fireweed-aphid-ladybird beetle system the predator can

leave a patch from its interior, although the observation of Kareiva and his collaborators is that a predator is far more likely to leave from the edge.)

It will turn out that the different hypotheses we make will lead to significantly different predictions from the models. We now analyze and interpret each of the four cases basically in turn, following some basic mathematical background material common to all the cases. In all but the first case (i.e., unlimited predator supply with no aggregation) additional mathematical development is required, and so we present the requisite information as it becomes pertinent.

**3.2. Some mathematical background.** Most of the effects of patch size on the prey in our models depend on the following result.

**THEOREM 3.1.** *Let  $D$ ,  $R$ , and  $B$  be positive constants. The model*

$$(3.4) \quad \begin{aligned} \frac{\partial v}{\partial t} &= D \left( \frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right) + Rv - Bv^2 \\ \text{for } 0 < x < l, \quad 0 < y < l, \quad t > 0, \\ v &= 0 \text{ for } x = 0, l, \quad y = 0, l \end{aligned}$$

has a unique equilibrium  $v^*(x, y)$  with  $v^*(x, y) > 0$  for  $0 < x < l$  and  $0 < y < l$  and with  $v \rightarrow v^*$  as  $t \rightarrow \infty$  if  $v(x, y, 0) \geq 0$ ,  $v(x, y, 0) \not\equiv 0$ , provided

$$(3.5) \quad R - (2\pi^2 D/l^2) > 0.$$

The equilibrium  $v^*(x, y)$  increases for each  $(x, y)$  if  $R$  is increased. If (3.5) does not hold then all positive solutions of (3.4) approach zero as  $t \rightarrow \infty$ .

*Remark.* The quantity  $2\pi^2 D/l^2$  is the principal eigenvalue for  $-D(\partial^2/\partial x^2 + \partial^2/\partial y^2)$  on the square of side  $l$  under the boundary conditions of (3.4). So  $2\pi^2$  is the principal Dirichlet eigenvalue of  $-(\partial^2/\partial x^2 + \partial^2/\partial y^2)$  on the square of side 1. If the basic underlying shape of the habitat patches is changed and  $\lambda_0$  denotes the principal Dirichlet eigenvalue of  $-(\partial^2/\partial x^2 + \partial^2/\partial y^2)$  when the linear dimension is 1, the value  $2\pi^2 D/l^2$  in (3.5) is changed to  $D\lambda_0/l^2$ , and this is the only effect of altering the basic shape of the habitat patches. In the case of circles,  $\lambda_0$  is the square of the first zero  $j_0$  of the Bessel function  $J_0$ . This value is approximately 5.783.

*Discussion.* This is a version of the type of results for KISS models that were introduced in [19, 30]. (3.5) gives the idea of a minimum characteristic length (in this case  $l = \pi\sqrt{2D/R}$ ) required to sustain a population. Much more general results of this sort are discussed in [3-5]; see also [21]. In particular, as noted, there is no qualitative change in the results if we have a patch shape other than a square. In our models the quantity corresponding to  $R$  will often depend on  $l$  and other parameters, so that (3.5) will lead to more complicated sorts of dependence on  $l$ . The fact that  $v^*$  increases with  $R$  (and decreases with  $B$ ) follows from results in [6, §4] based on sub- and supersolution methods.

For some purposes we will be interested in how the equilibrium  $v^*$  in Theorem 3.1 depends on the parameters in (3.4).

**THEOREM 3.2.** *For  $a > 2\pi^2$  let  $\theta_a(x, y)$  be the positive solution of*

$$(3.6) \quad \begin{aligned} \frac{\partial^2 \theta}{\partial x^2} + \frac{\partial^2 \theta}{\partial y^2} + a\theta - \theta^2 &= 0 \\ \text{in } (0, 1) \times (0, 1), \\ \theta(x, y) &= 0 \text{ for } x = 0, 1, \quad y = 0, 1, \end{aligned}$$

whose existence is implied by Theorem 3.1.

(i) If  $v^*$  is the positive solution of

$$(3.7) \quad \begin{aligned} D \left( \frac{\partial^2 v^*}{\partial x^2} + \frac{\partial^2 v^*}{\partial y^2} \right) + Rv^* - Bv^{*2} &= 0 \\ &\text{in } (0, l) \times (0, l), \\ v^*(x, y) &= 0 \text{ for } x = 0, l, \quad y = 0, l, \end{aligned}$$

then

$$(3.8) \quad v^*(x, y) = (D/Bl^2)\theta_{Rl^2/D}(x/l, y/l).$$

(Note that  $a = Rl^2/D > 2\pi^2$  is equivalent to (3.5).)

(ii) Let the total population corresponding to  $v^*(x, y)$  be denoted by

$$(3.9) \quad V^* = \int_0^l \int_0^l v^*(x, y) dx dy.$$

The average prey density  $V^*/l^2$  satisfies

$$(3.10) \quad V^*/l^2 \leq R/B;$$

in fact,  $0 \leq v^* \leq R/B$  on  $(0, l) \times (0, l)$ . If in (3.7) we have  $R = R(l)$  and  $B = B(l)$  such that for large  $l$  (3.5) holds,  $B(l)l^2 \rightarrow \infty$ , and the limit  $\lim_{l \rightarrow \infty} R(l)/B(l)$  exists, then

$$(3.11) \quad \lim_{l \rightarrow \infty} V^*/l^2 = \lim_{l \rightarrow \infty} R(l)/B(l).$$

(If  $R(l)/B(l) \rightarrow \infty$  as  $l \rightarrow \infty$  then  $V^*/l^2 \rightarrow \infty$  also.)

*Discussion.* Part (i) follows from the uniqueness of  $v^*$  (which follows from Theorem 3.1) and the observation that if the function  $\theta$  defined in (3.6) is rescaled as in (3.8), then the resulting function  $(D/Bl^2)\theta_{Rl^2/D}(x/l, y/l)$  satisfies (3.7). The fact that  $v^* < R/B$  is a standard result in the theory of diffusive logistic equations and follows directly from the maximum principle, as in [3]. Integrating over  $(0, l) \times (0, l)$  and dividing by  $l^2$  yields (3.10). If we let  $x' = x/l$ ,  $y' = y/l$  in the expression on the right in (3.8) we have  $v^*(x, y) = w(x', y')$ , where  $w$  can be seen (after some calculation) to satisfy

$$(3.12) \quad \begin{aligned} \frac{D}{B(l)l^2} \left[ \frac{\partial^2 w}{(\partial x')^2} + \frac{\partial^2 w}{(\partial y')^2} \right] + \frac{R(l)}{B(l)}w - w^2 &= 0 \\ &\text{in } (0, 1) \times (0, 1), \\ w(x', y') &= 0 \text{ for } x = 0, 1, \quad y = 0, 1. \end{aligned}$$

(Hence  $w(x', y') = (D/Bl^2)\theta_{Rl^2/D}(x', y')$ , in agreement with (3.8)). Suppose  $\lim_{l \rightarrow \infty} R(l)/B(l)$  is finite and let  $K_0 = \lim_{l \rightarrow \infty} R(l)/B(l)$ . For any  $\varepsilon > 0$  we can choose  $l$  large enough that

$$(3.13) \quad K_0 - \varepsilon < R(l)/B(l) < K_0 + \varepsilon.$$

Let  $\bar{w} > 0$  satisfy

$$(3.14) \quad \begin{aligned} \frac{D}{B(l)l^2} \left( \frac{\partial^2 \bar{w}}{(\partial x')^2} + \frac{\partial^2 \bar{w}}{(\partial y')^2} \right) + (K_0 + \varepsilon)\bar{w} - \bar{w}^2 &= 0 \\ &\text{on } (0, 1) \times (0, 1), \\ \bar{w} &= 0 \text{ for } x = 0, 1, \quad y = 0, 1, \end{aligned}$$

and let  $\underline{w} > 0$  satisfy

$$(3.15) \quad \begin{aligned} \frac{D}{B(l)l^2} \left( \frac{\partial^2 \underline{w}}{(\partial x')^2} + \frac{\partial^2 \underline{w}}{(\partial y')^2} \right) + (K_0 - \varepsilon)\underline{w} - \underline{w}^2 &= 0 \\ &\text{in } (0, 1) \times (0, 1), \\ \underline{w} &= 0 \text{ for } x = 0, 1, \quad y = 0, 1. \end{aligned}$$

The method of sub- and supersolutions and the uniqueness of positive equilibria for diffusive logistic equations imply that  $\underline{w} \leq w \leq \bar{w}$  when (3.13) holds, since  $w$  is a supersolution to (3.15) and a subsolution to (3.14). See [3] for discussion and references. The method of sub- and supersolutions was used in various ways in [1, 2, 6, 21] and is discussed at some length in [9, 20].

It follows from results of [3, §4] that as  $l \rightarrow \infty$ ,  $\bar{w} \rightarrow K_0 + \varepsilon$  and  $\underline{w} \rightarrow K_0 - \varepsilon$  uniformly on compact subsets of  $(0, 1) \times (0, 1)$ . (This requires  $D/B(l)l^2 \rightarrow 0$  as  $l \rightarrow \infty$ .) Thus, for any compact subset of  $(0, 1) \times (0, 1)$  we have  $K_0 - \varepsilon < w < K_0 + \varepsilon$  for  $l$  sufficiently large. Since  $\varepsilon > 0$  was arbitrary, we conclude that  $w \rightarrow K_0 = \lim_{l \rightarrow \infty} R(l)/B(l)$  as  $l \rightarrow \infty$ , uniformly on compact subsets of  $(0, 1) \times (0, 1)$ . Since  $w$  is bounded (e.g., by  $0 \leq w \leq K_0 + 1$ ) for large  $l$  and the square  $(0, 1) \times (0, 1)$  has unit area, we have

$$(3.16) \quad \lim_{l \rightarrow \infty} \int_0^1 \int_0^1 w(x', y') dx' dy' = \lim_{l \rightarrow \infty} R(l)/B(l).$$

On the other hand,

$$(3.17) \quad \begin{aligned} V^*/l^2 &= (1/l^2) \int_0^l \int_0^l v^*(x, y) dx dy \\ &= (1/l^2) \int_0^1 \int_0^1 w(x', y') l^2 dx' dy' \\ &= \int_0^1 \int_0^1 w(x', y') dx' dy' \end{aligned}$$

since the Jacobian of the change of coordinates  $(x, y) \mapsto (x', y') = (x/l, y/l)$  is  $\partial(x, y)/\partial(x', y') = l^2$ . Hence (3.11) follows from (3.16), (3.17). If  $R(l)/B(l) \rightarrow \infty$  as  $l \rightarrow \infty$  we would use the comparison  $v^* \geq \underline{w} > 0$  with  $\underline{w} \rightarrow K_1$  as  $l \rightarrow \infty$ ,  $K_1$  arbitrarily large, then use (3.17).

**3.3. Unlimited predator supply, no aggregation.** In this case we need consider only a single patch, since patches are not coupled. The model is given by equation (2.4); that is, we assume (2.2) and then substitute the equilibrium for the predator equation of (2.3) into the prey equation for (2.4). (The predator equilibrium is globally asymptotically stable and does not depend on the prey density.) Under hypothesis (2.5) we obtain

$$\begin{aligned} \frac{\partial v}{\partial t} &= D \left( \frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right) - rv - \frac{rv^2}{K} - cP_A(i/e)l^{p-q-2}v \\ &\text{for } 0 < x < l, \quad 0 < y < l, \quad t > 0, \\ v &= 0 \text{ for } x = 0, l, \quad y = 0, l. \end{aligned}$$

The quantity corresponding to  $R$  in (3.4) is

$$(3.18) \quad R = r - cP_A(i/e)l^{p-q-2};$$

the inequality corresponding to (3.5) and characterizing when the prey can persist is

$$r - cP_A(i/e)l^{p-q-2} - 2\pi^2 D l^{-2} > 0,$$

or equivalently

$$(3.19) \quad r > cP_A(i/e)l^{p-q-2} + 2\pi^2 D l^{-2}.$$

It is clear that if (3.19) is to hold  $l$  cannot be too small, since  $l^{-2} \rightarrow \infty$  as  $l \rightarrow 0$ . On the other hand, since  $p - q - 2 > 0$  then  $l^{p-q-2} \rightarrow \infty$  as  $l \rightarrow \infty$ , and  $l$  cannot be too large. The parameter dependence of (3.19) can be described graphically by noting that (3.19) will be satisfied when  $r > f(l) \equiv cP_A(i/e)l^{p-q-2} + 2\pi^2 D l^{-2}$ . The case yields a maximum patch size which will sustain a prey equilibrium as well as the usual minimum patch size.

**3.4. Equilibrium and pseudoequilibrium for finite predator populations.** The relevant models are (2.8) and (2.13)-(2.15). The total predator population  $C$  may be fixed or may vary with patch size or the number of patches as in (3.2) or (3.1), respectively. The predator equations in (2.8) are a coupled linear system of ordinary differential equations. Before proceeding further we must analyze that system. We shall see that it always has a unique asymptotically stable positive equilibrium. In (2.13) there is a corresponding "pseudoequilibrium" for any fixed prey populations  $V_1, \dots, V_N$ .

Let  $\bar{P}^* = (P_1^*, \dots, P_N^*)$  be the equilibrium for the predator equations in (2.8). Then

$$(3.20) \quad 0 = i l_n^p \left( C - \sum_{k=1}^N P_k^* \right) - e l_n^q P_n^*, \quad n = 1, \dots, N$$

or equivalently

$$(3.21) \quad 0 = (i/e) l_n^{p-q} \left( C - \sum_{k=1}^N P_k^* \right) - P_n^*, \quad n = 1, \dots, N.$$

Summing over  $n$  in (3.21) and noting that if we sum over  $n$  then  $n$  and  $k$  are interchangeable as indices of summation, we find

$$(3.22) \quad 0 = \left( \sum_{k=1}^N (i/e) l_k^{p-q} \right) \left( C - \sum_{k=1}^N P_k^* \right) - \sum_{k=1}^N P_k^*,$$

so that we can solve for  $\sum_{k=1}^N P_k^*$  and obtain

$$\sum_{k=1}^N P_k^* = \frac{C(i/e) \sum_{k=1}^N l_k^{p-q}}{1 + (i/e) \sum_{k=1}^N l_k^{p-q}}.$$

Substituting into (3.20) and solving for  $P_n^*$  yields

$$(3.23) \quad P_n^* = \frac{i C l_n^{p-q}}{i \sum_{k=1}^N l_k^{p-q} + e}, \quad n = 1, \dots, N.$$

We have the following result on stability.

**THEOREM 3.3.** *The equilibrium  $\bar{P}^*$  of (2.8) given by (3.23) is asymptotically stable.*

*Proof.* Let  $\bar{P}$  satisfy (2.8) and define  $\bar{z} = \bar{P} - \bar{P}^*$ . Observe that  $\bar{z}$  satisfies

$$(3.24) \quad \frac{d\bar{z}}{dt} = Q\bar{z},$$

where  $Q$  is the  $N \times N$  matrix with the  $n$ th diagonal entry given by  $-(i l_n^p + e l_n^q)$  and with all the other entries in the  $n$ th row equal to  $-i l_n^p$ . To show that the equilibrium  $\bar{P}^*$  is stable we must show that  $\bar{z} \rightarrow 0$  as  $t \rightarrow \infty$ . To do that we shall use Lyapunov's second method. Specifically, we shall construct a Lyapunov function  $E(\bar{z})$  so that  $E(\bar{z}) > 0$  for  $\bar{z} \neq 0$  but  $dE/dt < 0$  on trajectories of (3.24) with  $\bar{z} \neq 0$ . We observe that the matrix  $Q$  in (3.24) has the form

$$Q = \begin{pmatrix} -a_1 - b_1 & -a_1 & \cdots & -a_1 \\ -a_2 & -a_2 - b_2 & \cdots & -a_2 \\ \vdots & \vdots & \ddots & \vdots \\ -a_N & \cdots & \cdots & -a_N - b_N \end{pmatrix},$$

where  $a_n = i l_n^p > 0$ ,  $b_n = e l_n^q > 0$ . Let  $S$  be the positive definite (diagonal)  $N \times N$  matrix where for each  $n$  the  $n$ th diagonal entry is  $1/a_n$  and the entries off the diagonal are all zero. Since  $1/a_n > 0$  the matrix  $S$  is positive definite so  $\bar{z}^T S \bar{z} > 0$  for  $\bar{z} \neq 0$ . If we let  $E(\bar{z}) = \bar{z}^T S \bar{z}$  then computation shows that  $dE/dt = \bar{z}^T (Q^T S + S Q) \bar{z}$ . To establish asymptotic stability we need only show that the matrix  $Q^T S + S Q$  is negative definite. We have

$$Q^T S + S Q = -2 \begin{pmatrix} 1 + b_1/a_1 & 1 & \cdots & 1 \\ 1 & 1 + b_2/a_2 & \cdots & 1 \\ \vdots & \vdots & \ddots & \vdots \\ 1 & \cdots & \cdots & 1 + b_N/a_N \end{pmatrix},$$

so that

$$(3.25) \quad \begin{aligned} \bar{z}^T [Q^T S + S Q] \bar{z} &= -2 \left[ \sum_{n=1}^N z_n^2 + 2 \sum_{\substack{m,n=1 \\ m \neq n}}^N z_m z_n + \sum_{n=1}^N (b_n/a_n) z_n^2 \right] \\ &= -2 \left[ (z_1 + \cdots + z_N)^2 + \sum_{n=1}^N (b_n/a_n) z_n^2 \right] \\ &\leq -2 \sum_{n=1}^N (b_n/a_n) z_n^2. \end{aligned}$$

Thus  $Q^T S + S Q$  is negative definite and it follows by standard Lyapunov theory that the equilibrium for (2.8) is stable.

*Remark.* In the case of predator aggregation the predator equations are (2.13). For any fixed values of the prey populations  $V_n$  the system (2.13) would have the same structure as (2.8), so if the prey populations were held fixed the system (2.13) would also have a unique, stable equilibrium  $\bar{P}^*$  given in terms of the prey populations  $V_k$  by

$$(3.26) \quad P_n^* = \frac{i C V_n l_n^{p-q-2}}{i \sum_{k=1}^N l_k^{p-q-2} V_k + e}.$$



We shall sometimes need to rewrite (3.23) and (3.26) in slightly different forms. The analysis of (2.13) with  $V_1, \dots, V_N$  fixed is done in exactly the same way as that of (2.8). Of course,  $V_1, \dots, V_N$  will generally vary with time, but our modeling assumption is that predator aggregation occurs so rapidly that predator populations at time  $t$  remain at the "pseudoequilibrium" corresponding to the values of  $V_1, \dots, V_N$  at time  $t$ . Our analysis of the remaining cases will make systematic use of (3.23) and (3.26).

**3.5. Finite predator population, no aggregation.** In this case the relevant equations are (2.8). The predator populations tend asymptotically to the equilibrium given by (3.23). Substituting into the prey equations yields

$$(3.27) \quad \frac{\partial v_n}{\partial t} = D \left( \frac{\partial^2 v_n}{\partial x^2} + \frac{\partial^2 v_n}{\partial y^2} \right) + r \left( 1 - \frac{v_n}{K} \right) v_n - \left( \frac{icCl_n^{p-q-2}}{i \sum_{k=1}^N l_k^{p-q} + e} \right) v_n$$

for  $0 \leq x \leq l_n, 0 \leq y \leq l_n,$   
 $v_n(t, x, y) = 0$  for  $x = 0, l_n, y = 0, l_n, n = 1, \dots, N.$

For each  $n$ , (3.27) is a diffusive logistic equation which can be written in the form (3.4) with

$$(3.28) \quad B = r/K, \quad R = R_n = r - \frac{icCl_n^{p-q-2}}{i \sum_{k=1}^N l_k^{p-q} + e}.$$

Notice that  $R$ , the intrinsic growth rate at low densities, is reduced by the presence of predators. The behavior of the equations in (3.27) depends on our assumptions about how the total predator population  $C$  depends (or does not depend) on the size or number of patches. The criterion (3.5) using  $R$  from (3.28) will determine whether a given patch would sustain a prey population. Explicitly that condition for the  $n$ th patch is

$$(3.29) \quad r - \frac{icCl_n^{p-q-2}}{i \sum_{k=1}^N l_k^{p-q} + e} - \frac{2\pi^2}{l_n^2} D > 0.$$

We shall first briefly consider the case where the total predator population remains fixed as the patch size varies. To understand how patch size affects the predictions of the model, let us suppose that the size of the first patch varies but the others do not. It is convenient to write (3.29) for  $n = 1$  as

$$(3.30) \quad r > \frac{1}{l_1^2} \left[ \frac{icCl_1^{p-q}}{il_1^{p-q} + \left( i \sum_{k=2}^N l_k^{p-q} + e \right)} + 2\pi^2 D \right] \equiv g(l_1).$$

Since the expression in brackets on the right side of (3.30) is always bounded in  $l_1$  for any  $p$  and  $q$  (not just for those satisfying (3.3)), it follows that (3.30) will hold for  $l_1$  large since the expression in brackets is multiplied by  $1/l_1^2$ . Thus, in this case, any sufficiently large patch must sustain a prey population. This is not surprising since if the number of predators is fixed and the size of a patch increases enough, eventually the average predator density must approach zero so that the effect on the prey becomes negligible. On the other hand, when (3.3)

holds, i.e.,  $p - q > 2$ , the situation for moderate values of  $l_1$  is simple in some cases and more complex for others. The reason is that the right-hand side of (3.30) fails to be monotonically decreasing for all  $l_1 > 0$  if the predatory impact  $cC$  is large enough. For some values of  $r$ , this feature results in "excluded middle" ranges of  $l_1$  for which corresponding patches do not sustain prey populations even though there are patches of smaller and larger sizes which do sustain prey populations.

We leave the analysis of the preceding situation to the interested reader and turn to the situation where  $C$  depends on the total area of patches as in (3.2). In this case (3.29) becomes

$$(3.31) \quad r > \frac{icC_0 \left( \sum_{k=1}^N l_k^2 \right) l_1^{p-q-2}}{i \sum_{k=1}^N l_k^{p-q} + e} + \frac{2\pi^2 D}{l_1^2}$$

$$= \frac{icC_0 l_1^{p-q} + icC_0 l_1^{p-q-2} \left( \sum_{k=2}^N l_k^2 \right)}{il_1^{p-q} + \left( i \sum_{k=1}^N l_k^{p-q} + e \right)} + \frac{2\pi^2 D}{l_1^2}.$$

The first observation is that again the critical lower limit on the size of patch which can sustain a prey population is larger than the critical size determined by  $r > 2\pi^2 D/l_1^2$  in a simple KISS model without predators. This is similar to the case where the total predator population is a fixed constant. The second observation is that as  $l_1 \rightarrow \infty$ , with  $l_2, \dots, l_N$  held fixed or taken equal to  $l_1$ , the right side of (3.31) has a limit  $cC_0$ , so to conclude that all sufficiently large patches would sustain a prey population we would need  $r > cC_0$ . If  $r < cC_0$  then there may in fact be no patch size which can sustain a prey population. (The same turns out to be true if  $r = cC_0$  but that requires more delicate analysis.) The general case of (3.31) is somewhat complicated to analyze, so let us consider the special case where all the patches are the same size. If  $l_1 = l_2 = \dots = l_N = l$  then (3.31) becomes

$$(3.32) \quad r > \frac{icC_0 N l^{p-q}}{i N l^{p-q} + e} + \frac{2\pi^2}{l^2} D \equiv h(l).$$

The sign of  $h'(l)$  is determined by the expression (obtained by differentiating, combining fractions, taking the numerator, and simplifying)

$$icC_0 N (p - q) e l^{p-q+2} - 4\pi^2 (i N l^{p-q} + e)^2 D.$$

This expression is negative for  $l \approx 0$  and for  $l \approx \infty$  as  $p - q > 2$ , but will be positive for some values of  $l$  if  $cC_0$  is large enough. Thus, the sort of qualitative behavior noted above for the case of  $C$  fixed, namely, having patches of intermediate size not sustaining prey populations while having patches of both smaller and larger sizes sustaining prey populations, can also occur if (3.2) holds. The primary difference between the cases of fixed  $C$  and  $C = C_0$  "times" total patch area is that in the first case any sufficiently large patch will sustain a prey population, while the behavior of the second case depends in a more delicate way on the parameters. In particular, there may be no patch size which can sustain a prey population, or there may be an excluded range of patch sizes. There may even be situations where the total predator population is proportional to the total patch area in which there is a maximum patch size that can sustain a prey population. For example, (3.32) will be satisfied for  $l = 1$  if  $r > icC_0 N / (iN + e) + 2\pi^2 D$ , but  $icC_0 N / (iN + e) + 2\pi^2 D < cC_0$  provided

$2\pi^2 D(iN + e) < ecC_0$ , which will be satisfied if  $cC_0$  is large or  $D$  is small. In that case values of  $r$  in the interval  $((icC_0N/(iN + e)) + 2\pi^2 D, cC_0)$  would admit a positive prey equilibrium for some values of  $l$  (specifically for  $l = 1$ ) but not for large  $l$ . Thus, there would be a maximum patch size which could sustain a prey population.

In this case the effective carrying capacity  $R/B$  is given by

$$R/B = \frac{K}{r} \left( r - \frac{icC_0 N l^{p-q}}{iN l^{p-q} + e} \right) < K.$$

As  $l \rightarrow \infty$ ,  $R/B \rightarrow K(1 - (cC_0/r))$ , so we would always expect the effective carrying capacity to be less than  $K$  if the number of predators is proportional to the total patch area. As we saw already on the basis of examining  $R$  alone, if  $r < cC_0$  then sufficiently large patches will not sustain a prey population.

**3.6. Unlimited predator supply with predator aggregation.** In this third case the basic equations are (2.10)–(2.12). Recall that  $V_n$  represents the total prey population on the  $n$ th patch, that is,  $V_n$  is the integral over the  $n$ th patch of the density  $v_n$ . As in the scenario of an unlimited predator supply without aggregation there is no coupling between patches, so we shall consider only a single patch of side  $l$ . Assuming that the immigration and emigration rates obey (2.5) and (3.3), we have the pseudoequilibrium predator population on the patch given by (2.11), which becomes

$$(3.33) \quad P = (i/e) P_A l^{p-q-2} V,$$

leading to the prey equation

$$(3.34) \quad \frac{\partial v}{\partial t} = D \left( \frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right) + r \left( 1 - \frac{v}{K} \right) v - c P_A (i/e) l^{p-q-4} V v$$

via (2.12). We assume as always that  $v = 0$  on the patch boundary, so that  $v(x, y, t) = 0$  for  $x = 0, l$  or  $y = 0, l$ . Equation (3.34) is a reaction-diffusion equation with a nonlocal term. We shall see that some of the fourth case scenarios also give rise to such equations but with different dependence on  $V$ . For a single patch the models we shall consider all take the form

$$(3.35) \quad \begin{aligned} \frac{\partial v}{\partial t} &= D \left( \frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right) + Rv - F(V)v - Bv^2 \\ &\text{for } 0 < x < l, \quad 0 < y < l, \quad t > 0, \\ v(x, y, t) &= 0 \text{ for } x = 0, l, \quad y = 0, l, \end{aligned}$$

with the additional property

$$(3.36) \quad F(0) = 0, \quad F'(V) > 0 \text{ for } V \geq 0.$$

Equation (3.35) resembles the standard reaction-diffusion equation (3.4) and turns out to have similar properties. We have the following analogue of Theorem 3.1.

**THEOREM 3.4.** *Under hypothesis (3.36) the model (3.35) has a unique equilibrium  $v^{**}(x, y)$  with  $v^{**}(x, y) > 0$  for  $0 < x < l, 0 < y < l$  such that  $v \rightarrow v^{**}$  as  $t \rightarrow \infty$  for any  $v$  satisfying (3.35) with  $v(x, y, 0) \geq 0, v(x, y, 0) \not\equiv 0$ , provided (3.5) holds; that is,*

$$R - (2\pi^2 D/l^2) > 0.$$

*If (3.5) does not hold then all solutions of (3.35) tend asymptotically to zero as  $t \rightarrow \infty$ . The equilibrium  $v^{**}(x, y)$  can be characterized in terms of solutions to (3.6) as*

$$v^{**}(x, y) = (D/Bl^2)\theta_{(R-Q)l^2/D}(x/l, y/l),$$

where  $Q$  is determined by the relation

$$(3.37) \quad F(V^{**}) = F \left( \int_0^l \int_0^l v^{**}(x, y) dx dy \right) = Q,$$

which (in view of (3.17) applied to  $v^{**}$ ) is equivalent to

$$(3.38) \quad F \left( \int_0^1 \int_0^1 (D/Bl^2)\theta_{(R-Q)l^2/D}(x', y') dx' dy' \right) = Q.$$

By Theorem 3.2, since  $Q > 0, v^{**} \leq R/B$  so  $V^{**}/l^2 < R/B$ .

*Remark.* This result indicates the crucial difference between our purely geometric models for predator immigration/emigration and those of our models which incorporate predator aggregation depending on average prey density. The second sort of model typically has the form (3.35) with (3.36) satisfied and hence predicts the same minimum patch size for the prey as do standard KISS models with no predation. This is in contrast with the case of the density-independent models discussed in the preceding sections, where the presence of predators always raised the minimum patch size needed to sustain a prey population. In fact, because we consider only models where (3.36) holds, we can write the terms describing the prey population dynamics as  $(R - F(V) - Bv)v$ , where  $F(V) \rightarrow 0$  and  $Bv \rightarrow 0$  as  $v \rightarrow 0$ . Thus the behavior of those terms at low prey densities is essentially determined by the linear growth rate  $Rv$ , which is unaffected by the presence of predators. (Recall that in our models of predator immigration/emigration without dependence on the prey density the prey growth rate at low densities was reduced by the presence of predators.) Biologically, this distinction is sensible because the models with predator immigration/emigration depending on prey density assume that predator emigration rates rise toward infinity as the prey density tends toward zero, so the effects of predation on prey populations at low densities become negligible. We shall see, however, that as  $l$  increases so that a larger prey population would be sustained on the patch in the absence of predators, the effects of predation in models such as (3.35) become more pronounced and may imply qualitative behavior as  $l \rightarrow \infty$  for the equilibrium  $v^{**}$  which is quite different from that for models with no predators.

*Discussion of Theorem 3.4.* The key point in analyzing (3.35) is to observe that the presence of the nonlocal term  $F(V)$  does not invalidate many of the arguments used to study standard reaction-diffusion equations. In particular, since  $|V| \leq l^2 \sup |v|$  the mapping  $v \rightarrow F(V)$  will be well defined and as smooth as  $F$  on function spaces which embed in  $C([0, l] \times [0, l])$ . Those include the Sobolev spaces  $W^{2,p}$  for  $p$  large enough and the interpolation spaces  $X^\alpha$  obtained from them via fractional powers of the Laplace operator, as used in [3, 5, 10, 11]. Thus the existence and uniqueness of solutions to (3.35) can be obtained via the same functional analytic arguments (e.g., the Banach fixed point theorem for contraction mappings, semigroup theory, etc.) used in those references for standard semilinear parabolic (i.e., reaction-diffusion) equations. Furthermore, any solution of (3.35) can be interpreted as satisfying a linear parabolic equation

$$\frac{\partial v}{\partial t} = D \left( \frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right) + f(x, y, t)v \text{ for } 0 < x < l, \quad 0 < y < l, \quad t > 0,$$

which satisfies a maximum principle [9, 20, 28, 31, 35] so that  $v(x, y, t) \geq 0$  if  $v(x, y, 0) \geq 0$  and in fact  $v(x, y, t) > 0$  for  $0 < x < l, 0 < y < l$  and  $t > 0$  if  $v(x, y, 0) \not\equiv 0$ . Finally, if  $u$

and  $v$  satisfy

$$(3.39) \begin{cases} u_t - D \left( \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) - Ru + F(U)u + Bu^2 \\ \geq v_t - D \left( \frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right) - Rv + F(V)v + Bv^2 \\ \text{on } (0, l) \times (0, l) \text{ with } u(x, y, t) = v(x, y, t) = 0 \text{ for } x = 0, l, y = 0, l \end{cases}$$

and we have  $u(x, y, 0) \geq v(x, y, 0)$  then either  $u(x, y, t) > v(x, y, t)$  for all  $(x, y) \in (0, l) \times (0, l)$  and  $t > 0$  or  $u(x, y, t) = v(x, y, t)$  for all  $(x, y, t)$ . This comparison principle follows as in the usual reaction-diffusion case from the Nagumo-Westphal lemma and/or the maximum principle. Comparison principles are discussed and applied in general contexts in [9, 20, 28, 31, 35] and in more specific situations in [1, 2, 6, 7, 21]. The results in [7] apply to a competition system with nonlocal terms.

The significance here is that we can apply the method of sub- and supersolutions used earlier in this section to study (3.4) in our study of (3.35). As before, we can follow the reasoning in [1, 2] (see also [6, 9, 13, 21]) and conclude that solutions of (3.35) with initial data starting at sub- and supersolutions to the corresponding steady state problem must converge monotonically to equilibria of (3.35) as  $t \rightarrow \infty$ . We observe that if  $v$  satisfies (3.35) and  $w$  is a solution to (3.4) with  $w(x, y, 0) \geq v(x, y, 0)$  then  $w$  is a supersolution to (3.35). It follows from Theorem 3.1 that if  $R - (2\pi^2 D/l^2) \leq 0$  then all solutions of (3.4) tend to zero as  $t \rightarrow \infty$ , so all solutions of (3.35) must as well. On the other hand, since  $F(s) \rightarrow 0$  as  $s \rightarrow 0$ , for  $R - (2\pi^2 D/l^2) > 0$  and  $\varepsilon > 0$  sufficiently small we have that the eigenfunction  $\varepsilon \sin(\pi\sqrt{D}x/l) \sin(\pi\sqrt{D}y/l)$  is a subsolution to the equilibrium problem corresponding to (3.35), as for (3.4). (See [6].) Thus, for  $R - 2\pi^2 D/l^2 > 0$  equation (3.35) has the property that all solutions with positive initial data tend asymptotically as  $t \rightarrow \infty$  toward a set bounded above and below by maximal and minimal positive equilibria. This follows because all positive solutions of (3.35) can be bounded above by solutions whose initial data is a large constant and hence a supersolution to the equilibrium problem and bounded below by a solution whose initial data has the form  $\varepsilon \sin(\pi\sqrt{D}x/l) \sin(\pi\sqrt{D}y/l)$  with  $\varepsilon$  small and hence is a subsolution to the equilibrium problem.

To finish our analysis we must determine the equilibria of (3.35). We have already seen that for  $R - 2\pi^2 D/l^2 \leq 0$  all positive solutions must decay toward zero as  $t \rightarrow \infty$ . Suppose  $R - 2\pi^2 D/l^2 > 0$  and notice that any equilibrium for (3.35) must satisfy the equations

$$(3.40) \quad 0 = D \left( \frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right) + [R - F(Z)]v - Bv^2$$

$$\text{for } 0 < x < l, \quad 0 < y < l,$$

$$v(x, y) = 0 \text{ for } x = 0, l, y = 0, l, \text{ and}$$

$$(3.41) \quad Z = \int_0^l \int_0^l v(x, y) dy dx = V$$

and any solution to (3.40), (3.41) defines an equilibrium of (3.35). To see that (3.35) has the unique equilibrium given in Theorem 3.4, we observe that as long as  $R - 2\pi^2 D/l^2 - F(Z) > 0$  the existence a unique equilibrium  $v_Z^*(x, y) > 0$  for (3.40) is guaranteed by Theorem 3.1. If we take  $Z = 0$  we have  $F(Z) = 0$  so

$$(3.42) \quad Z = 0 < \int_0^l \int_0^l v_Z^*(x, y) dy dx = V_Z^*.$$

If we then allow  $Z$  to increase, the left side of (3.42) increases. On the other hand,  $R - F(Z)$  decreases, so by Theorem 3.1 the unique positive equilibrium  $v_Z^*$  of (3.40) also decreases. We always have  $v_Z^*(x, y) \leq v_0^*(x, y)$ . As we increase  $Z$  the left side of (3.42) increases without bound while the right side decreases. Hence, equality must be achieved for some value of  $Z$ . For that value of  $Z$ , (3.41) holds and we have an equilibrium  $v^{**} = v_Z^*$ . Increasing  $Z$  further would further reduce  $v^*(x, y)$  so that (3.41) would fail, so the value of  $Z$  for which (3.40), (3.41) are both satisfied is unique and hence so is the equilibrium  $v^{**} = v_Z^*$ . If we let  $Q = F(Z)$  for the value of  $Z$  for which  $v_Z^* = v^{**}$  then the remaining characterizations of  $v^{**}$  in Theorem 3.4 follow from Theorem 3.2. (We note that an alternate approach to the analysis of the equilibrium problem for (3.35) would be to use the bifurcation theoretic methods discussed in [3, 5]. Those methods apply with only minor modifications to the present situation.)

We now return to the question of determining how the model (3.34) behaves as  $l \rightarrow \infty$ . By Theorem 3.4, (3.34) has a unique stable positive equilibrium  $v^{**}$  if  $r - 2\pi^2 D/l^2 > 0$ . Since  $v^{**}$  is positive on  $(0, l) \times (0, l)$  and is zero on the boundary, we have that the outward normal derivative  $\partial v^{**}/\partial n$  is nonpositive on the boundary of the domain  $(0, l) \times (0, l)$ . Thus, if we write the equilibrium equation in the form

$$-D \left( \frac{\partial^2 v^{**}}{\partial x^2} + \frac{\partial^2 v^{**}}{\partial y^2} \right) = rv^{**} - \frac{r}{K}(v^{**})^2 - cP_A(i/e)l^{p-q-4}V^{**}v^{**},$$

integrate over  $(0, l) \times (0, l)$ , and apply the divergence theorem to the derivative terms on the left side, we obtain the inequality

$$(3.43) \quad 0 \leq rV^{**} - \frac{r}{K} \int_0^l \int_0^l (v^{**})^2 dx dy - cP_A(i/e)l^{p-q-4}(V^{**})^2.$$

If we apply the Cauchy-Schwarz inequality to the integral of  $(v^{**})^2$  we obtain

$$(3.44) \quad (V^{**})^2 = \left( \int_0^l \int_0^l v^{**} dx dy \right)^2 \leq \left( \int_0^l \int_0^l (v^{**})^2 dx dy \right) \left( \int_0^l \int_0^l 1 dx dy \right) \\ = l^2 \int_0^l \int_0^l (v^{**})^2 dx dy.$$

Dividing (3.44) by  $l^2$  and using the result in (3.43) yields the inequality

$$(3.45) \quad 0 \leq rV^{**} - \frac{r}{Kl^2}(V^{**})^2 - cP_A(i/e)l^{p-q-4}(V^{**})^2.$$

Since  $V^{**} > 0$ , (3.45) implies that

$$(3.46) \quad V^{**} \leq \frac{r}{[(r/Kl^2) + cP_A(i/e)l^{p-q-4}]}.$$

Since  $p - q > 2$ , it follows from (3.46) that the average prey density  $V^{**}/l^2$  tends asymptotically to zero as  $l \rightarrow \infty$ . (If  $p - q > 4$ , then the total prey population  $V^{**}$  itself tends asymptotically to zero.) Consequently, there must be an inverse relation between patch size and average prey density.

**3.7. Finite predator population with predator aggregation: A single patch.** In this case the relevant equations are (2.13)–(2.15) and (3.26). We shall first consider the case of a single patch since it illustrates many features of the general case and since the case of several patches will require some additional mathematical analysis. For a single patch, substituting

the predator pseudoequilibrium  $P^*$  given in (3.26) (with  $N = 1$ ) into (2.15) yields

$$(3.47) \quad \begin{aligned} \frac{\partial v}{\partial t} &= D \left( \frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right) + r \left( 1 - \frac{v}{K} \right) v - \frac{icCVl^{p-q-4}v}{il^{p-q-2}V + e} \\ &\text{for } 0 < x < l, \quad 0 < y < l, \quad t > 0, \\ v(x, y, t) &= 0 \text{ when } x = 0, l, \quad y = 0, l. \end{aligned}$$

(Recall that  $C$  is the total predator population and  $c$  describes the rate at which predators consume prey.) Equation (3.47) has the form (3.35) and so can be analyzed via Theorem 3.4. In this case the variables in Theorem 3.4 can be taken to be  $R = r$ ,  $B = r/K$ , and  $F(V) = icCl^{p-q-4}V/(il^{p-q-2}V + e)$ . If  $C$ , the number of predators, is independent of  $l$  we can observe that  $F(V) \leq cCl^{-2}$  for all  $V \geq 0$ , so that the quantity  $Q$  in (3.37) of Theorem 3.4 satisfies  $Q \leq cCl^{-2}$ , and thus by Theorem 3.4 we have

$$\begin{aligned} v^{**}(x, y) &= (DK/r l^2) \theta_{(R-Q)l^2/D}(x/l, y/l) \\ &\geq (DK/r l^2) \theta_{(r-cC)/D}(x/l, y/l) = u(x, y), \end{aligned}$$

where  $u(x, y)$  satisfies (by Theorem 3.2)

$$\begin{aligned} 0 &= D \left( \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) + [r - (cC/l^2)]u - \frac{ru^2}{K} \text{ on } (0, l) \times (0, l), \\ u(x, y) &= 0 \text{ for } x = 0, l, \quad y = 0, l. \end{aligned}$$

By (3.11) of Theorem 3.2 we have

$$(3.48) \quad \lim_{l \rightarrow \infty} (1/l^2) \int_0^l \int_0^l u(x, y) dy dx = K.$$

On the other hand,  $v^{**}$  is a positive subsolution to the basic equation

$$0 = D \left( \frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right) + r \left( 1 - \frac{v}{K} \right) v \text{ in } (0, l) \times (0, l)$$

with the same boundary conditions, so we have  $v^{**} \leq v \leq K$  where the second inequality follows by Theorem 3.2. Thus, in this case, we have  $V^{**}/l^2$  bounded above by  $K$  and below by the quantity in the limit in (3.48). Since the lower bound on  $V^{**}/l^2$  given by the expression in (3.48) approaches  $K$  as  $l \rightarrow \infty$  we must have

$$\lim_{l \rightarrow \infty} V^{**}/l^2 = K.$$

This is not surprising since for a sufficiently large patch the effects on the prey from any fixed number of predators can be expected to become negligible. If we allow the number of predators in the system to increase in proportion to patch area so that  $C = C_0 l^2$  then the asymptotic behavior as  $l \rightarrow \infty$  may change. There are two cases, namely,  $r > cC_0$  and  $r \leq cC_0$ . (Since we assume here that  $p - q > 2$  the powers of  $l$  occurring in the expression for  $F(V)$  in this case will tend toward infinity as  $l \rightarrow \infty$ .) We have  $F(V) = icC_0 l^{p-q-2} V / (il^{p-q-2} V + e)$ . Let us consider the case  $r > cC_0$ . In this case we first observe that  $F(V) \leq cC_0$ , so that any equilibrium solution to (3.47) is a supersolution to

$$(3.49) \quad \begin{aligned} 0 &= D \left( \frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2} \right) + (r - cC_0)w - \frac{rw^2}{K} \text{ on } (0, l) \times (0, l), \\ w(x, y) &= 0 \text{ for } x = 0, l, \quad y = 0, l. \end{aligned}$$

If  $l$  is large enough then  $r - cC_0 - 2\pi^2/l^2 > 0$ , so (3.49) has a unique positive solution  $\underline{w}^*$  and hence  $v^{**} \geq \underline{w}^* > 0$  on  $(0, l) \times (0, l)$ . Furthermore, by Theorem 3.2,

$$(3.50) \quad (1/l^2) \int_0^l \int_0^l \underline{w}^*(x, y) dy dx \rightarrow [1 - (cC_0/r)]K > 0$$

as  $l \rightarrow \infty$ , so for  $l$  sufficiently large we must have  $V^{**}/l^2 \geq (1/2)[1 - (cC_0/r)]K > 0$ , and hence we must have  $\lim_{l \rightarrow \infty} F(V^{**}) = cC_0$  since  $l^{p-q-2}V^{**} \rightarrow \infty$  as  $l \rightarrow \infty$ . It follows that for any  $\varepsilon > 0$  and  $l$  sufficiently large,  $v^{**}$  is a subsolution to

$$(3.51) \quad \begin{aligned} 0 &= D \left( \frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2} \right) + (r - cC_0 + \varepsilon)w - \frac{rw^2}{K} \text{ on } (0, l) \times (0, l), \\ w(x, y) &= 0 \text{ for } x = 0, l, \quad y = 0, l. \end{aligned}$$

For large  $l$  (3.51) will have a unique positive solution  $\bar{w}_\varepsilon^*$ , and since  $v^{**}$  is a subsolution (and any large constant is a supersolution) we have  $v^{**} \leq \bar{w}_\varepsilon^*$ . By Theorem 3.2,

$$(3.52) \quad \lim_{l \rightarrow \infty} (1/l^2) \int_0^l \int_0^l \bar{w}_\varepsilon^*(x, y) dy dx = K(r - cC_0 + \varepsilon)/r,$$

so using  $\underline{w}^* \leq v^{**} \leq \bar{w}_\varepsilon^*$  and applying (3.50) and (3.52) shows that for any  $\varepsilon > 0$

$$(3.53) \quad \begin{aligned} K[1 - (cC_0/r)] &\leq \liminf_{l \rightarrow \infty} V^{**}/l^2 \\ &\leq \limsup_{l \rightarrow \infty} V^{**}/l^2 \leq K[1 - (cC_0/r) + (\varepsilon/r)]. \end{aligned}$$

Since (3.53) must hold for any  $\varepsilon > 0$  we may conclude  $\lim_{l \rightarrow \infty} V^{**}/l^2 = K[1 - (cC_0/r)]$ . We see that the effect of predation in this scenario is to reduce the average density of the prey, but not so much that the density declines toward zero as patch size increases. *This is essentially the same behavior (even at the quantitative level) as  $l \rightarrow \infty$  that occurs in the case of purely geometric emigration and immigration rates when  $C = C_0 l^2$  and  $r > cC_0$ . The difference is that in the purely geometric case the minimum patch size needed to sustain a prey population is increased by the presence of predators but in the aggregative case the minimum patch size is unaffected by predation.* We shall see next that the geometric and aggregative models have different behavior as  $l \rightarrow \infty$  when  $r < cC_0$ , but both predict that a larger patch may have a smaller population than a smaller patch for some size ranges. Suppose then that  $C = C_0 l^2$ ,  $p - q > 2$ , and  $r < cC_0$ . Suppose that  $\lim_{l \rightarrow \infty} V^{**} \neq 0$ . (Recall that  $V^{**}$  is the total prey and in general  $V^{**} = V^{**}(l)$ .) Then there must exist  $\varepsilon > 0$  and a sequence  $\{l_j\}$  with  $l_j \rightarrow \infty$  as  $j \rightarrow \infty$  such that

$$(3.54) \quad V^{**}(l_j) \geq \varepsilon$$

for each  $j$ . We then would have

$$(3.55) \quad \begin{aligned} F(V^{**}(l_j)) &= \frac{icC_0 l_j^{p-q-2} V^{**}(l_j)}{il_j^{p-q-2} V^{**}(l_j) + e} \\ &\geq \frac{icC_0 \varepsilon l_j^{p-q-2}}{il_j^{p-q-2} \varepsilon + e}. \end{aligned}$$

As  $j \rightarrow \infty$ , the second expression on the right in (3.55) has limit  $cC_0$ , so if  $cC_0 > r$  then for  $j$  sufficiently large we must have  $F(V^{**}(l_j)) > r$ . However,  $v^{**}(l_j)$  must then satisfy (3.40) with  $R - F(Q) = r - F(V^{**}(l_j)) < 0$ . By Theorem 3.1 an equation of the form (3.40) will

admit a positive solution only if  $R - F(Q) - 2\pi^2/l^2 > 0$ . Thus we must have  $v^{**}(l_j) \equiv 0$  for  $j$  sufficiently large and hence  $V^{**}(l_j) = 0$ , contradicting (3.54). It follows that to avoid the contradiction we must have  $\lim_{l \rightarrow \infty} V^{**} = 0$ . Thus we see that if  $r < cC_0$ , the model with predator aggregation and a predator supply that increases proportionally with patch area predicts that the prey population will tend toward zero as the patch size tends toward infinity. Since in the models with aggregation any patch with  $r - 2\pi^2 D/l^2 > 0$  will sustain a prey population, this indicates that a maximum prey population will occur for some finite  $l$  and the population will be smaller on patches of larger size. This is similar to what happens in the purely geometric case but less extreme.

**3.8. Finite predator population with aggregation: Many patches.** The relevant equations are given by (2.15) where  $P_n^*(V_1, \dots, V_N)$  is given by (3.26). (Recall that we assume the time scale for predator aggregation to be much faster than that for prey population dynamics, so the predators are assumed to "track" the prey populations by staying at the pseudoequilibrium defined by (3.26).) Explicitly, we obtain the system

$$(3.56) \quad \frac{\partial v_n}{\partial t} = D \left( \frac{\partial^2 v_n}{\partial x^2} + \frac{\partial^2 v_n}{\partial y^2} \right) + r \left( 1 - \frac{v_n}{k} \right) v_n - \frac{icCV_n l_n^{p-q-4} v_n}{i \sum_{k=1}^N l_k^{p-q-2} V_k + e}$$

for  $0 < x < l_n, 0 < y < l_n, n = 1, \dots, N$ , and with

$$v_n = 0 \text{ for } x = 0, l_n, y = 0, l_n.$$

We observe that the equations are coupled only in the last terms involving the prey populations  $V_k$  on the  $N$  patches. If we write the system in the more abstract form

$$\frac{\partial v_n}{\partial t} = D \left( \frac{\partial^2 v_n}{\partial x^2} + \frac{\partial^2 v_n}{\partial y^2} \right) + F_n(v_n, V_1, \dots, V_N)$$

we observe that increasing  $v_k$  increases  $V_k$  and hence for  $n \neq k$  increases

$$F_n(v_n, V_1, \dots, V_N) = r \left( 1 - \frac{v_n}{K} \right) v_n - \frac{icCl_n^{p-q-4} V_n v_n}{i \sum_{k=1}^N l_k^{p-q-2} V_k + e}$$

Systems with this property are called quasimonotone or cooperative and have a number of special properties; see [9, 13, 20, 25]. The key observation for our purposes is that a quasimonotone, i.e., cooperative, reaction-diffusion system admits the same sort of comparison principle as does a single reaction-diffusion equation (see [9, Chap. 5] or [20, Chap. 1]) so that the methods we have used already to study the single equation (3.35) can also be applied to the system (3.56). (More abstract formulations of the same ideas are discussed in [13] and used in [5] to study a single equation.) If we view the terms on the right of (3.56) as effective growth rates, then it is natural from the biological viewpoint that the system is cooperative, because with a finite predator population predator aggregation will cause the number of predators on the  $k$ th patch to increase as the prey density increases. That will in turn draw predators away from the other patches and hence make them more favorable to the prey. The system (3.56) involves the nonlocal terms  $V_k$  but that does not affect the theory to any great extent. (Compare, for example, the monotone methods used for a competition system with local interactions in [6] with those used in [7] for a related system involving integral terms.) The main point is that we can establish the existence of maximal and minimal equilibria by starting with a super- and subsolution, respectively, for the equilibrium system associated with (3.56). Arguments similar to those used in [1, 2] then imply that if we use a subsolution to

the equilibrium system as initial data for (3.56) it will increase with time, and if we use a supersolution to the equilibrium problem for initial data it will decrease with time, and if the initial subsolution is below the initial supersolution the corresponding solutions of (3.56) will converge to equilibria. We shall see that in fact (3.56) can have only one positive equilibrium; hence, the convergence from above and below of the special solutions constructed with super- and subsolutions as initial data, together with the comparison principle, implies the stability of the (unique) positive equilibrium. In our analysis we shall describe only the appropriate sub- and supersolutions to the equilibrium problem for (3.56) (and give conditions for the existence of the subsolution) and then show the uniqueness of the positive equilibrium for (3.56).

**THEOREM 3.5.** *Suppose that for  $n = 1, \dots, N$  we have  $r - 2\pi^2 D/l_n^2 > 0$ . Then (3.56) has a unique equilibrium  $(v_1^{**}, \dots, v_N^{**})$  which is positive in each component such that any solution  $(v_1, \dots, v_N)$  of (3.56) with  $v_n(x, y, 0) \geq 0, v_n(x, y, 0) \not\equiv 0$  approaches  $(v_1^{**}, \dots, v_N^{**})$  as  $t \rightarrow \infty$ . If  $r - 2\pi^2 D/l_n^2 < 0$  for some  $n$  then for any nonnegative solutions  $(v_1, \dots, v_N)$  of (3.56) we have  $v_n \rightarrow 0$  as  $t \rightarrow \infty$ .*

*Discussion of Theorem 3.5.* By the arguments given immediately prior to the statement of the theorem it suffices to find arbitrarily small subsolutions and arbitrarily large supersolutions to the equilibrium problem for (3.56) and then to show that the equilibrium is unique. We observe that the vector  $(\bar{v}_1, \dots, \bar{v}_N) = (M, \dots, M)$  satisfies

$$0 \geq D \left( \frac{\partial^2 \bar{v}_n}{\partial x^2} + \frac{\partial^2 \bar{v}_n}{\partial y^2} \right) + r \left( 1 - \frac{\bar{v}_n}{K} \right) \bar{v}_n - \frac{icC\bar{V}_n l_n^{p-q-4} \bar{v}_n}{i \sum_{k=1}^N l_k^{p-q-2} \bar{V}_k + e}$$

for all  $n$  provided  $M \geq K$ , so we have immediately our arbitrarily large supersolution to the equilibrium problem for (3.56). Also, if we have  $r - 2\pi^2 D/l_n^2 > 0$  for all  $n$  we may choose  $\phi_n = \sin(\pi x/l_n) \sin(\pi y/l_n)$  (i.e.,  $\phi_n$  is the normalized principal eigenfunction of the Laplace operator  $\partial^2/\partial x^2 + \partial^2/\partial y^2$  with Dirichlet boundary conditions on the  $n$ th patch). Observe that if  $(\underline{v}_1, \dots, \underline{v}_N) = (\varepsilon\phi_1, \dots, \varepsilon\phi_N)$  then

$$\begin{aligned} & D \left( \frac{\partial^2 \underline{v}_n}{\partial x^2} + \frac{\partial^2 \underline{v}_n}{\partial y^2} \right) + r \left( 1 - \frac{\underline{v}_n}{K} \right) \underline{v}_n - \frac{icCl_n^{p-q-4} \underline{V}_n \underline{v}_n}{i \sum_{k=1}^N l_k^{p-q-2} \underline{V}_k + e} \\ & \geq D \left( \frac{\partial^2 \underline{v}_n}{\partial x^2} + \frac{\partial^2 \underline{v}_n}{\partial y^2} \right) + r \underline{v}_n - \left[ \frac{r \underline{v}_n}{K} + \frac{icCl_n^{p-q-4} \underline{V}_n}{e} \right] \underline{v}_n \\ & = \left[ \left( r - \frac{2\pi^2 D}{l_n^2} \right) - \frac{r}{K} \underline{v}_n - \frac{icCl_n^{p-q-4} \underline{V}_n}{e} \right] \underline{v}_n \\ & = \left[ r - \frac{2\pi^2 D}{l_n^2} - \frac{r}{K} \varepsilon \phi_n - \frac{icCl_n^{p-q-4} (\varepsilon \Phi_n)}{e} \right] \underline{v}_n \\ & \geq 0 \end{aligned}$$

if  $\varepsilon > 0$  is sufficiently small. (By  $\Phi_n$  we mean  $\phi_n(x, y)$  integrated over the  $n$ th patch.) Hence, we have an arbitrarily small subsolution to the equilibrium problem for (3.56). Combined with the arbitrarily large supersolution  $(\bar{v}_1, \dots, \bar{v}_N) = (M, \dots, M)$ , the existence of such a subsolution implies via monotonicity the existence of minimal and maximal positive equilibria, denoted  $(\underline{v}_1^{**}, \dots, \underline{v}_N^{**})$  and  $(\bar{v}_1^{**}, \dots, \bar{v}_N^{**})$ , respectively, for (3.56). Also, since the subsolution to the equilibrium problem can be arbitrarily small, any positive solution of (3.56) will lie

above some subsolution to the equilibrium problem. Since solutions to (3.56) with initial data given by  $(\underline{v}_1, \dots, \underline{v}_N)$  must increase toward  $(\underline{v}_1^{**}, \dots, \underline{v}_N^{**})$  (again, by standard monotonicity arguments), it follows that any positive solution to (3.56) is bounded below by a solution which approaches  $(\underline{v}_1^{**}, \dots, \underline{v}_N^{**})$  as  $t \rightarrow \infty$ . Similarly, by comparison with a solution of (3.56) starting at  $(\bar{v}_1, \dots, \bar{v}_N) = (M, \dots, M)$  (with  $M$  large enough), we find that any positive solution to (3.56) is bounded above by a solution which approaches  $(\bar{v}_1^{**}, \dots, \bar{v}_N^{**})$  as  $t \rightarrow \infty$ . If we can show that (3.56) has a unique equilibrium then the above argument implies its stability. We shall show by contradiction that any equilibrium must equal the minimal equilibrium  $(\underline{v}_1^{**}, \dots, \underline{v}_N^{**})$ . The argument is based on eigenvalue comparisons and is patterned after a result of Hess [12]; similar ideas were used to study diffusive logistic equations by Skellam [30] and by the authors in [3, 5]. The first observation is that if  $(v_1^{**}, \dots, v_N^{**})$  is any positive equilibrium for (3.56) then each of the Schrödinger-type eigenvalue problems

$$(3.57) \quad D \left( \frac{\partial^2 \psi}{\partial x^2} + \frac{\partial^2 \psi}{\partial y^2} \right) + \left[ \left( r - \frac{v_n^{**}}{K} \right) - \frac{icCl_n^{p-q-4} V_n^{**}}{i \sum_{k=1}^N l_k^{p-q-2} V_k^{**} + e} \right] \psi = \sigma \psi$$

for  $0 < x < l_n, 0 < y < l_n,$   
 $\psi = 0$  for  $x = 0, l_n, y = 0, l_n$

has principal eigenvalue  $\sigma = 0$  with eigenfunction a multiple of  $v_n^{**}$ . Suppose now that  $(v_1^{**}, \dots, v_N^{**})$  is an equilibrium not equal to  $(\underline{v}_1^{**}, \dots, \underline{v}_N^{**})$ . Since  $(\underline{v}_1^{**}, \dots, \underline{v}_N^{**})$  is minimal, we must have  $v_n^{**} \geq \underline{v}_n^{**}$  for all  $n$  and  $v_n^{**} > \underline{v}_n^{**}$  for some  $n$ . Thus,

$$(3.58) \quad \sum_{k=1}^N l_k^{p-q-2} V_k^{**} < \sum_{k=1}^N l_k^{p-q-2} \underline{V}_k^{**}.$$

We next show that for some  $n$  we must have

$$(3.59) \quad \frac{icCl_n^{p-q-4} \underline{V}_n^{**}}{i \sum_{k=1}^N l_k^{p-q-2} \underline{V}_k^{**} + e} < \frac{icCl_n^{p-q-4} V_n^{**}}{i \sum_{k=1}^N l_k^{p-q-2} V_k^{**} + e}.$$

Suppose (3.59) fails for all  $n$ . Summing over  $n$  then yields

$$(3.60) \quad \frac{cC \left( i \sum_{n=1}^N l_n^{p-q-2} \underline{V}_n^{**} \right)}{\left( i \sum_{k=1}^N l_k^{p-q-2} \underline{V}_k^{**} \right) + e} \geq \frac{cC \left( i \sum_{n=1}^N l_n^{p-q-2} V_n^{**} \right)}{\left( i \sum_{k=1}^N l_k^{p-q-2} V_k^{**} \right) + e}.$$

But the function  $cCx/(x+e)$  is strictly increasing in  $x$ , so (3.60) contradicts (3.58) and hence (3.59) must hold for some  $n$ . Choose an  $n$  for which (3.59) holds. Multiplying (3.59) by  $l_n^{-2}$  and using the result together with the observation  $v_n^{**} \geq \underline{v}_n^{**}$  yields

$$(3.61) \quad r - \frac{v_n^{**}}{K} - \frac{icCl_n^{p-q-4} V_n^{**}}{i \sum_{k=1}^N l_k^{p-q-2} V_k^{**} + e} > r - \frac{v_n^{**}}{K} - \frac{icCl_n^{p-q-4} \underline{V}_n^{**}}{i \sum_{k=1}^N l_k^{p-q-2} \underline{V}_k^{**} + e}.$$

Inequality (3.61) now implies a contradiction via the fact that (3.57) must have principal eigenvalue zero for any equilibrium, and hence for both  $(\underline{v}_1^{**}, \dots, \underline{v}_N^{**})$  and  $(v_1^{**}, \dots, v_N^{**})$ .

The contradiction arises because if we denote the "potentials" in (3.57) by

$$E_n(x, y) = r - \frac{v_n^{**}}{K} - \frac{icCl_n^{p-q-4} V_n^{**}}{i \sum_{k=1}^N l_k^{p-q-2} V_k^{**} + e}$$

and

$$\underline{E}_n(x, y) = r - \frac{v_n^{**}}{K} - \frac{icCl_n^{p-q-4} \underline{V}_n^{**}}{i \sum_{k=1}^N l_k^{p-q-2} \underline{V}_k^{**} + e},$$

we have  $E_n < \underline{E}_n$  by (3.61), but by (3.57) the problems

$$D \left( \frac{\partial^2 \psi}{\partial x^2} + \frac{\partial^2 \psi}{\partial y^2} \right) + E_n \psi = \sigma \psi$$

for  $0 < x < l_n, 0 < y < l_n,$   
 $\psi = 0$  for  $x = 0, l_n, y = 0, l_n$

and

$$D \left( \frac{\partial^2 \psi}{\partial x^2} + \frac{\partial^2 \psi}{\partial y^2} \right) + \underline{E}_n \psi = \sigma \psi$$

for  $0 < x < l_n, 0 < y < l_n,$   
 $\psi = 0$  for  $x = 0, l_n, y = 0, l_n$

must both have principal eigenvalues equal to zero. That is impossible when  $\underline{E}_n > E_n$  by standard eigenvalue comparison results (see for example [6, 8, 24]). It follows that to avoid a contradiction there cannot be any equilibrium for (3.56) which is larger than the minimal equilibrium. Hence the uniqueness of the positive equilibrium is established, and stability follows from the previous discussion.

In the case where  $r - 2\pi^2 D/l_n^2 < 0$  for some  $n$ , we simply observe that  $v_n$  must satisfy

$$\frac{\partial v_n}{\partial t} \leq D \left( \frac{\partial^2 v_n}{\partial x^2} + \frac{\partial^2 v_n}{\partial y^2} \right) + r \left( 1 - \frac{v_n}{K} \right) v_n,$$

so  $v_n$  is a subsolution for the diffusive logistic equation

$$(3.62) \quad \frac{\partial v}{\partial t} = D \left( \frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right) + r \left( 1 - \frac{v}{K} \right) v.$$

Hence, if we take  $v$  to be the solution of (3.62) with  $v(x, y, 0) = v_n(x, y, 0)$  then we have  $v_n \leq v$  for all  $t$  by the standard comparison principle for a single reaction-diffusion equation. However, if  $r - 2\pi^2 D/l_n^2 < 0$  it follows by Theorem 3.1 that  $v \rightarrow 0$  as  $t \rightarrow \infty$ , so we must have  $v_n \rightarrow 0$  as  $t \rightarrow \infty$  also. This concludes our discussion of Theorem 3.5.

We have established that to understand the behavior of (3.56) it suffices to understand how the unique equilibrium  $(v_1^{**}, \dots, v_N^{**})$  behaves as patch sizes vary. We have seen that the minimal patch size is the same as in a situation with no predation. We shall next examine how  $(v_1^{**}, \dots, v_N^{**})$  behaves as the size of some patch (or perhaps all patches) tends toward infinity. As before, the behavior of the system depends on how the predator population  $C$  changes with the scaling of patch size.

In the simplest case all the patches are identical, so that  $l_n = l$  for each  $n$  and the equilibrium of (3.56) is given by  $v_n^{**} = v^{**}$  for  $n = 1, \dots, N$ , where  $v^{**}$  satisfies

$$(3.63) \quad 0 = D \left( \frac{\partial^2 v^{**}}{\partial x^2} + \frac{\partial^2 v^{**}}{\partial y^2} \right) + r \left( 1 - \frac{v^{**}}{K} \right) v^{**} - \frac{icCl^{p-q-4} V^{**} v^{**}}{iNl^{p-q-2} V^{**} + e}$$

for  $0 < x < l, 0 < y < l,$   
 $v^{**} = 0$  for  $x = 0, l, y = 0, l.$

Equation (3.63) is equivalent to the equilibrium equation for the case of a single patch (3.47) if the constants  $C$  and  $e$  in (3.47) are replaced by  $C/N$  and  $e/N$ . If we let  $l \rightarrow \infty$  with  $C$  (the total predator population) held constant then as for a single patch the effect of the predators becomes negligible and  $V^{**}/l^2 \rightarrow K$ , so  $V_n^{**}/l^2 \rightarrow K$  since  $V^{**} = V_n^{**}$ . If the number of predators is proportional to the size of the patches then  $C = C_0 l^2$ , and since the asymptotic behavior for a single patch as  $l \rightarrow \infty$  depends only on  $K, r, c,$  and  $C_0$  in this situation and not on  $e$ , we may replace  $C = C_0 l^2$  with  $C/N = (C_0/N)l^2$  and  $e$  with  $e/N$  and still obtain  $V^{**}/l^2 \rightarrow K[1 - \frac{cC_0}{Nr}]$  as  $l \rightarrow \infty$  if  $r > cC_0/N$  and  $V^{**}/l^2 \rightarrow 0$  as  $l \rightarrow \infty$  if  $r \leq cC_0/N$ . Hence the model with  $N$  identical patches behaves exactly as does the model for a single patch as  $l \rightarrow \infty$  except that the effects of predation are equally divided among the  $N$  patches and thus reduce the effective value of  $C_0$  by a factor of  $1/N$  in the asymptotic analysis.

We now discuss the case where the patches may be of different sizes but the size of one, say the first, is increased toward infinity. If we assume the predator population to be proportional to total patch area we have  $C = C_0(\sum_{k=1}^N l_k^2)$ . To understand the behavior of the equilibrium densities  $V_n^{**}/l_n^2$  in this case we shall need to compare the system equilibrium with equilibria of various equations having the form discussed in Theorem 3.4. We shall estimate our equilibrium  $(v_1^{**}, \dots, v_N^{**})$  for (3.56) by showing that the components must be sub- or supersolutions to equilibrium equations of the sort occurring in "single patch" models as treated in Theorem 3.4. We shall assume  $r - cC_0 > 0$ , but  $r - cC_0$  may be small. We begin with an upper bound for  $v_1^{**}$  and hence for  $V_1^{**}/l_1^2$ . Since

$$\frac{icC_0 \left( \sum_{k=1}^N l_k^2 \right) l_1^{p-q-4} V_1}{i \sum_{k=1}^N l_k^{p-q-2} V_k + e} \geq \frac{icC_0 l_1^{p-q-2} V_1}{il_1^{p-q-2} V_1 + \left[ i \sum_{k=2}^N l_k^{p-q} K + e \right]}$$

we find that  $v_1^{**}$  is a subsolution to the equilibrium problem

$$0 = D \left( \frac{\partial^2 \bar{v}_1^{**}}{\partial x^2} + \frac{\partial^2 \bar{v}_1^{**}}{\partial y^2} \right) + r \left( 1 - \frac{\bar{v}_1^{**}}{K} \right) \bar{v}_1^{**} - \frac{icC_0 l_1^{p-q-2} \bar{v}_1^{**}}{il_1^{p-q-2} \bar{V}_1 + \left[ iK \sum_{k=2}^N l_k^{p-q} + e \right]}$$

for  $0 < x < l_1, 0 < y < l_1,$   
 $\bar{v}_1^{**} = 0$  for  $x = 0, l_1, y = 0, l_1.$

Hence, we have  $v_1^{**} \leq \bar{v}_1^{**}$ . By our analysis of the case of a single patch with predator aggregation and a finite predator supply scaled proportionally to the patch area, we have  $\bar{V}_1^{**}/l_1^2 \rightarrow K[1 - (cC_0/r)]$  as  $l_1 \rightarrow \infty$ . Thus, for  $l_1$  large enough we have for any  $\varepsilon > 0$

$$(3.64) \quad V_1^{**}/l_1^2 \leq K(1 + \varepsilon)[1 - (cC_0/r)].$$

On the other hand, for  $l_1$  large enough we have for any given  $\alpha > 0$

$$\frac{icC_0 \left( \sum_{k=1}^N l_k^2 \right) l_1^{p-q-4}}{i \sum_{k=1}^N l_k^{p-q-2} V_k + e} \leq \frac{icC_0 \left[ 1 + \sum_{k=2}^N (l_k^2/l_1^2) \right] l_1^{p-q-2}}{il_1^{p-q-2} V_1 + e}$$

$$\leq \frac{icC_0(1 + \alpha)l_1^{p-q-2}}{il_1^{p-q-2} V_1 + e},$$

so that  $v_1^{**}$  is a supersolution to

$$0 = D \left( \frac{\partial^2 \underline{v}_1^{**}}{\partial x^2} + \frac{\partial^2 \underline{v}_1^{**}}{\partial y^2} \right) - r \left( 1 - \frac{\underline{v}_1^{**}}{K} \right) \underline{v}_1^{**} - \frac{icC_0 l_1^{p-q-2} (1 + \alpha) \underline{v}_1^{**}}{il_1^{p-q-2} \underline{V}_1 + e}$$

for  $0 < x < l_1, 0 < y < l_1,$   
 $\underline{v}_1^{**} = 0$  for  $x = 0, l_1$  or  $y = 0, l_1.$

Again appealing to the case of a single patch discussed in the preceding section, we have (for  $\alpha$  small enough that  $1 - cC_0(1 + \alpha)/r > 0$ ) the limiting behavior  $\underline{V}_1^{**}/l_1^2 \rightarrow K[1 - cC_0(1 + \alpha)/r]$  as  $l_1 \rightarrow \infty$ , so since  $v_1^{**} \geq \underline{v}_1^{**}$  we have

$$V_1^{**}/l_1^2 \geq K(1 - \beta)[1 - cC_0(1 + \alpha)/r]$$

for arbitrarily small  $\alpha$  and  $\beta$  provided  $l_1$  is sufficiently large. By continuity and the fact that  $\alpha$  and  $\beta$  can be taken to be arbitrarily small we have

$$(3.65) \quad V_1^{**}/l_1^2 \geq K(1 - \gamma)[1 - cC_0/r]$$

for  $l_1$  sufficiently large, where  $\gamma$  is also arbitrarily small. It follows from (3.64), (3.65), and the fact that  $\varepsilon > 0$  and  $\gamma > 0$  are arbitrary that  $\lim_{l_1 \rightarrow \infty} V_1^{**}/l_1^2 = K[1 - cC_0/r]$ . This is the same result as in the case of a single patch and indicates that as far as the largest patch in this scenario is concerned the presence of the other patches is irrelevant if that largest patch is sufficiently large. (If we had assumed  $r < cC_0$  a similar sort of argument would imply  $\lim_{l_1 \rightarrow \infty} V_1^{**}/l_1^2 = 0$ , but we shall not pursue that point further.) We ask next how  $V_n^{**}/l_n^2$  behaves in this scenario as  $l_1 \rightarrow \infty$ . We shall establish a lower bound independent of the quantity  $cC_0$  provided  $l_1$  is sufficiently large. The biological interpretation is that the largest patch in effect draws the predators away from the other patches. (Remember that although we scale the predator population with total area we assume that it is finite. Perhaps it is quite large, if  $l_1$  is large, but it is still finite.) To understand the behavior of  $V_n^{**}/l_n^2$  we again compare  $v_n^{**}$  with the unique solution of an equilibrium problem for which  $v_n^{**}$  is a supersolution. We have for large  $l_1$

$$(3.66) \quad \frac{icC_0 \left( \sum_{k=1}^N l_k^2 \right) l_n^{p-q-4} V_n^{**}}{i \sum_{k=1}^N l_k^{p-q-2} V_k^{**} + e} \leq \frac{icC_0 \left( l_1^2 + \sum_{k=2}^N l_k^2 \right) l_n^{p-q-2} (V_n^{**}/l_n^2)}{il_1^{p-q} (V_1^{**}/l_1^2) + e}$$

For our equilibrium problem we have  $V_n^{**}/l_n^2 \leq K$  and for large  $l_1$  we have  $V_1^{**}/l_1^2 \geq K(1 - \gamma)[1 - cC_0/r]$  with  $\gamma$  arbitrarily small, so  $V_1^{**}/l_1^2$  is bounded below by a positive

constant and hence since  $p - q > 2$  the right side of (3.66) approaches zero as  $l_1 \rightarrow \infty$ . It follows that for any  $\mu_n > 0$  we can choose  $l_1$  large enough that  $v_n^{**}$  is a supersolution to

$$(3.67) \quad 0 = D \left( \frac{\partial^2 v_n^{**}}{\partial x^2} + \frac{\partial^2 v_n^{**}}{\partial y^2} \right) + r \left( 1 - \frac{v_n^{**}}{K} \right) v_n^{**} - \mu_n v_n^{**}$$

for  $0 < x < l_n, 0 < y < l_n,$   
 $v_n^{**} = 0$  for  $x = 0, l_n, y = 0, l_n.$

Thus, for  $l_1$  large,  $v_n^{**} \geq \underline{v}_n^{**}$  where  $\underline{v}_n^{**}$  is the unique positive solution of (3.67). (We require  $\mu_n$  to be small enough that  $\underline{v}_n^{**} > 0$  exists.) Note that this does not depend on  $cC_0$ . How large  $l_1$  must be so that  $v_n^{**}$  is a supersolution to (3.67) for a given  $\mu_n$  will depend on  $cC_0$ , but for any  $\mu_n > 0$  and any  $cC_0$  it will be the case that  $v_n^{**}$  is a supersolution to (3.67) for  $l_1$  sufficiently large. If for each  $n$  we choose  $\mu_n$  so that  $r - \mu_n - 2\pi^2 D/l_n^2 > 0$  we see that for each  $n$  (3.67) has a positive equilibrium  $\underline{v}_n^{**}$  with  $v_n^{**} \geq \underline{v}_n^{**}$ . Hence we have for  $l_1$  large  $V_n^{**}/l_n^2 \geq \underline{V}_n^{**}/l_n^2$ , where the lower bound is independent of  $cC_0$  as long as  $r - cC_0 > 0$ . If  $cC_0$  is close enough to  $r$  that for each  $n$

$$(3.68) \quad K[1 - (cC_0/r)] < \underline{V}_n^{**}/l_n^2,$$

then since  $V_1^{**}/l_1^2 \rightarrow K[1 - (cC_0/r)]$  as  $l_1 \rightarrow \infty$  and  $V_n^{**}/l_n^2 \geq \underline{V}_n^{**}/l_n^2$  for  $l_1$  sufficiently large we may conclude that the average prey density  $V_1^{**}/l_1^2$  on the largest patch is smaller than the average prey density on any other patch if the largest patch is large enough. This shows there are parameter values for which a larger patch may have a lower prey density.

**4. General conclusions.** We have constructed and analyzed several models for spatial aspects of the interactions of a logistically growing prey population and an immigrating/emigrating predator. All of our models assume that the time scale for immigration and emigration of predators is much faster than that for the population dynamics of the prey, and in turn the time scale for the population dynamics of the prey is much faster than that for the population dynamics of the predator. Hence we always assume that the predators do not reproduce but quickly achieve an equilibrium (or pseudoequilibrium) population via immigration and emigration while the prey grow logistically. In the ladybird beetle/aphid system which initially motivated our work, the aphids disperse at short range through a single patch of host plants while the ladybirds fly around and between patches at much longer ranges. Consequently, in our models the predators perceive the environment as a collection of patches, with each patch a continuous habitat for the prey. We consider this development of models at two distinct spatial scales as well as two distinct time scales to be one of the more important aspects of our work. We consider models where the predators immigrate and emigrate at rates which depend only on the patch size and geometry, and also models in which the predator emigration rate decreases with prey density in addition to its geometric dependence on the patch. This second type of model describes a simple form of area-restricted search by the predators. Finally, we consider cases where the predator population is effectively unlimited in the sense that the size of the pool of predators available for immigration is unaffected by the number of predators immigrating to the patches containing the prey, and other cases where the total predator population is finite. In the second case we consider the possibility that the total predator population remains fixed regardless of patch size or the number of patches, and also the possibility that the predator population increases with patch size or numbers. This last scaling hypothesis reflects the idea that as patches become sufficiently large or numerous they must encompass a larger geographic area which would be expected to contain a larger number of predators. The hypothesis of an unlimited predator supply reflects the idea that there is a large source of predators near the prey patches.

Our mathematical modeling and analysis of the scenarios described above leads us to some general conclusions about the behavior of the system as patch size increases. In all cases the models either have a unique positive equilibrium or prey densities tend toward zero asymptotically in time. All of the models which assume that the predator supply is unlimited or that the total predator population is proportional to the total patch area display the phenomenon that for at least some values of the parameters describing prey growth rates, predator immigration and emigration rates, and the impact of predation on the prey, the average population density of the prey at equilibrium will be smaller on sufficiently large patches than on patches of moderate size. This is in sharp contrast with the case of simple KISS models for the prey alone, in which the prey density approaches logistic carrying capacity as patch size approaches infinity. The effect is most pronounced in the cases where the predator immigration and emigration rates depend only on the patch geometry and where the predator population is unlimited. In those cases there is typically a maximum patch size which can sustain a prey population; on larger patches the prey population must become extinct. The effect is somewhat weaker but still apparent in cases with an unlimited predator supply and a predator emigration rate inversely proportional to average prey density. In those situations the equilibrium prey density or even the total prey population typically approaches zero as patch size increases, but there is no maximum patch size. In our models the prey population diffuses through a continuous environment with a hostile exterior so there is always a minimum patch size necessary to sustain a prey population. The minimum patch size is increased when the predator immigration and emigration rates are purely geometric, and the intrinsic rate of increase of the prey population at low densities is decreased. In the cases where the predator emigration rate is inversely proportional to the average prey density the minimal patch size is unaffected by predation, as is the intrinsic growth rate for the prey at low densities. The difference is that in cases where the predator emigration rate increases as prey density decreases the number (and hence the impact) of predators becomes small at low prey densities. Thus, the effects of predation are negligible when the patch is near the minimal size needed to sustain a prey population since then the prey density will be small because of the usual KISS phenomenon of dispersal into the hostile exterior of the patch. Similarly, since the effect of predation will be reduced whenever the prey density is small, the prey population will not be completely driven to extinction and can grow with little interference from predators if it starts at a low enough density. The models in which the predator population is fixed independent of patch size or numbers all indicate, not surprisingly, that the effect of predation becomes negligible as patch size increases toward infinity. The behavior of the models in the intermediate cases, where the predator population is finite but grows proportionally to the total area of the patch or patches, depends in a more delicate way on the various parameters in the system. Again, purely geometric dependence of immigration and emigration rates can lead to an increase in minimal patch size and a decrease in intrinsic growth rate for the prey, while an emigration rate inversely proportional to average prey density does not affect those features of the prey population dynamics. In these scenarios the equilibrium prey density may go toward zero as patch size increases, but the detailed behavior of the prey equilibrium relative to patch size depends in delicate ways on the parameters of the models and may be quite complicated in some cases. In particular, some of the models with purely geometric predator immigration and emigration rates and a total predator population depending on patch size admit parameter values for which moderately small or very large patches can sustain prey populations but very small or moderately large patches cannot. This phenomenon is fairly delicate and it is not clear that it occurs in nature. On the other hand, the phenomenon of "larger patch, smaller prey density" is quite robust, and it seems plausible to us that it might occur in some natural systems involving slowly dispersing prey and rapidly immigrating/emigrating predators. A graph comparing the relationship between patch size and average prey density for our various modeling regimes is given in Figure 1.



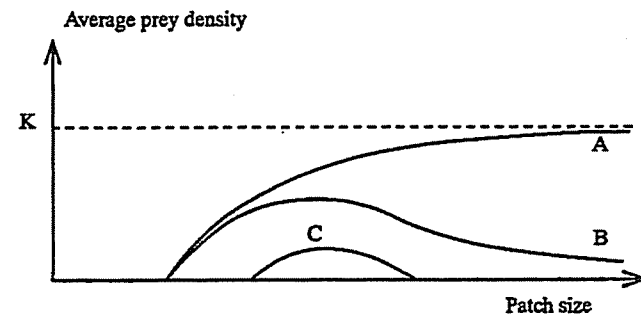


FIG. 1. The graphs indicate schematically how the average prey density on a patch varies as the patch size increases under three different sets of modeling hypotheses. The dashed line indicates the carrying capacity  $K$  for the basic logistic model for the prey. The graph A illustrates the case of a simple diffusive logistic model, i.e., a KISS model, for the prey in the absence of predators. In that case the average prey density approaches the carrying capacity asymptotically as the patch size increases. In the cases illustrated by graphs B and C the number of predators is assumed to increase proportionally with the total area of all of the patches and the intensity of predation and/or the size of the predator population are assumed to be relatively large with respect to the intrinsic growth rate  $r$  of the prey. The graph B illustrates the case where the predators aggregate in response to the prey density as well as patch size and geometry. In that case the minimum patch size required to sustain a prey population is the same as in the absence of predators, but the average prey density approaches zero asymptotically as the patch size increases. The graph C illustrates the case where the predators immigrate to and emigrate from patches as rates depending upon geometric factors only but not on prey density. In that case the minimum patch size needed to sustain a prey population is increased and there is also a maximum patch size that can sustain a prey population. Other sorts of behavior are also possible in the scenarios that include predators. The details of the asymptotic behavior of the average prey density with respect to increasing patch size in those scenarios depend on several of the parameters in the models.

The above conclusions are all based on the predictions of our models. We also have some conclusions about the models themselves. Our approach has been to use models where the predator dynamics were described by a patch model while the prey dynamics within patches were described by a KISS model (i.e., a reaction-diffusion model) with predation. This sort of model is somewhat more difficult to analyze than a pure patch model, but can be treated by methods not too different from those already widely used in reaction-diffusion theory. It gives a much richer description of the effects of patch size in small to moderate size ranges than does a pure patch model and would allow other sorts of analysis which we have not explored here, e.g., consideration of the effects of patch shape or of the degree of hostility of the environment outside the patches. We believe that this modeling approach may have broader applications to systems involving a patchily distributed, slowly dispersing prey and a rapidly dispersing predator. These could perhaps include some types of plant-herbivore systems. We also believe that this sort of model is the most realistic for the aphid/ladybird system which inspired our work. In summary, the problem of modeling populations that interact at a variety of scales is an important issue in ecology, and we hope that this work will encourage further investigation of this topic.

**Acknowledgment.** The authors thank Peter Kareiva for suggesting the topic of this article and for helpful discussions of the ecological motivation for the sort of models we consider.

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