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IDEAL FREE DISPERSAL IN A PREDATOR-PREY SYSTEM

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Abstract. Roughly speaking, a population is said to have an ideal free distribution on a spatial region if all of its members can and do locate themselves in a way that optimizes their fitness, allowing for the effects of crowding. Dispersal strategies that can lead to ideal free distributions of populations that use them have been shown to exist and to be evolutionarily stable in a number of models for a single population. Those models include reaction-diffusion-advection equations and the analogous models using discrete diffusion or nonlocal dispersal described by integrodifferential equations. Furthermore, in the case of reaction-diffusion-advection models and their nonlocal analogues, for environments that are static in time there are strategies that allow populations to achieve an ideal free distribution by using only local information about environmental quality and/or gradients. In this paper, we extend some of these ideas and results to certain Lotka-Volterra type predator-prey systems. In the case of single-species models it is often possible to do the analysis via methods based on monotonicity, but in the predator-prey context those fail so we use methods based on a Lyapunov functional.

1. Introduction.

The evolution or adoption of dispersal strategies has been a topic of interest in evolutionary ecology and foraging theory for decades; see for example [12, 19, 20, 24, 27, 34] among many others. One focus of that interest has been on understanding whether individuals or populations can develop dispersal strategies that are optimal in some sense. Addressing that issue requires some notion of optimality. Two major approaches that have been used to characterize optimal dispersal strategies are game theory and adaptive dynamics. In the game theoretic approach it is typical to define and compute payoffs that arise from using specified strategies, then use those to decide which strategies correspond to Nash equilibria, evolutionarily stable strategies, etc. These properties can be characterized in part by comparing the payoffs of different strategies. The adaptive dynamics approach avoids the direct computation of payoffs by looking directly at the problem of whether a population using one strategy can invade or resist invasion by populations using other strategies. That approach is more feasible than directly calculating payoffs in the case of complex models such as reaction-advection-diffusion equations, where it is difficult to obtain explicit solutions but qualitative properties such as the stability of equilibria can often be determined. An important idea about optimal dispersal or foraging is the ideal free distribution [30, 31]. It is based on the

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idea that if organisms have complete knowledge of their environment and are able to move freely, they will locate themselves to optimize their fitness. The ideal free distribution has been treated mathematically from the viewpoints of game theory [25, 26, 42, 33] and adaptive dynamics [5, 11, 13, 14, 15, 16, 17, 18, 24, 45]. A large fraction of those treat single species models. For single species models, in many cases dispersal strategies that lead to an ideal free distribution have been shown to be optimal in some sense. However, the situation for coevolution of movement in predator-prey models is more complicated; see [28, 29, 42]. Game theoretic treatments have considered predator-prey systems. Vlastimal Křivan has worked extensively in that area; see [38, 39, 40, 41] among others. Křivan et al. provide a game theoretic definition of the ideal free distribution for two species in a two patch environment and show that it is evolutionarily stable in the game theoretic sense in [42]. In this body of work populations are typically assumed to achieve their spatial distribution on a fast timescale that is effectively instantaneous relative to other timescales in the model. Mean field games, which extend classical game theoretic ideas and are motivated by a type of stochastic optimization, were used in [33] to study the ideal free distribution for a predator-prey system. They considered a continuous environment, but in their models movement was assumed to be instantaneous, and they used a game theoretic type of optimization criterion. The background theory of mean field games is somewhat complicated, but detailed discussions including a description of how they can be related to the ideal free distribution are given in [33, 46]. However, other than some basic results obtained in [11], to our knowledge the adaptive dynamics approach to the ideal free distribution has not been applied to predator-prey models. There is a limited amount of work related to the ideal free distribution and/or to comparing dispersal strategies in multispecies models. A treatment of three species competition and the ideal free distribution is given in [44]. It is worth noting that our understanding of the evolution of dispersal in general for interacting populations is much more limited than for single populations. A recent issue of Philosophical Transactions B, (379 (1907), 12 August 2024) was devoted to the theme “Diversity-dependence of dispersal: interspecific interactions determine spatial dynamics.” In the beginning of the table of contents the editors state “Our mechanistic understanding of single species dispersal dynamics has progressed rapidly over the last decade, but the inclusion of interactions between species as drivers of dispersal over ecological and evolutionary time scales is largely missing.” A detailed discussion is given in the introduction [6] of the issue.

The goal of the present study is to apply the adaptive dynamics approach to predator-prey systems and show that in some cases dispersal strategies leading to an ideal free distribution in predator-prey systems are evolutionarily stable. Other approaches to optimal dispersal and/or the ideal free distribution in predator-prey systems are developed in [7, 28, 29, 33, 38, 39, 40, 48, 49, 50, 51, 53, 54], among others. The papers [7, 28, 29, 53] focus on mechanisms that might or might not lead to an ideal free distribution. A numerical approach to the ideal free distribution for reaction-diffusion-advection models for predator prey systems is developed in the papers [51, 54], which include additional references to related topics. We will also consider predator-prey systems in the setting of reaction-diffusion-advection models. Our approach is analytic, in terms of theorems and proofs. We will define a version of the ideal free distribution in the reaction-diffusion-advection context and prove that it is typically evolutionarily stable from the viewpoint of adaptive dynamics.

2. **Preliminaries.**

2.1. **The modeling approach.**

We start with Lotka-Volterra predator-prey models with diffusion and advection on a bounded region $\Omega \subset \mathbb{R}^n$ with boundary $\partial\Omega$ of class $C^{2+\alpha}$ for some $\alpha \in (0,1)$. Our models have the form

$$\begin{aligned} \frac{\partial u}{\partial t} &= Lu + (a(x) - b(x)u - c(x)v)u \\ \frac{\partial v}{\partial t} &= Mv + (-d(x) + e(x)u - f(x)v)v \quad \text{on } (0,\infty) \times \Omega \end{aligned} \tag{1}$$

where $a, b, c, d, e, f \in C^{\alpha}(\overline{\Omega})$, with $a, b, c, d,$ and e positive and f nonnegative.

We will always assume that a, b, c, d, e and f are such the ODE system corresponding to (1) has a positive equilibrium $(u^*(x), v^*(x))$ for all $x \in \overline{\Omega}$. (When it exists such an equilibrium is unique and globally asymptotically stable among positive solutions to the ODE system.)

For our main results we will also want to assume one or the other of the hypotheses in Hypothesis 1:

Hypothesis 1.

$$\begin{aligned} &(Ha) \quad f(x) > 0 \textit{ and for some constant } \alpha > 0,\ \max_{x \in \overline{\Omega}}(|\alpha c(x) - e(x)|^2 - 4\alpha b(x) f(x) \\ &\qquad < 0)), \\ &or \\ &(Hb) \quad f(x) \equiv 0 \textit{ and for some constant } \alpha_0 > 0,\ e(x) = \alpha_0 c(x). \end{aligned} \tag{2}$$

The hypothesis Hb means that the rate of production e of new predators is proportional to the rate c at which predators consume prey, and does not depend on location but only on predator physiology, which is simplistic but not unreasonable. If $e(x) = \alpha_0 c(x)$ then we could choose $\alpha = \alpha_0$ and Ha would be satisfied if b and$f$ are positive everywhere. In general Ha requires roughly that the spatial variation in the amount of prey needed to produce a new predator is not too large relative to the logistic self limitation terms defined by b and f.

The conditions Ha and Hb are needed for technical reasons in deriving our results. It is not clear to us what happens if the conditions Ha and Hb fail. In the case of models in discrete space, we found in [11] that roughly speaking, strategies that produce an ideal free distribution in predator-prey systems are typically locally evolutionarily stable if there is self limitation in the predator equation, which in (1) would mean $f > 0$ as in Ha. In the case where $f \equiv 0$ we were not able to obtain similar results in [11]. We think it is likely that if $f > 0$ and the parameters in the system (1) are restricted so that (1) always has a unique asymptotically stable positive equilibrium for admissible parameters, then strategies that produce an ideal free distribution will be evolutionarily stable. However, to our knowledge, the detailed dynamics of Lotka-Volterra predator-prey systems with dispersal are still not completely understood, even in the case of simple diffusion. For simple diffusion in one space dimension the uniqueness of the positive equilibrium was shown in [43]. In higher dimensions the structure of the set of positive equilibria for diffusive Lotka-Volterra predator-prey models continues to be a topic of active research; see [52, 55]. For that reason we are uncertain about how far our present results can be extended.

The operators L and M describe movements of predators and prey by combinations of diffusion and advection. Those movements are assumed to depend on the local environment but not on the densities of predators or prey. We will use the forms

$$\begin{aligned} Lu &= \nabla \cdot D_u(x)[\nabla u - u\nabla P(x)] \\ Mv &= \nabla \cdot D_v(x)[\nabla v - v\nabla Q(x)]) \quad \text{on } \Omega \end{aligned} \tag{3}$$

with no-flux boundary conditions

$$[\nabla u - u\nabla P(x)] \cdot \vec{n} = [\nabla v - v\nabla Q(x)] \cdot \vec{n} = 0 \quad \text{on } \partial\Omega, \tag{4}$$

in where $\vec{n}$ denotes the outward unit normal vector, $D_u(x)$ and $D_v(x)$ are diffusion rates which are bounded below by positive constants, $D_u(x), D_v(x) \in C^{1+\alpha}(\overline{\Omega})$, and there is directed movement by advection up the gradients of $P(x)$ and $Q(x)$ with $P(x), Q(x) \in C^{2+\alpha}(\overline{\Omega})$.

We want to compare pairs of predator-prey populations that use different movement strategies. The key idea is to interpret the diffusion rates and advection terms in the model as defining dispersal strategies and to compare strategies from the viewpoint of adaptive dynamics via invasion analysis. This approach is used to study the evolution of dispersal in the context of single populations in [5, 13, 14, 15, 16, 17, 18, 27, 34], among many other studies. The general background for this type of modeling is discussed in the section of [24] on evolution. In the framework of adaptive dynamics, the traits that can be expected to evolve are those that allow a small population that has them to invade any population that does not, and allow an established population to resist invasion by populations that have other traits. Traits are interpreted as strategies. Strategies that allow a population to invade populations using other strategies are known as neighborhood invader strategies (NIS). Strategies that allow a population to resist invasion by populations using other strategies are known as evolutionarily stable or evolutionarily steady (ESS). We will show that in the coevolution of dispersal strategies for a specialized predator and its prey, strategies that produce an ideal free distribution are neighborhood invaders and evolutionarily stable.

The ideal free distribution is a theoretical description of how a population subject to crowding effects would distribute itself if all individuals were ideal in that they could sense their reproductive fitness in any given location, allowing for crowding, and were free to locate themselves so as to maximize it [30, 31]. It follows that when at equilibrium, all individuals will have equal fitness, since otherwise some would move to increase their fitness. Also, there would be no net movement, because by moving to another location, an individual would increase crowding there and reduce its fitness, unless individuals just changed places. For population models in continuous time, the reproductive fitness is described by the overall growth rate terms, but to have equal fitness everywhere and no population growth, the fitness everywhere must be zero, so the population distribution should have the population in equilibrium at each point the same as it would be with no movement. Thus, if (u, v) is an equilibrium of (1) corresponding to an ideal free distribution, we should have $(u, v) = (u^*, v^*)$ where $(u^*(x), v^*(x))$ is the equilibrium for the ODE system corresponding to (1) at the point x. Then the movement operators must satisfy

$$Lu^* = Mv^* = 0 \quad \text{on} \quad \overline{\Omega}, \tag{5}$$

and u^* and v^* must satisfy the boundary conditions in (4).

To verify that strategies that produce an ideal free distribution are ESS and NIS versus strategies that are not, we will consider a model where another pair of populations with densities (w, y) that are ecologically identical to those with densities (u, v) are present in the same region Ω. That leads to the system

$$\begin{aligned}
\frac{\partial u}{\partial t} &= Lu + [a(x) - b(x)(u+w) - c(x)(v+y)]u \qquad (6)\\
\frac{\partial v}{\partial t} &= Mv + [-d(x) + e(x)(u+w) - f(x)(v+y)]v\\
\frac{\partial w}{\partial t} &= \tilde{L}w + [a(x) - b(x)(u+w) - c(x)(v+y)]w\\
\frac{\partial y}{\partial t} &= \tilde{M}y + [-d(x) + e(x)(u+w) - f(x)(v+y)]y \quad \text{on } (0,\infty)\times\Omega,
\end{aligned}$$

with operators $\tilde{L}$ and $\tilde{M}$ having the same form and the same type of boundary conditions as as L and M:

$$\begin{aligned}
\tilde{L}w &= \nabla\cdot\tilde{D}_w(x)[\nabla w - w\nabla\tilde{P}(x)] \qquad (7)\\
\tilde{M}y &= \nabla\cdot\tilde{D}_y(x)[\nabla y - y\nabla\tilde{Q}(x)]) \quad \text{on } \Omega
\end{aligned}$$

with no-flux boundary conditions

$$[\nabla w - w\nabla\tilde{P}(x)]\cdot\vec{n} = [\nabla y - y\nabla\tilde{Q}(x)]\cdot\vec{n} = 0 \quad \text{on } \partial\Omega. \qquad (8)$$

Standard local existence theory and regularity theory apply to (6) with boundary conditions (4) and (8). This can be seen by using the change of variables $U = e^{-P}u$, $V = e^{-Q}v$, $W = e^{-\tilde{P}}w$, $Y = e^{-\tilde{Q}}y$ to convert (6) to

$$\begin{aligned}
\frac{\partial U}{\partial t} &= D_u(x)\Delta U + [\nabla D_u(x) + D_u(x)\nabla P]\cdot\nabla U \qquad (9)\\
&\quad + [a(x) - b(x)(e^P U + e^{\tilde{P}}W) - c(x)(e^Q V + e^{\tilde{Q}}Y)]U\\
\frac{\partial V}{\partial t} &= D_v(x)\Delta V + [\nabla D_v(x) + D_v(x)\nabla Q]\cdot\nabla V\\
&\quad + [-d(x) + e(x)(e^P U + e^{\tilde{P}}W) - f(x)(e^Q V + e^{\tilde{Q}}Y)]V\\
\frac{\partial W}{\partial t} &= \tilde{D}_w(x)\Delta W + [\nabla\tilde{D}_w(x) + \tilde{D}_w(x)\nabla\tilde{P}]\cdot\nabla W\\
&\quad + [a(x) - b(x)(e^P U + e^{-\tilde{P}}W) - c(x)(e^Q V + e^{\tilde{Q}}Y)]W\\
\frac{\partial Y}{\partial t} &= \tilde{D}_y(x)\Delta Y + [\nabla\tilde{D}_y(x) + \tilde{D}_y(x)\nabla\tilde{Q}]\cdot\nabla Y\\
&\quad + [-d(x) + e(x)(e^P U + e^{\tilde{P}}W) - f(x)(e^Q V + e^{\tilde{Q}}Y]Y\\
&\text{on } (0,\infty)\times\Omega.
\end{aligned}$$

This change of variables also converts the boundary conditions (4) and (8) to homogeneous Neumann conditions

$$\nabla U\cdot\vec{n} = \nabla V\cdot\vec{n} = \nabla W\cdot\vec{n} = \nabla Y\cdot\vec{n} = 0 \quad \text{on } \partial\Omega. \qquad (10)$$

Returning to the condition (5) for L and M to produce an ideal free distribution and writing it in terms of the variables $U^* = e^{-P}u^*$ and $V^* = e^{-Q}v^*$ we obtain

$$\begin{aligned}
&D_u(x)\Delta U^* + [\nabla D_u(x) + D_u(x)\nabla P]\cdot\nabla U^* = 0 \qquad (11)\\
&D_v(x)\Delta V^* + [\nabla D_v(x) + D_v(x)\nabla Q]\cdot\nabla V^* = 0 \quad \text{on } \Omega.
\end{aligned}$$

with homogeneous Neumann boundary conditions. The differential operators in (9) and (11) with Neumann boundary conditions satisfy a maximum principle and have principal eigenvalues which are simple and have eigenfunctions that can be chosen to be positive; see for example [36]. Observe that $U^* \equiv 1$ and $V^* \equiv 1$ are solutions to (11), so any principal eigenfunctions are constants which can be chosen to be positive. Thus we must have $U^* = e^{-P}u^* = C$ for some constant C, so $P = \ln(u^*) - \ln C$. Similarly, $Q = \ln(v^*) - \ln C$ for some C. Hence we have

$$\nabla P = \frac{\nabla u^*}{u^*} \quad \text{and} \quad \nabla Q = \frac{\nabla v^*}{v^*}. \tag{12}$$

2.2. **Basic properties of the models.** The operators in (9) are in standard form, and the boundary conditions in (10) are classical, so the standard methods and results on reaction-diffusion-advection equations discussed in [3, 4, 9, 10, 35, 36, 37, 47] and in the references in those sources can be applied. In particular, the local existence and uniqueness of classical solutions to the initial value problem for (9), (10) is guaranteed, and the system generates a smooth semiflow on $\{(U, V, W, Y) \in [C^1(\overline{\Omega})]^4 : \nabla U \cdot \vec{n} = \nabla V \cdot \vec{n} = \nabla W \cdot \vec{n} = \nabla Y \cdot \vec{n} = 0 \quad \text{on } \partial\Omega.\}$. Since the map between (U, V, W, Y) and (u, v, w, y) is smooth and invertible, we can work with either the system (9) and (10) or the system (6), (4) and (8) in establishing properties of the semiflow. In particular, we will want to show that the system has a compact global attractor so that we can apply the LaSalle invariance principle, and then find a suitable Lyapunov functional. We will use whichever form of the system is most convenient in any particular calculation. The analysis is very similar to that used in [10] for systems of the form (1) where L and M are multiples of the Laplacian. The only significant difference is that we need to verify that certain types of arguments used in [10] still apply in the case of the more general operators and boundary conditions defined in (3), (4), (7) and (8), which will sometimes require using the forms (9) and (10). We will give a sketch of the analysis to show that such is the case and to provide clarity for the convenience of readers.

In addition to being in the standard form for applying classical results on existence, regularity, etc., the operators in the system (9) and (10) have the correct form to have maximum principles. The full system is not monotone but it is still possible to get some information about solutions by using maximum principles for the single equations making up the system. In the case where $f(x) > 0$ that information is sufficient to imply that the systems (9) and (10) or the system (6), (4) and (8) have global solutions, are dissipative, and have compact attractors. The case of (1) with constant coefficients was treated by related methods in [21]. We have

Lemma 1. *Any solution to (9), (10) for $0 < t < T$ with nonnegative initial data is nonnegative for $t > 0$. Each component U, V, W or Y is either strictly positive or identically 0 on $\overline{\Omega}$ for $0 < t < T$. There are constants $C_0(U)$ and $C_0(W)$ depending on the initial data for U and W respectively, but independent of the other components of the solution and independent of T such that $U \leq C_0(U)$ and $W \leq C_0(W)$ for $0 < t < T$. If $f(x) \geq f_0 > 0$ for all $x \in \overline{\Omega}$ then there are analogous constants constants $C_0(V)$ and $C_0(Y)$ independent of T so that $V \leq C_0(V)$ and $Y \leq C_0(Y)$ for $0 < t < T$. In that case solutions to (9), (10), and hence to (4),(6), and (8) exist globally in t, and the systems are dissipative and have compact global attractors in the subspaces of functions in $[C^1(\overline{\Omega})]^4]$ that satisfy the appropriate boundary conditions (4) and (8) in the case of (6), and (10) in the case of (9).*

Proof. We first describe the case of U in detail. The other cases use similar ideas. Any solution U to the first equation in (9) satisfies an equation of the form

$$\frac{\partial U}{\partial t} = D_u(x)\Delta U + [\nabla D_u(x) + D_u(x)\nabla P] \cdot \nabla U + h(t,x)U \text{ on } (0,T)\times\Omega, \tag{13}$$

with homogeneous Neumann boundary conditions, where $h(t,x)$ is some continuous function of x and t. It follows from the maximum principle and the boundary conditions on U that $U(t,x) \geq 0$ for $0 < t < T$ if $U(0,x) \geq 0$, and either $U > 0$ or $U \equiv 0$ for $0 < t < T$. The same argument applies to V, W and Y. Furthermore, any solution U to the first equation in (9) satisfying the boundary condition (10) is also a subsolution to the equation

$$\frac{\partial Z}{\partial t} = D_u(x)\Delta Z + [\nabla D_u(x) + D_u(x)\nabla P] \cdot \nabla Z + [a(x) - b(x)e^P Z]Z \tag{14}$$

with homogeneous Neumann boundary conditions and the same initial data as U. It follows that $U \leq Z$ for $0 \leq t < T$. There is a positive constant C_1 so that $[a(x) - b(x)e^P C] < 0$ if $C > C_1$, so in that case $\overline{Z} = C$ is a supersolution to (14). If we choose $C_0(U) > max\{C_1, ||U(0,x)||_\infty\}$ then it follows from the comparison principle that $Z(t,x) < \overline{Z} = C_0(U)$, and hence $U \leq C_0(U)$, for $0 \leq t < T$. The case of W is essentially the same.

Suppose now that $f(x) \geq f_0 > 0$ for all $x \in \overline{\Omega}$, and consider the equation (9) for V. We know that $U \leq C_0(U)$ and $W \leq C_0(W)$ for $0 < t < T$, so V is a subsolution to the equation

$$\begin{aligned}\frac{\partial S}{\partial t} &= D_v(x)\Delta S + [\nabla D_v(x) + D_v(x)\nabla Q] \cdot \nabla S \\ &\quad + [-d(x) + e(x)(e^P C_0(U) + e^{\tilde{P}} C_0(W)) - f_0 e^Q S]S\end{aligned} \tag{15}$$

with homogeneous Neumann boundary conditions. If we choose a solution S to (15) with $S(0,x) > V(0,x)$ then $V(t,x) < S(t,x)$ for $0 < t < T$. Since $f(x) \geq f_0 > 0$ and $e^Q \geq e^{minQ} \geq Q_0$ for some $Q_0 > 0$, equation (15) is again a logistic equation with diffusion and advection, and any sufficiently large constant is a supersolution to it. Choosing such a constant $C_0(V)$ so that $C_0(V) > S(0,x)$, we obtain $S(t,x) \leq C_0(V)$ and hence $V(t,x) < C_0(V)$ for $0 < t < T$, with $C_0(V)$ independent of T. The argument for Y is similar.

Note that in the case where $f(x) \geq f_0 > 0$ for all $x \in \overline{\Omega}$ we have pointwise bounds for U, V, W and Y that do not depend on T, so that solutions to (9) and (10) can be extended forward arbitrarily in time and remain uniformly bounded, that is, solutions are global in time. See [3, 4] or the discussion in [10], for example. Once we know that solutions are global we can recall that U is a subsolution to (14) with homogeneous Neumann boundary conditions. It is well known that for logistic equations with diffusion and advection such as (14) all solutions with nonnegative initial data converge to either 0 or to a unique positive equilibrium as $t \to \infty$. If (14) has a positive equilibrium $\theta(x)$ then any positive solution of (14) will satisfy $0 \leq Z \leq 1 + \max\limits_{\overline{\Omega}} \theta(x)$ within finite time, so the component U in the solution of (9), (10) with the same initial data will do the same thing. The same argument applies to W. If there is no positive equilibrium for (14) we can replace $\theta(x)$ with 0. The analogous argument applies to W. Since $\theta(x)$ is bounded there is a constant C_1 such that for any initial data $0 \leq U \leq C_1$ and $0 \leq W \leq C_1$ after some finite time. Thus we have that in finite time the component V of the solution to (9), (10) is a subsolution of

$$\frac{\partial S}{\partial t} = D_v(x)\Delta S + [\nabla D_v(x) + D_v(x)\nabla Q]\cdot\nabla S \\ + [-d(x) + (e(x)(e^P + e^{\tilde{P}})C_2 - f_0 e^Q S]S \tag{16}$$

with homogeneous Neumann boundary conditions. Equation (16) is again a logistic equation with diffusion and advection, so again there is a constant C_3 independent of the initial data such that $0 \le S \le C_3$ after an additional finite time, and hence $0 \le S \le C_3$ in finite time. The same argument applies to Y. It follows that the system (9), (10) is dissipative relative to $[C^(\overline{\Omega})]^4$. It then follows by parabolic regularity that the system is dissipative relative to $[W^{1,p}(\Omega)]^4$ for $1 < p < \infty$, and hence by embedding with respect to $[C^\alpha(\overline{\Omega})]^4$. Using parabolic regularity again, the system is dissipative relative to $[C^{1+\alpha}(\overline{\Omega})]^4$, which embeds compactly in $[C^1(\overline{\Omega})]^4$. It follows that (9), (10) is dissipative in $\{(U,V,W,Y) \in [C^1(\overline{\Omega})]^4 : \nabla U\cdot\vec{n} = \nabla V\cdot\vec{n} = \nabla W\cdot\vec{n} = \nabla Y\cdot\vec{n} = 0 \quad \text{on } \partial\Omega\}$, with a compact global attractor. Changing variables back to (u,v,w,y) shows that the system (6), (4), (8) is dissipative with a compact global attractor in the subspace of $[C^1(\overline{\Omega})]^4$ consisting of functions satisfying the boundary conditions (4) and (8). ☐

The case where $f(x) \ge 0$, but we allow $f(x) = 0$, is more delicate. It uses the estimates on U and W from Lemma 1 but uses methods and results from [2] to bound V and v, and similarly Y and y.

Lemma 2. *The conclusions of Lemma 1 remain valid for $f(x) \ge 0$.*

Proof. The proof consists of verifying the conditions needed for the proof of Theorem 4.1 of [2]. Standard results, for example from [32], imply that the diagonal matrix of differential operators in (9) with Neumann boundary conditions (10) generates an analytic semigroup on $[L^p(\Omega)]^4$ for any $p \in (1,\infty)$. This is one of the things needed to extend the proof of Theorem 4.1 of [2] to our system (9) and (10), or equivalently (6),(4), and (8). We also need to show that solutions to (9) exist globally in time. The estimates for U and W in Lemma 1 are still valid, so for any initial data there are constants $C_0(U)$ and $C_0(W)$ such that $U \le C_0(U)$ and $W \le C_0(W)$ for $0 < t < T$, independent of T, if the solution to (9) exists on that interval. This will allow us to show global existence, will imply dissipativity in $C(\overline{\Omega})$ for U and W, and will be used to obtain another condition that we need, which is the dissipativity of V and Y relative to $L^1(\Omega)$. For $0 < t < T$, V is a subsolution to

$$\frac{\partial S}{\partial t} = D_v(x)\Delta S + [\nabla D_v(x) + D_v(x)\nabla Q]\cdot\nabla S \\ + [-d(x) + e(x)(e^P C_0(U) + e^{\tilde{P}} C_0(W))]S. \tag{17}$$

Since there is a constant C_4 such that $-d(x) + e(x)(e^P C_0(U) + e^{\tilde{P}} C_0(W)) \le C_4$, we have that $\overline{S} = C_5 e^{C_4 t}$ is a supersolution to (17) for $C_5 > 0$, so by choosing C_5 larger than $V(0,x)$ we obtain $V(t,x) \le C_5 e^{C_4 T}$ for $0 < t < T$. A similar estimate holds for Y. Since solutions of (9) remain finite on any interval $0 < t < T$, they exist globally in time. Since solutions are global in time, we have as in Lemma 1 that there is a constant C_6 such that for any initial data we have $0 \le U \le C_6$ and $0 \le W \le C_6$ after some finite time, which implies there is a constant C_7 independent of initial data so that for sufficiently large t, $0 \le u \le C_7$ and $0 \le w \le C_7$.

Let

$$z = k(u+w) + v, \tag{18}$$

where k is large enough that $kc(x) > e$. We have

$$\begin{aligned}
&\frac{\partial z}{\partial t} \\
&= k(Lu + \tilde{L}w) + Mv + k[a - b(u+w) - c(v+y)](u+w) + [-d + e(u+w)v \\
&= k(Lu + \tilde{L}w) + Mv + k[a - b(u+w) - cy + d](u+v) - d[k(u+w) + v] \\
&\quad + (e - ck)(u+w)v \\
&\le k(Lu + \tilde{L}w) + Mv + C_8 - dz,
\end{aligned} \tag{19}$$

where again C_8 is independent of initial conditions. Integrating over Ω and using the no-flux boundary conditions (4) yields

$$\int_\Omega z dt \le C_8|\Omega| - \min_{\overline{\Omega}} d(x) \int z dt. \tag{20}$$

It follows that there exists a constant C_9 such that for sufficiently large t we have $||v||_1 \le C_9$, so that for another constant C_{10}, we have

$$||V||_1 \le C_{10}, \tag{21}$$

with C_9 and C_{10} independent of initial data. The same arguments apply to Y. Finally, we need to verify that the equation for V in (9) yields an estimate of the form of equation (4.9) of [2]. We have $V \ge 0$ and for large t,

$$\frac{\partial V}{\partial t} \le D_v(x)\Delta V + [\nabla D_v(x) + D_v(x)\nabla Q] \cdot \nabla V + [-d(x) + e(x)(e^P + e^{\tilde{P}})C_6)]V \tag{22}$$

with C_6 independent of the initial data. If we multiply by V, then integrate and rearrange terms, then use Young's inequality, we obtain

$$\begin{aligned}
\frac{\partial}{\partial t}\int_\Omega V^2 dx &\le -\int_\Omega [\min_{\overline{\Omega}} D_v(x)|\nabla V|^2 dx + C_{11}V|\nabla V| + C_{12}V^2]dx \qquad (23)\\
&\le -\frac{1}{2}\min_{\overline{\Omega}} D_v(x)\int_\Omega [|\nabla V|^2 + V^2]dx + C_{13}\int_\Omega V^2 dx
\end{aligned}$$

for some constant C_{13} independent of the initial data. This is an inequality of the type shown in equation (4.9) of [2] where $\sigma = 1$ in that inequality. Multiplying (22) by V^3 and integrating similarly leads to an equation analogous to equation (4.13) of [2]. The corresponding estimates hold for Y. The remaining steps in the the proof of Theorem 4.1 of [2] then go through with only a few obvious minor adjustments. □

3. Main results.

The first main result is

Theorem 1. *Suppose that the domain $\overline{\Omega}$, the operators $L, M, \tilde{L}, \tilde{M}$, and the coefficients a, b, c, d, e, f have the forms and properties stated in section 2.1. Suppose further that the hypothesis Ha in (2) is satisfied for some positive constant α. If L and M satisfy the ideal free condition (5) but $\tilde{L}$ and $\tilde{M}$ do not, then $(u^*, v^*, 0, 0)$ is globally asymptotically stable among nonnegative solutions of (6) with u and v positive.*

Remark 1. *The asymptotic stability of $(u^*, v^*, 0, 0)$ implies that when both predators and prey adopt a dispersal strategy that produces an ideal free distribution, they* *can invade a community where neither predators nor prey have a dispersal strategy that produces an ideal free distribution, and can resist invasion by any such predator-prey pair. Therefore, in that case, the strategies that produce an ideal free distribution are evolutionarily stable (ESS) and neighborhood invaders (NIS) relative to those that do not.*

If $\tilde{L}u^* = 0$ *holds but* $\tilde{M}v^* \neq 0$ *, then (9) has equilibria of the form* $(su^*, v^*, (1-s)u^*, 0)$ *for* $s \in [0,1]$*; similarly, there are equilibria* $(u^*, sv^*, 0, (1-s)v^*)$ *if* $\tilde{M}v^* = 0$ *but* $\tilde{L}u^* \neq 0$.

We will prove Theorem 1 via a Lyapunov function argument as follows:

Lemma 3. *Suppose* (u, v, w, y) *is a positive solution to (6) with boundary conditions (4) and (8), hypothesis Ha of (2) is satisfied, and that* L *and* M *satisfy the ideal free condition (5). Let*

$$E(t, u, v, w, y)) = \int_\Omega H(u, v, w, y)dx \tag{24}$$

with

$$H(u, v, w, y) = \alpha[u - u^* - u^* \ln(u/u^*)] + \alpha w + v - v^* \ln(v/v^*) + y. \tag{25}$$

Then

$$\frac{dE}{dt} \leq 0 \tag{26}$$

with strict inequality unless

$$u - u^* + w = v - v^* + y = 0 \tag{27}$$

and

$$\frac{\nabla u}{u} - \frac{\nabla u^*}{u^*} = 0 \;\; \text{if} \;\; u > 0 \quad \text{and} \quad \frac{\nabla v}{v} - \frac{\nabla v^*}{v^*} = 0 \;\; \text{if} \;\; v > 0. \tag{28}$$

Remark: By the strong maximum principle, either $u > 0$ or $u \equiv 0$ on $\overline{\Omega}$, and similarly for v.

Proof. We have

$$\begin{aligned} \frac{dE}{dt} = \int_\Omega \frac{dH}{dt}dx = \int_\Omega \{&\alpha(1 - \frac{u^*}{u})Lu + \alpha\tilde{L}w + (1 - \frac{v^*}{v})Mv + \tilde{M}y \\ &+ \alpha[a - b(u + w) - c(v + y)][(u - u^*) + w] \\ &+ [-d + e(u + w) - f(v + y)][(v - v^*) + y)]\}dx. \end{aligned} \tag{29}$$

The equilibria u^* and v^* satisfy

$$a - bu^* - cv^* = -d + eu^* - fv^* = 0, \tag{30}$$

so

$$\begin{aligned} &\alpha[a - b(u + w) - c(v + y)](u - u^* + w) \\ &= -\alpha[b(u - u^*) + bw - c(v - v^*) + cy](u - u^* + w) \\ &= -\alpha b(u - u^* + w)^2 - \alpha c(u - u^* + w)(v - v^* + y). \end{aligned} \tag{31}$$

Similarly,

$$\begin{aligned} &[-d + e(u + w) - f(v + y)][(v - v^*) + y)](v - v^* + y) \\ &= -f(v - v^* + y)^2 + e(u - u^* + w)(v - v^* + y). \end{aligned} \tag{32}$$

Adding (31) and (32) and choosing α so that the inequality in hypothesis Ha of (2) is satisfied gives

$$\begin{aligned}
&\alpha[a-b(u+w)-c(v+y)](u-u^*+w)]+[-d+e(u+w)-f(v+y)][(v-v^*)+y)]\\
&=-\alpha b(u-u^*+w)^2+(e-\alpha c)(u-u^*+w)(v-v^*+y)-f(v-v^*+y)^2\\
&\leq -\epsilon[(u-u^*+w)^2+(v-v^*+y)^2]
\end{aligned}\tag{33}$$

for some $\epsilon > 0$. (The inequality in Ha implies that the quadratic form in the second line of (33) is negative definite for some choice of α. The meaning of the inequality in Ha is that the predator-prey interaction is not too strong relative to the strength of the logistic self limitation terms in the model.)

The constant multiples of the integrals of $Lu, \tilde{L}w, Mv$ and $\tilde{M}w$ over Ω that are present in (29) are zero because of the no flux boundary conditions (4) and (8). For the remaining terms, we have (again using (4)

$$\begin{aligned}
-\int_\Omega \frac{u^*}{u} Lu\, dx \quad &= -\int_\Omega \frac{u^*}{u}\nabla\cdot D_u[(\nabla u - u\frac{\nabla u^*}{u^*})]dx\\
&=\int_\Omega \nabla\left(\frac{u^*}{u}\right)\cdot D_u[(\nabla u - u\frac{\nabla u^*}{u^*})]dx\\
&=\int_\Omega D_u\frac{(u\nabla u^* - u^*\nabla u)}{u^2}\cdot[(\nabla u - u\frac{\nabla u^*}{u^*})dx]\\
&=-\int_\Omega D_u\left(\frac{u^*}{u^2}\right)|\nabla u - u\frac{\nabla u^*}{u^*}|^2 dx\\
&=-\int_\Omega D_u u^*\left|\frac{\nabla u}{u}-\frac{\nabla u^*}{u^*}\right|^2 dx.
\end{aligned}\tag{34}$$

An analogous calculation shows that

$$-\int_\Omega \frac{v^*}{v} Mv\, dx = -\int_\Omega D_v v^*\left|\frac{\nabla v}{v}-\frac{\nabla v^*}{v^*}\right|^2 dx. \tag{35}$$

Using (33), (34) and (35) in (29) yields

$$\begin{aligned}
\frac{dE}{dt}\leq\quad &-\alpha\int_\Omega D_u u^*\left|\frac{\nabla u}{u}-\frac{\nabla u^*}{u^*}\right|^2 dx-\int_\Omega D_v v^*\left|\frac{\nabla v}{v}-\frac{\nabla v^*}{v^*}\right|^2 dx\\
&-\epsilon\int_\Omega[(u-u^*+w)^2+(v-v^*+y)^2]dx.
\end{aligned}\tag{36}$$

The conclusion of the lemma then follows. □

Proof of Theorem 1:

Proof. Let $X\subset[C^1(\overline{\Omega})]^4$ be the subspace of functions that satisfy boundary conditions (4) and (8). By Lemma 1, the semiflow on the set X^+ of nonnegative functions in X that is generated by (6) has a compact global attractor, so that the LaSalle invariance principle applies; see for example [35]. Specifically, let $\mathcal{M}$ be the subset of X^+ such that $\dfrac{dE(t,u,v,w,y)}{dt}=0$ for $(u,v,w,y)\in\mathcal{M}$, where E is the Lyapunov function defined in (24) and (25), and let $\mathcal{M}'$ be the maximal invariant subset of $\mathcal{M}$. Then for solutions (u,v,w,y) of (6) in X^+, we have $(u,v,w,y)\to\mathcal{M}'$ as $t\to\infty$. By Lemma 3, for $(u,v,w,y)\in\mathcal{M}$ we have $u^*=u+w$ and $v^*=v+y$. Since

$(u^*(x), v^*(x))$ is the positive equilibrium for (1), it follows that in $\mathcal{M}$

$$\frac{\partial u}{\partial t} = Lu, \quad \frac{\partial v}{\partial t} = Mv, \quad \frac{\partial w}{\partial t} = \tilde{L}w, \quad \text{and} \quad \frac{\partial y}{\partial t} = \tilde{M}v. \tag{37}$$

Also, by (28) we have

$$\frac{\nabla u}{u} - \frac{\nabla u^*}{u^*} = 0 \text{ if } u > 0 \quad \text{and} \quad \frac{\nabla v}{v} - \frac{\nabla v^*}{v^*} = 0 \text{ if } v > 0. \tag{38}$$

.

It follows that that for $u > 0$ we have $\nabla \ln u = \nabla \ln u^*$ so that $\nabla \ln(u/u^*) = 0$ and hence u/u^* is independent of x, so $u = C_u(t)u^*$ for some positive function $C_u(t)$. If $u \equiv 0$ then this remains true with $C_u(t) \equiv 0$. Since u is differentiable in t by parabolic regularity, $C_u(t)$ is also differentiable in t. The analogous argument shows that $v = C_v(t)v^*$ with $C_v(t)$ nonnegative and differentiable. By (38) we have $C_u'(t)u^* = \frac{\partial u}{\partial t} = Lu = C_u(t)Lu^*$. The ideal free condition (5) requires $Lu^* = 0$, so $C_u'(t) = 0$ and hence $C_u(t) = C_u$ for some nonnegative constant C_u. It then follows from (27) that $w = (1 - C_u)u^*$, with $1 - C_u$ nonnegative. It follows from (37) that $0 = \frac{\partial[(1-C_u)u^*]}{\partial t} = \frac{\partial w}{\partial t} = \tilde{L}w = (1 - C_u)\tilde{L}u^*$. If $C_u \neq 1$ then it follows that $\tilde{L}u^* = 0$. This contradicts the assumption that $\tilde{L}$ does not produce an ideal free distribution relative to u^*. Thus we must have $C_u = 1$ so that $u = u^*$ and $w = 0$. An exactly parallel argument shows that since $\tilde{M}$ is assumed not to produce an ideal free distribution relative to v^* we must have $y = 0$ and $v = v^*$. Thus $\mathcal{M}' = (u^*, v^*, 0, 0)$, so that $(u^*, v^*, 0, 0)$ is globally asymptotically stable. □

Remark 2. *Since the parallel arguments for the predator and prey are independent of each other, if* $\tilde{L}u^* = 0$ *but* $\tilde{M}v^* \neq 0$ *we can still conclude that that for* $(u, v, w, y) \in \mathcal{M}$ *we have* $(u, v, w, y) \in \{(C_u u^*, v^*, (1 - C_u)u^*, 0) : C_u \in [0, 1]\}$, *and analogously if* $\tilde{L}u^* \neq 0$ *but we have* $\tilde{M}v^* = 0$ *then* $(u, v, w, y) \in \{u^*, C_v v^*, 0, (1 - C_v)v^*) : C_v \in [0, 1]\}$. *In other words, two ideal free predators or two ideal free prey could coexist, but the total predator population (respectively prey population) would still end up at* u^* *(respectively* v^**), and any population that does not use an ideal free dispersal strategy would still be excluded.*

We now consider the case where Hb holds in (2). We have

Lemma 4. *Suppose* (u, v, w, y) *is a positive solution to (6) with boundary conditions (4) and (8), hypothesis Hb of (2) is satisfied, and that* L *and* M *satisfy the ideal free condition (5). Let*

$$E(t, u, v, w, y)) = \int_\Omega H(u, v, w, y)dx \tag{39}$$

with

$$H(u, v, w, y) = \alpha_0[u - u^* - u^* \ln(u/u^*)] + \alpha_0 w + v - v^* \ln(v/v^*) + y. \tag{40}$$

Then

$$\frac{dE}{dt} \leq 0 \tag{41}$$

with strict inequality unless

$$u - u^* + w = 0 \tag{42}$$

and

$$\frac{\nabla u}{u} - \frac{\nabla u^*}{u^*} = 0 \text{ if } u > 0 \quad \text{and} \quad \frac{\nabla v}{v} - \frac{\nabla v^*}{v^*} = 0 \text{ if } v > 0. \tag{43}$$

Proof. If we again define E by (24) and (25) and choose $\alpha = \alpha_0$, then we have

$$\begin{aligned}\frac{dE}{dt} &= \int_\Omega H dx \\ &= \int_\Omega \{\alpha_0(1-\frac{u^*}{u})Lu + \alpha_0\tilde{L}w + (1-\frac{v^*}{v})Mv + \tilde{M}y \\ &\quad + \alpha_0[a-b(u+w)-c(v+y)][(u-u^*)+w] + [-d+e(u+w)][(v-v^*)+y]\}dx.\end{aligned} \tag{44}$$

We can still use (31), and instead of (32) we have

$$[-d+e(u+w)][(v-v^*)+y)](v-v^*+y) = e(u-u^*+w)(v-v^*+y), \tag{45}$$

and we have $a = bu^* + cv^*$ and $eu^* = d$ (since $f \equiv 0$), so (using Hb)

$$\begin{aligned}&\alpha_0[a-b(u+w)-c(v+y)][(u-u^*)+w] + [-d+e(u+w)][(v-v^*)+y] \\ &= -\alpha_0 b(u-u^*+w)^2 + (e-\alpha_0 c)(u-u^*+w)(v-v^*+y) \\ &= -\alpha_0 b(u-u^*+w)^2.\end{aligned} \tag{46}$$

The terms in (44) involving $L, \tilde{L}, M$ and $\tilde{M}$ are the same as those occurring in (29) with $\alpha = \alpha_0$, so we have

$$\frac{dE}{dt} = -\alpha_0 \int_\Omega D_u u^* \left|\frac{\nabla u}{u} - \frac{\nabla u^*}{u^*}\right|^2 dx - \int_\Omega D_v v^* \left|\frac{\nabla v}{v} - \frac{\nabla v^*}{v^*}\right|^2 dx - \alpha_0 b(u-u^*+w)^2. \tag{47}$$

The conclusions of the Lemma then follow from (47). ☐

To state the second main theorem we will need to state another hypothesis and make some definitions.

Hypothesis 2. *(Hc) There is a constant $C_v \in [0,1)$ such that*

$$\frac{\tilde{L}u^*}{cu^*} + (1-C_v)v^* \geq 0 \tag{48}$$

and

$$\tilde{M}\left[\frac{\tilde{L}u^*}{cu^*} + (1-C_v)v^*\right] = 0. \tag{49}$$

Remark 3. *In general the inequality in (48) will not hold, but it will for some operators $\tilde{L}$. Recall that $\tilde{L}u^* = \nabla \cdot \tilde{D}_w(x)[\nabla u^* - u^*\nabla\tilde{Q}(x)]$, so in the case where $\tilde{D}_w(x) = \delta\tilde{D}_0(x)$ for some $\tilde{D}_0(x) > 0$, if $\delta > 0$ is sufficiently small then $\tilde{L}u^*$ will be small enough that the inequality in (48) will hold.*

Definition: If Hc holds, let

$$y^* := \frac{\tilde{L}u^*}{cu^*} + (1-C_v)v^*. \tag{50}$$

To satisfy Hc, we must have $\tilde{M}y^* = 0$. As we will show below, there are choices of $\tilde{Q}$ for which $\tilde{M}y^* = 0$.Thus, Hc will be satisfied sometimes.

Note that unless $\tilde{M}[\frac{\tilde{L}u^*}{cu^*}] = 0$ the equation in (49) can hold for at most one value of C_v. However, if $\tilde{M}[\frac{\tilde{L}u^*}{cu^*}] = 0$ and $C_v \neq 1$, so that $y^* \neq 0$, then the equation (49) implies $\tilde{M}v^* = 0$, which can occur only if $\tilde{M}$ produces an ideal free distribution. Thus, the value of C_v for which (49) is satisfied is unique if $\tilde{M}$ does not produce an ideal free distribution, that is, $\tilde{M}v^* \neq 0$.

In our analysis we will want to consider solutions of the equation

$$\tilde{M}y = 0. \tag{51}$$

Using (7) and setting $Y = e^{-\tilde{Q}}y$ as in (9) in (51) yields

$$\tilde{D}_y(x)\Delta Y + [\nabla \tilde{D}_y(x) + \tilde{D}_y(x)\nabla \tilde{Q}] \cdot \nabla Y = 0 \tag{52}$$

where Y satisfies a Neumann boundary condition. Thus $Y = C_0$ for some constant C_0, so $y = C_0 e^{\tilde{Q}}$.

We will want to impose (49) as part of Hc, so we want

$$\tilde{M}y^* = 0. \tag{53}$$

This is possible for some cases of $\tilde{Q}$. Note that $\tilde{D}_y$ can be any smooth strictly positive function so choosing $\tilde{Q}$ does not completely determine $\tilde{M}$.

If we have

$$\tilde{Q} = \ln(y^*) = \ln(\frac{\tilde{L}u^*}{cu^*} + (1 - C_v)v^*) \tag{54}$$

then y^* satisfies (53). Also, any nonzero solution of (51) is a multiple of y^*.

Theorem 2. *Suppose that the domain $\overline{\Omega}$, the operators $L, M, \tilde{L}, \tilde{M}$, and the coefficients a, b, c, d, e, f have the forms and properties stated in section 2.1. Suppose further that the hypothesis Hb in (2) is satisfied and L and M satisfy the ideal free condition (5) but $\tilde{L}$ and $\tilde{M}$ do not, so that $Lu^* = Mv^* = 0$, $\tilde{L}u^* \neq 0$, and $\tilde{M}v^* \neq 0$.*
i) If Hc is NOT satisfied then $(u^*, v^*, 0, 0)$ is globally asymptotically stable among nonnegative solutions of (6) with u and v positive.
ii) If Hc is satisfied then there is a unique value of $C_v \in [0, 1)$ such that (48) holds. For y^* defined by (50) we have

$$(u, v, w, y) \to \{(u^*, v^*, 0, 0), (0, C_v v^*, u^*, y^*))\} \tag{55}$$

as $t \to \infty$ for solutions of (6) with u, v, w and y positive.

Proof. As in the proof of Theorem 1, let $X \subset [C^1(\overline{\Omega})]^4$ be the subspace of functions that satisfy the boundary conditions (4) and (6). By Lemma 2, under hypothesis Hb the semiflow on the set X^+ of nonnegative functions in X that is generated by (6) has a compact global attractor, so again the LaSalle invariance principle applies. Let $\mathcal{M}$ be the subset of X^+ such that $\frac{\partial E(t,u,v,w,y)}{\partial t} = 0$ for $(u, v, w, y) \in \mathcal{M}$, where E is the Lyapunov function defined in (24) and (25), and let $\mathcal{M}'$ be the maximal invariant subset of $\mathcal{M}$. For solutions to (u, v, w, y) of (6) in X^+, we have $(u, v, w, y) \to \mathcal{M}'$ as $t \to \infty$. By Lemma 4, for $(u, v, w, y) \in \mathcal{M}'$ we have $u^* = u + w$. We then have $-d + eu^* = 0$ under hypothesis Hb since $f \equiv 0$, so by (6) we have

$$\frac{\partial v}{\partial t} = Mv \quad \text{and} \quad \frac{\partial y}{\partial t} = \tilde{M}y. \tag{56}$$

Also, as in the case of Ha, (38) holds on $\mathcal{M}'$ so $u = C_u(t)u^*$ and $v = C_v(t)v^*$. We then have

$$C_v'(t)v^* = \frac{\partial v}{\partial t} = Mv = C_v(t)Mv^* = 0 \tag{57}$$

since M produces an ideal free distribution. Hence $v = C_v v^*$ for some constant $C_v \geq 0$. Also, we have

$$0 = \frac{\partial u^*}{\partial t} = \frac{\partial u}{\partial t} + \frac{\partial w}{\partial t} = Lu + \tilde{L}w + (a - bu^* - c(v + y))(u + w) = Lu + \tilde{L}w + c(v^* - v - y)u^* \tag{58}$$

(since $a - bu^* = cv^*$). Integrating gives

$$0 = \int_\Omega c(v^* - v - y)u^* dx. \tag{59}$$

Integrating the equation for u in (6) and using (59), $u = C_u(t)u^*$, $u + w = u^*$, and the ideal free condition $Lu^* = 0$ gives

$$C_u'(t)\int_\Omega u^* dx = \int_\Omega \frac{\partial u}{\partial t} dx = C_u(t)\int_\Omega Lu^* + c(v^* - v - y)u^* dx = 0 \tag{60}$$

so that $C_u'(t) = 0$ and thus $u = C_u u^*$ and $w = (1 - C_u)u^*$ for some constant $C_u \in [0, 1]$.

Returning to the equation for u in (6) then gives

$$0 = C_u[Lu^* + (a - bu^* - c(v + y))u^*)] = C_u c(v^* - v - y)u^* = C_u c[(1 - C_v)v^* - y]u^*, \tag{61}$$

so either $(1 - C_v)v^* = y$ or $C_u = 0$. If $C_u \neq 0$ then y is constant in time so that by (56) $\tilde{M}y = 0$, so $\tilde{M}(1 - C_v)v^* = 0$. If $C_v \neq 1$ then $\tilde{M}v^* = 0$, which violates the assumption that $\tilde{M}$ does not produce an ideal free distribution, that is, $\tilde{M}v^* \neq 0$. Thus we must have either $C_v = 1$ so that $v = v^*$ and $y = 0$, or $C_v < 1$ and $C_u = 0$. If $v = v^*$ and $y = 0$ then since $u + w = u^*$ and $w = (1 - C_u)u^*$, the equation for w in (6) becomes $0 = (1 - C_u)\tilde{L}u^*$, so by the assumption that $\tilde{L}$ does not produce an ideal free distribution (so that $\tilde{L}u^* \neq 0$) we must have $C_u = 1$, which leads to $(u, v, w, y) = (u^*, v^*, 0, 0)$. The case of $C_u = 0$ (which can only occur if $C_v < 1$) is more complicated.

If $C_u = 0$ then $u \equiv 0$ and $w = u^*$, and we still have $v = C_v v^*$ (with $C_v < 1$) and $a - bu^* = cv^*$, so the equation for w in (6) implies

$$0 = \tilde{L}u^* + c[(1 - C_v)v^* - y]u^*. \tag{62}$$

Differentiating in t then gives

$$0 = -cu^*\frac{\partial y}{\partial t} = -cu^*\tilde{M}y \tag{63}$$

for $(u, v, w, y) \in \mathcal{M}'$ since $u + w = u^*$ and so $-d + e(u + w) = 0$. Thus we have

$$\tilde{M}y = 0. \tag{64}$$

Solving (62) for y gives

$$y = \frac{\tilde{L}u^*}{cu^*} + (1 - C_v)v^* = y^*, \tag{65}$$

where y^* is defined in (50).

If Hc does not hold then (65) yields a contradiction since we must have $y^* \geq 0$. In that case the possibility that $C_u = 0$ is eliminated and we have $\mathcal{M}' = (u^*, v^*, 0, 0)$. If Hc holds then by (48) the right side of (65) is nonnegative. Also, since we assume $\tilde{M}$ does not produce an ideal free distribution for v^*, then since $\tilde{M}v^* \neq 0$, the value of C_v is uniquely determined by (49). Then we can have $C_u = 0$, so $u = 0$, so that $w = u^*$. If $C_u = 0$ there is a unique equilibrium in $\mathcal{M}'$ different from $(u^*, v^*, 0, 0)$ given by $(0, C_v v^*, u^*, y^*)$. □

Remark 4. *Hc requires rather special assumptions about $\tilde{L}$ and $\tilde{M}$ so it would be expected to occur only rarely. Interestingly, when Hc holds, the possible equilibrium different from $(u^*, v^*, 0, 0)$ has the prey population density w equal to u^*, which would correspond to something like an ideal free distribution for the prey population, but for $C_v \neq 0$ the predator population is split into two parts with densities $v = C_v v^*$ and $y = y^*$ that do not add up to v^*. The population with density v still has the property that $Mv = 0$, and the population with density $y = y^*$ has $\tilde{M}y = 0$, so that there is no net movement of those populations at equilibrium. Thus in the possible* *case where Hc holds, the second equilibrium retains some features of the ideal free distribution. The mechanisms that allow Hc to occur and therefore make it possible to have* $w = u^*$ *at equilibrium are not entirely clear to us. Note that since we assume that* $\tilde{L}u^* \neq 0$*, there is a nonzero movement term in the equilibrium equation of the population with density* w *at the evolutionary equilibrium* $(0, C_v v^*, u^*, y^*)$*, which then must be balanced somehow by the population dynamics of the system. It may be that the absence of logistic self limitation on the predators in this case allows them more flexibility so that the predator with density* y *can exploit the population dynamical behavior of the prey by moving correctly, which might be related to why the density* y^* *has the ideal free feature* $\tilde{M}y^* = 0$*.*

We do not know the stability of the equilibrium $(0, C_v v^*, u^*, y^*)$ *in the case where it occurs. We suspect that it may be unstable. If it is, then the equilibrium* $(0, C_v v^*, u^*, y^*)$ *might simply represent the best approximation to an ideal free distribution that is possible if the prey population with density* u *is not present in the system. However, these ideas are speculative and we do not really have a good understanding of the biology that might produce this phenomenon.*

4. Discussion.

Our results show that in a class of Lotka-Volterra type models for a specialist predator and its prey, in the case where there is logistic self-limitation for the predator, dispersal strategies that produce a joint ideal free distribution of predators and prey are always evolutionarily stable and are neighborhood invaders. In that case the equilibrium $(u^*, v^*, 0, 0)$ is globally asymptotically stable, which is consistent with the typical predictions for single species models involving the ideal free distribution. If there is no logistic self limitation of the predator the same is true except in a very special case where the dispersal operators $\tilde{L}$ and $\tilde{M}$ and the equilibrium prey density u^* for the nonspatial model satisfy the particular relations (48) and (49). In that special case there is another equilibrium $(0, C_v v^*, u^*, y^*)$ where y^* is defined in (50), so that the predator with density y, which is not ideal free in the usual sense, and the predator with density v, which is, can coexist. Also, the equilibrium density of prey species w is equal to u^*, the prey density for the nonspatial equilibrium. Thus, although $(0, C_v v^*, u^*, y^*)$ is not an ideal free distribution in the usual sense, it has features that are related to the ideal free distribution. We do not have a clear understanding of the biological mechanisms behind this special case. In a different direction, preliminary calculations suggest that results similar to those obtained in this paper should hold for some models with a functional response, but the conditions on the coefficients would be more complicated. In general, a system with a functional response may have a limit cycle, and it is unclear to us whether these is anything analogous to the ideal free distribution in that cases. However, there are some cases where the nonspatial system for a model with a functional response may have a unique globally attracting positive equilibrium and admit a Lyapunov function for some parameter ranges; see for example [8]. More broadly, results related to ours are obtained by similar methods in [44] for a model of three competing species, which suggests that the general approach should work for other systems that admit appropriate Lyapunov functions. We should note that in [33] the authors consider Rosenzweig-MacArthur models which may have limit cycles and find that optimal dispersal can eliminate them, but they use a different modeling approach than we do and assume instantaneous movement.

As in the case of models for a single population in a static environment, it is possible for the populations in our model to attain an ideal free distribution based on local information, namely the values of the equlibrium densities $u^*(x)$ and $v^*(x)$ predicted by the nonspatial model. However, it is not clear that it is generally feasible for organisms to sense those values, even locally. It may be that in real systems the predators and prey actually use their current observations of their own and each other's local densities and/or the density of the prey's resource, or some simple proxy for fitness based on those. Those sorts of ideas are explored in [28, 29]. However, to capture movement based on population densities would require some sort on nonlinear advection and/or diffusion, for example as in [22, 23], which would complicate the analysis.

Our results require that the system of ordinary differential equations in the nonspatial model has coefficients that are static in time and has a globally stable positive equilibrium. In the case of a single equation, ideas and results on optimal dispersal that are related to the ideal free distribution can be extended to the case of time periodic coefficients (see [17, 18]). We hope to address that case in future work.

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