

A comparison of foraging strategies in a patchy environment¹

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Abstract

In this paper we compare foraging strategies that might be used by predators seeking prey in a patchy environment. The strategies differ in the extent to which predators aggregate in response to prey density. The approach to the comparison is suggested by the idea of evolutionarily stable strategies. A strategy is said to be evolutionarily stable if it cannot be invaded by another strategy. Thus we examine scenarios where a small number of individuals using one strategy are introduced into a situation where a large number of individuals using the other strategy are already present. However, our foraging models do not explicitly incorporate predator population dynamics, so we use net energy uptake as a surrogate for reproductive fitness. In cases where all of the patches visited by predators sustain prey populations, we find that for any pair of strategies one of them will have a higher net energy uptake than the other whether it is the resident or the introduced strain. However, which one is higher will typically depend on the total predator population, which is determined by the resident strain. If the predators leave prey densities high, the more aggregative strain will have the advantage. If the predators reduce prey densities to low levels the less aggregative strain will have the advantage. In cases where one strain of predators aggregates in response to prey density and the other does not, then there might be patches which do not contain prey but do contain (non-aggregating) predators. In those cases, there is the possibility that whichever strategy is used by the introduced strain will yield a higher energy uptake than that used by the resident strain. This suggests that if some patches are empty of prey then aggregative

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and non-aggregative strategies may be able to coexist. © 1999 Elsevier Science Inc. All rights reserved.

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1. Introduction

In this paper we compare some foraging strategies which might be used by predators seeking prey in a patchy environment. The prototype for our study is the ladybird beetle–aphid–fireweed community which arose in the aftermath of the explosion of Mt. St. Helens. Consequently, the strategies for comparison are based on behavioral mechanisms (random search, area restricted search), known to be employed by beetles [1]. The strategies differ in the extent to which predators aggregate in response to prey density. To compare strategies we examine scenarios where a small number of individuals using one strategy are introduced into a system where a large number of individuals using the other strategy are already resident. The comparison is then made by computing the net rates of energy uptake of the resident and introduced strains. Our approach to the comparison is suggested by Maynard Smith's definition of an evolutionarily stable strategy ([2], pp. 10–11) and related ideas in the mathematical theory of persistence (or permanence) in dynamical systems [3,4]. According to Maynard Smith's original definition, an evolutionarily stable strategy is one which is uninvadable by any other available strategy. In the other direction, results from persistence theory give a rigorous formulation of the ecological maxim 'invasibility implies coexistence'; see [4]. However, we do not use the idea of invasibility directly, because that requires a model which incorporates predator population dynamics. The model we use to describe the foraging strategies does not include predator population dynamics. It is based solely on the searching behavior of the predators. We assume that some fixed number of predators are resident in the system and then compare different foraging strategies under that assumption. In principle we could construct a true population dynamical model from the foraging model, but the foraging model is already complex enough that its analysis is somewhat complicated. Hence we examine scenarios of the sort which would occur in an actual invasion, where a few individuals using one strategy are introduced into a system where many individuals using the other strategy are already resident. However, we do not directly model the population dynamics of the competing strains using the different strategies. Instead, we follow a common biological custom and use the net rate of energy uptake per unit time as a surrogate for reproductive fitness; see [5]. We also describe how predator population dynamics could be incorporated into the models, but do not give a detailed analysis.

The models we employ are extensions and generalizations of an established model for predator–prey systems at multiple scales [6]. The work described in Ref. [6] was initially motivated by field observations by Kareiva and his collaborators [7] on the fireweed–aphid–ladybug beetle system which emerged from the ruins of Mt. St. Helens following its 1980 eruption. The differences in the temporal and spatial scales for movement and reproduction in the prey (aphid) and predator (ladybird beetle) species meant that conventional modelling approaches were unsuitable. For instance, the host plants were configured into patches upon which populations of the prey resided. The prey could move freely throughout any patch via diffusion, but were prevented from moving from patch to patch by their minute dispersal scale and the harshness of the landscape between patches. In contrast, the predators had a sufficiently long dispersal scale spatially so as to regard the environment as a collection of patches among which they could immigrate and emigrate at will by flight. Additionally, the time scale for predator dispersal and foraging was very short in comparison with the reproductive time scale of the prey which in turn was somewhat short in comparison with the reproductive time scale of the predator. As a consequence of these considerations, we modelled the system using a hybrid which coupled a diffusion equation for the prey dispersal and population dynamics on each patch with an immigration–emigration model for predator dispersal and foraging among the patches. No population dynamics for the predator were introduced, because we were mainly interested in examining how the different dispersal patterns of the predators affected the spatial distribution of the prey.

To summarize briefly, our models in Ref. [6] envision the environment as a collection of patches, some of which are inhabited by a resource or prey species that views each patch as a continuum through which it diffuses and reproduces. On and surrounding the patches initially is a consumer or predator species that moves freely among the patches by flight. A predator immigrates to a patch and forages and then emigrates to some other patch. This activity occurs on a time scale short enough in comparison to the reproductive scale of the prey species that the predator population quickly reaches an ‘equilibrium’ on the patches and in the air surrounding them in terms of the present density of the prey population. The system is then left undisturbed so as to come to a steady-state in the prey density. Because of the disparity in time scales between predators and prey we followed the derivation of resource competition models in [8,9] and assumed that the predator population on a patch equilibrates immediately in response to the current prey population on that patch. Substituting the resulting predator ‘pseudoequilibria’ into the predation terms of the diffusion equations for the prey led to a system of non-local reaction–diffusion equations the asymptotics of which we then analyzed.

The models in [6] were informed in large part by two sets of assumptions regarding the predators. First, the total predator population could be

regarded as finite or as essentially unlimited, a distinction which controlled whether prey population dynamics on one patch were linked to prey population dynamics on the other patches. For our present purposes we will always assume a finite predator population, because we want to calculate per capita energy uptake rates. It turns out that the size of the predator population affects the average prey density, which in turn affects which strategies are more advantageous. Second, we assumed that the predator species may or may not aggregate in response to average prey density by using area restricted search [1,10,11]. Such aggregative behavior was modelled by letting the emigration rate from host plant patches be inversely proportional to average prey density. Additionally, the predators were always assumed to be sensitive to the geometry of the environment, the canonical expression of which was an emigration rate directly proportional to the perimeter-to-area ratio of a habitat patch. In order to focus on the two predator characteristics just described, predator immigration rates and predator functional response to prey kept the same form throughout our modelling and analysis. (See [6] for further detail.)

The idea of using an emigration rate which is inversely proportional to prey density to model aggregation by area restricted search was introduced in Ref. [1]. The mechanism is simple: if predators quickly leave patches without prey and continue searching but stay for a long time on patches where there are prey, then soon there will be a concentration of predators on the patches where prey are present.

We should note that our goal here is to compare foraging strategies which are available to the predators in our system, namely ladybird beetles. We do not attempt to find a strategy which is globally optimal in the sense of yielding the maximum possible net energy uptake of any conceivable strategy. That is because not all conceivable strategies are feasible for beetles. For example, the ideal free distribution described in [12] is widely used to model the spatial distribution of consumers. However, the ideal free distribution requires that individuals select the best habitat currently available. Such a selection requires an assessment of the quality of available habitats. That is plausible when the species can sample and remember, as in the case of large vertebrates, but does not appear to be consistent with the observed behavior of beetles [1].

Our purpose here is to view aggregation through area restricted search as a foraging strategy. To this end, we extend the model of [6] by allowing the emigration rate to be inversely proportional to a power (between 0 and 1) of average prey density. (We choose this form because it is the simplest one that captures the phenomenon.) In so doing we obtain a continuum of aggregative behaviors or foraging strategies starting with an emigration rate that is independent of average prey density and increasing along a scale of increasing sensitivity to prey density to an emigration rate inversely proportional to

average prey density. We then compute the net energy uptake rates for a resident strain and for an introduced strain using a different strategy and compare them. We expect that the strain with the higher net energy uptake would have a reproductive advantage over the other strain and hence an actual invasion would succeed or fail depending on whether the advantage lay with the resident or the introduced strain. However, we do not attempt to model the dynamics of an invasion *per se*.

Our analysis is as follows. In Section 2 we formulate expressions for the net per capita energy uptake for the introduced and resident predator strains, making use of the extended version of the model in Ref. [6]. The mathematical tractability of these expressions is greatly enhanced by the simplifying assumption that all host plant patches in our system are the same size and shape, although we do not assume that all patches harbor aphid populations. In Section 3, we show how comparisons of net per capita energy uptakes depend on the value of the average prey density. We are thus led to a qualitative and quantitative analysis of this dependence which we perform in Section 4. We conclude in Section 5 with a description of biological conclusions supported by the mathematical analysis.

2. The models

As noted above, the models in Ref. [6] were classified according to two sets of assumptions about the predators in the system. First, the predator supply could be regarded as either (i) effectively unlimited because of a nearby source population or (ii) finite, though possibly proportional to the total area or number of host plant patches. Second, predator emigration from a host plant patch could be taken (i) to depend solely on the geometric characteristics of the patch or (ii) to be inversely proportional to average prey density on the patch. Having an unlimited supply of predators does not allow computation of a net per capita energy uptake. Consequently, in this article, we shall assume throughout that the predator supply is finite, sometimes with the additional assumption that it is proportional to total patch area or number of patches. Our principal purpose here is to compare foraging strategies of different strains of predators, where strategies are differentiated according to predator aggregation. The strategies were modeled in terms of area restricted search. The level of predator aggregation is reflected by the dependence of the emigration rate from the host plant patches on average prey density. We want a more robust treatment than can be provided by just considering the two alternatives in emigration regimes examined in Ref. [6]. As a result, we make a more general assumption about predator emigration that includes the two regimes from [6] as special cases. More specifically, we consider a family E_μ of emigration rates, where $\mu \in [0, 1]$ and

$$E_\mu = \frac{e_\mu}{\ell} \left/ \left(\frac{V}{\ell^2} \right)^\mu \right. . \quad (1)$$

In formula (1), ℓ is the linear dimension of a square patch, while V is the total prey population in the patch (and hence V/ℓ^2 is the average prey density). Consequently, the emigration rate is inversely proportional to the μ th power of average prey density, which for $\mu > 0$ represents a crude form of area restricted search, and is directly proportional to the perimeter to area ratio of the patch. In Eq. (1), the parameter μ indicates the sensitivity of a predator's emigration rate to aggregation, and ranges from emigration that depends only on geometric factors at $\mu = 0$ to having an emigration rate inversely proportional to average prey density at $\mu = 1$. For any fixed μ , the constant of proportionality e_μ may be tuned to accelerate or retard the emigration rate without changing its essential sensitivity to aggregation. (Notice that the units of e_μ necessarily depend on μ .) As μ increases, the predator's tendency to leave a patch with a low average prey density becomes more pronounced while its tendency to leave a patch with a high average prey density becomes less pronounced.

One may well ask why we favor (1) as a means of interpolating between the alternatives for emigration rates considered in [6]. Certainly, there are other possibilities. However, the power law used in (1) provides the simplest mathematical formulation of E_μ so that the tendency of a predator strain to aggregate in response to average prey density becomes more pronounced as μ increases. Any other formulation of E_μ with this property would lead to results which are qualitatively the same as those we shall describe in this paper. Consequently, in the absence of more specific biological information, the formulation of E_μ given in Eq. (1) seems the most reasonable choice.

We extend the model in Ref. [6] so as to incorporate the continuum of possible predator emigration rates given by Eq. (1). As noted, the model envisions a finite collection (say N) of host plant patches, each of which may be inhabited by a prey species that views an individual patch as a continuum through which it diffuses and reproduces. The habitat patches are idealized as squares, with the n th patch having side length ℓ_n . The prey density on the n th patch is denoted by $v_n(x, y, t)$ where (x, y) indicates patch location and t time. On the patches and in the air surrounding them is a population (of total size C) of a predator species that can move freely from one patch to another in search of the prey. For each fixed $\mu \in [0, 1]$, the model is given by a coupled system of $2N$ equations, one for the prey population density and one for the predator population number on each of the N patches. The system is coupled by the immigration and emigration of the predators among the host plant patches, and N of the equations track this movement with $P_n(t)$ denoting the number of predators on the n th patch at time t . Immigration to the n th patch is from the airborne predators and is proportional to patch area. Emigration from the n th patch is given by Eq. (1). Reflecting our concentration on differences in

emigration from habitat patches, the constant of proportionality for immigration, denoted i , is assumed independent of μ . To account for prey population dynamics and dispersal on each patch and for predation, the immigration–emigration equations for the predators are augmented by a diffusive logistic equation with predation for each of the N patches. The parameters in these equations are common ones in diffusive logistic models with predation, namely the diffusivity of the prey (D), intrinsic growth rate of the prey at low densities (r), prey carrying capacity (K), and predation rate (c). Explicitly, the model is given by

$$\begin{aligned} \frac{dP_n}{dt} &= i \left(C - \sum_{k=1}^N P_k \right) \ell_n^2 - \frac{e_\mu P_n}{\ell_n} / \left(\frac{V_n}{\ell_n^2} \right)^\mu, \\ \frac{\partial v_n}{\partial t} &= D \left(\frac{\partial^2 v_n}{\partial x^2} + \frac{\partial^2 v_n}{\partial y^2} \right) + r \left(1 - \frac{v_n}{K} \right) v_n - c \left(\frac{P_n}{\ell_n^2} \right) v_n \\ \text{for } 0 < x < \ell_n, \quad 0 < y < \ell_n, \\ v_n(x, y, t) &= 0 \quad \text{for } x = 0, \ell_n, y = 0, \ell_n, \quad n = 1, \dots, N. \end{aligned} \tag{2}$$

Note that the total prey population V_n in the top equations is the integral of the prey density v_n over the n th patch; i.e. $V_n(t) = \int_0^{\ell_n} \int_0^{\ell_n} v_n(x, y, t) \, dx \, dy$.

A fundamental premise of [6], as noted in Section 1, is that predator dispersal occurs on a sufficiently accelerated time scale to justify assuming that the predator population on any patch effectively reaches equilibrium almost immediately. As a consequence, following along lines used by MacArthur ([8,9]) we assume the P_n adjust to the V_n so quickly that the predator populations stay at whatever equilibrium would be determined by the V_n . The top equations in (2) then yield the “pseudoequilibrium” (P_1^*, \dots, P_N^*) where

$$P_n^* = \frac{iC\ell_n^3(V_n/\ell_n^2)^\mu}{i \sum_{k=1}^N \ell_k^3(V_k/\ell_k^2)^\mu + e_\mu}, \tag{3}$$

so that the long term dynamics of Eq. (3) are determined by

$$\begin{aligned} \frac{\partial v_n}{\partial t} &= D \left(\frac{\partial^2 v_n}{\partial x^2} + \frac{\partial^2 v_n}{\partial y^2} \right) + r \left(1 - \frac{v_n}{K} \right) v_n - \frac{icC(V_n/\ell_n^2)^\mu \ell_n v_n}{(i \sum_{k=1}^N \ell_k^3(V_k/\ell_k^2)^\mu + e_\mu)} \\ \text{for } 0 < x < \ell_n, \quad 0 < y < \ell_n, \quad n = 1, \dots, N, \\ v_n &= 0 \quad \text{for } x = 0, \ell_n; y = 0, \ell_n. \end{aligned} \tag{4}$$

The system (4) is coupled by the dependence of the predator pseudoequilibrium (P_1^*, \dots, P_N^*) on all of the habitat patches. When $\mu = 0$, the effect of predation is to suppress the intrinsic growth rate of the prey (see Ref. [6; section 3.5]). As a result, the prey density may equilibrate to zero on some patches, and some patches with no prey may still contain predators. However, when $\mu > 0$, the coupling is through the non-local terms V_n and in essence the carrying capacities of the prey densities are affected. For $\mu > 0$, predators will only be found

in patches that contain prey. The system is quasimonotone (i.e. cooperative) for $\mu \in (0, 1)$ just as in the case $\mu = 1$, and its asymptotic behavior is qualitatively the same for any $\mu \in (0, 1]$. (A coupled system of differential equations $\vec{y}' = \vec{f}(\vec{y})$ is said to be quasimonotone, i.e. cooperative, if $\partial f_i / \partial y_j > 0$ for $i \neq j$. The key property of such systems is that they are order preserving. These ideas extend to reaction–diffusion systems.) Namely, Eq. (4) has a unique globally attracting equilibrium $(v_1^{**}(\mu), \dots, v_N^{**}(\mu))$ with $v_n^{**}(\mu) > 0$ on $(0, \ell_n) \times (0, \ell_n)$ if $r/D > 2\pi^2/\ell_n^2$ and $v_n^{**}(\mu) \equiv 0$ if $r/D \leq 2\pi^2/\ell_n^2$. The models developed in [6] and used here assume that the population dynamics of the prey (in the absence of predators) are logistic. If that assumption is changed, for example by introducing an Allee effect, then the system (4) may not have a unique attracting equilibrium. In such cases the spatial distribution of the prey might be more complicated or might depend on ‘historical’ factors such as how many prey originally colonized a patch. It is likely that such changes could affect the relative effectiveness of predator foraging strategies, but we will not pursue this point further in the present article.

Our aim now is to formulate an expression for the net per capita energy uptake \mathcal{E}_μ for the μ strain of predators. We compute \mathcal{E}_μ in terms of the available prey. In order that this expression be simple enough for us readily to compare energy uptakes for different strains of predators, we make (for the remainder of this article) the additional assumption that

$$\ell_n = \ell \tag{5}$$

for $n = 1, \dots, N$. In this case, the components of the globally attracting equilibrium to (4) are all equal, so that $v_n^{**}(\mu) = v^{**}(\mu)$, where $v^{**}(\mu) \geq 0$ satisfies

$$0 = D \left(\frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right) + r \left(1 - \frac{v}{K} \right) v - \frac{icC(V/\ell^2)^\mu \ell v}{iN\ell^3(V/\ell^2)^\mu + e_\mu}$$

for $0 < x < \ell, \quad 0 < y < \ell$

$$v = 0 \quad \text{for } x = 0, \ell, \quad y = 0, \ell. \tag{6}$$

The predation term in Eq. (6) becomes

$$\frac{icC_0N\ell^3(V/\ell^2)^\mu v}{iN\ell^3(V/\ell^2)^\mu + e_\mu} \tag{7}$$

when the number of patches is held fixed but the total predator population C is assumed to be proportional to the total habitat area (i.e. $C = C_0N\ell^2$) and becomes

$$\frac{icC_0N\ell(V/\ell^2)^\mu v}{iN\ell^3(V/\ell^2)^\mu + e_\mu} \tag{8}$$

when each patch size is held fixed but the total predator population C is assumed to be proportional to the total number of patches (i.e. $C = C_0N$). We introduce these forms of predation terms because we will later examine how the

predictions of our models are affected as the size or number of patches become large. It turns out that the results depend on how C is scaled.

We shall denote the net per capita energy uptake for the μ strain of predators by \mathcal{E}_μ , and we have

$$\begin{aligned} \mathcal{E}_\mu &= \{ \text{Total resource consumption} \\ &\quad - \text{total energy cost of flying} \\ &\quad - \text{total energy cost of activity within a patch} \} \\ &\quad / \text{total number of predators} \\ &= \frac{\{ \sum_{n=1}^N cP_n(V_n/\ell^2) - \delta(C - \sum_{n=1}^N P_n) - \gamma(\sum_{n=1}^N P_n) \}}{C}, \end{aligned} \tag{9}$$

where δ and γ represent per capita energy costs of flying and patch activity, respectively. Unless otherwise noted, we shall assume throughout this article that

$$\delta > \gamma, \tag{10}$$

reflecting the assumption that flying requires more energy than foraging within a patch.

An assumption implicit in the formulation of (9) is that all patches under consideration support prey populations. By (1), such an assumption is completely general if $\mu > 0$. However, if the predator’s emigration rate is based solely upon the geometric characteristics of potential habitat patches (i.e., $\mu = 0$), it may well be possible that the number of host plant patches (M) exceeds the number occupied by the prey (N). As we shall see, the presence of patches free of prey can change the predictions of the model. We shall treat this case separately later in this section, but for now let us return to Eq. (9). Our aim is to use net per capita energy uptake to compare the foraging strategy of a resident population of one predator strain with that of a second, potentially invading strain, which is introduced in small numbers. We make this comparison at a point at which the resident predator–prey system has reached equilibrium. Assumption (5) tells us that the equilibrium prey population is the same on each patch. So we set $V_n = V^{**} = V$ where $V^{**} = \int_0^\ell \int_0^\ell v^{**} dx dy$ and we have by (3) that

$$\begin{aligned} \mathcal{E}_\mu &= \frac{icN\ell^3(V/\ell^2)^\mu(V/\ell^2)}{iN\ell^3(V/\ell^2)^\mu + e_\mu} - \delta + \frac{(\delta - \gamma)iN\ell^3(V/\ell^2)^\mu}{iN\ell^3(V/\ell^2)^\mu + e_\mu} \\ &= \frac{iN\ell^3}{iN\ell^3 + e_\mu/(V/\ell^2)^\mu} \{ c(V/\ell^2) + (\delta - \gamma) \} - \delta \\ &= \frac{iN\ell^3}{iN\ell^3 + \ell E_\mu} \{ c(V/\ell^2) + \delta - \gamma \} - \delta. \end{aligned} \tag{11}$$

since $E_\mu = (e_\mu/\ell)/(V/\ell^2)^\mu$ by Eq. (1).

When $\mu = 0$ and there are $M - N$ host plant patches unoccupied by prey formula (9) must be adapted to

$$\mathcal{E}_0 = \frac{\left\{ \sum_{n=1}^N cP_n(V_n/\ell_n^2) - \delta(C - \sum_{n=1}^M P_n) - \gamma(\sum_{n=1}^M P_n) \right\}}{C}. \quad (12)$$

In this case, we have

$$P_n = \frac{iC\ell^3}{iM\ell^3 + e_0} \quad (13)$$

for $n = 1, \dots, M$ by assumption (5). Using Eq. (13) and the fact that $V_n = V$ for $n = 1, \dots, N$, Eq. (12) simplifies to

$$\mathcal{E}_0 = \frac{icN\ell^3(V/\ell^2)}{iM\ell^3 + \ell_0 E_0} + (\delta - \gamma) \frac{iM\ell^3}{iM\ell^3 + \ell E_0} - \delta. \quad (14)$$

By virtue of the underlying assumption of the models that predator strains ‘track’ the mean prey density, the formulations of net per capita energy uptake given in Eq. (11) and Eq. (14) do not depend upon whether the predator strain in question is the resident or the invader. In particular, there is no explicit dependence in the formulas on the total population size of either strain of predator. However, it is important to note that the value of V/ℓ^2 is the equilibrium value determined by the interaction of the prey with the resident strain of predator. Consequently, the size C of the population of the resident predator does affect which strain of predator has the higher net per capita energy uptake, while the number of introduced predators does not.

Since the size of the resident predator population affects the relative effectiveness of different foraging strategies, a complete evolutionary treatment of our model system would require a model for the year-to-year population dynamics of the predators. We shall not attempt to give a full evolutionary treatment in the present paper. Our goal is more modest, namely to show how the spatial aspects of foraging strategies can be described and compared. However, we will now give a brief discussion of how population models could be constructed. Recall that our models are based on a system where the predators reproduce only once per year, so that the resident predator population (denoted by C) is assumed to be constant within any given year. Suppose that only a single strain of predators is present and denote the population in year T as C_T . Since the predators reproduce only once per year, it is appropriate to use a discrete time model for C_T . If reproductive success depends only on resource uptake, the model should take the form

$$C_{T+1} = C_T f(\mathcal{E}(V(C_T))),$$

where f is an increasing function of the resource uptake \mathcal{E} . Recall that $V(C)$ is a decreasing function of C and \mathcal{E} is an increasing function of V . If $f(\mathcal{E}(V(0))) > 1$ then the predator population will increase at low densities and can be expected to persist. If $f(\mathcal{E}(V(C))) < 1$ for C large then the model will typically

have a unique and stable equilibrium C^* such that $f(\mathcal{E}(V(C^*))) = 1$. If there are two strains of predators the situation becomes more complicated. To give a full treatment of a situation where there were two predator populations C_1 and C_2 using different strategies we would need to return to the modeling of [6] to determine an average prey density $V(C_1, C_2)$. The predator population model would then take the form

$$C_{1(T+1)} = C_{1T}f_1(\mathcal{E}_1(V(C_{1T}, C_{2T}))),$$

$$C_{2(T+1)} = C_{2T}f_2(\mathcal{E}_2(V(C_{1T}, C_{2T}))).$$

However, even in this case, it should be possible to say something about coexistence from the viewpoint of permanence or uniform persistence (see [3,4]) strictly on the basis of single-strain models. Permanence provides a rigorous theoretical formulation of the idea that ‘invasibility implies coexistence’, and the question of invasibility can be addressed via single species models. If only C_1 is present it should satisfy a single-strain population model

$$C_{1(T+1)} = C_{1T}f_1(\mathcal{E}_1(V(C_{1T}, 0)));$$

similarly, if only C_2 is present then

$$C_{2(T+1)} = C_{2T}f_2(\mathcal{E}_2(V(0, C_{2T}))).$$

If these models have unique equilibria C_1^*, C_2^* then the first strain can invade when the second is resident provided $f_1(\mathcal{E}_1(V(0, C_2^*))) > 1$. Similarly, the second strain could invade when the first is resident if $f_2(\mathcal{E}_2(V(C_1^*, 0))) > 1$. The point of this discussion is that $C_1^*, C_2^*, V(C_1^*, 0)$ and $V(0, C_2^*)$ could all be determined in principle on the basis of single-strain models, which in turn could be formulated directly from the models in [6].

3. Energy comparisons

Let us now assume that for both strains the net per capita energy uptake is given by Eq. (11). Such is the case if both μ_1 and μ_2 are positive or if one of μ_1 and μ_2 is 0 but all host plant patches under consideration are occupied by prey. By (10), it follows from the form of \mathcal{E}_{μ_1} and \mathcal{E}_{μ_2} in Eq. (11) that

$$\mathcal{E}_{\mu_1} > \mathcal{E}_{\mu_2} \iff E_{\mu_1} < E_{\mu_2}, \tag{15}$$

where E_{μ_1} and E_{μ_2} are given by Eq. (1).

Now consider E_{μ_1} and E_{μ_2} . Notice that

$$\frac{E_{\mu_1}}{E_{\mu_2}} = \frac{e_{\mu_1}}{e_{\mu_2}} (V/\ell^2)^{\mu_2 - \mu_1}. \tag{16}$$

If $\mu_1 \neq \mu_2$, we see from Eq. (16) that E_{μ_1}/E_{μ_2} is a strictly monotonic function of V/ℓ^2 . If $\mu_1 \neq \mu_2$, there is a unique numerical value of V/ℓ^2 for which $E_{\mu_1} = E_{\mu_2}$, namely $V/\ell^2 = (e_{\mu_2}/e_{\mu_1})^{1/(\mu_2 - \mu_1)}$. We express this value in terms of the prey

carrying capacity K . (It follows from the maximum principle that $0 \leq V/\ell^2 \leq K$.) We thus define $\alpha = \alpha(\mu_1, \mu_2)$ by

$$E_{\mu_1} = E_{\mu_2} \text{ if } V/\ell^2 = \alpha K, \quad (17)$$

so that $\alpha = [(e_{\mu_2}/e_{\mu_1})^{1/(\mu_2-\mu_1)}]/K$. It follows from Eqs. (16) and (17) that if $\mu_1 > \mu_2$,

$$E_{\mu_1} < E_{\mu_2} \iff V/\ell^2 > \alpha K. \quad (18)$$

Thus, if $\alpha > 1$, the bound on the average prey density implies that $\mathcal{E}_{\mu_2} > \mathcal{E}_{\mu_1}$ independent of V/ℓ^2 . However, if $\alpha < 1$, the value of V/ℓ^2 determines which of \mathcal{E}_{μ_1} and \mathcal{E}_{μ_2} is the larger. Consequently, in this case, we need to examine the dependence on V/ℓ^2 more closely, a task we undertake in the next section.

If now $\mu_2 = 0$ and there are $M - N$ host plant patches unoccupied by prey, the net per capita energy uptake \mathcal{E}_{μ_1} is given by (11) while \mathcal{E}_0 is given by (14), so that

$$\begin{aligned} \mathcal{E}_0 &= \frac{iN\ell^3}{iM\ell^3 + \ell E_0} (cV/\ell^2) + \frac{iM\ell^3}{iM\ell^3 + \ell E_0} (\delta - \gamma) - \delta, \\ \mathcal{E}_{\mu_1} &= \frac{iN\ell^3}{iN\ell^3 + \ell E_{\mu_1}} (cV/\ell^2) + \frac{iN\ell^3}{iN\ell^3 + \ell E_{\mu_1}} (\delta - \gamma) - \delta. \end{aligned} \quad (19)$$

Deciding which of \mathcal{E}_0 and \mathcal{E}_{μ_1} is larger is no longer tantamount to deciding which of E_0 and E_{μ_1} is smaller. For example, for the sake of specificity, suppose $E_0 = E_{\mu_1}$ (which implies $V/\ell^2 = \alpha K = ((e_{\mu_1})/(e_0))^{1/\mu_1}$). Then, comparing the terms in (4) for \mathcal{E}_0 and \mathcal{E}_{μ_1} ,

$$\frac{iN\ell^3}{iM\ell^3 + \ell E_0} (cV/\ell^2) < \frac{iN\ell^3}{iN\ell^3 + \ell E_{\mu_1}} (cV/\ell^2), \quad (20)$$

while

$$\frac{iM\ell^3}{iM\ell^3 + \ell E_0} (\delta - \gamma) > \frac{iN\ell^3}{iN\ell^3 + \ell E_{\mu_1}} (\delta - \gamma), \quad (21)$$

so long as Eq. (10) holds (i.e. $\delta > \gamma$). In Eq. (20), having $M > N$ confers a disadvantage to the strain of predator which incorporates only the geometry of the host plant patches into its emigration regime, as it is better to forage where there is a food supply. However, in Eq. (21), having $M > N$ confers an advantage to the 0 strain as long as there is a higher energy cost associated with flying than with patch activity and movement. Which effect wins out depends on the disparity between M and N and the relative sizes of c and $\delta - \gamma$. For instance, if $M = N + 1$, c is relatively large and $\delta - \gamma$ is relatively small, we expect $\mathcal{E}_{\mu_1} > \mathcal{E}_0$. Indeed, if E_0 continues to equal E_{μ_1} but now $\delta = \gamma$ (so there is no additional energy cost to flying), $\mathcal{E}_{\mu_1} > \mathcal{E}_0$ for any $M > N$ and $c > 0$. If $\mu_1 = 1$, (19) can be rewritten

$$\begin{aligned} \mathcal{E}_0 &= \frac{icN\ell^3\alpha K - (\delta e_0 + \gamma iM\ell^3)z}{z(iM\ell^3 + e_0)}, \\ \mathcal{E}_1 &= \frac{icN\ell^3\alpha K - \gamma iN\ell^3z - \delta e_0z^2}{z(iN\ell^3 + e_0z)}, \end{aligned} \tag{22}$$

where $\alpha K = (e_1)/(e_0)$ and $z = (\alpha K)/(V/\ell^2)$. Then $\mathcal{E}_1 > \mathcal{E}_0$ is equivalent to

$$\begin{aligned} &(icN\ell^3\alpha K - \gamma iN\ell^3z - \delta e_0z^2)(iM\ell^3 + e_0) \\ &> (icN\ell^3\alpha K - [\delta e_0 + \gamma iM\ell^3]z)(iN\ell^3 + e_0z), \end{aligned}$$

which in turn simplifies to

$$\begin{aligned} &(\delta - \gamma)ie_0M\ell^3z^2 + ie_0N\ell^3[c\alpha K - \delta + \gamma]z + iNc\alpha K\ell^3(i(N - M)\ell^3 - e_0) \\ &< 0. \end{aligned} \tag{23}$$

Since $N \leq M$, the last term on the left-hand side of Eq. (23) is negative, so that the corresponding quadratic equation in z has one positive root z^+ and one negative root z^- , as long as $\delta > \gamma$. It follows that in this case,

$$\mathcal{E}_1 > \mathcal{E}_0 \iff 0 < \frac{\alpha K}{V/\ell^2} < z^+. \tag{24}$$

If $N = M$, Eq. (23) reduces to

$$(\delta - \gamma)z^2 + (c\alpha K - \delta + \gamma)z - c\alpha K < 0$$

and it can be seen by inspection that $z^+ = 1$, so that Eq. (24) coincides with Eq. (18) for $\mu_1 = 1$ and $\mu_2 = 0$.

4. Dependence on V/ℓ^2

We saw in the preceding section that in the model system described by Eq. (2) and Eq. (5) if all host plant patches may be viewed as being occupied by prey (effectively that $M = N$) and an exotic strain of predator is introduced into a resident predator–prey system that has reached equilibrium, then whether the resident or the introduced variety has a higher net per capita energy uptake depends solely on the average prey density V/ℓ^2 at the equilibrium. In particular, we require knowledge of the value of V/ℓ^2 in relation to αK , where $\alpha = \alpha(\mu_1, \mu_2)$ is the proportion of K at which the emigration rates E_{μ_1} and E_{μ_2} for the two predator strains are equal. In this section, we shall examine the value of V/ℓ^2 under various assumptions about patch size, number of patches and number of predators. In the case $M = N$ it turns out that whether V/ℓ^2 exceeds αK or not depends only on the number C of resident predators and is independent of which strain of predator is resident. This fact has significant ramifications as to the most effective strategy for a resident strain of predator. Our result here is as follows.

Theorem 4.1. *Suppose that $M = N$ and suppose that $r/D > 2\pi^2/\ell^2$. If $\mu_1 > \mu_2$ and $E_{\mu_1} = E_{\mu_2}$ when $V/\ell^2 = \alpha K$, then*

$$V_{\mu_1}/\ell^2 < V_{\mu_2}/\ell^2 \iff V_{\mu_1}/\ell^2 > \alpha K.$$

Proof: Having $E_{\mu_1} > E_{\mu_2}$ when $V/\ell^2 = \alpha K$ requires that $e_{\mu_2} = e_{\mu_1}(\alpha K)^{\mu_2 - \mu_1}$. Consequently, if v_{μ_1} denotes the solution to Eq. (6) with $\mu = \mu_1$, we have $v_{\mu_1} > 0$ and that

$$\begin{aligned} D\left(\frac{\partial^2 v_{\mu_1}}{\partial x^2} + \frac{\partial^2 v_{\mu_1}}{\partial y^2}\right) &+ \left[r - \frac{icC\ell(V_{\mu_1}/\ell^2)^{\mu_2}}{iN\ell^3(V_{\mu_1}/\ell^2)^{\mu_2} + e_{\mu_2}}\right]v_{\mu_1} - r\frac{v_{\mu_1}^2}{K} \\ &= v_{\mu_1} \left[\frac{icC\ell(V_{\mu_1}/\ell^2)^{\mu_1}}{iN\ell^3(V_{\mu_1}/\ell^2)^{\mu_1} + e_{\mu_1}} - \frac{icC\ell(V_{\mu_1}/\ell^2)^{\mu_2}}{iN\ell^3(V_{\mu_1}/\ell^2)^{\mu_2} + e_{\mu_1}(\alpha K)^{\mu_2 - \mu_1}} \right] \\ &= \frac{e_{\mu_1} icC\ell v_{\mu_1} [(\alpha K)^{\mu_2 - \mu_1} (V_{\mu_1}/\ell^2)^{\mu_1} - (V_{\mu_1}/\ell^2)^{\mu_2}]}{[iN\ell^3(V_{\mu_1}/\ell^2)^{\mu_1} + e_{\mu_1}][iN\ell^3(V_{\mu_1}/\ell^2)^{\mu_2} + e_{\mu_1}(\alpha K)^{\mu_2 - \mu_1}]} \end{aligned} \tag{25}$$

It is easy to see that the sign of the right-hand side of Eq. (25) depends only on the sign of

$$(\alpha K)^{\mu_2 - \mu_1} (V_{\mu_1}/\ell^2)^{\mu_1} - (V_{\mu_1}/\ell^2)^{\mu_2}$$

or equivalently only on the sign of

$$1 - \left(\frac{\alpha K}{V_{\mu_1}/\ell^2}\right)^{\mu_1 - \mu_2} \tag{26}$$

Since $\mu_1 > \mu_2$, (26) is positive when $(\alpha K)/(V_{\mu_1}/\ell^2) < 1$, zero when $(\alpha K)/(V_{\mu_1}/\ell^2) = 1$, and negative when $(\alpha K)/(V_{\mu_1}/\ell^2) > 1$.

It follows that v_{μ_1} is a (strict) subsolution for (6) with $\mu = \mu_2$ if and only if $V_{\mu_1}/\ell^2 > \alpha K$. Moreover, the solution of Eq. (6) is unique and any sufficiently large constant is a super solution. Consequently, if $V_{\mu_1}/\ell^2 > \alpha K$, then $v_{\mu_2} > v_{\mu_1}$ on $(0, \ell) \times (0, \ell)$ by the method of sub- and super solutions. So $V_{\mu_2}/\ell^2 > V_{\mu_1}/\ell^2$. On the other hand, if $V_{\mu_2}/\ell^2 > V_{\mu_1}/\ell^2$ and $V_{\mu_1}/\ell^2 < \alpha K$, the fact that v_{μ_1} is then an upper solution for Eq. (6) with $\mu = \mu_2$ leads to the contradiction that $V_{\mu_2}/\ell^2 < V_{\mu_1}/\ell^2$. Hence if $V_{\mu_2}/\ell^2 > V_{\mu_1}/\ell^2$, $V_{\mu_1}/\ell^2 > \alpha K$. \square

We may use Theorem 4.1 to identify appropriate strategies for different strains of resident predators. To this end we suppose all patches are occupied with prey ($M = N$ and r/D is large enough) and that $\mu_1 > \mu_2$. Let us call the strain of predator associated with μ_1 Strain 1 and that associated with μ_2 Strain 2. Suppose that Strain 2 is the resident and that Strain 1 has the higher net per capita energy uptake. Then it must be the case that $\mathcal{E}_{\mu_1} > \mathcal{E}_{\mu_2}$ which by Eq. (15) is equivalent to $E_{\mu_1} < E_{\mu_2}$. Since $\mu_1 > \mu_2$, $E_{\mu_1} < E_{\mu_2}$ is equivalent by (18) to $V_{\mu_2}/\ell^2 > \alpha K$. In this case $V_{\mu_1}/\ell^2 > \alpha K$ also. Otherwise $V_{\mu_1}/\ell^2 < \alpha K$, and Theorem 4.1 implies $V_{\mu_2}/\ell^2 < V_{\mu_1}/\ell^2 < \alpha K$, a contradiction. So if $V_{\mu_2}/\ell^2 > \alpha K$, so is V_{μ_1}/ℓ^2 . Hence if Strain 1 is the resident predator, $E_{\mu_1} < E_{\mu_2}$ so that $\mathcal{E}_{\mu_1} > \mathcal{E}_{\mu_2}$

and Strain 1 still attains the higher net per capita energy. The reverse holds as well; that is, if in the equilibrium system with Strain 1 as resident Strain 2 attains the higher net per capita energy then Strain 2 would attain the higher net per capita energy as resident. What is suggested is that the strain with the more pronounced tendency to aggregate in response to average prey density (i.e. the one with the larger μ) should aim as resident to keep the average prey density above the point at which its emigration rate matches that of the introduced predator strain having a less pronounced tendency to aggregate in response to average prey density, whereas the strain with the less pronounced tendency to aggregate in response to average prey density (i.e. the one with the smaller μ) should aim as resident to keep the average prey density below the point at which its emigration rate matches that of an invader having a more pronounced tendency to aggregate in response to average prey density.

We now examine the value of V/ℓ^2 at equilibrium when all habitat patches are assumed to be occupied by prey (i.e. $M = N$) under various assumptions on the size and number of patches and on the total number of resident predators. Theorem 4.1 allows us to assume that $\mu_2 > 0$, and as a result, to adapt the results of section 3.8 of [6] to determine the value of V/ℓ^2 in various cases. Consequently, we omit proofs and refer the interested reader to [6]. In that which follows, we assume $\alpha \in (0, 1)$.

If the total number of predators is a fixed constant C , the effect of predation is marginalized if either the size of a patch becomes large ($\ell \rightarrow \infty$) or the number of patches becomes large ($N \rightarrow \infty$). Hence $\lim_{\ell \rightarrow \infty} V/\ell^2$ or $\lim_{N \rightarrow \infty} V/\ell^2$ is K in this case. As a result, if the number of patches or the size of patches becomes large, we should expect the strain of predators with the more pronounced tendency to aggregate in response to average prey density (i.e., the strain with the higher μ) to have the higher net per capita energy uptake, whether it is the resident in a predator–prey system at equilibrium or the introduced strain.

If the total number of predators is proportional to total habitat area (i.e. $C = C_0 N \ell^2$) and the size of patches become large ($\ell \rightarrow \infty$), V/ℓ^2 tends to $(1 - (cC_0)/(r))K$ when $cC_0 < r$ and 0 if $cC_0 \geq r$. (This follows from Eqs. (6) and (7)). If $1 - (cC_0)/(r) > \alpha$, the more aggregative strain of predator always has the higher net per capita energy uptake, whereas if $1 - (cC_0)/(r) < \alpha$, the situation is reversed and the strain with the less pronounced tendency to aggregate in response to average prey density has the higher net per capita energy uptake. Notice that for fixed values of C_0, r and α , $1 - (cC_0)/(r) > \alpha$ occurs if c is smaller and $1 - (cC_0)/(r) < \alpha$ when c is larger. This observation is consistent with the note regrading strategies for resident predator strains which follows Theorem 4.1.

When the total number of predators is proportional to the number of patches (i.e. $C = C_0 N$ as in Eq. (8)) and the number of patches becomes large ($N \rightarrow \infty$), the explicit dependence of the predation term (8) on the size of the

patch (i.e. ℓ) remains. As a consequence, $\lim_{N \rightarrow \infty} V/\ell^2$ depends on the solution to an elliptic partial differential equation. Specifically,

$$\lim_{N \rightarrow \infty} V/\ell^2 = \begin{cases} W/\ell^2 & \text{if } r > \frac{2\pi^2 D}{\ell^2} + \frac{cC_0}{\ell^2}, \\ 0 & \text{if } r \leq \frac{2\pi^2 D}{\ell^2} + \frac{cC_0}{\ell^2}, \end{cases} \tag{27}$$

where $W = \int_0^\ell \int_0^\ell w(x, y) dx dy$ and w is the unique positive solution to

$$\begin{aligned} -D \left(\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2} \right) &= \left(r - \frac{cC_0}{\ell^2} \right) w - \frac{r}{K} w^2 \text{ in } (0, \ell) \times (0, \ell) \\ w &= 0 \text{ on } \partial((0, \ell) \times (0, \ell)) \end{aligned} \tag{28}$$

when one exists (i.e. when $r > (2\pi^2 D)/(\ell^2) + (cC_0)/(\ell^2)$). It is evident from inspection that (8) is an increasing function of N . Consequently, the convergence to a limit in Eq. (27) is decreasing in N if the remaining parameters in the Eq. (6) are held fixed. Hence if $W/\ell^2 > \alpha K$ for some fixed choice of r, c, C_0 and $\ell, V/\ell^2 > \alpha K$ regardless of the number of host plant patches, and the strain of predators with the more pronounced tendency to aggregate in response to average prey density has the higher net per capita energy uptake. On the other hand, if $W/\ell^2 < \alpha K$ for a fixed selection of r, c, C_0 and ℓ , the strain of predators with the less pronounced tendency to aggregate in response to average prey density can be expected to have the higher net per capita energy uptake if there are a large number of host plant patches. Notice also that w (and hence W/ℓ^2) increases with r and decreases with c or C_0 , again consistent with our earlier findings

As the size of the host plant patches decreases, so does the equilibrium density of the prey population. Indeed, $v \equiv 0$ (and hence $V/\ell^2 = 0$) once $\ell \leq \sqrt{(2\pi D)/(r)}$. Moreover, such is the case even without predation pressure on the prey population. In this case, any strain of predator would experience a net energy loss and it is not meaningful to compare net per capita energy uptakes. As ℓ increases just past the threshold value of $\sqrt{(2\pi D)/(r)}$, V/ℓ^2 will necessarily be small and net per capita energy uptakes will remain negative. In fact, it is easy to see from Eq. (11) that $\mathcal{E}_\mu < 0$ so long as

$$V/\ell^2 < \gamma/c.$$

If $\gamma/c < \alpha K$, however, it is reasonable to expect there to be a range of sizes for host plant patches for which a strain of predators with a less pronounced tendency to aggregate in response to average prey density has a positive net per capita energy uptake which is higher than that of a more aggregative strain.

Let us now consider the case where there are host plant patches without prey and one of the predator strains emigrates from host plant patches solely on the basis of geometric cues (i.e. $M > N$ and $\mu_1 > \mu_2 = 0$). In this situation there is, as noted in Section 4, a trade-off between the detrimental effect of a non-aggregative predator strain's foraging on empty patches and the higher energy

cost associated with flying as opposed to that associated with patch activity and movement. This trade off may sometimes lead to a qualitatively different outcome in the interaction of an aggregative predator strain and a non-aggregative predator strain. Namely, whichever strain is introduced into the equilibrium system has the higher net per capita energy uptake. In order to focus on this possibility, we make an additional assumption for the remainder of the section designed to simplify the underlying mathematical analysis and the corresponding biological exposition. Namely, we shall assume that $\mu_1 = 1$; i.e., that the predator strain with the tendency to aggregate in response to average prey density emigrates from host plant patches at a rate inversely proportional to average prey density.

There is an analogue to Theorem 4.1 for the case $M > N$, $\mu_1 = 1$ and $\mu_2 = 0$. Its proof mimics that of Theorem 4.1, so we shall merely state it and leave it to the interested reader to check the proof.

Theorem 4.2. *Suppose that $M > N$ and suppose that $r/D > (2\pi^2)/(\ell^2)$. If $E_1 = E_0$ when $V/\ell^2 = \alpha K$, then*

$$V_1/\ell^2 < V_0/\ell^2 \iff V_1/\ell^2 > \left(\frac{1}{1 + (i\ell^3)/(e_0)(M - N)} \right) \alpha K.$$

Remark. Observe that $E_1 = E_0$ when $V/\ell^2 = \alpha K$ requires that $e_1 = e_0 \alpha K$.

We recall from (24) that the net per capita energy uptake for the μ_1 strain of predator (namely \mathcal{E}_1) exceeds that for the μ_2 strain (namely \mathcal{E}_0) precisely when the equilibrium value of the average prey density exceeds $\alpha K/z^+$, where z^+ denotes the positive root of the quadratic expression on the left hand side of (23), so we have

$$\mathcal{E}_1 > \mathcal{E}_0 \iff V/\ell^2 > \frac{\alpha K}{z^+} \tag{29}$$

while

$$V_0/\ell^2 > V_1/\ell^2 \iff V_1/\ell^2 > \frac{\alpha K}{(1 + (i\ell^3(M - N))/(e_0))}. \tag{30}$$

We noted in Section 3 that if $M = N$, $z^+ = 1$ and it is evident that $1 + (i\ell^3(M - N))/(e_0) = 1$ if $M = N$. When $M > N$, it is not difficult to show that $z^+ < 1 + (i\ell^3(M - N))/(e_0)$, and so if $M > N$,

$$\frac{\alpha K}{(1 + (i\ell^3(M - N))/(e_0))} < \frac{\alpha K}{z^+}. \tag{31}$$

If we now examine Eqs. (29) and (31), there is a contrast with the situation when $M = N$. If $M = N$, $z^+ = 1 = 1 + (i\ell^3(M - N))/(e_0)$, and both of V_{μ_1}/ℓ^2 and V_{μ_2}/ℓ^2 are less than threshold value αK or both exceed αK . This fact

guarantees the conclusion that if the equilibrium system determined by a first strain yields a higher net per capita energy uptake for the second strain, then the second strain would have a higher net per capita energy uptake if it determined the prey equilibrium. If $M > N$ and one of V_1/ℓ^2 and V_0/ℓ^2 is less than $(\alpha K)/((1 + (i\ell^3(M - N))/(e_0)))$, then the other is also. In this case, $V/\ell^2 < (\alpha K)/(z^+)$ for the prey equilibrium determined by the resident predator, whether it is the aggregative or non-aggregative strain that is the resident. Consequently, $\mathcal{E}_0 > \mathcal{E}_1$ whether the non-aggregative strain is the initial resident or the introduced strain. Similarly, $V_1/\ell^2 > (\alpha K)/(z^+)$ implies $V_1/\ell^2 > (\alpha K)/(1 + (i\ell^3(M - N))/(e_0))$, hence $V_0/\ell^2 > V_1/\ell^2 > (\alpha K)/(z^+)$, and the aggregative strain holds the advantage as resident or the introduced strain. But if $V_0/\ell^2 > (\alpha K)/(z^+)$, then $V_1/\ell^2 > (\alpha K)/(1 + (i\ell^3(M - N))/(e_0))$ is as much as may be deduced from Eq. (30). Consequently, we cannot immediately rule out the possibility that

$$\frac{\alpha K}{\left(1 + \frac{i\ell^3(M - N)}{e_0}\right)} < \frac{V_1}{\ell^2} < \frac{\alpha K}{z^+} < \frac{V_0}{\ell^2}. \quad (32)$$

If Eq. (32) obtains and the aggregative predator strain determines the prey equilibrium, $V_1/\ell^2 < (\alpha K)/(z^+)$ means that $\mathcal{E}_0 > \mathcal{E}_1$, whereas if Eq. (32) obtains and the non-aggregative strain determines the prey equilibrium, $V_0/\ell^2 > (\alpha K)/(z^+)$ means that $\mathcal{E}_1 > \mathcal{E}_0$. As a consequence, we would expect that the system displays mutual invasibility, and thus we would expect a prediction of coexistence from population models based on these strategies for resource uptake.

The question remains as to whether the model admits Eq. (32) as a possibility. We assert that the answer is yes. To see that such is the case, assume initially that $M = N$ and that $V_1/\ell^2 > 0$. Choose $\alpha \in (0, 1]$ so that $\alpha K = V_1/\ell^2$. If we now choose $e_0 = e_1/\alpha K$, it follows that $V_0/\ell^2 = \alpha K$ also. When $M = N$, $z^+ = 1$. Hence for $M = N$, $\alpha K = (\alpha K)/(1 + [(i\ell^3(M - N))/e_0]) = (V_1)/(\ell^2) = (\alpha K)/(z^+) = (V_0)/(\ell^2)$. Now let M increase so that $M > N$. The behavior of the predator strain which aggregates in response to average prey density does not change in this event so that V_1/ℓ^2 retains its initial value. However, it is clear from inspection that now $(\alpha K)/(1 + [(i\ell^3(M - N))/e_0]) < (V_1)/\ell^2$. Theorem 4.2 now implies $(V_1)/(\ell^2) < (V_0)/(\ell^2)$. Consequently, let us view $M > N$ and α, e_0 and e_1 as fixed as above, and examine $(\alpha K)/(z^+)$. For $M > N$ the value of z^+ depends on the difference $\delta - \gamma$, whereas V_1 and V_0 do not. (Recall that δ is the constant of proportionality associated with the energy cost of flying and γ the constant of proportionality associated with the energy cost of patch activity and movement.) As a result, we can adjust $\delta - \gamma$ without changing the values of $(\alpha K)/(1 + [(i\ell^3(M - N))/e_0])$, $(V_1)/(\ell^2)$ and $(V_0)/(\ell^2)$. It is a straightforward exercise in calculus to show that $\lim_{\delta - \gamma \rightarrow 0^+} z^+ = 1 + (i\ell^3(M - N))/(e_0)$ and that $\lim_{\delta - \gamma \rightarrow +\infty} z^+ = (N)/(M)$. As a result, as the difference $\delta - \gamma$ varies from

0 to $+\infty$, $(\alpha K)/(z^+)$ takes on every value in the interval $((\alpha K)/(1 + [(i\ell^3(M - N))/e_0]), (M)/(N)(\alpha K))$. It follows that there is a range of values of $\delta - \gamma$ for which Eq. (32) holds. It is also of interest to note that $z^+ = 1$ precisely when $\delta - \gamma = (i\ell^3 N \alpha K)/(e_0) = (i\ell^3 N c e_1)/(e_0^2)$, so that $(\alpha K)/(z^+) > \alpha K = V_1/\ell^2$ when $\delta - \gamma > (i\ell^3 N \alpha K)/(e_0)$.

One possible mechanism for the occurrence of Eq. (32) is as follows. If the non-aggregative strain of predator establishes the prey equilibrium, having $M > N$ pulls residents to empty patches, which allows a higher prey density on the non-empty patches, which is an advantage to the aggregative predator strain. On the other hand, if $\delta - \gamma$ is large enough, it may be better to be on an empty patch than it is to fly, which offers an advantage to the non-aggregative strain.

5. Conclusions

We have compared certain foraging strategies for predators that seek prey in an environment consisting of patches of plants which might or might not harbor prey. We have specifically considered a situation where the strategies used by different strains of predators differ in the extent to which predators aggregate in response to prey density. In our models the mechanism for predator aggregation is a version of area restricted search in which the emigration rate of predators from a patch of plants is inversely proportional to a power μ of the average prey density on the patch. Larger values of μ correspond to greater sensitivity to prey density. If $\mu = 0$ the predators ignore prey density and forage solely on the basis of the geometry of the patches of plants. We compared strategies by comparing the net rates of energy uptake of different strains of predators in scenarios where one strain was established as a resident and the other was introduced in small numbers. The choice of these scenarios was suggested by John Maynard Smith's definition (see [2]) of evolutionarily stable strategies as those which cannot be invaded by any competing strategy. Since our foraging models do not include predator population dynamics we used net energy uptake as a surrogate (see [5]).

If the emigration rate for the predator strain is inversely proportional to the zeroth power of average prey density, the strain employs only geometric cues in emigration and thus the strain can be expected to be present on prey habitat patches devoid of prey if there are any such patches. All strains which aggregate in response to average prey density, however, can be expected to be present only on patches occupied by prey. This behavioral difference in predator strains plays an important role in analyzing the model (2). Indeed, the results of our analysis are well described by considering two cases: (i) all habitat patches are occupied by prey and/or both the resident and invading predator strains tend to aggregate in response to average prey density; or (ii)

there are host plant patches which are unoccupied by prey and either the resident or invading predator strain emigrates by using geometric cues alone.

In the first case, we may assume with no loss in generality that the number M of host plant patches is the same as the number N of host plant patches occupied by the prey species. There is a unique threshold value of average prey density at which the emigration rates from host plant patches of both the resident and introduced predator strains are the same. We express this threshold as a multiple αK of the carrying capacity K of the prey. If average prey density is above αK , the strain with the more pronounced tendency to aggregate in response to average prey density emigrates from host plant patches more slowly than the other strain; the situation is reversed when average prey density is less than αK . Which strain achieves a higher net per capita energy uptake depends only on whether the average prey density at equilibrium exceeds the threshold αK or not, and moreover, whether or not the average prey density at equilibrium exceeds αK depends on the predator population C but is independent of which strain is resident and hence determines the equilibrium prey density (Theorem 4.1). If the average prey density at equilibrium exceeds αK , the strain with the more pronounced tendency to aggregate in response to average prey density has the advantage of a higher net per capita energy uptake either as resident or as the introduced strain. The situation is precisely reversed if the average prey density at equilibrium lies below the threshold αK . The maximum principle for elliptic partial differential equations guarantees that the average prey density at equilibrium is less than or equal to K . Consequently, one strategy in this scenario can be superior to a second strategy at all levels of equilibrium prey density only in the case $\alpha > 1$. In this case, the more aggregative strain always emigrates from host plant patches faster and consequently has a lower net per capita energy uptake. On the other hand, if $\alpha < 1$ and a predator strain has the advantage as resident, it has the advantage as the introduced strain also. Moreover, since a higher average prey density at equilibrium favors the more aggregative strain, a lower predation rate c favors the more aggregative strain, all other factors being equal.

If there are unoccupied host plant patches (so that $M > N$) and one of the strains of predator emigrates from host plant patches using geometric cues alone, competing effects come into play. Foraging on empty patches lowers the total resource consumption for a non-aggregative species. However, this detrimental effect may be offset if the disparity between the energy cost of flying and the energy cost of activity on a patch is sufficiently large to proffer an advantage to a non-aggregative strain of predator. These competing effects are reflected in the complexities added to the underlying mathematics of the model (2) when $M > N$. Just as in the case when $M = N$, there is a unique threshold value αK such that the aggregative strain emigrates from host plant patches more slowly than a non-aggregative strain precisely if the average prey density

at equilibrium exceeds αK . In the case $M = N$, if one predator strain determines an equilibrium average prey density greater or less than αK , so does the other. Moreover, if $M = N$, whether the average prey density at equilibrium exceeds αK or not determines which predator strain achieves the higher net per capita energy uptake. If $M > N$, there are again thresholds T_1 and T_2 in terms of average prey density at equilibrium so that if one strain determines an equilibrium average prey density above or below T_1 so does the other strain and so that whether the equilibrium average prey density exceeds T_2 or not determines how the strategies compare. However, if $M > N$, these thresholds T_1 and T_2 no longer necessarily equal αK or each other. In general, $T_1 < T_2$. When the aggregative strain emigrates from host plant patches at a rate inversely proportional to average prey density, $T_1 = (\alpha K)/(1 + (i\ell^3(M - N))/(e_0))$ and $T_2 = \frac{\alpha K}{z^+}$, where z^+ is the positive root of the quadratic of (3.9). The value of z^+ depends on the disparity in energy costs associated with flying and with patch activity as well as $M - N$ and the parameters of (2).

If $M > N$ and the equilibrium average prey density is less than T_1 , the predator strain which emigrates in response to geometric cues alone has the advantage either as resident or as the introduced strain. Consequently, low equilibrium average prey densities favor the non-aggregative predator strain just as in the case when $M = N$. If the aggregative strain of predator is the initial resident and the equilibrium average prey density is high enough (i.e. exceeds T_2), the aggregative strain has a higher net per capita energy uptake than the non-aggregative strain. However, if the non-aggregative strain is the initial resident and determines an equilibrium for Eq. (2) wherein the average prey density exceeds T_2 , we can only conclude that the aggregative strain would determine an average prey density at equilibrium exceeding T_1 . Indeed, we demonstrate that $T_1 < V_a/\ell^2 < T_2 < V_g/\ell^2$ sometimes occurs in the model if the disparity in energy costs for flying and patch activity is high enough, where V_a/ℓ^2 and V_g/ℓ^2 are the average densities at equilibria determined by the aggregative and non-aggregative strain of predator, respectively. In this situation the introduced strain has an advantage over the resident, independent of which strain is using which strategy. This suggests that in population dynamical models based on these strategies for resource uptake the two strains would be likely to display mutual invasibility, which would usually imply co-existence.

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