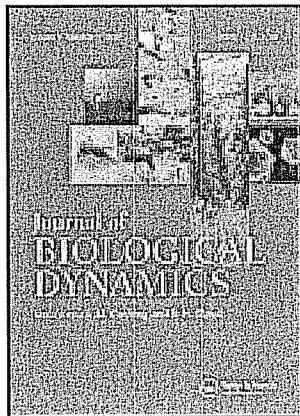


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Journal of Biological Dynamics

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tjbd20>

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Robert Stephen Cantrell^a, Chris Cosner^a, Donald L. Deangelis^b & Victor Padron^c

^a Department of Mathematics, University of Miami, USA

^b Department of Biology, University of Miami and U.S. Geological Survey, USA

^c Institute of Mathematics and its Applications, Minneapolis, USA

Version of record first published: 10 Aug 2007

To cite this article: Robert Stephen Cantrell, Chris Cosner, Donald L. Deangelis & Victor Padron (2007): The ideal free distribution as an evolutionarily stable strategy, *Journal of Biological Dynamics*, 1:3, 249-271

To link to this article: <http://dx.doi.org/10.1080/17513750701450227>

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The ideal free distribution as an evolutionarily stable strategy

ROBERT STEPHEN CANTRELL*†, CHRIS COSNER†, DONALD L. DEANGELIS‡
and VICTOR PADRON§

†Department of Mathematics, University of Miami, USA

‡Department of Biology, University of Miami and U.S. Geological Survey, USA

§Institute of Mathematics and its Applications, Minneapolis, USA

(Received 15 February 2007; in final form 17 April 2007)

We examine the evolutionary stability of strategies for dispersal in heterogeneous patchy environments or for switching between discrete states (e.g. defended and undefended) in the context of models for population dynamics or species interactions in either continuous or discrete time. There have been a number of theoretical studies that support the view that in spatially heterogeneous but temporally constant environments there will be selection against unconditional, i.e. random, dispersal, but there may be selection for certain types of dispersal that are conditional in the sense that dispersal rates depend on environmental factors. A particular type of dispersal strategy that has been shown to be evolutionarily stable in some settings is balanced dispersal, in which the equilibrium densities of organisms on each patch are the same whether there is dispersal or not. Balanced dispersal leads to a population distribution that is ideal free in the sense that at equilibrium all individuals have the same fitness and there is no net movement of individuals between patches or states. We find that under rather general assumptions about the underlying population dynamics or species interactions, only such ideal free strategies can be evolutionarily stable. Under somewhat more restrictive assumptions (but still in considerable generality), we show that ideal free strategies are indeed evolutionarily stable. Our main mathematical approach is invasibility analysis using methods from the theory of ordinary differential equations and nonnegative matrices. Our analysis unifies and extends previous results on the evolutionary stability of dispersal or state-switching strategies.

Keywords: Ideal free distribution; Evolutionarily stable strategy; Evolution of dispersal; Discrete diffusion

1. Introduction

How animals select their habitats has been a fundamental question addressed by ecologists. One possible model is random or unconditional dispersal, with no active choices being made. Another model is conditional dispersal, where organisms move in response to features of their environment. One model of habitat selection by conditional dispersal assumes active movement, such that all animals move around freely until they cannot do any better in terms

*Corresponding author. Department of Mathematics, University of Miami, Coral Gables, FL33124, USA. Email: rsc@math.miami.edu

of resource acquisition. The distribution thus produced is the 'ideal free distribution' of Fretwell and Lucas [1]. The original model was modified by Parker [2] to allow the suitability of habitat (i.e. the abundance of resources per animal) to diminish as the density of animals increases. In a landscape where the input of new resources is distributed unevenly, the population of free individuals develops a matching distribution, and ideal free distribution therefore develops into an inhomogeneous pattern such that each animal has the same resources available to it as every other animal.

Cressman *et al.* [3] recognized the game theoretic aspect that is implicit in the ideal free distribution because animals move in response to the locations of other animals. The authors used game theory to show that the ideal free distribution of a metapopulation inhabiting a two-patch environment is an evolutionarily stable strategy in the sense that it cannot be invaded by another species with similar ecological features but with a different pattern of distribution.

An important result from Cressman *et al.* [3] is that in single species and predator-prey models, and in some competition models, the ideal free distribution that arises is the same as the distribution that would arise when movement between patches is not allowed. In other words, if the populations follow the ideal free distribution, they have the same equilibrium values they would have in the case that the patches were isolated from each other, so that if the population were initially distributed to match the single patch equilibria there would be no movement between patches.

In a different line of research on the evolution of dispersal, Hastings [4] showed that for animals dispersing randomly in spatially heterogeneous but temporally constant environments with logistic dynamics in each patch there will be selection for lower dispersal rates, so that the only evolutionarily stable strategy based on random movement is the one where the dispersal rate is zero. Similar results have been obtained for other types of models [5–7]. The reason why random dispersal is not favored in heterogeneous environments is that it results in over exploitation of resources in some patches and underexploitation in others. If there is no movement between patches then the population on each patch will equilibrate at carrying capacity. McPeck and Holt [5] found that there are patterns of conditional dispersal in heterogeneous patchy environments which allow movement between patches but are evolutionarily stable. Those patterns have the feature that if the population on each patch is at the equilibrium it would attain in isolation then there is no net movement between patches. That type of conditional dispersal is known as balanced dispersal [8, 9]. It implies that at equilibrium individuals in any patch will have the same fitness, namely zero, because all populations are at carrying capacity. Since no individual can increase its fitness by moving to another patch, this is a type of ideal free distribution. The notion of balanced dispersal leading to an evolutionarily stable ideal free distribution is not restricted to models of physical dispersal in space. A similar phenomenon has been observed emerging from simulations of consumer/resource systems where the resources can switch between defended and undefended states [10–12].

Here we will investigate the connections between evolutionary stability and ideal free distributions arising from balanced dispersal or the equivalent state-switching strategy. We will not use game theory explicitly; instead, we will examine the invasibility of systems at ecological equilibrium under different sorts of dispersal strategies. The formulation of our results is fairly general; we can treat single species models, competition models, and consumer/resource models on n patches in either continuous or discrete time from the same viewpoint. It turns out that under rather general conditions the only possible evolutionarily stable strategies are ideal free. The conditions under which an ideal free strategy can be seen to be evolutionarily stable are somewhat more restrictive but still are satisfied in many reasonable models. Related results for single-species models on n patches have been obtained in [13–15], but our analysis unifies and extends those, and allows for multiple species. Technically our approach is based on using the theory of nonnegative matrices to determine the stability properties of systems of

differential or difference equations arising in the analysis of the invasibility of equilibria by a small population using a different dispersal or state-switching strategy.

The paper is structured as follows: in section 2 we formulate the models and state our main results, in section 3 we apply them to a number of different systems and scenarios, and in section 4 we give a brief nonmathematical discussion of our conclusions. The proofs of the main results are given in the Appendix.

2. Modeling framework and main results

2.1 The basic models

The models we will consider describe deterministic population dynamics and species interactions together with transfer or movements of individuals among a discrete set of states or patches. In most of the literature on the ideal free distribution, individuals are envisioned as dispersing among patches, but the same modeling framework applies to cases where they can shift between different states (e.g. defended vs. undefended; see [10–12]) or life history traits. The models are systems of differential or difference equations where the state variables are population densities indexed by patch or state and perhaps by species. The patches or states generally are not assumed to be identical, but that possibility is not excluded, and in fact may arise naturally in certain cases that will describe later. Movement rates are assumed to be constants, as in the case of discrete diffusion, but the rate of movement between patches (or states) may depend on the specific patches. We will consider situations where systems involve multiple species but only some of those species present variants with a new dispersal (or state-switching) strategy. Thus, we will formulate our continuous-time models as

$$\frac{du_{ki}}{dt} = F_{ki}(\mathbf{u})u_{ki} + \sum_{\substack{j=1 \\ j \neq i}}^n [d_{ij}^k u_{kj} - d_{ji}^k u_{ki}] \quad \text{for } i = 1, \dots, n \text{ and } k = 1, \dots, m, \quad (1)$$

where $i, j = 1, \dots, n$ indicate the patch or state, $k = 1, \dots, m$ indicates the species, and $\mathbf{u} = (u_{11}, u_{12}, \dots, u_{mn})^T$ is the vector of densities of all species on all patches or in all states. Thus, holding the first subscript on u constant at k and sweeping through the second subscript from 1 to n yields the vector of densities of the k th species on patches 1 through n . On the other hand, holding the second subscript fixed at i and sweeping through the first from 1 to m yields the vector of densities of the 1st through m th species on patch i . The system (1) can be written as

$$\frac{d\mathbf{u}_k}{dt} = \mathcal{F}_k(\mathbf{u}) + A_k \mathbf{u}_k \quad (2)$$

where $\mathbf{u}_k = (u_{k1}, \dots, u_{kn})^T$, $\mathcal{F}_k(\mathbf{u}) = (F_{k1}(\mathbf{u})u_{k1}, \dots, F_{kn}(\mathbf{u})u_{kn})^T$, and $A_k = ((a_{ij}^k))$ with

$$a_{ij}^k = \begin{cases} d_{ij}^k & \text{for } j \neq i \\ -\sum_{\substack{\ell=1 \\ \ell \neq i}}^n d_{\ell i}^k & \text{for } j = i. \end{cases} \quad (3)$$

We will always assume $d_{ij}^k \geq 0$ for all i, j, k . The coefficient d_{ij}^k describes the rate at which individuals of species k move from patch or state j to patch or state i . In some modeling situations we may want to take $A_k = 0$, indicating that the k th species does not move or

change state. Otherwise we will assume A_k is irreducible, so that all individuals have access to all possible patches or states. A special case of (1) occurs if we envision the k th species as a single consumer population that consumes resource species in all patches or states. That might occur if the consumer species operates on a larger spatial scale than the resource and in effect experiences the entire environment as a single patch. Normally that sort of scenario would be described by using a single equation for the consumer population, but such a formulation would not fit our modeling framework (1). An equivalent model for a situation can be formulated in the framework of (1) by using n copies of the appropriate single equation with the same initial conditions; e.g. by using $A_k = 0$, $F_{ki}(\mathbf{u}) = F_k(\mathbf{u})$ for $i = 1, \dots, n$, and assuming $u_k(0) = u_{ki}(0)$ for $i = 1, \dots, n$. In that case the system (2) reduces to n copies of the equation

$$\frac{du_k}{dt} = F_k(\mathbf{u})u_k \quad (4)$$

with $u_{ki} = u_k$ for $i = 1, \dots, n$. In such a case u_k would normally be viewed as a uniform density across patches or states, so that $F_{ki}(\mathbf{u}) = F_k(\mathbf{u})$ could depend on $u_{\ell j}$ for any or all ℓ and j . In many other cases $F_{ki}(\mathbf{u})$ would depend only on $u_{\ell i}$ for $\ell = 1, \dots, m$ since population dynamics and species interactions would be assumed to occur within patches.

Models analogous to (1) also can be formulated in discrete time. Suppose that at each time step the populations in patch or state k reproduce or interact and then disperse. The models would then take the form

$$u_{ki}(t+1) = \left(1 - \sum_{\substack{j=1 \\ j \neq i}}^n D_{ji}^k \right) F_{ki}(\mathbf{u})u_{ki} + \sum_{\substack{j=1 \\ j \neq i}}^n D_{ij}^k F_{kj}(\mathbf{u})u_{kj} \\ \text{for } i = 1, \dots, n, \quad k = 1, \dots, m. \quad (5)$$

The terms in (5) correspond to those in (1), except that D_{ij}^k denotes the fraction of the population of species k in patch or state j that moves to patch or state i in each time step. Thus, we still must have $D_{ij}^k \geq 0$, but we also must have

$$\sum_{\substack{i=1 \\ i \neq j}}^n D_{ij}^k \leq 1 \quad \text{for } j = 1, \dots, n, \quad k = 1, \dots, m. \quad (6)$$

We also must assume $F_{ki} \geq 0$ in (5). As in the case of (1), we may assume that for some k , $D_{ij}^k = 0$ for all i, j . This again describes the case where the k th species does not move or change state. By defining $B_k = ((b_{ij}^k))$ with

$$b_{ij}^k = \begin{cases} D_{ij}^k & \text{for } j \neq i \\ 1 - \sum_{\substack{\ell=1 \\ \ell \neq i}}^n D_{\ell i}^k & \text{for } j = i \end{cases} \quad (7)$$

we can write (5) as

$$\mathbf{u}_k(t+1) = B_k \mathcal{F}_k(\mathbf{u}(t)), \quad k = 1, \dots, m \quad (8)$$

in analogy to (2).

Note that models of the form (1) or (5) leave the nonnegative orthant invariant. We will assume that the functions F_{ki} are all of class C^2 . In the cases we consider we will assume that the system (1) or (5) has at least one stable nonzero equilibrium if there is no movement; equivalently we will assume that (2) and (8) have at least one stable nonzero equilibrium if $A_k = 0$ or $B_k = I$, respectively for $k = 1, \dots, m$. All of our results about evolutionary stability will be framed in terms of such ecologically stable equilibria.

2.2 Ideal free strategies, invasibility, and ESS's

We envision situations where a small number of individuals using a new movement or state-switching strategy attempt to invade a system which is at equilibrium. Suppose that the attempt at invasion is made by species $k = 1, \dots, \ell$, while species $k = \ell + 1, \dots, m$ are not subject to the invasion attempt. Let $v = (v_{11}, \dots, v_{\ell n})^T$ and $w = (w_{11}, \dots, w_{\ell n})^T$ denote the vectors of population densities of the resident and invading species, respectively, and let $y = (y_{(\ell+1)1}, \dots, y_{mn})^T$ denote the vector of densities of species not subject to invasion. In the basic models (1), (5) we would then have $u = \begin{pmatrix} v \\ y \end{pmatrix}$. Let $u^* = \begin{pmatrix} v^* \\ y^* \end{pmatrix}$ denote an asymptotically stable equilibrium of the original system (1) or (5) in the absence of dispersal that is nontrivial with respect to the species that are subject to the invasion attempt in the sense that $u_{ki}^* = v_{ki}^* \neq 0$ for $k = 1, \dots, \ell$ and $i = 1, \dots, n$. It follows that for (1) we have

$$0 = F_{ki}(u^*), \quad k = 1, \dots, \ell, \quad i = 1, \dots, n, \tag{9}$$

while for (5)

$$1 = F_{ki}(u^*), \quad k = 1, \dots, \ell, \quad i = 1, \dots, n, \tag{10}$$

We will use $u^{**} = \begin{pmatrix} v^{**} \\ y^{**} \end{pmatrix}$ to denote a generic equilibrium for (1) or (5).

DEFINITION A dispersal strategy is ideal free (relative to u^*) if there is no net movement of population when $u = u^*$; that is, in (1), if

$$\sum_{\substack{j=1 \\ j \neq i}}^n [d_{ij}^k u_{kj}^* - d_{ji}^k u_{ki}^*] = 0, \quad k = 1, \dots, \ell, \quad i = 1, \dots, n \tag{11}$$

and in (5)

$$0 = \sum_{\substack{j=1 \\ j \neq i}}^n [D_{ij}^k u_{kj}^* - D_{ji}^k u_{ki}^*], \quad k = 1, \dots, \ell, \quad i = 1, \dots, n. \tag{12}$$

The reason why such strategies correspond to a version of the ideal free distribution is that at the equilibrium u^* all individuals of species 1 through l in all patches have equal fitness (namely 0) if fitness is measured by the local recruitment rates F_{ki} , and at equilibrium there is no net movement of individuals of those species between patches (or states). Neither of these need be true for generic movement or state-switching strategies. The definition of ideal free strategies is given in terms of only those species corresponding to $k = 1, \dots, l$ because we will sometimes want to consider cases where some of the species in (1) or (5) are using strategies that are (or are not) ideal free, while we do not restrict the strategies of other species.

Remark If a dispersal strategy where some dispersal rates are nonzero is ideal free relative to u^* then for species $1, \dots, \ell$ we must have $u_{kj}^* \neq 0$ for all $j = 1, \dots, n$ if $u_{ki}^* \neq 0$ for at least

one value of i . Thus, the conditions (9) and (10) are reasonable for nontrivial equilibria that can admit ideal free dispersal strategies in the sense of (11) and (12), respectively. This observation follows from (11) or (12) and the assumption that the matrices A_k and B_k describing dispersal are irreducible if they are nonzero. Consider the case of (11). Suppose that $u_{kj}^* \neq 0$ for some j but that $u_{ki}^* = 0$ for some $i \neq j$. Let $I = \{1, \dots, n\}$ and let $I_1 \subseteq I$ be the subset of I such that $u_{ki}^* = 0$ for $i \in I_1$. We then would have $I_1 \neq \emptyset$ and $I_1 \neq I$. If $i \in I_1$ then (11) and the fact \mathbf{u}^* is an equilibrium imply

$$0 = \sum_{\substack{j=1 \\ j \neq i}}^n [d_{ij}^k u_{kj}^* - d_{ji}^k u_{ki}^*] + F_{ki}(\mathbf{u}^*) u_{ki}^* = \sum_{j \notin I_1} d_{ij}^k u_{kj}^*.$$

By assumption we would have $u_{kj}^* > 0$ for all $j \notin I_1$ so we must have $d_{ij}^k = 0$ for $i \in I_1, j \notin I_1$, which would contradict the irreducibility assumption on the dispersal matrix A_k . Thus, to avoid contradiction, we must have $u_{ki}^* = 0$ for either all $i \in I$ or for no $i \in I$. It follows that (9) must hold for any equilibrium that is nontrivial and can admit an ideal free strategy. The case of discrete time, (10) and (12), is similar.

If a small population of individuals using a different dispersal (or state-switching) strategy will increase when introduced to a system at an equilibrium $\mathbf{u}^{**} = (\mathbf{y}^{**})$ then the system is invadable by that strategy. If the small introduced population cannot increase then the system is not invadable. We envision situations where the invading population w is small relative to the equilibrium \mathbf{v}^{**} of the resident population \mathbf{v} but where w and \mathbf{v} are ecologically equivalent except for their movement (or state-switching) strategies. Thus, we assume that the invaders do not initially have a significant effect on the resident equilibrium except to augment it with their own population. This is plausible only if the resident equilibrium is stable, since otherwise any small perturbation could cause the system to move away from the equilibrium.

DEFINITION Suppose that $\mathbf{u}^{**} = (\mathbf{y}^{**})$ is an asymptotically stable equilibrium of (1), and the invaders $w = (w_{11}, \dots, w_{\ell n})^T$ are using strategies $(\tilde{d}_{ij}^k), k = 1, \dots, \ell$. The system (1) at equilibrium \mathbf{u}^{**} is invadable by w if $w = 0$ is unstable relative to nonnegative initial data in the system

$$\frac{dw_{ki}}{dt} = \sum_{\substack{j=1 \\ j \neq i}}^n [\tilde{d}_{ij} w_{kj} - \tilde{d}_{ji} w_{ki}] + F_{ki}(\mathbf{v}^{**} + w, \mathbf{y}^{**}) w_{ki}, \quad k = 1, \dots, \ell, \quad i = 1, \dots, n. \quad (13)$$

If $w = 0$ is stable relative to nonnegative initial data in (13) then the equilibrium \mathbf{u}^{**} is not invadable by w . If \mathbf{u}^{**} is an asymptotically stable equilibrium of (5) then the system (5) at equilibrium \mathbf{u}^{**} is invadable by w if $w = 0$ is unstable relative to nonnegative initial data in the system

$$w_{ki}(t+1) = \left(1 - \sum_{\substack{j=1 \\ j \neq i}}^n \tilde{D}_{ji}^k \right) F_{ki}(\mathbf{v}^{**} + w(t), \mathbf{y}^{**}) w_{ki}(t) + \sum_{\substack{j=1 \\ j \neq i}}^n \tilde{D}_{ij}^k F_{kj}(\mathbf{v}^{**} + w(t), \mathbf{y}^{**}) w_{ki}(t), \quad k = 1, \dots, \ell, \quad i = 1, \dots, n. \quad (14)$$

If $w = 0$ is stable relative to nonnegative initial data in (14) then the system at equilibrium \mathbf{u}^{**} is not invadable by w .

We will sometimes just say that the equilibrium u^{**} is or is not invadable by w without referring explicitly to the systems (1) or (5).

DEFINITION A dispersal strategy (d_{ij}^k) in (1) or (D_{ij}^k) in (5) (respectively) with corresponding asymptotically stable equilibrium $u^{**} = (v^{**}, y^{**})$ is evolutionarily stable with respect to v if it is not invadable by any small population w using another strategy, where invasibility is determined from (13) or (14).

We will use ESS as the standard abbreviation of evolutionarily stable strategy.

2.3 Main results

Again, let $v = (v_{11}, \dots, v_{\ell n})^T$, $w = (w_{11}, \dots, w_{\ell n})^T$, $y = (y_{\ell+11}, \dots, y_{mn})^T$.

Define $F(v, y)$ to be the vector function $F(v, y) = (F_{11}(v, y), \dots, F_{\ell n}(v, y))^T$. Denote by $\nabla_v F$ the Jacobian of F relative to v , so that $\nabla_v F$ is an $\ell n \times \ell n$ matrix.

THEOREM 1 Suppose that $u^* = (v^*, y^*)$ is an isolated asymptotically stable equilibrium for (1) in the absence of dispersal or state switching, i.e. in the case where $d_{ij}^k = 0$ for all i, j, k , so that u^* satisfies (9). Suppose that $\nabla_v F(u^*)$ satisfies

$$w^T \nabla_v F(u^*) w \leq -\gamma |w|^2 \quad (15)$$

for some $\gamma > 0$ and any $w \in \mathbb{R}_+^{\ell n}$ with $|w|$ sufficiently small, where $\mathbb{R}_+^{\ell n}$ is the nonnegative orthant of $\mathbb{R}^{\ell n}$. Then any strategy that is ideal free relative to u^* in the sense of (11) and for which u^* is asymptotically stable is an ESS relative to v .

Suppose that u^* is an isolated asymptotically stable equilibrium for (5) in the absence of dispersal or state switching, i.e. in the case $D_{ij}^k = 0$ for all i, j, k , so that u^* satisfies (10). Suppose that (15) holds for $w \in \mathbb{R}_+^{\ell n}$ with $|w|$ sufficiently small. Then any strategy that is ideal free relative to u^* in the sense of (12) and for which u^* is asymptotically stable in (5) is an ESS relative to v .

Proof See Appendix. ■

The condition (15) will play a central role in our analysis. It implies the evolutionary stability of ideal free strategies in the sense of noninvasibility. (Recall that we define invasibility and noninvasibility in the context of (13) or (14)). We will sometimes refer to (15) as an evolutionary stability condition.

Remarks In general it is not clear how (15) is related to the stability of u^* in (1) or (5). However, if $v = u_1$ so that there is only one invading species, and $F_{1i}(v, y^*)$ depends only on $v_i = u_{1i}$ so that population dynamics for v occur within patches, then (15) simply requires that $F_{1i}(v, y^*)$ is strictly decreasing in v_i for $i = 1, \dots, n$. In that case v^* will be an asymptotically stable equilibrium of the (uncoupled) system

$$\frac{dv}{dt} = \mathcal{F}(v, y^*). \quad (16)$$

In the analogous discrete time case the condition that $F_{1i}(\vec{v}, \vec{y}^*)$ is strictly decreasing in v_i for $i = 1, \dots, n$ is not sufficient for stability. Furthermore, it is conceivable that either (1) or (5) might admit Turing instabilities. It is also conceivable that the ideal free property rules out

Turing instabilities, but as far as we know that is an open question. We will revisit these points in our discussion of particular cases in the next section.

To continue our analysis we need the following results from matrix theory:

LEMMA 1 *Suppose that A is an $N \times N$ matrix with nonnegative off-diagonal entries, and that $\mathbf{u} \in \mathbb{R}^N$ is a vector with all components positive. Denote the i th components of $A\mathbf{u}$ and $\mathbf{u}^T A$ by $(A\mathbf{u})_i$ and $(\mathbf{u}^T A)_i$, respectively. Suppose $\mu \in \mathbb{R}$.*

(i) *If*

$$(A\mathbf{u})_i \geq \mu u_i, \quad i = 1, \dots, N \quad (17)$$

or

$$(\mathbf{u}^T A)_i \geq \mu u_i, \quad i = 1, \dots, N \quad (18)$$

then A has a real eigenvalue $\lambda \geq \mu$ with nonzero nonnegative eigenvector.

(ii) *If μ is an eigenvalue for A or A^T with eigenvector \mathbf{u} then any other eigenvalue λ of A (or A^T) has real part $\text{Re}\lambda \leq \mu$.*

(Note that \mathbf{u} is an eigenvector for A^T if $\mathbf{u}^T A = \mu \mathbf{u}^T$.)

Proof See Appendix.

We can now continue our discussion of the systems (1) and (5) and their linearizations. Let $\mathbf{u}^* = (\mathbf{v}^*, \mathbf{y}^*)$ be ideal free as in Theorem 1. Since $F_{ki}(\mathbf{v}^*, \mathbf{y}^*) = 0$ in (1) and $F_{ki}(\mathbf{v}^*, \mathbf{y}^*) = 1$ in (5), the linearizations of (13) and (14) around $\mathbf{w} = 0$ include only dispersal terms, so that the linearization of (13) is

$$\frac{d\mathbf{w}}{dt} = A\mathbf{w} \quad (19)$$

where A is the block-diagonal matrix with the matrices A_k as defined in (3) on the diagonal for $k = 1, \dots, \ell$. We may apply Lemma 1 to A . Note that $(1, \dots, 1)A = (0, \dots, 0)$ so 0 is an eigenvalue for A and no other eigenvalue has positive real part. Hence $\mathbf{w} = 0$ is neutrally stable at the linear level. Similarly, the linearization about $\mathbf{w} = 0$ in (14) is

$$\mathbf{w}(t+1) = B\mathbf{w}(t), \quad (20)$$

where B is the block diagonal matrix with matrices B_k on the diagonal as in (7). In this case $(1, \dots, 1)B = (1, \dots, 1)$, so no eigenvalue of B has real part greater than 1 by Lemma 1, so again $\mathbf{w} = 0$ is neutrally stable at the linear level.

Next we consider the case of resident population $\bar{\mathbf{u}} = (\mathbf{v})$ at an equilibrium $\bar{\mathbf{u}}^{**} = (\mathbf{v}^{**})$ where $\mathbf{v}^{**} \neq 0$ and where \mathbf{v} is using a strategy that is not ideal free relative to \mathbf{u}^{**} . For (1) in such a situation we must have $F_{ki}(\mathbf{u}^{**})v_{ki}^{**} \neq 0$ for some $k \in \{1, \dots, \ell\}$ and $i \in \{1, \dots, n\}$ since otherwise the strategy used by \mathbf{v} would be ideal free relative to \mathbf{u}^{**} . Similarly we must have $F_{ki}(\mathbf{u}^{**}) \neq 1$ for some $k \in \{1, \dots, \ell\}$ and $i \in \{1, \dots, n\}$ in the case of (5). Note that the linearization of (13) around $\mathbf{w} = 0$ is

$$\frac{dp_{ki}}{dt} = \sum_{\substack{j=1 \\ j \neq i}}^n [\bar{d}_{ij}^k p_{kj} - \bar{d}_{ji}^k p_{ki}] + F_{ki}(\mathbf{u}^{**}) p_{ki}, \quad k = 1, \dots, \ell, \quad i = 1, \dots, n. \quad (21)$$

Similarly, the linearization of (14) about $w = 0$ is

$$p_{ki}(t+1) = \left(1 - \sum_{\substack{j=1 \\ j \neq i}}^n \tilde{D}_{ji}^k\right) F_{ki}(u^{**}) p_{ki} + \sum_{\substack{j=1 \\ j \neq i}}^n \tilde{D}_{ij}^k F_{kj}(u^{**}) p_{kj},$$

$$k = 1, \dots, \ell, \quad i = 1, \dots, n. \quad (22)$$

Both (21) and (22) decouple relative to the species index k . Our second main result is that if the resident population of species k is using a dispersal or state switching strategy that is not ideal free relative to u^{**} then that population can be invaded by some small population using another strategy, so that no strategy which is not ideal free can be an ESS. ■

THEOREM 2 *If the system (1) (respectively, (5)) is at an equilibrium u^{**} where the population of the k th species is nonzero, and the resident population of species k is using a strategy that is not ideal free, then there is a strategy \tilde{d}_{ij}^k (respectively, \tilde{D}_{ij}^k) that can be chosen by an invading population of species k so that 0 is unstable in (21) (respectively, (22)) for that k . Thus, $w = 0$ is linearly unstable in (13) (respectively, (14)). The invading strategy can be chosen to be ideal free with respect to any asymptotically stable equilibrium u^* of the system corresponding to (1) (respectively, (5)) without movement or state-switching. Thus, no strategy that is not ideal free can be an ESS.*

Proof See the Appendix. ■

Remarks Results related to Theorems 1 and 2 have been obtained in various contexts by various researchers. McPeck and Holt [5] found in simulations of discrete time logistic type (specifically Ricker) models for a species inhabiting two patches that strategies satisfying (12) were evolutionarily stable. Derivations of the ideal free distribution as an ESS (and many other results) based on explicitly game theoretic ideas were given for continuous time models for one or two species on two patches in [3, 16, 17].

In the case of two competitors, Cressman *et al.* [3] and Krivan and Sirot [16] observed that it was possible to obtain a unique ESS with nonzero populations of both species on both patches only if the coexistence equilibrium was stable. We will explore this point further in examples, but it is worth noting that the hypotheses of Theorem 1 involve stability conditions and that Theorem 1 allows the possibility of distinct stable equilibria for the system without dispersal or strategy switching, with associated ideal free distributions that are ESS's which are also distinct.

Padrón and Trevisan [13] showed that the ideal free distribution was an ESS in the case of a logistic continuous time model for a single species on an arbitrary number of patches. Cressman and Krivan [14] derived a similar result by different methods in the single species case where the growth rate $F_i(u_i)$ on each patch is decreasing. Kirkland *et al.* [15] obtained analogous results for single species models in discrete time. The conditions for noninvasibility in [15] are formulated differently than ours or those given in [13, 14] but in their system the equilibrium is stable if it exists, and their condition on the dispersal/strategy-switching terms can be seen to be equivalent to (12).

In our formulation the cases of $\tilde{d}_{ij}^k = 0$ and $\tilde{D}_{ij}^k = 0$ for all i, j qualify as ideal free in the sense that they satisfy (11) and (12), respectively. There are a number of results indicating that in situations where there is spatial variation in habitat quality but where dispersal is independent of location, i.e. is 'unconditional' in the terminology of McPeck and Holt [5], the slowest disperser has an advantage. This was shown for models similar to (1) by Hastings

[4], for reaction–diffusion models by Dockery *et al.* [6], and for integrodifferential models by Hutson *et al.* [7]. It was observed in numerical simulations of discrete time models by McPeck and Holt [5]. In our models the corresponding situations would be where $d_{ij}^k = d^k$ or $D_{ij}^k = D^k$ for all i, j but where $u_{ki}^* \neq u_{kj}^*$ for some i and j . In our terminology we would consider $d^k = 0$ or $D^k = 0$ to be ideal free, so those choices would be ESS's if u^* had the necessary stability property (15). This is consistent with the results of Hastings [4] and McPeck and Holt [5]. We do not consider reaction–diffusion or integrodifferential models here.

2.4 Variations on the models and analysis

We have focused our attention on the scenario where a small population using a new pattern of dispersal or strategy switching is attempting to invade a resident population at equilibrium. Other sorts of perturbations are possible. Suppose that we consider a system that might be far from equilibrium or where a fraction of the existing population changes its pattern of dispersal. In such cases the description of the process given by (13) or (14) are not adequate. We would need to consider in place of (13) the system

$$\begin{aligned} \frac{dv_{ki}}{dt} &= \sum_{\substack{j=1 \\ j \neq i}}^n [d_{ij}^k v_{kj} - d_{ji}^k v_{ki}] + F_{ki}(v + w, y) v_{ki} \\ \frac{dw_{ki}}{dt} &= \sum_{\substack{j=1 \\ j \neq i}}^n [\tilde{d}_{ij}^k w_{kj} - \tilde{d}_{ji}^k w_{ki}] + F_{ki}(v + w, y) w_{ki} \\ &\text{for } k = 1, \dots, \ell, \quad i = 1, \dots, n, \quad \text{and} \end{aligned} \tag{23}$$

$$\frac{dy_{ki}}{dt} = \sum_{\substack{j=1 \\ j \neq i}}^n [d_{ij}^k y_{kj} - d_{ji}^k y_{ki}] + F_{ki}(v + w, y) y_{ki} \quad k = \ell + 1, \dots, m, \quad i = 1, \dots, n.$$

The analogous system in the discrete time case is

$$\begin{aligned} v_{ki}(t+1) &= \left[1 - \sum_{\substack{j=1 \\ j \neq i}}^n D_{ji}^k \right] F_{ki}(v(t) + w(t), y(t)) v_{ki}(t) \\ &\quad + \sum_{\substack{j=1 \\ j \neq i}}^n D_{ij}^k F_{kj}(v(t) + w(t), y(t)) v_{kj}(t) \\ &\quad \vdots \\ w_{ki}(t+1) &= \left[1 - \sum_{\substack{j=1 \\ j \neq i}}^n \tilde{D}_{ji}^k \right] F_{ki}(v(t) + w(t), y(t)) w_{ki}(t) \\ &\quad + \sum_{\substack{j=1 \\ j \neq i}}^n \tilde{D}_{ij}^k F_{kj}(v(t) + w(t), y(t)) w_{kj}(t) \\ &\quad \text{for } k = 1, \dots, \ell, \quad i = 1, \dots, n, \quad \text{and} \end{aligned}$$

$$\begin{aligned}
 y_{ki}(t+1) &= \left[1 - \sum_{\substack{j=1 \\ j \neq i}}^n D_{ji}^k \right] F_{ki}(v(t) + w(t), y(t)) y_{ki}(t) \\
 &\quad + \sum_{\substack{j=1 \\ j \neq i}}^n D_{ij}^k F_{kj}(v(t) + w(t), y(t)) y_{kj}(t) \\
 &\text{for } k = \ell + 1, \dots, m, \quad i = 1, \dots, n.
 \end{aligned}
 \tag{24}$$

Suppose that $u_0^* = (\nu_0^*, y_0^*)$ is an equilibrium for (1) or (5) in the absence of dispersal or state switching, so that (9) or (10) holds. Suppose further that the strategies (d_{ij}^k) or (D_{ij}^k) are ideal free relative to u_0^* , i.e. satisfy (11) or (12). Consider a situation in (23) or (24) where some subpopulation w_0 of ν_0^* changes to a different strategy (\tilde{d}_{ij}^k) or (\tilde{D}_{ij}^k) that is ideal free relative to u_0^* . Since the strategy used by w_0 is ideal free relative to u_0^* , it is easy to see that $(\nu_0^* - w_0, w_0, y_0^*)$ is an equilibrium of (23) or (24). (This follows because if $v + w = \nu_0^*$ then $F_{ki}(v + w, y_0^*) = F_{ki}(\nu_0^*, y_0^*) = F_{ki}(u_0^*)$.) Hence, such a perturbation shifts the system to a new equilibrium, where it remains unless otherwise perturbed. In that sense the equilibrium $(\nu_0^*, 0, y_0^*)^T$ of (23) or (24) is neutrally stable with respect to ideal free perturbations that do not increase the total population of any species on any patch (or in any state.)

Suppose we do not restrict (\tilde{d}_{ij}^k) to be ideal free. If (23) is linearized about $(\nu_0^*, 0, y_0^*)^T$ then the terms p_{ki} corresponding to w in the linearization satisfy

$$\frac{d}{dt} p_{ki} = \sum_{\substack{j=1 \\ j \neq i}}^n [\tilde{d}_{ij}^k p_{kj} - \tilde{d}_{ji}^k p_{ki}], \quad k = 1, \dots, \ell, \quad i = 1, \dots, n.
 \tag{25}$$

Analogously, for (24) we would have

$$p_{ki}(t+1) = \left[1 - \sum_{\substack{j=1 \\ j \neq i}}^n \tilde{D}_{ji}^k \right] p_{ki}(t) + \sum_{\substack{j=1 \\ j \neq i}}^n \tilde{D}_{ij}^k p_{kj}(t).$$

Using matrix notation as in (2), the system (25) can be written as

$$\frac{dp}{dt} = \tilde{A}p$$

where \tilde{A} is the block diagonal matrix with diagonal blocks \tilde{A}_k given by (\tilde{a}_{ij}^k) , $k = 1, \dots, \ell$, where the entries \tilde{a}_{ij}^k are defined relative to the coefficients \tilde{d}_{ij}^k of (25) as in (3). The off-diagonal terms in \tilde{A} are nonnegative; also, $(1, \dots, 1)\tilde{A} = 0$. If the matrix \tilde{A}' obtained by replacing the diagonal terms of \tilde{A} with zeroes is irreducible, it then follows from the general theory of non-negative matrices that \tilde{A}' and hence \tilde{A} must have a unique eigenvalue with real part larger than any other eigenvalue and characterized by having positive left and right eigenvectors [18, 19]. Thus, the eigenvalues associated with eigenvectors having nonzero components in the terms corresponding to w in the linearization of (23) about $(\nu_0^*, 0, y_0^*)$ must all have nonpositive real parts. In that sense the linearization of (23) about $(\nu_0^*, 0, y_0^*)^T$ is neutrally stable with respect to perturbations where the terms p corresponding to w in (23) are nonzero. The case of (24) is analogous. This neutral stability at the linear level is why we need to consider higher order terms in the analysis underlying Theorem 1.

3. Examples and discussion

3.1 Framing the issues

Theorem 2 of the previous section shows that under quite general conditions any dispersal or state-switching strategy which is not ideal free can be invaded by certain other strategies, some of which are ideal free. It follows that in a wide range of models only ideal free strategies can be evolutionarily stable. Theorem 1 gives conditions under which an ideal free strategy will be an ESS in the sense of noninvasibility, but those conditions impose specific requirements which vary in detail from system to system and which do not hold for some common types of models.

The issues that arise in continuous time and discrete time models are mostly similar; the only obvious exception is that equilibria for discrete-time single-species models may lose stability via routes that are not present in continuous time single species models. For that reasons we will focus our attention mainly on how Theorem 1 does or does not apply to continuous time models for a single species, a set of competing species, or a consumer/resource system. The collection of examples is not intended to be exhaustive, but merely to illustrate the scope and limitations of the theory.

3.2 Single species models

If we consider only a single species we may omit the species index k and write $\mathbf{u} = (u_1, \dots, u_n)^T$. We do not need the notation $\mathbf{u} = (v, y)$ and we can identify \mathbf{u} with v in the notation of section 2.

Suppose that we are in the continuous-time case (1) and that the population dynamics in each patch depend only on the density in that patch, so that $F_i(\mathbf{u}) = F_i(u_i)$. Suppose further that $F_i(u_i^*) = 0$ and $u_i^* \geq 0$ for each i , so that $\mathbf{u} = (u_1^*, \dots, u_n^*)$ is an equilibrium for (1) in the absence of dispersal or state switching. Any strategy $A = (d_{ij})$ that is ideal free relative to \mathbf{u}^* will be an ESS if the evolutionary stability condition (15) holds. In this case (15) becomes

$$\sum_{i=1}^n F_i'(u_i^*) w_i^2 \leq -\gamma |w|^2 \quad (26)$$

which will be true if and only if

$$F_i'(u_i^*) \leq -\gamma, \quad i = 1, \dots, n. \quad (27)$$

Condition (27) is the condition for asymptotic stability for $u_i = u_i^* > 0$ in the equations

$$\frac{du_i}{dt} = F_i(u_i)u_i, \quad i = 1, \dots, n. \quad (28)$$

Furthermore, if we consider the linearization of (1) about \mathbf{u}^* in this case, we have (in notation analogous to (2))

$$\frac{d\mathbf{u}}{dt} = A\mathbf{u} + \nabla\mathcal{F}(\mathbf{u}^*)\mathbf{u}, \quad (29)$$

where $\nabla\mathcal{F}(\mathbf{u}^*)$ is the diagonal matrix with entries $F_i'(u_i^*)u_i^*$ on the diagonal as in (15). Let $f_1 = -\min\{F_i'(u_i^*)u_i^* + a_{ii}, i = 1, \dots, n\}$. Suppose A is irreducible so that $A + \nabla\mathcal{F}(\mathbf{u}^*) + f_1 I$ is a nonnegative irreducible matrix. By the general theory of nonnegative matrices

[18, 19] $A + \nabla\mathcal{F}(\vec{u}^*) + f_1 I$ will have a unique positive principal eigenvalue λ_0 with positive eigenvector \mathbf{u} . Also, we have

$$[A + \nabla\mathcal{F}(\mathbf{u}^*)]\mathbf{u} = (\lambda_0 - f_1)\mathbf{u}, \tag{30}$$

and any other eigenvalue λ of $A + \nabla\mathcal{F}(\vec{u}^*)$ has $Re\lambda \leq \lambda_0 - f_1$. Let $f_2 = -\max\{F'_i(u_i^*)u_i^*, i = 1, \dots, n\}$. We have

$$(A\mathbf{u})_i \geq (\lambda_0 - f_1 + f_2)u_i, \quad i = 1, \dots, n, \tag{31}$$

so by Lemma 1, A must have a real eigenvalue $\lambda_1 \geq \lambda_0 - f_1 + f_2$. On the other hand $(1, \dots, 1)^T A = \mathbf{0}$ so any eigenvalue of A must have real part less than or equal to zero. Thus, $0 \geq \lambda_1 \geq \lambda_0 - f_1 + f_2$ or

$$\lambda_0 - f_1 \leq -f_2 = \max\{F'_i(u_i^*)u_i^*, i = 1, \dots, n\} \leq 0. \tag{32}$$

Hence, by (27), the eigenvalues of $A + \nabla\mathcal{F}(\vec{u}^*)$ must have negative real parts if $u_i^* > 0$ for each i , so \mathbf{u}^* is stable in the full system (1).

It follows that in the continuous-time single-species case with population dynamics all occurring within patches, condition (15) implies not only that \mathbf{u}^* is stable in (28) but also in (1). The logic behind the argument is similar to that which is used to show that single species models do not support Turing instabilities.

In discrete time models that situation is somewhat different. The condition (15) does not necessarily coincide with the stability condition for an equilibrium \mathbf{u}^* of

$$\mathbf{u}(t + 1) = \mathcal{F}(\mathbf{u}(t)) = F(\mathbf{u}(t))^T \mathbf{u}(t). \tag{33}$$

Consider the case of a single species on a single patch. In the case of the Beverton–Holt model $F_i(u) = a_i/(1 + b_i u)$, it is well known that there is a unique globally stable positive equilibrium for each equation in (33) with $a_i > 1$. On the other hand, the Ricker model $F_i(u) = \exp(a_i - b_i u)$ has period doubling bifurcations leading to chaos as a_i increases (see [20]). Both models satisfy (15), but in the case of Ricker dynamics our theory applies only when \mathbf{u}^* is stable.

It is worth noting that there may be more than one stable equilibrium \mathbf{u}^* for (28) or (33), and if so there will be different ideal free strategies associated with the different equilibria. This could happen in the case where the functions \mathcal{F}_i are bistable, i.e. if on each patch there is an Allee effect so that $u = 0$ and $u = u_i^* > 0$ are both stable equilibria.

Discussion: There has been a considerable amount of work on single species models. An important class of models are spatial logistic models. In the continuous case those would have $F_i(u) = r_i(1 - [u/K_i])$. In the discrete case there are various possible ‘logistic’ models, but the Beverton–Holt and Ricker models described previously are popular. They can be written in terms of carrying capacities by taking $F_i(u) = r_i/(1 + [(r_i - 1)/K_i]u)$ and $F_i(u) = \exp(r_i(1 - [u/K_i]))$, respectively. In logistic models the only possible stable equilibrium is $\mathbf{u}^* = (K_1, \dots, K_n)$. In that case the condition for dispersal to be ideal free is

$$\sum_{\substack{j=1 \\ j \neq i}}^n d_{ij} K_j = K_i \left(\sum_{\substack{j=1 \\ j \neq i}}^n d_{ji} \right).$$

In the two-patch case this reduces to the well-known relation $d_{12}/d_{21} = K_1/K_2$ for ‘balanced dispersal,’ as derived by McPeck and Holt [5] in simulations of coupled pairs of Ricker models with stable equilibria. (In a later paper [21] they considered the case where the Ricker models

had complex dynamics and found that the simulation there was quite different.) Padron and Trevisan [13] obtained results similar to those of this paper for continuous time logistic models. Cressmann and Krivan [14] obtained such results for continuous time single species models with $F_i(u_i)$ decreasing for each i . Kirkland *et al.* [15] obtained similar results (formulated in slightly different terms) for a class of discrete time single-species models including Beverton–Holt type models.

3.3 Competition models

Typical models for competition between species assume something like logistic self-limitation on each species (arising from intraspecific competition) and a negative impact of each species on the growth rate of the other species (arising from interspecific competition.) A continuous time nonspatial model for the densities u_1, \dots, u_m of m competitors would have the form

$$\frac{du_k}{dt} = F_k(\mathbf{u})u_k, \quad k = 1, \dots, m,$$

with the functions F_k satisfying

$$\frac{\partial F_k}{\partial u_\ell} \leq 0 \quad \text{for } k, \ell = 1, \dots, m,$$

usually with strict inequality for $k = \ell$. (In the Lotka–Volterra case $\partial F_k/\partial u_\ell$ will be a nonpositive constant for each k and ℓ .) Suppose that the competitors inhabit a system of n patches but that interactions occur only within patches, and let u_{ki} denote the density of the k th competitor on the i th patch. The spatial model is then

$$\frac{du_{ki}}{dt} = F_{ki}(u_{1i}, \dots, u_{mi})u_{ki} + \sum_{\substack{j=1 \\ j \neq i}}^n [d_{ij}^k u_{kj} - d_{ji}^k u_{ki}], \quad (34)$$

$$k = 1, \dots, m, \quad i = 1, \dots, n,$$

with

$$\frac{\partial F_{ki}}{\partial u_{hj}} \leq 0 \quad \text{for all } i, j, h, k. \quad (35)$$

(Note that $\partial F_{ki}/\partial u_{hj} = 0$ if $i \neq j$.)

Suppose that \mathbf{u}^* is an isolated asymptotically stable equilibrium for (34) in the case where $d_{ij}^k = 0$ for all i, j, k . If the coefficients d_{ij}^k satisfy the ideal free condition (11) relative to \mathbf{u}^* then \mathbf{u}^* is still an equilibrium for (34), and if the coefficients are small it will still be isolated and asymptotically stable. In some competition models it is possible for spatial heterogeneity and dispersal to interact in ways that change the dynamics of the model. This point is noted by Cressman *et al.* [3] in a game theoretic treatment of the ideal free distribution on two patches. Related results for reaction–diffusion models of competitions on spatially heterogeneous regions are obtained in [22, 23]. Thus, in the case of competition, the requirement that \mathbf{u}^* must still be stable in the model with dispersal imposes a genuine restriction. It may be possible to rule out destabilization by dispersal in some competition models, but we will not address that issue here. In any case, continuity of eigenvalues implies that the asymptotic stability of \mathbf{u}^* is unaffected by small perturbations of (34). We can consider cases where some or all of the competing populations are subject to an attempted invasion by other populations of the same species with different dispersal strategies. Suppose that we want to consider a situation where small populations of competitors with indices $k = 1, \dots, \ell$ attempt to invade.

We would take $\mathbf{v} = (u_1, \dots, u_\ell)^T$ and $\mathbf{y} = (u_{\ell+1}, \dots, u_m)$ in the formulation of Theorem 1. Suppose that the resident populations are using a strategy that is ideal free relative to \mathbf{u}^* in the sense of (11). All the entries in $\nabla_{\mathbf{v}} F(\mathbf{u}^*)$ are nonpositive by (35). If (for example) each species is logistically self-limiting so that $\partial F_{ki} / \partial u_{ki} \leq -\gamma < 0$ for $\mathbf{u} = \mathbf{u}^*$ then (15) holds, so any strategy that is ideal free relative to \mathbf{u}^* will be an ESS in the sense of noninvasibility by Theorem 1. Any strategy that is not ideal free will be invisable by some ideal free strategy by Theorem 2.

In general, \mathbf{u}^* need not be uniquely determined. Models such as (34) may have multiple stable equilibria; for example, in the case of two species with strong competition the equilibria with only one competitor present may both be stable. Thus, there may be several different types of strategies which are ideal free relative to different equilibria, and the resident equilibrium may be determined by the order of coloniation of the system. A similar observation was made by Krivan and Sirot [16] in a two-patch model; see also [3]. The case of discrete time competition is similar to the continuous time case in most respects, so we will not discuss it in detail. As for single-species models, the main difference is that some extra conditions may be needed to insure the stability of equilibria.

3.4 Consumer/resource or predator/prey models

We will consider a number of different situations involving consumer–resource or predator–prey systems. In most models for consumer–resource systems the resources are assumed to have some type of self-limitation, but that is not always the case for the consumers. This point turns out to be relevant in establishing the evolutionary stability condition (15) of Theorem 1 in some cases. In particular, if there is no self-limitation on the consumers it is possible for the system to have an asymptotically stable equilibrium for which (15) does not hold.

Another issue that may be relevant for consumer–resource systems is the possibility of Turing instabilities, but as we noted previously an asymptotically stable equilibrium will not be destabilized by the addition of dispersal or state-switching to the model if the coefficients d_{ij}^k or D_{ij}^k are sufficiently small.

The first case we will consider is where members of the resource or prey species may disperse or switch between defended and undefended states, but the consumers or predators do not. This case is motivated by the systems studied in [10–12], where the resource species had inducible defenses. In the case of state-switching by resource species it is natural to think of the consumers as a single population without a state structure and hence without movement between states. In the case of dispersal among patches by the resource species, the situation where consumers do not disperse among patches could occur if consumers are sessile (as in some aquatic systems), or if they experience the matrix between patches as more difficult to cross than it is for the resources, or if they form groups that defend territories. If we write $\mathbf{u} = \begin{pmatrix} \mathbf{v} \\ \mathbf{y} \end{pmatrix}$ where \mathbf{v} is a vector of resource/prey densities and \mathbf{y} the vector of consumer/predator densities, with both indexed by i , then a typical consumer/resource model would have the form

$$\begin{aligned} \frac{dv_i}{dt} &= f_i(v_i)v_i - g_i(v_i, y_i)y_i \\ \frac{dy_i}{dt} &= (G_i(\mathbf{v}, y_i) - a_i)y_i, \quad i = 1, \dots, n \end{aligned} \tag{36}$$

where f_i would usually be logistic and g_i would be a functional response of some sort. In the case of local interactions between populations on distinct spatial patches we would take $G_i(\mathbf{v}, y_i) = e_i g_i(v_i, y_i)$. To describe the case of a single consumer population interacting with resources in various states (or a single consumer population distributed uniformly across

patches) we would take $G_i(\mathbf{v}, y_i) = G_i(\mathbf{v}) = \sum_{j=1}^n e_j g_j(v_j)$ and $a_i = a$ for each i . In that case the consumers would satisfy n copies of the same equation, so the set $\{\mathbf{y} : y_1 = y_2 = \dots = y_n\}$ would be invariant, and all equilibria for (36) would have \mathbf{y} in that set. (We would assume that any initial data had \mathbf{y} in the set.) The full model corresponding to (36) is

$$\begin{aligned} \frac{dv_i}{dt} &= f_i(v_i)v_i - g_i(v_i, y_i)y_i + \sum_{\substack{j=1 \\ j \neq i}}^n (d_{ij}v_j - d_{ji}v_i) \\ \frac{dy_i}{dt} &= (G_i(\mathbf{v}, y_i) - a_i)y_i, \quad i = 1, \dots, n. \end{aligned} \quad (37)$$

If $\mathbf{u}^* = (\mathbf{v}^*, \mathbf{y}^*)$ is an asymptotically stable equilibrium of (36) which is also asymptotically stable in (37) and the dispersal or state-switching strategy $((d_{ij}))$ is ideal free, it will be an ESS by Theorem 1 if (15) holds. If we write $g_i(v_i, y_i)y_i = h_i(v_i, y_i)v_i y_i$ (which is possible for all standard forms of the functional response) then $\nabla_{\mathbf{v}} F$ in (15) is an $n \times n$ diagonal matrix with diagonal entries $df_i/dv_i + (\partial h_i/\partial v_i)y_i$ evaluated at $\mathbf{v} = \mathbf{v}^*, \mathbf{y} = \mathbf{y}^*$. Thus, (15) holds if

$$\left. \frac{df_i}{dv_i} - \left(\frac{\partial h_i}{\partial v_i} \right) y_i \right|_{\left(\begin{smallmatrix} \mathbf{v}^* \\ \mathbf{y}^* \end{smallmatrix} \right)} < -\gamma, \quad i = 1, \dots, n, \quad (38)$$

and in that case a strategy that is ideal free with respect to \mathbf{v} relative to \mathbf{u}^* will be an ESS by Theorem 1.

Condition (38) is related to the stability condition for an equilibrium of (36) in some cases. Suppose that in (36) $G_i(\mathbf{v}, y_i) = e_i g_i(v_i, y_i)$, so that the system decouples into n pairs of equations. Dropping the index i and computing the Jacobian for the linearization of such a pair at a positive equilibrium (where we use the equilibrium conditions to simplify) yields

$$J = \begin{pmatrix} \left[\frac{df}{dv} - \left(\frac{\partial h}{\partial v} \right) y \right] v & \left[-h - \left(\frac{\partial h}{\partial y} \right) y \right] v \\ e y \frac{\partial(hv)}{\partial v} & e \left(\frac{\partial h}{\partial y} \right) v y \end{pmatrix} \quad (39)$$

evaluated at the equilibrium (v^*, y^*) . If $g = hv$ is independent of y and is nondecreasing in v , as in the Lotka–Volterra or Holling type 2 cases, then the matrix in (39) has the form

$$\begin{pmatrix} P & Q \\ R & O \end{pmatrix} \quad (40)$$

with $Q < 0$ and $R > 0$. Thus, the eigenvalues $\lambda = (P \pm \sqrt{P^2 + 4RQ})/2$ have negative real parts if and only if $P < 0$, which is equivalent to (38). Hence, in those cases, (15) is automatically satisfied for any asymptotically stable equilibrium of (36). This is analogous to what happens in the single species case.

In the case of dispersal among patches, as opposed to state-switching, it makes sense to consider cases where the consumers also disperse and may change their dispersal strategies. For the cases where consumers can move we will assume that $G_i(\mathbf{v}, y_i) = e_i g_i(v_i, y_i)$ for each i . We will simply state condition (15) for the cases where only consumers move and where both consumers and resources move. We will deviate slightly from our standard notation in the first of those cases by continuing to denote consumers by \mathbf{y} and resources by \mathbf{v} even though the

consumers are the organisms that can disperse and can select dispersal strategies. In the case where only consumers move the condition (15) is equivalent to

$$e_i \frac{\partial g_i}{\partial y_i} \bigg|_{\begin{pmatrix} v^* \\ y^* \end{pmatrix}} \leq -\gamma < 0, \quad i = 1, \dots, n. \tag{41}$$

This condition cannot be satisfied unless the functional response g_i is consumer-dependent, e.g. in the Beddington–DeAngelis case. However, if the equations for the consumers are modified to include density-dependent mortality so that in (36) y_i satisfies

$$\frac{dy_i}{dt} = (e_i g_i(v_i, y_i) - a_i - b_i y_i) y_i \tag{42}$$

then (41) would become

$$e_i \frac{\partial g_i}{\partial y_i} - b_i \bigg|_{\begin{pmatrix} v^* \\ y^* \end{pmatrix}} \leq -\gamma < 0, \quad i = 1, \dots, n, \tag{43}$$

which will be satisfied if $b_i > 0$ and g_i does not depend on y_i . Conditions (41) and (43) are consistent with the asymptotic stability of the linearized system based on (39) but for most standard types of models some additional conditions are still required. However, both (41) and the presence of density-dependent mortality in (42) reflect some sort of intraspecific competition or interference by consumers.

If both consumers and resources are allowed to disperse and G_i depends only on v_i and y_i then (15) will hold if and only if the matrices

$$M_i = \begin{pmatrix} \left[\frac{df_i}{dv_i} - \left(\frac{\partial h_i}{\partial v_i} \right) y_i \right] & \left[-h_i - \left(\frac{\partial h_i}{\partial y_i} \right) y_i \right] \\ e_i \left[h_i + v_i \frac{\partial h_i}{\partial v_i} \right] & e_i v_i \frac{\partial h_i}{\partial y_i} \end{pmatrix} \bigg|_{\begin{pmatrix} v^* \\ y^* \end{pmatrix}} \tag{44}$$

have the property $w^T M_i w \leq -\gamma |w|^2$ for all nonnegative $w = (w_1, w_2)^T$ for each i . Recall that $g_i = v_i h_i$ so the term $e_i v_i (\partial h_i / \partial y_i)$ is equivalent to $e_i \partial g_i / \partial y_i$. Thus, for (15) to hold we must require both (38) and (41), so that the functional response must be consumer-dependent. As in the case where only the consumers move, we could avoid that requirement by adding density-dependent mortality as in (42). A comparison of the matrices in (39) and (44) shows that the form J can be obtained by multiplying the first row of M_i by v and the second by y . Such a modification can stabilize or destabilize the corresponding linear system, so although the matrices for stability in (36) and for condition (15) are related, the connection between (15) and stability is not clear in general.

4. Discussion

Our approach to assessing the evolutionary stability of dispersal or state-switching strategies in terms of invasibility allows us to examine a number of different types of models from the same conceptual viewpoint. That generality enables us to gain some insight into the properties that determine the evolutionary stability of strategies across a variety of systems. On the other

hand, our approach is not based on behavioral mechanisms such as optimal foraging [24], does not explicitly formulate models in terms of evolutionary game theory [3] and does not give any insight into what, if anything, those strategies that are stable in the sense of noninvasibility might optimize [13]. Thus, the trade-off for obtaining a level of generality that allows us to draw some broad conclusions about many systems and types of models is that we cannot obtain as much detailed information about the mechanisms involved in specific systems.

It turns out that in many situations the strategies which are predicted to be evolutionarily stable have some of the features of the ideal free distribution [1], and of balanced dispersal [5, 8, 9]. Specifically, they have the features that at equilibrium the fitnesses of populations in different patches or states all have the same value (namely zero) and there is no net movement of individuals between patches or states. These features are present in the strategy of no movement at all. If strategies are constrained (for example, by requiring all rates of dispersal to be equal even though patches differ in quality) it may be that the only evolutionarily stable strategy under the constraint is that of no dispersal at all. This observation is consistent with the results of [4–7].

We derive both necessary and sufficient conditions for a strategy that admits an ecologically stable equilibrium to be evolutionarily stable. The ideal free/balanced dispersal property is necessary under very general conditions. Essentially, if there are differences in fitness between patches when the system is at equilibrium, it is possible to devise strategies that can invade the resident strategy. The sufficient conditions for an ideal free strategy to be evolutionarily stable are more subtle. They appear to require something like self-limitation via intraspecific competition or density dependent mortality. These are standard assumptions in single species models and models for competition, but they are not always present in consumer/resource models. Self-limitation can sometimes have a stabilizing effect on models but it does not rule out the possible destabilization of equilibria by Turing instabilities or other effects.

In the case of single species models in continuous time our sufficient condition for the evolutionary stability of strategies that are ideal free with respect to some equilibrium implies that the equilibrium must be ecologically stable, with or without dispersal. In discrete-time or multi-species models the stability of the equilibrium is not guaranteed and generally must be assumed as a separate hypothesis.

All of the models we consider treat space or the set of possible states as being discrete and finite. Our analytic methods do not extend directly to models where the solution space is infinite dimensional, such as reaction–diffusion or integro-difference models, or even spatially discrete models with infinitely many patches. It would be of interest to know whether results analogous to ours can be extended to the infinite dimensional case.

Acknowledgements

Research partially supported by NSF Grant DMS 0514839 (RSC, CC).

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Appendix

Proof of Theorem 1 Suppose that w is a solution of (13) in \mathbb{R}_+^n with $v^{**} = v^*$, $y^{**} = y^*$. Let

$$V(w) = \sum_{k=1}^l \sum_{i=1}^n w_{ki}. \quad (\text{A1})$$

We have (by summing (13) over k and i , $k = 1, \dots, l$, $i = 1, \dots, n$),

$$\begin{aligned} \frac{dV(w)}{dt} &= \sum_{k=1}^l \sum_{i=1}^n F_{ki}(v^* + w, y^*) w_{ki} \\ &= \sum_{k=1}^l \sum_{i=1}^n \left[F_{ki}(v^*, y^*) + \sum_{h=1}^l \sum_{j=1}^n \frac{\partial F_{ki}}{\partial v_{hj}}(v^*, y^*) w_{hj} + o(|w|) \right] w_{ki} \quad (\text{A2}) \\ &= w^T \nabla_v F(v^*, y^*) w + o(|w|^2) \end{aligned}$$

Let $W_c = \{w \in \mathbb{R}_+^{ln} : V(w) < c\}$. Since $V(0) = 0$ and u^* is isolated we can choose c small enough that $w = 0$ is the only equilibrium of (13) in W_c and $w^T \nabla_v F(v^*, y^*) w + o(|w|^2) < 0$ for $w \in W_c, w \neq 0$. It follows from (A2) and the invariance of \mathbb{R}_+^{ln} in (13) that $w \rightarrow 0$ as $t \rightarrow \infty$, which proves the theorem in the case of (1).

The ideas behind the proof for (5) are similar to the case of (1) but there are a few differences in the details. If we compute $V(w)$ for (5) we get

$$V(w)(t+1) = \sum_{k=1}^l \sum_{i=1}^n F_{ki}(v^* + w, y^*) w_{ki}(t). \quad (A3)$$

We have

$$F_{ki}(v^* + w, y^*) = F_{ki}(v^*, y^*) + \int_0^1 \sum_{h=1}^l \sum_{j=1}^n \frac{\partial F_{ki}}{\partial v_{hj}}(v^* + sw, y^*) w_{hj} ds \quad (A4)$$

so since $F_{ki}(v^*, y^*) = 1$, multiplying (A4) by w_{ki} , summing $k = 1, \dots, l$ and $i = 1, \dots, n$, then substituting into (A3) yields

$$V(w)(t+1) = V(w)(t) + \int_0^1 w^T \nabla F(v^* + sw, y^*) w ds$$

so that for c small and $w \in W_c$ we have

$$\begin{aligned} V(w)(t+1) - V(w)(t) &\leq -(\gamma/2)|w(t)|^2 \\ &\leq -(\gamma/6)[V(w)(t)]^2. \end{aligned} \quad (A5)$$

Since \mathbb{R}_+^{ln} is invariant we have $V \geq 0$, so by (A5) $V(w)(t) \rightarrow V_0 \geq 0$ as $t \rightarrow \infty$; but again by (A5), $0 \leq (-\gamma/2)V_0^2$ so we must have $V_0 = 0$. This completes the proof.

Proof of Lemma 1 Recall that if B is a positive $N \times N$ matrix then by the Perron–Frobenius theorem B and B^T have a unique positive eigenvalue $\lambda_1(B)$ which is equal to the spectral radius of B and is characterized as the unique eigenvalue for B or B^T with a positive eigenvector. Furthermore if λ is any other eigenvalue of B then $\operatorname{Re} \lambda < \lambda_1$. (See, for example, [18,19]). Choose R_0 large enough that $A + R_0 I$ is nonnegative and $\mu + R_0 \geq 0$. Let $((\varepsilon))$ be the $N \times N$ matrix with all entries equal to ε , and suppose $\varepsilon > 0$. If (i) of (17) holds then for $B = A + R_0 I + ((\varepsilon))$ we have

$$(Bu)_i \geq (Au)_i + (R_0 + \varepsilon)u_i \geq (\mu + R_0 + \varepsilon)u_i > 0 \quad \text{for } i = 1, \dots, N. \quad (A6)$$

It follows from (A6) that

$$\sum_{i=1}^N (Bu)_i^2 \geq (\mu + R_0 + \varepsilon)^2 \sum_{i=1}^N u_i^2 \quad (A7)$$

so that $\|Bu\| \geq (\mu + R_0 + \varepsilon)\|u\|$. Hence the spectral radius of B is greater than or equal to $\mu + R_0 + \varepsilon$, so $\lambda_1(B) \geq \mu + R_0 + \varepsilon$. The eigenvector corresponding to $\lambda_1(B)$ is positive. If we normalize the eigenvector and let $\varepsilon \rightarrow 0$ it follows by continuity that $A + R_0 I$ has an eigenvalue $\Lambda \geq \mu + R_0$, with nonnegative eigenvector. Since the eigenvalues of A and $A + R_0 I$ have the same eigenvectors and since λ is an eigenvalue of A if and only if $\Lambda = \lambda + R_0$

is an eigenvalue of $A + R_0I$, the conclusion of (i) follows. The argument for the case (18) is analogous. Suppose (ii) holds. Choose B as above; then

$$0 < (Bu)_i = (\mu + R_0)u_i + \varepsilon \sum_{j=1}^n u_j \quad \text{for } i = 1, \dots, N \quad (\text{A8})$$

So

$$\begin{aligned} \sum_{i=1}^N (Bu)_i^2 &\leq \sum_{i=1}^N \left[(\mu + R_0)^2 u_i^2 + [2\varepsilon(\mu + R_0) + \varepsilon^2] \left(\sum_{i=1}^N u_i \right)^2 \right] \\ &\leq ((\mu + R_0)^2 + N[2\varepsilon(\mu + R_0) + \varepsilon^2]) \sum_{i=1}^N u_i^2. \end{aligned} \quad (\text{A9})$$

It follows that the spectral radius of B is less than or equal to $((\mu + R_0)^2 + N[2\varepsilon(\mu + R_0) + \varepsilon^2])^{1/2}$, so $\lambda_1(B) \leq ((\mu + R_0)^2 + N[2\varepsilon(\mu + R_0) + \varepsilon^2])^{1/2}$. All other eigenvalues λ of B have $\text{Re}\lambda < \lambda_1(B)$. As $\varepsilon \rightarrow 0$ we have that $\text{Re}\lambda \leq \mu + R_0$ for any eigenvalue of $A + IR_0$, so $\text{Re}\lambda \leq \mu$ for any eigenvalue of A . The case where μ is an eigenvalue of A^T is analogous.

Proof of Theorem 2 In notation analogous to that of (2) we can write the part of (21) corresponding to the k th species as

$$\frac{dp}{dt} = \tilde{A}_k p + F_k(u^{**})p = Mp, \quad (\text{A10})$$

where the entries of \tilde{A}_k are as in (3) with d_{ij}^k replaced by \tilde{d}_{ij}^k , $F_k = (F_{k1}(u^{**}), \dots, F_{kn}(u^{**}))$, and M is the matrix obtained by adding the terms $F_{ki}(u^{**})$ to the diagonal terms \tilde{a}_{ii}^k of \tilde{A}_k . Since u^{**} is an equilibrium of (1) we have

$$0 = \sum_{\substack{j=1 \\ j \neq i}}^n [d_{ij}^k v_{kj}^{**} - d_{ji}^k v_{ki}^{**}] + F_{ki}(u^{**})v_{ki}^{**}, \quad i = 1, \dots, n. \quad (\text{A11})$$

Summing (A11) over i yields

$$0 = \sum_{i=1}^n F_{ki}(u^{**})v_{ki}^{**}. \quad (\text{A12})$$

Some of the terms in (A12) must be nonzero since the resident strategy is not ideal free, so at least one must be positive, so $F_{ki}(u^{**})$ must be positive for some i . Without loss of generality assume $F_{k1}(u^{**}) = F_0 > 0$. If we compute Mp_0 for the vector $p_0 = (1, \varepsilon, \dots, \varepsilon)^T \in \mathbb{R}_+^n$, the first entry is

$$\sum_{j=2}^n \tilde{d}_{1j}^k \varepsilon - \sum_{j=2}^n \tilde{d}_{j1}^k + F_0. \quad (\text{A13})$$

The i th entry in Mp_0 is

$$\tilde{d}_{i1}^k + \varepsilon \left[\sum_{\substack{j=2 \\ j \neq i}}^n \tilde{d}_{ij}^k - \sum_{\substack{j=1 \\ j \neq i}}^n \tilde{d}_{ji}^k + F_{ki}(u^{**}) \right]. \quad (\text{A14})$$

For $\delta > 0$ sufficiently small, there are strategies $((\tilde{d}_{ij}^k))$ with $\tilde{d}_{i1} \geq \delta > 0$ for $i = 1, \dots, n$ that satisfy

$$\sum_{j=2}^n \tilde{d}_{j1}^k < F_0/3. \quad (\text{A15})$$

For any such strategy we can take $\varepsilon > 0$ sufficiently small so that the quantity in (A13) is larger than $F_0/3$, and for $i = 2, \dots, n$ the quantities in (A14) are all larger than $\delta/2$. For such choices of p_0 and $((\tilde{d}_{ij}^k))$ we have

$$(Mp_0)_i \geq \delta_0 p_{0i} \quad \text{for } i = 1, \dots, n, \quad (\text{A16})$$

where $\delta_0 = \min\{F_0/3, \delta/2\}$. It follows from Lemma 1 that M has an eigenvalue greater than or equal to $\delta_0 > 0$ with a nonnegative eigenvector. Thus, $p = 0$ is unstable in (A10), with the unstable eigenvector nonnegative. Since the only restrictions on the coefficients \tilde{d}_{ij}^k are that the \tilde{d}_{i1} 's must be positive but satisfy (A15), they can be chosen to be ideal free relative to any stable equilibrium u^* . (If $((\tilde{d}_{ij}^k))$ is ideal free relative to u^* then so is $((s\tilde{d}_{ij}^k))$ for any $s > 0$, so we can always choose ideal free dispersal terms to be as small as we want.)

The analysis for the case (22) is similar to that for (21). We can write the part of (22) corresponding to the k th species in form of (8) as

$$p_k(t+1) = \tilde{B}_k \mathcal{F}_k(u^{**}) p_k(t) = Lp_k(t). \quad (\text{A17})$$

We have (from (5) and the fact u^{**} is an equilibrium)

$$v_{ki}^{**} = \left(1 - \sum_{\substack{j=1 \\ j \neq i}}^n D_{ji}^k \right) F_{ki}(u^{**}) v_{ki}^{**} + \sum_{\substack{j \neq 1 \\ j \neq i}}^n D_{ij}^k F_{kj}(u^{**}) v_{kj}^{**} \quad \text{for } i = 1, \dots, n.$$

Summing over i , we have

$$\sum_{i=1}^n v_{ki}^{**} = \sum_{i=1}^n F_{ki}(u^{**}) v_{ki}^{**}. \quad (\text{A18})$$

If the resident strategy is not ideal free then not all of terms $F_{ki}(u^{**})$ can be equal to 1, so at least one must be larger than 1 by (A18), and again we may assume that $F_{k1}(u^{**}) > 1$. The first entry in Lp_k from (A17) is

$$\left(1 - \sum_{j=2}^n \tilde{D}_{j1}^k \right) F_{k1}(u^{**}) p_{k1} + \sum_{j=2}^n \tilde{D}_{1j}^k F_{kj}(u^{**}) p_{kj} \quad (\text{A19})$$

and the i th entry for $i = 2, \dots, n$ is

$$\tilde{D}_{i1}^k F_{k1}(u^{**}) p_{k1} + \sum_{\substack{j=2 \\ j \neq i}}^n \tilde{D}_{ij}^k F_{kj}(u^{**}) p_{kj} + \left(1 - \sum_{\substack{j=1 \\ j \neq i}}^n \tilde{D}_{ji}^k \right) F_{ki}(u^{**}) p_{ki}. \quad (\text{A20})$$

As in the continuous time case, we can choose $p_{k1} = 1$, $p_{ki} = \varepsilon$ for $i = 2, \dots, n$, and \tilde{D}_{ij}^k positive and small in such a way that the expression in (A19) is larger than $(1 - \delta)F_{k1}(u^{**})$ for some $\delta > 0$ such that $(1 - \delta)F_{k1}(u^{**}) = 1 + \delta_0 > 1$. Also, the expressions in (A20) are larger than $\tilde{D}_{i1}^k F_{k1}(u^{**})$, which will be larger than $(1 + \delta_0)\varepsilon$ if $\varepsilon > 0$ is sufficiently small. Thus,

the i th component of $L(1, \varepsilon, \dots, \varepsilon)^T$ will be larger than $(1 + \delta_0)$ times the i th component of $(1, \varepsilon, \dots, \varepsilon)$, so by Lemma 1 the matrix L will have an eigenvalue larger than or equal to $1 + \delta_0$ with a nonnegative eigenvector. Thus, $p_k = 0$ is unstable with respect to such a strategy. Again, the only restrictions on the coefficients \bar{D}_{ij}^k are that some must be positive but small, so the invading strategy can be chosen to be ideal free relative to an arbitrary equilibrium u^{**} of the system (5) without dispersal or state switching. This completes the proof.