

Evolutionarily Stable Strategies in Multistage Biological Systems

T. L. VINCENT^{1*} and J. S. BROWN²

¹*Aerospace and Mechanical Engineering, University of Arizona, Tucson, AZ, USA,*

²*Department of Biological Sciences, University of Illinois at Chicago, Chicago, IL, USA*

(Received: 29 June 2001,

Accepted: 9 October 2001)

It has been shown that the ESS Maximum Principle, used to find evolutionarily stable strategies, is applicable to a large class of population dynamic models. These include both differential and difference equation models. To date, this principle has been used to find an evolutionarily stable strategy (ESS) for single-stage systems. That is, systems in which the density of all individuals of a given species or phenotype are represented by a scalar. There are many situations in which more detail is needed in order to properly model the state of a system (e.g. within a given species or phenotype, juveniles may effect the fitness of adults and vice versa). In this case, the density of a species or phenotype is more properly represented by a vector. Each component of the vector represents the density of a particular life stage. We show here that the ESS Maximum Principle may be extended to include multistage systems in a very natural way. In the scalar case, we have used a scalar G -function (fitness generating function) to model the system and formulate the ESS Maximum Principle. We have shown that it is necessary for the G -function, when evaluated at equilibrium, to take on a maximum with respect to the ESS strategy. Here we show, for multistage systems that a G -matrix may be used to model the system and the ESS Maximum Principle may be stated in terms of a G -matrix. In this case the real part of the dominant eigenvalue of the G -matrix, when evaluated at equilibrium, must take on a maximum with respect to the ESS strategy. Two multistage examples are given to illustrate use of the theory.

Keywords: ESS, multistage population, adaptive dynamics, adaptive landscape, life history evolution, ESS Maximum Principle, projection matrix, evolutionary game theory

1. Introduction

Traditional optimization approaches to life history evolution are giving way to game theoretic ones that consider density-dependence, frequency-dependence, and adaptive dynamics (Stearns, 2000). In all likelihood, demographic parameters relating to age- or stage-specific births and deaths are density dependent. Density-dependence raises issues regarding the most appropriate measure of

fitness (e.g. instantaneous growth rate, r , or net reproductive value, R_0 ?); (Dieckmann et al., 1998; Brommer, 2000; Metz and Gyllenberg, 2001) and places the adaptive dynamics of evolution within an explicit framework of population dynamics (Tuljapurkar, 1989; Ferriere and Clobert, 1992). The introduction of density-dependence into a life history model of evolution also introduces frequency-dependence (Kawecki, 1993). At the very least, the life history traits of other individuals influence population sizes that in turn influence an individual's prospects; and even more likely the traits of others directly influence an individual's prospects for survival and reproduction.

* Corresponding author: T. L. Vincent, Aerospace and Mechanical Engineering, University of Arizona, P. O. Box 210119 Tucson, AZ 85721-0119, USA, fax: 520 621-8191 E-mail: vincent@u.arizona.edu

Because of frequency-dependence, the evolution of life history traits is a game in which an individual's fitness (payoff) becomes influenced by its own trait value (its strategy), the trait values of others in the population (the strategies of others) and population size (Vincent and Brown, 1988). Advances in life history evolution as a game include the balance between growth and reproduction in size-structured populations (Calasina and Saldana, 1999; Heino and Kaitala, 1999), evolutionary effects on the complexity of population dynamics (Doebeli and Koella, 1995; Sinervo et al., 2000), evolution of reaction norms (Kisdi et al., 1998), and evolution in spatially-structured populations (Brown and Pavlovic, 1992; Holt and Gaines, 1992; Metz and Gyllenberg, 2001). All of these applications of evolutionary game theory, require an explicit or implicit fitness formulation that considers the successes of different strategies with respect to each other. Also, there must be some means of permitting evolutionary change either through adaptive dynamics or the invasion of rare alternative strategies.

Fitness formulations for non-structured populations are simpler than more complex life history of structured population models. The evolutionary game formulation can be a fitness generating function (Brown and Vincent, 1987; Vincent et al., 1996; Schoombie and Getz, 1998; Cohen et al., 1999; Schreiber et al., 2000; Holmgren and Getz, 2000), a fitness function that considers the fitness of a mutant strategy when immersed in a population composed of a particular resident strategy (Abrams et al., 1993; Geritz et al., 1998), or an explicit model of adaptive dynamics with evolutionary branching (Metz et al., 1996; Geritz et al., 1997). The fitness formulation determines the tools available for modeling evolutionary dynamics, convergent stable points, and for evaluating evolutionarily stable strategies (see Maynard Smith and Price, 1973). Here, we are interested in extending the tools of the fitness generating function (*G*-function) to life history and population-structured models of evolution.

Using a *G*-function to model evolutionary games has certain advantages, and it formalizes

other successful fitness function methods used in adaptive dynamics (see for example Marrow et al., 1992a, b; Dieckmann et al., 1995; Geritz, 1998; Cohen et al., 1999). For a general discussion of *G*-functions and comparable approaches see Abrams (2001a) and Cohen et al. (2001). The *G*-function uses a virtual variable to determine the fitness of a focal individual using a particular strategy against a particular biotic environment that includes the numbers and strategies of others. The *G*-function allows one to alter the dimensionality of the ecological model by increasing or decreasing the number of extant strategies (or species). The fitness consequences of an individual's strategy can be plotted and viewed as an adaptive landscape. The function can be used to identify strategies with maximal fitness (those resistant to invasion) and those that are convergent stable. The *G*-function can be used to apply the ESS Maximum Principle: at an ESS the *G*-function takes on a maximum with respect to the focal individual's strategy (Vincent and Brown, 1988; Vincent et al., 1996). And, the *G*-function can be used to model adaptive dynamics (Vincent et al., 1993).

Specifically, we will consider population dynamics that use projection matrices to model populations that are structured into discrete categories according to age, stage, gender, spatial location (e.g. metapopulation), or some other attribute. We let the elements of the projection matrix be influenced by density and by an evolutionary strategy. We show how the resulting game can produce a **G**-matrix that determines the fitness of a focal individual in the context of a particular biotic environment. Under the assumption of equilibrium population dynamics and a stable stage (or age) distribution, an explicit *G*-function emerges that represents the real part of the dominant eigenvalue of the **G**-matrix. We relate the **G**-matrix and *G*-function to the definition of an ESS, to the ESS maximum principle, to adaptive dynamics, and to techniques for finding the ESS. We illustrate its application using two examples: a simple stage-structured population, and a structured population spread over two habitats (Brown and Pavlovic, 1992; Holt and Gaines, 1992).

2. Population dynamics

We begin with the idea that there is an ecological community composed of n_x types or species.¹ Each species shares a similar life history that has n_s life stages. These stages may represent age classes (as in a standard life history table, Deevey, 1947), developmental stages (as in models with ontogenetic niche shifts, Werner and Gilliam, 1984), or states within a structured population (as in individuals occupying different habitats or places within a metapopulation, Hanski, 1991). Species are identified by their respective population sizes, \mathbf{x}_i , and strategies, \mathbf{u}_i . A species' population size includes the number of individuals of that species within each life history stage. A species' strategy is the species' phenotype for some relevant set of heritable traits. In the following, we show how these elements combine to model each species population dynamics as a population projection matrix that is both density- and frequency-dependent. Density-dependent in that the species population growth rate may be a function of the combined population sizes of all of the species, and frequency-dependent in that a species population growth rate may be influenced by the actual strategy values of each species.

Let the column vector

$$\mathbf{x} = [\mathbf{x}_1 \dots \mathbf{x}_{n_x}]^T$$

be a vector of densities associated with n_x species in a community. The superscript T denotes transpose. All vectors will be defined as column vectors. Assume that the density of each species, $i = 1, \dots, n_x$, is also a column vectors

$$\mathbf{x}_i = [x_{i1} \dots x_{in_s}]^T$$

made up of n_s life stages. For example, x_{23} is the population density of the third stage of species two. It follows that \mathbf{x} is an $n_x = n_s \times n_x$ dimensional column vector. Let the strategies used by species i be given by

¹ We are using what may be an unfamiliar subscript notation (e.g. n_x) in order to avoid a proliferation of symbols. The advantage of this notation is that it is mnemonic and hierarchical (e.g. n_x refers to the number of \mathbf{x} 's).

$$\mathbf{u}_i = [u_1 \dots u_{n_u}]^T$$

We allow the possibility, through evolution, for $\mathbf{u}_i = \mathbf{u}_j, j \neq i$. The strategies \mathbf{u}_i maybe scalars ($n_u = 1$) or vectors ($n_u > 1$). Collectively they form an $n_u \times n_x$ dimensional column vector

$$\mathbf{u} = [\mathbf{u}_1 \dots \mathbf{u}_{n_x}]^T.$$

Let each strategy vector \mathbf{u}_i , be distinct and be drawn from the same set of evolutionarily feasible strategies (as will be required later in our definition of evolutionarily identical individuals), which we will designate by

$$\mathbf{u} \in \mathcal{U} \quad (1)$$

where \mathcal{U} is a subset of an n_u dimensional strategy space that represents the feasible strategy choices after all (if any) constraints have been imposed. The meaning of (1) is that each strategy must satisfy

$$\mathbf{u}_i \in \mathcal{U} \quad i = 1, \dots, n_x.$$

For quantitative traits, the constraints are simply upper and lower bounds placed on the components of the strategy vector.

Let $I = (i - 1) n_s$ and $J = in_s$, in terms of this notation, we model the dynamics of species i 's population densities, \mathbf{x}_i , in terms of a system of differential equations of the form.

$$\begin{aligned} \dot{x}_{i1} &= x_{i1} H_{(I+1)1}(\mathbf{u}, \mathbf{x}) + x_{i2} H_{(I+1)2}(\mathbf{u}, \mathbf{x}) + \\ &\quad + \dots + x_{in_s} H_{(I+1)n_s}(\mathbf{u}, \mathbf{x}) \\ \dot{x}_{i2} &= x_{i1} H_{(I+2)1}(\mathbf{u}, \mathbf{x}) + x_{i2} H_{(I+2)2}(\mathbf{u}, \mathbf{x}) + \\ &\quad + \dots + x_{in_s} H_{(I+2)n_s}(\mathbf{u}, \mathbf{x}) \\ &\vdots = \vdots \\ \dot{x}_{in_s} &= x_{i1} H_{J1}(\mathbf{u}, \mathbf{x}) + x_{i2} H_{J2}(\mathbf{u}, \mathbf{x}) + \\ &\quad + \dots + x_{in_s} H_{Jn_s}(\mathbf{u}, \mathbf{x}) \end{aligned} \quad (2)$$

where $i = 1, \dots, n_x$ and the dot denotes differentiation with respect to time. For example, sup-

pose that there are two species, $n_x = 2$, each of which have three life stages, $n_s = 3$. Leaving off the arguments, the equations in this case would be written as

$$\begin{aligned}\dot{x}_{11} &= x_{11}H_{11} + x_{12}H_{12} + x_{13}H_{13} \\ \dot{x}_{12} &= x_{11}H_{21} + x_{12}H_{22} + x_{13}H_{23} \\ \dot{x}_{13} &= x_{11}H_{31} + x_{12}H_{32} + x_{13}H_{33} \\ \dot{x}_{21} &= x_{21}H_{41} + x_{22}H_{42} + x_{23}H_{43} \\ \dot{x}_{22} &= x_{21}H_{51} + x_{22}H_{52} + x_{23}H_{53} \\ \dot{x}_{23} &= x_{21}H_{61} + x_{22}H_{62} + x_{23}H_{63}.\end{aligned}$$

In matrix form, (2) may be written as

$$\dot{\mathbf{x}}_i = [\mathbf{H}_i(\mathbf{u}, \mathbf{x})]\mathbf{x}_i \quad (3)$$

where

$$H_i(u, x) = \begin{bmatrix} H_{(i+1)1}(\mathbf{u}, \mathbf{x}) & H_{(i+1)2}(\mathbf{u}, \mathbf{x}) & \cdots & H_{(i+1)n_s}(\mathbf{u}, \mathbf{x}) \\ H_{(i+2)1}(\mathbf{u}, \mathbf{x}) & H_{(i+2)2}(\mathbf{u}, \mathbf{x}) & \cdots & H_{(i+2)n_s}(\mathbf{u}, \mathbf{x}) \\ \vdots & \vdots & \ddots & \vdots \\ H_{j1}(\mathbf{u}, \mathbf{x}) & H_{j2}(\mathbf{u}, \mathbf{x}) & \cdots & H_{j n_s}(\mathbf{u}, \mathbf{x}) \end{bmatrix} \quad (4)$$

is the population projection matrix (Caswell, 1989; Stearns, 1992) for individuals of type i . We assume that $\mathbf{H}_i[\mathbf{u}, \mathbf{x}(t)]$ has continuous partial derivatives with respect to \mathbf{x} and \mathbf{u} .

2. Ecological stability

The population projection matrix is used to calculate the population dynamics both within the stages of each population and among the different species. Because population sizes must remain non-negative, yet finite, these dynamics must accurately model persistence. Only some species in the initial community will be able to coexist at positive population sizes. Even in isolation, limits to growth insures that no population can grow to infinite size. In the following, we characterize issues of non-zero population sizes, the persistence of a species, and the coexistence of several species. While persistence of a population simply requires population dynamics bounded from zero (including the possibility of limit cycles and chaotic dynamics), we will restrict our pres-

ent formalism to the case where the population dynamics achieve stable equilibria. With the condition of equilibrium population dynamics, we will conclude this section with a definition of fitness (per capita growth rate) for species i as the real part of the dominant eigenvalue of its projection matrix, $\mathbf{H}_i(\mathbf{u}, \mathbf{x})$.

Because population density is a non-negative quantity, the dynamical model given by (2) must produce trajectories of population density that satisfy $\mathbf{x}(t) \geq \mathbf{0}$ for all $t \geq \mathbf{0}$. For a given strategy vector \mathbf{u} and non-negative initial population densities $\mathbf{x}(\mathbf{0})$, the population trajectory, $\mathbf{x}(t)$, generated by (2) is n_x dimensional and must remain in the non-negative space, \mathbf{O} , defined as the set of points in the n_x dimensional real state space, R^{n_x} satisfying

$$\mathbf{O} = \{\mathbf{x} \in R^{n_x} \mid \mathbf{x} \geq \mathbf{0}\} \quad (5)$$

Since any realistic model will not generate solutions in which any component of \mathbf{x} becomes arbitrarily large, the system trajectories must remain in a bounded subset of \mathbf{O} . Many types of motion are possible, including stable motion to an equilibrium point, periodic orbits, and chaos (May, 1973, 1976). Here we will focus on conditions pertinent to stable equilibrium points.

We need to distinguish between species (one or more) whose equilibrium populations have at least one stage positive, $\mathbf{x}_i^* \succ \mathbf{0}$ (the notation \succ is used to imply that every component of the vector is $\geq \mathbf{0}$ with at least one component $> \mathbf{0}$) and those whose equilibrium populations have every component zero, $\mathbf{x}_i^* = \mathbf{0}$. We will refer to the first group through the indices $\mathbf{1} \dots n_c$ and the second group through the indices $n_c + \mathbf{1} \dots n_x$. This dichotomy of indices leads us to the following definition of an ecological equilibrium.

Definition 1 (Ecological Equilibrium) Given a strategy vector $\mathbf{u} \in \mathcal{U}$, a point $\mathbf{x}^* \in \mathbf{O}$ is said to be an ecological equilibrium point for (2) provided that

$$\dot{\mathbf{x}}_i = \mathbf{0}, \mathbf{x}_i^* > \mathbf{0} \text{ for } i = 1, \dots, n_c$$

$$\dot{\mathbf{x}}_i = \mathbf{0}, \mathbf{x}_i^* = \mathbf{0} \text{ for } i = n_c + 1, \dots, n_x$$

where n_c may take on any value between 1 and n_x .

We will now examine the stability of an ecological equilibrium point. For this, we will need to define points in the neighborhood of \mathbf{x}^* . The concept of a **ball** is useful in this regard a ball \mathcal{B} centered at x^* is the set of points in the n_x -dimensional state space, with a Euclidean norm, E^{n_x} , satisfying

$$\mathcal{B} = \{ \mathbf{x} \in E^{n_x} \mid \| \mathbf{x} - \mathbf{x}^* \| < \varepsilon \}$$

We will assume that for every strategy vector $\mathbf{u} \in \mathcal{U}$, an ecological equilibrium solution \mathbf{x}^* exists. For an ecological equilibrium point to be stable, we require that every trajectory which begins in a non-negative neighborhood of the point remain in that neighborhood for all t , and converge to the equilibrium as $t \rightarrow \infty$. If an ecological equilibrium point has this property, we will refer to it as an **ecologically stable equilibrium**.

Definition 2 (ESE) Given a strategy vector $\mathbf{u} \in \mathcal{U}$, an ecological equilibrium point $\mathbf{x}^* \in \mathbf{O}$ is said to be an **ecologically stable equilibrium (ESE)** if there exists a ball \mathcal{B} such that for any $\mathbf{x}(0) \in \mathbf{O} \cap \mathcal{B}$ the trajectory generated by (2) satisfies $\mathbf{x}(t) \in \mathbf{O}$ for all $t > 0$ and asymptotically approaches \mathbf{x}^* as $t \rightarrow \infty$. If the radius of the ball can be made arbitrarily large, the ecological equilibrium point is said to be a **global ESE**, otherwise it is said to be a **local ESE**.

ESE Theorem. Given $\mathbf{u} \in \mathcal{U}$, if an ecological equilibrium point \mathbf{x}^* is an ESE then all of the eigenvalues of the matrices

$$\mathcal{D} = \begin{bmatrix} \frac{\partial(H_1 \mathbf{x}_1)}{\partial \mathbf{x}_1} & \cdots & \frac{\partial(H_1 \mathbf{x}_1)}{\partial \mathbf{x}_{n_c}} \\ \vdots & \ddots & \vdots \\ \frac{\partial(H_{n_c} \mathbf{x}_{n_c})}{\partial \mathbf{x}_1} & \cdots & \frac{\partial(H_{n_c} \mathbf{x}_{n_c})}{\partial \mathbf{x}_{n_c}} \end{bmatrix}_{(\mathbf{u}, \mathbf{x}^*)} \quad (7)$$

$$\mathcal{H} = \begin{bmatrix} H_{n_c+1} & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & H_{n_x} \end{bmatrix}_{(\mathbf{n}, \mathbf{x}^*)} \quad (8)$$

must have non-positive real parts. Furthermore, if the eigenvalues of \mathcal{D} and \mathcal{H} have negative real parts, then \mathbf{x}^* is local ESE.

Proof: See the appendix for a proof.

We will now use this theorem to develop a lemma to be used in the proof of the ESS maximum principle in the next section.

Since $\dot{\mathbf{x}}_i = \mathbf{0}$ for all n_c at an ecological equilibrium point it follows from (3) that for there to exist a non-trivial solution for \mathbf{x}_i^* the following condition must hold.

$$\text{del}[H_i(\mathbf{u}, \mathbf{x}^*)] = \mathbf{0} \text{ for } i = 1, \dots, n_c. \quad (9)$$

This requirement and the \mathcal{H} part of the ESE Theorem maybe restated as a lemma using the concept of a **dominant eigenvalue**.

Let $\lambda_i [\lambda_{i1} \dots \lambda_{im_s}]$ be the eigenvector corresponding to $H_i|_{(\mathbf{u}, \mathbf{x}^*)}$ and **real** (λ_i) be the vector of real parts. Let **max**(**real** (λ_i)) be the value of the maximum components of the vector (while the maximum value is unique, there may be more than one component with this value). By definition, those components of the eigenvector that have this maximum value are dominant eigenvalues. Finally the following notation will be used

$$\text{dom}[H_i|_{(\mathbf{u}, \mathbf{x}^*)}] = \text{max}(\text{real}(\lambda_i)).$$

Lemma 1: At an ESE it is necessary that

$$\text{dom}[H_i|_{(\mathbf{u}, \mathbf{x}^*)}] = 0 \quad i = 1, \dots, n_c \quad (10)$$

$$\text{dom}\left[\mathbf{H}_i\Big|_{(\mathbf{u}, \mathbf{x}^*)}\right] \leq 0 \quad i = n_c + 1, \dots, n_x \quad (11)$$

Proof: For every $i = 1, \dots, n_c$, it follows from (9) that at least one eigenvalue of $\mathbf{H}_i\Big|_{(\mathbf{u}, \mathbf{x}^*)}$ must be zero. Because of the stability requirement, none of the remaining eigenvalues can have positive real parts. Hence the first condition follows. The ESE Theorem requires that all of the eigenvalues of \mathcal{H} must have non-positive real parts. The second condition follows from the fact that the eigenvalues of a diagonal block form are equal to the eigenvalues of each block.

In summary, for any community of n_x species, an ESE exists if one or more of the species (species $i = 1, \dots, n_c$) achieve stable population densities with $\mathbf{x}_i^* \succ \mathbf{0}$ while the other species ($i = n_c + 1, \dots, n_x$) have stable population densities with $\mathbf{x}_i^* = \mathbf{0}$. For species with positive population densities and zero population densities, respectively, $\text{dom}\left[\mathbf{H}_i\Big|_{(\mathbf{u}, \mathbf{x}^*)}\right]$ will be zero and non-positive. In fact, $\text{dom}\left[\mathbf{H}_i\Big|_{(\mathbf{u}, \mathbf{x}^*)}\right]$ provides a useful definition of fitness. Under a stable stage distribution, $\text{dom}\left[\mathbf{H}_i\Big|_{(\mathbf{u}, \mathbf{x}^*)}\right]$, defines fitness while \mathbf{H}_i defines the per capita growth rate of species i . This property will become useful in developing the \mathbf{G} -matrix and the G -function concepts below.

4. Evolutionary stability

In the above formulation, the number of extant strategies within the community determines the number of projection matrices and the dimensionality of the problem. However, to evaluate the consequences of alternative strategies (perhaps not yet present in the community) and to permit evolution by natural selection it becomes necessary to 1. have the ability to determine the fitness consequences to a focal individual of possessing some arbitrary strategy drawn from \mathcal{U} , and 2. have the flexibility to scale up or down the number of resident strategies within the population in response to invasions or extirpations of strategies. Other similar fitness formulations for evolutionary games achieve (1) by specifying a variable for a rare mutant strategy within the

existing community of strategies (Abrams et al., 1993; Dieckmann and Law, 1996) and (2) by establishing a new fitness function each time a new distinct strategy or species is added to the community (Geritz et al., 1997). However, the fitness generating function, G -function, allows one to achieve (1) and (2) seamlessly with a single formulation of the evolutionary game.

If individuals are evolutionarily identical, then a single \mathbf{G} -matrix can be used to describe all of the possible projection matrices that can be produced by all possible $\mathbf{u} \in \mathcal{U}$. Individuals with different strategies or of different species are evolutionarily identical (Vincent and Brown, 1989) if all individuals share the same strategy set \mathcal{U} and share the same ecological consequences of using strategies from \mathcal{U} (Vincent and Brown, 1984). For those readers familiar with the G -function method, the following definitions will be familiar. Indeed, if the \mathbf{G} -matrix is a scalar, then the following definitions reduce to those we have used before. That is, the \mathbf{G} -matrix is identical to the G -function. However, if \mathbf{G} is a true matrix, then there is an important difference. As we will see below, the \mathbf{G} -matrix is used to “generate” the \mathbf{H} matrices. However, we will still be able to obtain a G -function from the \mathbf{G} -matrix. This G -function will play the same role as before.

Definition 3 (G-Matrix) A matrix $\mathbf{G}(\mathbf{v}, \mathbf{u}, \mathbf{x})$ is said to be a \mathbf{G} -matrix for a group of evolutionarily identical types if

$$\mathbf{G}(\mathbf{v}, \mathbf{u}, \mathbf{x})\Big|_{\mathbf{v}=\mathbf{u}_i} = \mathbf{H}_i(\mathbf{u}, \mathbf{x}) \quad (12)$$

for all of the indices i corresponding to the various types or species in the group.

The \mathbf{G} -matrix does not fix *a priori* the number of different populations or species. The number of species (defined here as populations of individuals that do not interbreed with other populations), n_x , specifies the dimension of \mathbf{u} . Setting \mathbf{v} equal to an element of \mathbf{u} generates the specific projection matrix for that species.

In what follows we assume that the entire community of individuals (all n_x types) can be described in terms of a single \mathbf{G} -matrix. Of course, a given community would generally be composed of more than one evolutionarily identical group,

each with their own \mathbf{G} -matrix. This more general setting has been discussed in detail elsewhere (Vincent and Brown, 1989; Brown and Vincent, 1992).

The \mathbf{G} -matrix generates the population projection matrices for an individual, \mathbf{H}_i by selecting \mathbf{u}_i from the vector \mathbf{u} and setting \mathbf{v} equal to that individual's strategy, \mathbf{u}_i . In terms of the \mathbf{G} -matrix, the system dynamics (2) may be written as

$$\dot{\mathbf{x}}_i = \mathbf{G}(\mathbf{v}, \mathbf{u}, \mathbf{x}) \Big|_{\mathbf{v}=\mathbf{u}_i} \mathbf{x}_i. \quad (13)$$

If we assume that the system dynamics achieve an ESE, then we can distinguish between those strategies that survive at positive population sizes and those that have gone extinct. We will refer to combination of strategies among the survivors as a **coalition vector**. With this in mind we define:

Definition 4 (coalition vector) If for the system (2) there exists an ecological equilibrium point \mathbf{x}^* [$x_i^* > 0$ for the indices $1, \dots, n_c \geq 1$ and $x_i^* = 0$ for the indices $n_c + 1, \dots, n_x$] corresponding to the strategy vector $\mathbf{u} \in \mathcal{U}$, then the composite of the strategies for the first group of indices is called a coalition vector, $\mathbf{u}_c = [\mathbf{u}_1, \dots, \mathbf{u}_{n_c}]$, and the composite strategies of the second group of indices is designated by the vector $\mathbf{u}_m = \mathbf{u}_{n_c+1}, \dots, \mathbf{u}_{n_x}$.

A coalition vector describes an inclusive set of strategies that can persist together, but it may not be exclusive. By adding different strategies to the initial vector of strategies, the resulting coalition vector may change in size (more or fewer strategies) and/or composition. A coalition vector may not be evolutionarily stable as per the introduction. It may be possible for a novel strategy to invade and change its character. In the following definition of the ESS, we identify the subset of coalition vectors that are simultaneously inclusive and exclusive.

Definition 5 (ESS) A coalition vector \mathbf{u}_c is said to be an evolutionarily stable strategy (ESS) for the equilibrium point \mathbf{x}^* if, for all $n_x > n_c$ and all strategies $\mathbf{u}_m \in \mathcal{U}$, the

equilibrium point \mathbf{x}^* is an ecologically stable equilibrium (ESE).

The ESS will be a local ESS if \mathbf{x}^* is a local ESE and the ESS will be a global ESS if \mathbf{x}^* is a global ESE. Note that under this definition an ESS must be an ESE, but given an arbitrary \mathbf{u}_c , with an ecologically stable equilibrium \mathbf{x}^* , it does not imply that \mathbf{u}_c will be an evolutionarily stable strategy.

Thus the ESS is made up of the same number of species as there are strategies contained in the coalition vector \mathbf{u}_c . However, the vector \mathbf{u}_m maybe made up either of strategies corresponding to species different from those in the coalition vector or strategies corresponding to phenotypes of the species in the coalition vector or some combination of both. From this perspective, the definition requires stability with respect to both intraspecific and interspecific interactions. Furthermore, this definition of an ESS insures that the ESS is convergent stable (see Cohen et al., 1999) and is resistant to invasion by rare alternative strategies (Brown and Vincent, 1987). We have found this ESS definition to be useful because it is inclusive. It keeps the ESS concept abreast of new discoveries regarding the properties of evolutionary equilibria and reduces the proliferation of terms regarding the different stability properties inherent in the outcomes of natural selection under frequency dependent selection (Eshel, 1996).

ESS Maximum Principle. Let $\mathbf{G}(\mathbf{v}, \mathbf{u}, \mathbf{x})$ be the \mathbf{G} -matrix for a community. If \mathbf{u}_c is an ESS, then $\text{dom}[\mathbf{G}(\mathbf{v}, \mathbf{u}, \mathbf{x}^*)]$ must take on a maximum with respect to $\mathbf{v} \in \mathcal{U}$ at $\mathbf{u}_1, \dots, \mathbf{u}_{n_c}$.

Proof: Since \mathbf{x}^* is an ecologically stable equilibrium, the dominant eigenvalue of $\mathbf{G}(\mathbf{v}, \mathbf{u}, \mathbf{x}^*)$ must be zero. Let $n_x > n_c$, it follows from Lemma 1 that for any $i = 1, \dots, n_c$ and any $j = n_c + 1, \dots, n_x$

$$0 = \text{dom}[\mathbf{H}_i(\mathbf{u}, \mathbf{x}^*)] \geq \text{dom}[\mathbf{H}_j(\mathbf{u}, \mathbf{x}^*)]$$

which, from the definition of G , implies

$$0 = \text{dom}[\mathbf{G}(\mathbf{u}_i, \mathbf{u}, \mathbf{x}^*)] \geq \text{dom}[\mathbf{G}(\mathbf{u}_j, \mathbf{u}, \mathbf{x}^*)]$$

which proves the theorem.

We finally arrive at a natural definition of fitness. For a given \mathbf{u} and \mathbf{x} we first define a fitness generating function as:

$$G(\mathbf{v}, \mathbf{u}, \mathbf{x}) = \text{dom}[G(\mathbf{v}, \mathbf{u}, \mathbf{x})]$$

with the fitness of individuals using the strategy \mathbf{u} defined by

$$H_i(\mathbf{u}, \mathbf{x}) = G(\mathbf{v}, \mathbf{u}, \mathbf{x}) \Big|_{\mathbf{v}=\mathbf{u}_i}.$$

Working in terms of the G -function $G(\mathbf{v}, \mathbf{u}, \mathbf{x})$ has several advantages over using the \mathbf{G} -matrix directly. In some cases $G(\mathbf{v}, \mathbf{u}, \mathbf{x})$ can be used to solve analytically for a potential ESSs and it can be used to plot the adaptive landscape for any given fixed values of \mathbf{u} and \mathbf{x} . The adaptive landscape is defined as the relationship between $G(\mathbf{v}, \mathbf{u}, \mathbf{x})$ and \mathbf{v} . As we will see below, it shows the fitness consequences to a focal individual of using any arbitrary strategy within the current community. When an ESS exists the adaptive landscape is then determined from $G(\mathbf{v}, \mathbf{u}, \mathbf{x}^*)$ so that it must have a global peak at each strategy of the ESS (in accord with the ESS Maximum Principle) and at each of these peaks the population has a zero per capita growth rate. The adaptive landscape is also the surface along which adaptive dynamics occur.

5. Adaptive dynamics

In order for evolution to take place there must be a process that introduces novel species into the community (usually as rare mutant strategies) and/or a strategy dynamic that permits evolutionary change in the mean strategy value of the existing species within the community. The introduction of species permits invasion-structuring of the community (Roughgarden, 1987) and strategy dynamics is adaptive dynamics (Metz et al., 1996). Invasion-structuring provides the most flexibility for natural selection to explore the adaptive landscape because, in theory, novel strategies can be introduced as new species from anywhere in the strategy set. In practice, however, new mutations arise within species and much evolutionary change involves changes in the strategy composition of an interbreeding species. When the heritable variation in strategy values

exists within a particular interbreeding species, the distribution of strategies results in adaptive dynamics (Dieckmann and Law, 1996). With this heritable variation, \mathbf{u}_i simply characterizes the mean strategy values of species i and \mathbf{x}_i is the sum of the densities of all of the strategies of that species.

Adaptive dynamics have been derived for evolutionary games in unstructured population models. When a G -function exists, we obtain an adaptive dynamic that is analogous to those derived for non-matrix fitness generating functions (Vincent et al., 1993; Cohen et al., 1999):

$$\begin{aligned} \dot{\mathbf{u}}_i &= k_i \frac{\partial G(\mathbf{v}, \mathbf{u}, \mathbf{x})}{\partial \mathbf{v}} \Big|_{\mathbf{v}=\mathbf{u}_i} = \\ &= k_i \frac{\partial \text{dom}[G(\mathbf{v}, \mathbf{u}, \mathbf{x})]}{\partial \mathbf{v}} \Big|_{\mathbf{v}=\mathbf{u}_i} = \end{aligned} \quad (14)$$

where k_i is an evolutionary speed term that increases with the amount of heritable variation within the population (it combines heritability of the trait and the existing amount of additive genetic variability) and $\frac{\partial G}{\partial \mathbf{v}}$ is the slope of the adaptive landscape evaluated at the mean strategy of the species.

The \mathbf{G} -matrix provides a general formulation of an evolutionary game in age-, stage- or population-structured models. The ESS maximum principle, $\text{dom}[G(\mathbf{v}, \mathbf{u}, \mathbf{x})]$, and adaptive dynamics provide tools for solving for the game's ESSs and for considering the likely consequences of natural selection acting on the game.

6. Elementary example

The life cycle in the following example does not conform directly to actual taxa, rather it illuminates features of the theory (the second example applies to an actual question in evolutionary ecology). In this life cycle, the creature has two stages: a competitive reproductive stage, and a non-competitive non-reproductive stage. An organism in the reproductive stage produces offspring (immediately recruited into this reproductive stage), suffers mortality that increases with the density of reproductives, and has some probability

of becoming non-reproductive. Individuals in the non-reproductive stage suffer mortality that increases with the density of reproductives, and have some probability of becoming reproductive (births, deaths and transition probabilities are independent of the density of non-reproductives). Let a scalar-valued strategy of an individual affect two aspects of the life cycle. First, an individual's likelihood of shifting from reproductive to non-reproductive increases linearly with its strategy. Second, this same strategy of the individual influences its reproduction rate when it is in the reproductive stage. We let the strategies of others weight the mortality effect that reproductives have on those in the reproductive stage.

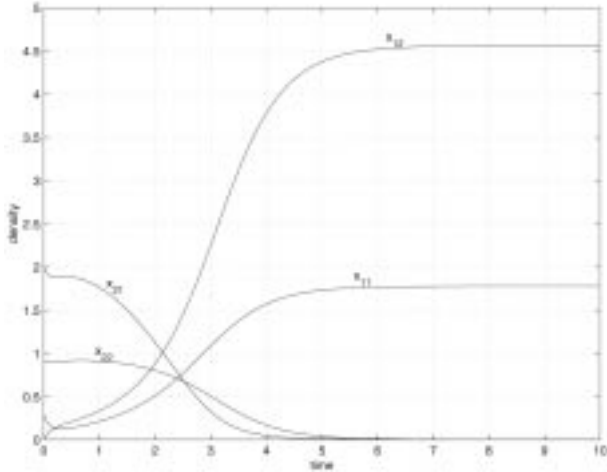


FIG. 1. A multistage ESS

We incorporate these assumptions into the following model of population growth. The model describes the rate of change in population density of stage 1 (reproductives) and stage 2 (non-reproductives) of the i th species (as influenced by \mathbf{u} and \mathbf{x}):

$$\dot{x}_{i1} = \left(f(u_i) - \sum_{j=1}^{n_x} u_j x_{j1} \right) x_{i1} + u_i x_{i2}$$

$$\dot{x}_{i2} = u_i x_{i1} - \left(\sum_{j=1}^{n_x} x_{j2} \right) x_{i2}$$

The \mathbf{G} -matrix for this case is given by

$$\mathbf{G}(\nu, \mathbf{u}, \mathbf{x}) = \begin{bmatrix} f(\nu) - \sum_{j=1}^{n_x} u_j x_{j1} & \nu \\ \nu & - \left(\sum_{j=1}^{n_x} x_{j1} \right) \end{bmatrix}.$$

Note how the \mathbf{G} -matrix highlights the effects on fitness of the focal individual's strategy, ν , the strategies of others, $\mathbf{u} = (u_1, \dots, u_{n_x})$, and the effects of population densities, $\mathbf{x} = (x_1, \dots, x_{n_x})$. Since the \mathbf{G} -matrix is symmetric, the eigenvalues will be real.

Let the relationship between reproduction rate and the individual's strategy conform to a downward parabola that reaches a peak value at $\nu = 2$:

$$f(\nu) = -1 + 4\nu - \nu^2$$

The strategy $\nu = 2$ would maximize fitness if the model were density-independent (independent of \mathbf{x}) and frequency-independent (independent of \mathbf{u}). In this example, the \mathbf{G} -matrix is density- and frequency-dependent.

We can now seek an ESS composed of a coalition of one species. We do this by setting $n_x = 1$. Furthermore, we can write $\mathbf{G}^*(\nu)$ if we assume that the species population size is at equilibrium:

$$\mathbf{G}(\nu, \mathbf{u}, \mathbf{x}^*) = \mathbf{G}^*(\nu) = \begin{bmatrix} -1 + 4\nu - \nu^2 - u_1 x_{11}^* & \nu \\ \nu & -x_{11}^* \end{bmatrix}$$

By solving for the dominant eigenvalue (using MAPLE) yields the G^* -function:

$$G^*(\nu), \text{ dom}[G^*(\nu)] = -\frac{1}{2} + 2\nu - \frac{1}{2}\nu^2 - \frac{1}{2}u_1 x_{11}^* + \frac{1}{2}\sqrt{A+B}$$

where

$$A = 1 - 8\nu u_1 x_{11}^* - 8\nu + 22\nu^2 + 2\nu^2 u_1 x_{11}^* + (x_{11}^*)^2 - 8\nu^3 - 2x_{11}^* \nu^2$$

$$B = v^4 - 2x_{11}^* + 8vx_{11}^* + 2u_1x_{11}^* - 2u_1(x_{11}^*)^2 + u_1^2(x_{11}^*)^2.$$

We can apply the conditions of the ESS Maximum Principle by setting $\frac{\partial G^*}{\partial v} = \mathbf{0}$ which yields the following solution

$$v = \frac{1}{4}u_1x_{11}^* - \frac{1}{4}x_{11}^* + \frac{3}{2} + \frac{1}{4}\sqrt{u_1^2(x_{11}^*)^2 - 2u_1(x_{11}^*)^2 - 4u_1x_{11}^* + (x_{11}^*)^2 + 4x_{11}^* + 20}$$

The ESE equilibrium conditions x_{11}^* and x_{22}^* yield

$$(-1 + 4v - v^2 - u_1x_{11}^*)x_{11}^* + vx_{12}^* = 0$$

$$vx_{11}^* - x_{11}^*x_{12}^* = 0.$$

For an ESS with a single strategy, set $v = u_1$ in the above three equations and solving these equations simultaneously

$$u = \frac{1}{4}u_1x_{11}^* - \frac{1}{4}x_{11}^* + \frac{3}{2} + \frac{1}{4}\sqrt{u_1^2(x_{11}^*)^2 - 2u_1(x_{11}^*)^2 - 4u_1x_{11}^* + (x_{11}^*)^2 + 4x_{11}^* + 20}$$

$$0 = (-1 + 4u_1 - u_1^2 - u_1x_{11}^*)x_{11}^* + u_1x_{12}^*$$

$$0 = u_1x_{11}^* - x_{11}^*x_{12}^*$$

yielding the result

$$x_{11}^* = \frac{3}{4} + \frac{1}{4}\sqrt{17} = 1.7808$$

$$x_{12}^* = \frac{5}{2} + \frac{1}{2}\sqrt{17} = 4.5616$$

$$u_1 = \frac{5}{2} + \frac{1}{2}\sqrt{17} = 4.5616.$$

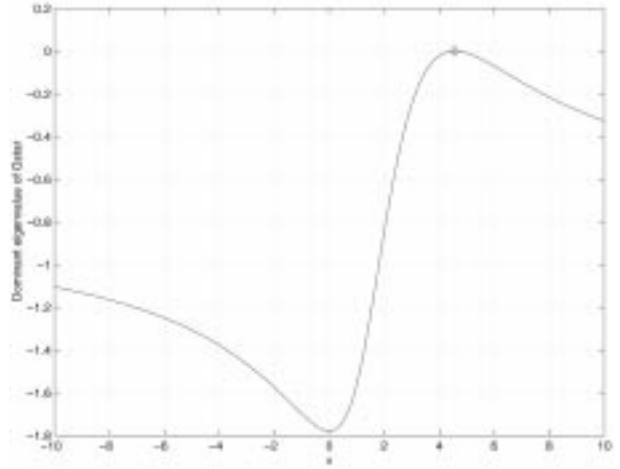


FIG. 2. The dominant eigenvalue takes on a maximum at the ESS

The solution $u_1 = \mathbf{4.5616}$ can be shown to be the ESS in two ways as is demonstrated in Figures 1 and 2. When the solution, u_1 , is played against a fixed strategy $u_2 = \mathbf{1}$, the mutant strategy (even when introduced at higher numbers) dies out with time (Fig. 1). In accordance with the ESS definition, we use simulations to show that the mutants die off irrespective of their strategies or the initial number of different mutants seeded into the population. This resistance to invasion occurs because the solution occupies a global peak on the adaptive landscape at the ESS (Fig. 2). Furthermore, the solution can be shown to be convergent stable through simulation of the strategy and population dynamics; adaptive dynamics on strategy values in the neighborhood of the ESS return the species' strategy to the ESS. In this example, the ESS appears to be global for any initial strategy value \mathbf{u} , any initial population size, $\mathbf{x}(\mathbf{0}) > \mathbf{0}$, and any number of initial species, n_x .

While this elementary model may not fit or address any specific question in life history evolution, it does show how a variety of life history scenarios can generate a similar projection matrix. We chose to interpret the stages as a reproductive vs. non-reproductive stage. Alternatively, these could have been population densities within a source and sink habitat. The next example takes up directly this question of ESSs under migration and gene flow.

7. Gene flow

The following model follows the structure of (Brown and Pavlovic, 1992) and (Meszina and Czibula, 1998). It shows how a **G**-matrix addresses evolution within structured metapopulations (Metz and Gyllenberg, 2001). Imagine two habitats coupled by migration that is a fixed property of the organism's ecology and environment (the individuals cannot control their migration rates). This allows the model to provide an evolutionary game perspective on gene flow models from population and quantitative genetics (Kisdi and Geritz, 1999). The model's intellectual roots trace back to (Levins, 1968) question regarding the evolution of generalists and specialists within fine (high migration rate) or coarse grained (low migration rate) environments. The model could be applied to any number of habitats and any functional form for competitive interactions among individuals within patches. Here, we will assume that population interactions within each of two habitats conform to Lotka–Volterra competition equations and that movement among habitats occurs via a density independent and fixed migration rate.

The strategy of an individual influences the carrying capacity that it would experience in habitats 1 and 2. The strategy of others is assumed to have no direct influence on an individual's fitness. Density-dependence occurs via competition among individuals within a habitat. We assume that all inter- and intra-specific competition coefficients equal one. In summary, imagine two habitats where populations grow logistically, there is migration between patches, and carrying capacity is influenced by the individual's strategy. There is explicit dependence on population size and the focal individual's strategy, but not on the strategies of others. Changes in the population size of species i within habitats **1** and **2**, respectively, can be given as:

$$\dot{x}_{i1} = \left[\frac{r}{K_1(u_i)} \left(K_1(u_i) - \sum_{j=1}^{n_x} x_{j1} \right) - m \right] x_{i1} + m x_{i2}$$

$$\dot{x}_{i2} = \left[\frac{r}{K_2(u_i)} \left(K_2(u_i) - \sum_{j=1}^{n_x} x_{j2} \right) - m \right] x_{i2} + m x_{i1}$$

Let a normal curve describe the relationship between carrying capacity and the individual's strategy. Habitats can vary in the maximum attainable carrying capacity, B_j , and in the strategy value that achieves this maximum, γ_j :

$$K_j(v) = B_j \exp \left(- \frac{(\gamma_j - v)^2}{2\sigma_k^2} \right)$$

Under this functional relationship between carrying capacity and strategy, habitats vary in quality based on the value of B_j . If the strategy that maximizes K in the two habitats vary, $\gamma_1 \neq \gamma_2$, then an individual's strategy represents a trade-off between fitness in habitat 1 and fitness in habitat 2. Assuming that $\gamma_1 > \gamma_2$, then $u_i \in [\gamma_1, \gamma_2]$ represent the active edge of Levins' fitness set (those strategies that actually trade-off K_1 and K_2). All other values for u are on the interior of the fitness set in that they could never be favored by natural selection because such strategies can be replaced by those that simultaneously improve fitness in both habitats (Levins, 1962, 1968).

The population projection **G**-matrix in this case is given by

$$\mathbf{G}(v, \mathbf{u}, \mathbf{x}) = \begin{bmatrix} \frac{r}{K_1(v)} \left(K_1(v) - \sum_{j=1}^{n_x} x_{j1} \right) - m & m \\ m & \frac{r}{K_2(v)} \left(K_2(v) - \sum_{j=1}^{n_x} x_{j2} \right) - m \end{bmatrix}$$

Here the fitness of a focal individual appears directly influenced by its own strategy the population densities of each species and the distribution of each species' population among the two habitats. While the strategies of others do not directly influence fitness they will matter, and frequency-dependence enters the model via the effect of each species strategy on population sizes and distributions (see Heino et al., 1998, for a discussion of frequency-dependent selection).

The dominant eigenvalue of this **G**-matrix provides a simple *G*-function. Unlike the elementary example, an analytical solution to an ESS is very involved. It is easier to use strategy dynamics to obtain convergent stable points by integrating equations (13) and (14). The adaptive landscape at these convergent stable points can then be inspected to reveal whether they conform to the ESS Maximum Principle and are ESS.

Consider the following parameters: $r = \mathbf{0.2}$, $B_1 = \mathbf{100}$, $B_2 = \mathbf{75}$, $m = \mathbf{0.1}$, $\gamma_1 = \mathbf{0}$, $\gamma_2 = \mathbf{1}$, $\text{CCC} = \mathbf{4}$. Using a single strategy with an initial value of $u(\mathbf{0}) = \mathbf{2}$, with initial conditions for the two stages $\mathbf{x}(\mathbf{0}) = [\mathbf{10} \ \mathbf{20}]^T$ and “speed” term $k = \mathbf{0.5}$, we obtain the equilibrium solution $u^* = \mathbf{0.4629}$ and $\mathbf{x}^* = [\mathbf{90.6423} \ \mathbf{78.1309}]^T$. Figure 3 illustrates that this equilibrium value for u^* is indeed an ESS.

In this model m , is a bifurcation parameter determining whether the ESS has a single compromise strategy or whether there is a two strategy ESS. For example, keeping all the parameters the same as above but changing $m = \mathbf{0.005}$ and rerunning the simulation with the same initial conditions we obtain the equilibrium solution $u^* = \mathbf{0.3540}$ and $\mathbf{x}^* = [\mathbf{97.7845} \ \mathbf{71.8254}]^T$. However this solution is not an ESS as illustrated in Figure 4. In fact, if only a single species is allowed to evolve, it will evolve to a local minimum on the adaptive landscape.

This suggests the possibility of an ESS coalition of two. Once again we integrate equations (14) and (15) with the same parameters as before, but with

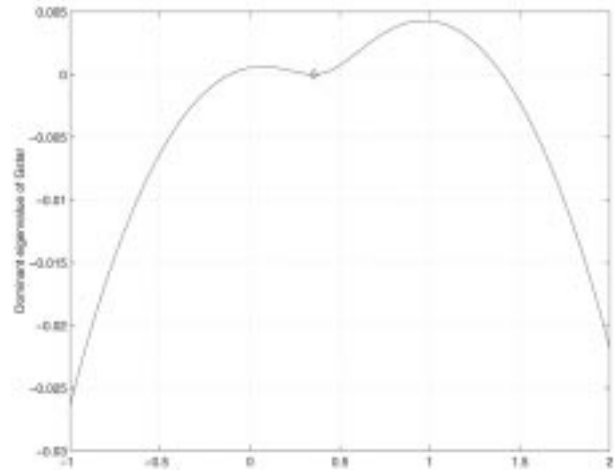


FIG. 4. With $m = \mathbf{0.005}$ a single strategy evolves to a local minimum on the adaptive landscape

initial conditions $u_1(\mathbf{0}) = \mathbf{0.3540}$, $u_2(\mathbf{0}) = \mathbf{0.35}$, $\mathbf{x}_1(\mathbf{0}) = [\mathbf{97.7845} \ \mathbf{71.8254}]^T$, $\mathbf{x}_2(\mathbf{0}) = [\mathbf{5} \ \mathbf{3}]^T$ and $k_1 = k_2 = \mathbf{0.5}$. These initial conditions were chosen to simulate “speciation” from a minimum in the *G*-functions as discussed in Cohen et al. (1999). The equilibrium solutions $u_1^* = \mathbf{0.0440}$, $\mathbf{x}_1^* = [\mathbf{86.6590} \ \mathbf{17.5590}]^T$ and $u_2^* = \mathbf{0.9561}$, $\mathbf{x}_2^* = [\mathbf{11.3252} \ \mathbf{55.9256}]^T$ are obtained. We see from Figure 5 that the ESS is a coalition of two.

In this model, σ_k can also play the role of a bifurcation parameter. For example keeping all the parameters the same as above, except increasing $m = \mathbf{0.05}$, we once again obtain a coalition of one ESS with $u^* = \mathbf{0.4240}$. $\mathbf{x}^* = [\mathbf{93.2731}$

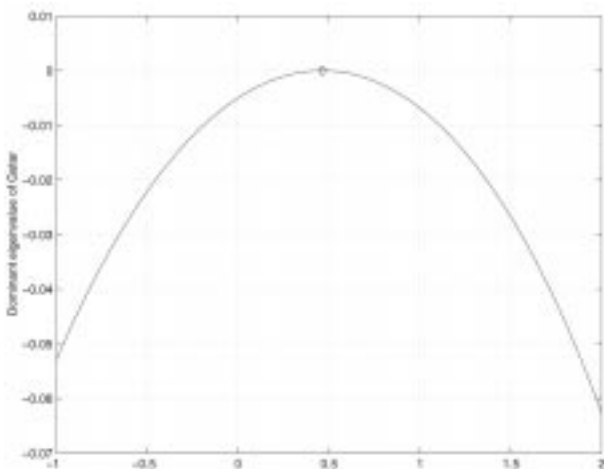


FIG. 3. With $m = \mathbf{0.1}$ the ESS is a coalition of one

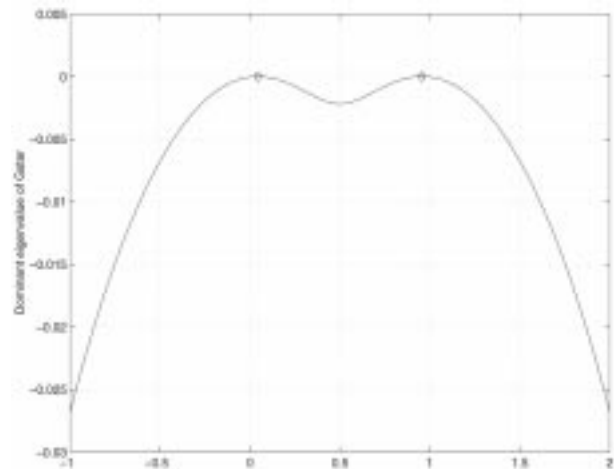


FIG. 5. With $m = \mathbf{0.005}$ the ESS is a coalition of two

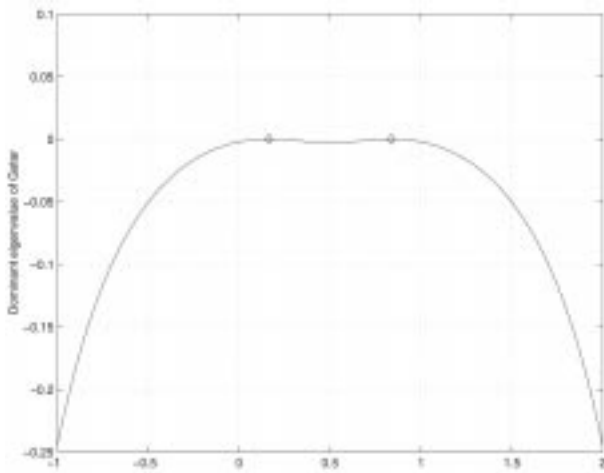


FIG. 6. Decreasing σ_k can also result in an ESS coalition of two

$76.0123 \mathbf{j}^T$. Decreasing $\sigma_k = 0.75$, keeping all other parameters the same results in an ESS coalition of two with $u_1^* = 0.8369$, $\mathbf{x}_1^* = [12.5865 \ 38.4630 \mathbf{j}^T$ and $u_2^* = 0.1631$, $\mathbf{x}_2^* = [68.6518 \ 22.4612 \mathbf{j}^T$ as illustrated in Figure 6.

8. Discussion

We extend the idea of a fitness generating function, G -function, to include life history models of evolution. This extension allows for the determination of ESSs for multistage systems by using the population projection matrix to form a \mathbf{G} -matrix. The elements of the \mathbf{G} -matrix may be influenced by the strategy of a focal individual, the strategies of others in the population, and each strategy's population density. In this form, life history evolution becomes a game that can incorporate frequency- and density-dependent selection, adaptive dynamics, adaptive speciation, and coevolution among species. This modeling applies well to projection matrices where the different stages (rows and columns of the matrix) represent typical age classes, gender, reproductive states, ontogenetic niches, and subpopulations within a metapopulation. The theory to life history evolution as described by the \mathbf{G} -matrix is more inclusive and has parallels to works modeling age and/or size at maturity (Berrigan and Koella, 1994), growth versus reproduction (Calsina and

Saldana, 1999), and evolution of dispersal (Metz and Gyllenberg, 2001). The \mathbf{G} -matrix allows extensions of the ESS definition, adaptive dynamics, and the adaptive landscape to a broader class of problems.

The determination of a \mathbf{G} -matrix begins with an ecological scenario involving populations of one or more species whose populations can be subdivided into distinct stages. Next, one uses the scenario and population structure to build a projection matrix that describes the population dynamics of each stage. The elements of this matrix are likely density-dependent. Then, one adds an evolutionary dimension to the model by letting an evolutionary strategy influence the elements of the projection matrix. Finally, a \mathbf{G} -matrix is formulated for all individuals, populations and species that share the same strategy set, the same life history stages, and the same ecological consequences of possessing a particular strategy (we call these individuals evolutionarily identical). The \mathbf{G} -matrix comes about by expressing the explicit relationship between the elements of the projection matrix and the strategy of a focal individual, v , the strategies of others, \mathbf{u} , and their population sizes, \mathbf{x} .

Holt and Gaines (1992) also use dominant eigenvalued when modeling evolution of specialization under source-sink population dynamics, and, similarly, Blarer and Doebeli (1996) used r from Euler's equation in modeling the evolutionary trade-off between growth and reproduction. As a G -function one can apply prior results and tools of evolutionary game theory, namely those of adaptive dynamics, the ESS Maximum Principle, and adaptive landscapes. Combining these tools becomes an effective means of evaluating whether a strategy or coalition of strategies is ESS. Inspection of the adaptive landscape evaluated at the ESS will reveal whether it is a global maximum and hence, resistant to invasion. And, strategy dynamics can be used to verify convergence stability when the values of strategies are perturbed from their ESS values. Adaptive dynamics can be used to produce convergent stable points that may not be ESS. They may either be local maxima on the adaptive landscape (Cohen et al., 1999) or evolutionarily stable minima (Abrams et al., 1993b) that may be conducive to adaptive speciation (Brown and

Pavlovic, 1992; Dieckmann and Doebeli, 1999; Geritz and Kisdi, 2000) and evolutionary branching (Geritz et al., 1998).

We considered two examples to illustrate the application of a **G**-matrix to life history evolution. The elementary example shows how an analytic solution of the ESS is possible when there are equilibrium population dynamics and the dominant eigenvalue of the **G**-matrix is used as a *G*-function. In the example the ESS always has a single strategy that is global (with respect to initial population sizes).

The second example examines (Levins, 1968) original problem of evolving generalists or specialists in heterogeneous environments. The two stages represent metapopulation structure where individuals reside in two habitats. An evolutionary strategy represents a fitness trade-off between performance in the two habitats. As anticipated from Levins (1968), fine- and coarse-grained environments (decreasing the migration rate among habitats increases grain size) select for an ESS with one generalist species and two specialist species, respectively. Furthermore, when the ESS has two species, adaptive dynamics operating on a single species will achieve an evolutionarily stable minima that encourages adaptive speciation and evolution to the ESS (Brown and Pavlovic, 1992; Meszena et al., 1997). This two habitat model shows how gene flow per se is not a force of evolution. Rather, migration between patches become part of the ecological circumstances to which natural selection responds. The resulting ESS balances the strategy's experience of each habitat. So, while an individual is never fully adapted to its current habitat, its strategy represents an adaptation to the statistical experience that the strategy can expect to have of the two habitats. The model also offers some attractive prospects by increasing the number of habitats (possibility for revisiting stepping stone, ring, and random models of flow), and altering the within habitat competition function to explicitly consider the influence of others' strategy (Vincent et al., 1993).

What if the population dynamics do not produce stable equilibria? The population dynamics within a life history model may produce limit cycles, chaotic dynamics or may be subject to stochasticity

(Tuljapurkar, 1989). The **G**-matrix still applies and can model the population dynamics. Furthermore, the ESS concept of resistance to invasion and convergence stability still apply. However, the definitions for the ESE, ESS, ESS Maximum Principle and adaptive dynamics do not apply. Evolutionary change can still be modeled by periodically introducing rare alternative strategies into the community. The community becomes invasion structured if these novel strategies are drawn from the strategy set without regard to the resident strategies. Or, a kind of adaptive dynamic is introduced when novel strategies are introduced into some small neighborhood of resident strategies. Run for long enough, these procedures reveal strategies or coalitions of strategies resistant to invasion. Convergence stability can be demonstrated by showing that populations with strategies near but not at the ESS can be invaded by strategies closer to the strategy values of the ESS.

Even with non-equilibrium or stochastic dynamics it is possible to recover and use adaptive landscapes and strategy dynamics along the landscape. If the dynamics result in a periodic solution, then a compound **G**-matrix can be modeled in a manner analogous to using geometric mean fitness as a *G*-function in simpler evolutionary games with periodic dynamics (Vincent and Brown, 1987). With stochastic dynamics and life history evolution (Schmidt et al., 2000) provide a lead. In a two habitat model with migration as the evolutionary strategy, the population dynamics were run for sufficiently long to produce a complete spectrum of population sizes for some resident strategy. The resident strategy and the sequence of population sizes could then be used as a standard. The adaptive landscape for this standard could be generated by evaluating the geometric mean fitness of a focal individual's strategy, v , experiencing the standard. The resulting landscape shows how the resident strategy compares to rare alternative strategies. If not ESS, then the number or positions of the strategies can be changed to reflect adaptive speciation or adaptive dynamics along the gradient of the landscape.

References

- ABRAMS, P. A. (2001a): Adaptive dynamics: Neither F nor G. *Evolut. Ecol. Res.* **3**:369–373.
- ABRAMS, P. A. (2001b): Modelling the adaptive dynamics of traits involved in inter- and intraspecific interactions: An assessment of three methods. *Ecol. Lett.* **4**:166–175.
- ABRAMS, P. A., HARADA, Y. and MATSUDA, H. (1993): On the relationships between quantitative genetics and ESS. *Evolution* **47**:982–985.
- ABRAMS, P. A., MATSUDA, H. and HARADA, Y. (1993): Evolutionary unstable fitness maxima and stable fitness minima of continuous traits. *Evol. Ecol.* **7**:465–487.
- BERRIGAN, D. and KOELLA, J. C. (1994): The evolution of reaction norms – simple models for age and size at maturity. *J. Evol. Biol.* **7**:549–566.
- BLARER, A. and DOEBELI, M. (1996): Heuristic optimization of the general life history problem: A novel approach. *Evol. Ecol.* **10**:81–96.
- BROMMER, J. E. (2000): The evolution of fitness in life-history theory. *Biol. Rev. Camb. Philos. Soc.* **75**:377–404.
- BROWN, J. S. and PAVLOVIC, N. B. (1992): Evolution in heterogeneous environments: Effects of migration on habitat specialization. *Evol. Ecol.* **6**:360–382.
- BROWN, J. S. and VINCENT, T. L. (1987): A theory for the evolutionary game. *Theor. Popul. Biol.* **31**:140–166.
- BROWN, J. S. and VINCENT, T. L. (1992): Organization of predator-prey communities as an evolutionary game. *Evolution* **46**:1269–1283.
- CALSINA, A. and SALDANA, J. (1999): Global dynamics and optimal life history of a structured population model. *Siam J. Appl. Math.* **59**:1667–1685.
- CASWELL, H. (1989): *Matrix Population Models: Construction, Analysis and Interpretation*. Sinauer, Sunderland, MA.
- COHEN, Y., VINCENT, T. L. and BROWN, J. S. (1999): A G-function approach to fitness minima, fitness maxima, evolutionary stable strategies and adaptive landscapes. *Evol. Ecol. Res.* **1**:923–942.
- COHEN, Y., VINCENT, T. L. and BROWN, J. S. (2001): Does the G-function deserve an F? *Evol. Ecol. Res.* **3**:375–377.
- DEEVEY, E. S. (1947): Life tables for natural populations of animals. *Q. Rev. Biol.* **22**:283–314.
- DIECKMANN, O., GYLLENBERG, M., METZ, J. A. J. and THIEME, H. R. (1998): On the formulation and analysis of general deterministic structured population models – I. Linear theory. *J. Math. Biol.* **36**:349–388.
- DIECKMANN, U. and DOEBELI, M. (1999): On the origin of species by sympatric speciation. *Nature* **400**:354–357.
- DIECKMANN, U. and LAW, R. (1996): The dynamical theory of coevolution: A derivation from stochastic ecological processes. *J. Math. Biol.* **34**:579–613.
- DIECKMANN, U., MARROW, P. and LAW, R. (1995): Evolutionary cycling in predator-prey interactions: Populations dynamics and the red queen. *J. Theor. Biol.* **176**:91–102.
- DOEBELI, M. and KOELLA, J. C. (1995): Evolution of simple population-dynamics. *Proc. R. Soc. Lond. B* **260**:119–125.
- ESHEL, I. (1996): On the changing concept of population stability as a reflection of a changing problematics in the quantitative theory of evolution. *J. Math. Biol.* **34**:485–510.
- FERRIERE, R. and CLOBERT, J. (1992): Evolutionarily stable age at 1st reproduction in a density-dependent model. *J. Math. Biol.* **157**:253–267.
- GERITZ, S. A. H. (1998): Co-evolution of seed size and seed predation. *Evol. Ecol.* **12**:891–911.
- GERITZ, S. A. H., KISDI, E., MESZENA, G. and METZ, J. A. J. (1998): Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* **12**:35–57.
- GERITZ, S. A. H., METZ, J. A. J., KISDI, E. and MESZENA, G. (1997): The dynamics of adaptation and evolutionary branching. *Phys. Rev. Lett.* **78**:2024–2027.
- GERITZ, S. A. H. and KISDI, E. (2000): Adaptive dynamics in diploid, sexual populations and the evolution of reproductive isolation. *Proc. R. Soc. Lond. B* **267**:1671–1678.
- GOH, B. S. (1980): *Management and Analysis of Biological Populations*. Elsevier, New York.
- HANSKI, I. (1991): *Metapopulation Ecology*. Oxford University Press, Oxford, U.K.
- HEINO, M. and KAITALA, V. (1999): Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *J. Evol. Biol.* **12**:423–429.
- HEINO, M., METZ, J. A. J. and KAITALA, V. (1998): The enigma of frequency-dependent selection. *Trends Ecol. Evolut.* **13**:367–370.
- HOLMGREN, N. M. A. and GETZ, W. M. (2000): Evolution of host plant selection in insects under perceptual constraints: A simulation study. *Evol. Ecol. Res.* **2**:81–106.
- HOLT, R. D. and GAINES, M. S. (1992): Analysis of adaption in heterogeneous landscapes: Implication for the evolution of fundamental niches. *Evol. Ecol.* **6**:433–447.
- KAWECKI, T. J. (1993): Age and size at maturity in a patchy environment – fitness maximization versus evolutionary stability. *Oikos* **66**:309–317.
- KISDI, E. and GERITZ, S. A. H. (1999): Adaptive dynamics in allele space: Evolution of genetic polymorphism by small mutations in a heterogeneous environment. *Evolution* **53**:993–1008.
- KISDI, E., MESZENA, G. and PASZTOR, L. (1998): Individual optimization: Mechanisms shaping the optimal reaction norm. *Evol. Ecol.* **12**:211–221.
- LEVINS, R. (1962): Theory of fitness in a heterogeneous environment: 1. The fitness set and adaptive function. *Amer. Nat.* **96**:361–373.
- LEVINS, R. (1968): *Evolution in Changing Environment*. Princeton University Press, Princeton, NJ.
- MARROW, P., LAW, R. and CANNINGS, C. (1992): The coevolution of population interactions: ESSs and red queen dynamics. *Proc. R. Soc. Lond. B* **250**:133–141.
- MAY, R. M. (1973): *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, NJ.
- MAY, R. M. (1976): Simple mathematical models with very complicated dynamics. *Nature* **266**:459–467.
- MAYNARD SMITH, J. and PRICE, G. R. (1973): The logic of animal conflicts. *Nature* **246**:15–18.
- MESZENA, G., CZIBULA, I. and GERITZ, S. A. H. (1997): Adaptive dynamics in a 2-patch environment: A toy model for allopatric speciation. *J. Biol. Syst.* **5**:265–284.
- METZ, J. A., GERITZ, S. A. H., MESZENA, G., JACOBS, F. J. A.

- and VAN HEERWAARDEN, J. S. (1996): *Adaptive Dynamics, a Geometrical Study of the Consequences of Near Faithful Reproduction*. Royal Academy of Arts and Sciences, North Holland, Amsterdam.
- METZ, J. A. J. and GYLLENBERG, M. (2001): How should we define fitness in structured metapopulation models? Including an application to the calculation of evolutionarily stable dispersal strategies. *Proc. R. Soc. Lond. B* **268**:499–508.
- ROUGHGARDEN, J. (1987): Community coevolution: A comment. *Evolution* **41**:1130–1134.
- SCHMIT, K. A., EARNHARDT, J. M., BROWN, J. S. and HOLT, R. D. (2000): Habitat selection under temporal heterogeneity: Sinking the ghost of competition past. *Ecology* **81**:2622–2630.
- SCHOOMBIE, S. W. and GETZ, W. M. (1998): Evolutionary stable strategies and trade-offs in generalized Beverton and Holt models. *Tehro. Popul. Biol.* **53**:216–235.
- SCHREIBER, S. J., FOX, L. R. and GETZ, W. M. (2000): Coevolution of contrary choices in hot-parasitoid systems. *Amer. Nat.* **155**:637–648.
- SINERVO, B., SVENSSON, E. and COMENDANT, T. (2000): Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* **406**:985–988.
- STEARNS, S. C. (1992): *The Evolution of Life Histories*. Oxford University Press, Oxford, U.K.
- STEARNS, S. C. (2000): Life history evolution: Successes, limitations, and prospects. *Naturwissenschaften* **87**:476–486.
- TULJAPURKAR, S. (1989): An uncertain life – demography in random-environments. *Theor. Popul. Biol.* **35**:227–294.
- VINCENT, T. L. and BROWN, J. S. (1984): Stability in an evolutionary game. *Theor. Popul. Biol.* **26**:408–427.
- VINCENT, T. L. and BROWN, J. S. (1987): Evolution under nonequilibrium dynamics. *Math. Model.* **8**:766–771.
- VINCENT, T. L. and BROWN, J. S. (1988): The evolution of ESS theory. *Annu. Rev. Ecol. Syst.* **19**:423–443.
- VINCENT, T. L. and BROWN, J. S. (1989): The evolutionary response to a changing environment. *Appl. Math. Comp.* **32**:185–206.
- VINCENT, T. L., COHEN, Y. and BROWN, J. S. (1993): Evolution via strategy dynamics. *Theor. Popul. Biol.* **44**:149–176.
- VINCENT, T. L., VAN, M. V. and GOH, B. S. (1996): Ecological stability, evolutionary stability and the ESS maximum principle. *Evol. Ecol.* **10**:567–591.
- WERNER, E. E. and GILLIAM, J. F. (1984): The ontogenetic niche and species iterations in size-structured populations. *Annu. Rev. Ecol. Syst.* **15**:393–425.

APPENDIX

Proof of ESE Theorem: Given $\mathbf{u} \in \mathcal{U}$, a first order Taylor series expansion of (3) about \mathbf{x}^* yields the following perturbation equations

$$\delta \dot{\mathbf{x}}_i = \frac{\partial(\mathbf{H}_i \mathbf{x}_i)}{\partial \mathbf{x}_1} \Big|_{(\mathbf{u}, \mathbf{x}^*)} \delta \mathbf{x}_1$$

or equivalently

$$\begin{aligned} \delta \dot{\mathbf{x}}_i = & \frac{\partial(\mathbf{H}_i \mathbf{x}_i)}{\partial \mathbf{x}_1} \Big|_{(\mathbf{u}, \mathbf{x}^*)} \delta \mathbf{x}_1 + \frac{\partial(\mathbf{H}_i \mathbf{x}_i)}{\partial \mathbf{x}_2} \Big|_{(\mathbf{u}, \mathbf{x}^*)} \delta \mathbf{x}_2 + \\ & + \dots + \frac{\partial(\mathbf{H}_i \mathbf{x}_i)}{\partial \mathbf{x}_{n_x}} \Big|_{(\mathbf{u}, \mathbf{x}^*)} \delta \mathbf{x}_{n_x} \end{aligned}$$

where $\delta \mathbf{x}_i$ is the perturbation in \mathbf{x}_i from the ecological equilibrium solution. In terms of all the individual types, these equations may be written in matrix notation as

$$\begin{bmatrix} \delta \dot{\mathbf{x}}_1 \\ \vdots \\ \delta \dot{\mathbf{x}}_{n_c} \\ \text{-----} \\ \delta \dot{\mathbf{x}}_{n_c+1} \\ \vdots \\ \delta \dot{\mathbf{x}}_{n_x} \end{bmatrix} = \begin{bmatrix} \frac{\partial(\mathbf{H}_1 \mathbf{x}_1)}{\partial \mathbf{x}_1} & \dots & \frac{\partial(\mathbf{H}_1 \mathbf{x}_1)}{\partial \mathbf{x}_{n_c}} \\ \vdots & \ddots & \vdots \\ \frac{\partial(\mathbf{H}_{n_c} \mathbf{x}_{n_c})}{\partial \mathbf{x}_1} & \dots & \frac{\partial(\mathbf{H}_{n_c} \mathbf{x}_{n_c})}{\partial \mathbf{x}_{n_c}} \\ \text{---} & \text{---} & \text{---} \\ \frac{\partial(\mathbf{H}_{n_c+1} \mathbf{x}_{n_c+1})}{\partial \mathbf{x}_1} & \dots & \frac{\partial(\mathbf{H}_{n_c+1} \mathbf{x}_{n_c+1})}{\partial \mathbf{x}_{n_c}} \\ \vdots & \ddots & \vdots \\ \frac{\partial(\mathbf{H}_{n_x} \mathbf{x}_{n_x})}{\partial \mathbf{x}_1} & \dots & \frac{\partial(\mathbf{H}_{n_x} \mathbf{x}_{n_x})}{\partial \mathbf{x}_{n_c}} \end{bmatrix} \begin{bmatrix} \frac{\partial(\mathbf{H}_1 \mathbf{x}_1)}{\partial \mathbf{x}_{n_c+1}} & \dots & \frac{\partial(\mathbf{H}_1 \mathbf{x}_1)}{\partial \mathbf{x}_{n_x}} \\ \vdots & \ddots & \vdots \\ \frac{\partial(\mathbf{H}_{n_c} \mathbf{x}_{n_c})}{\partial \mathbf{x}_{n_c+1}} & \dots & \frac{\partial(\mathbf{H}_{n_c} \mathbf{x}_{n_c})}{\partial \mathbf{x}_{n_x}} \\ \text{---} & \text{---} & \text{---} \\ \frac{\partial(\mathbf{H}_{n_c+1} \mathbf{x}_{n_c+1})}{\partial \mathbf{x}_{n_c+1}} & \dots & \frac{\partial(\mathbf{H}_{n_c+1} \mathbf{x}_{n_c+1})}{\partial \mathbf{x}_{n_x}} \\ \vdots & \ddots & \vdots \\ \frac{\partial(\mathbf{H}_{n_x} \mathbf{x}_{n_x})}{\partial \mathbf{x}_{n_c+1}} & \dots & \frac{\partial(\mathbf{H}_{n_x} \mathbf{x}_{n_x})}{\partial \mathbf{x}_{n_x}} \end{bmatrix} \begin{bmatrix} \delta \mathbf{x}_1 \\ \vdots \\ \delta \mathbf{x}_{n_c} \\ \text{-----} \\ \delta \mathbf{x}_{n_c+1} \\ \vdots \\ \delta \mathbf{x}_{n_x} \end{bmatrix}_{(\mathbf{u}, \mathbf{x}^*)}$$

Each term in the matrix is itself a matrix. These matrices, in turn, divide up into four blocks according to n_c . Consider now actually evaluating the

1

lower two blocks. Any term on the diagonal of the lower right hand block is of the form

$$\frac{\partial(\mathbf{H}_i \mathbf{x}_i)}{\partial \mathbf{x}_i} = \begin{bmatrix} \left(x_{i1} \frac{\partial H_{(l+1)1}}{\partial x_{11}} + \dots + x_{in_s} \frac{\partial H_{(l+1)n_s}}{\partial x_{11}} \right) & \dots & \left(x_{i1} \frac{\partial H_{(l+1)1}}{\partial x_{1(n_s)}} + \dots + x_{in_s} \frac{\partial H_{(l+1)n_s}}{\partial x_{1(n_s)}} \right) \\ \vdots & \ddots & \vdots \\ \left(x_{i1} \frac{\partial H_{j1}}{\partial x_{11}} + \dots + x_{in_s} \frac{\partial H_{jn_s}}{\partial x_{11}} \right) & \dots & \left(x_{i1} \frac{\partial H_{j1}}{\partial x_{1(n_s)}} + \dots + x_{in_s} \frac{\partial H_{jn_s}}{\partial x_{1(n_s)}} \right) \end{bmatrix}$$

where $i = (n_c+1, \dots, n_x)$ and all other terms in the lower two blocks are of the form

$$\frac{\partial(\mathbf{H}_i \mathbf{x}_i)}{\partial \mathbf{x}_j} = \begin{bmatrix} \left(x_{i1} \frac{\partial H_{(l+1)1}}{\partial x_{11}} + \dots + x_{in_s} \frac{\partial H_{(l+1)n_s}}{\partial x_{11}} \right) & \dots & \left(x_{i1} \frac{\partial H_{(l+1)1}}{\partial x_{1(n_s)}} + \dots + x_{in_s} \frac{\partial H_{(l+1)n_s}}{\partial x_{1(n_s)}} \right) \\ \vdots & \ddots & \vdots \\ \left(x_{i1} \frac{\partial H_{j1}}{\partial x_{11}} + \dots + x_{in_s} \frac{\partial H_{jn_s}}{\partial x_{11}} \right) & \dots & \left(x_{i1} \frac{\partial H_{j1}}{\partial x_{1(n_s)}} + \dots + x_{in_s} \frac{\partial H_{jn_s}}{\partial x_{1(n_s)}} \right) \end{bmatrix}$$

where $i = (n_c+1, \dots, n_x)$ $j = (1, \dots, n_x)$, $i \neq j$. Evaluating the lower two blocks using (6) results in

$$\begin{bmatrix} \delta \dot{\mathbf{x}}_1 \\ \vdots \\ \delta \dot{\mathbf{x}}_{n_c} \\ \text{---} \\ \delta \dot{\mathbf{x}}_{n_c+1} \\ \vdots \\ \delta \dot{\mathbf{x}}_{n_x} \end{bmatrix} = \begin{bmatrix} \frac{\partial(\mathbf{H}_1 \mathbf{x}_1)}{\partial \mathbf{x}_1} & \dots & \frac{\partial(\mathbf{H}_1 \mathbf{x}_1)}{\partial \mathbf{x}_{n_c}} & \frac{\partial(\mathbf{H}_1 \mathbf{x}_1)}{\partial \mathbf{x}_{n_c+1}} & \dots & \frac{\partial(\mathbf{H}_1 \mathbf{x}_1)}{\partial \mathbf{x}_{n_x}} \\ \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ \frac{\partial(\mathbf{H}_{n_c} \mathbf{x}_{n_c})}{\partial \mathbf{x}_1} & \dots & \frac{\partial(\mathbf{H}_{n_c} \mathbf{x}_{n_c})}{\partial \mathbf{x}_{n_c}} & \frac{\partial(\mathbf{H}_{n_c} \mathbf{x}_{n_c})}{\partial \mathbf{x}_{n_c+1}} & \dots & \frac{\partial(\mathbf{H}_{n_c} \mathbf{x}_{n_c})}{\partial \mathbf{x}_{n_x}} \\ \text{---} \\ 0 & \dots & 0 & H_{n_c+1} & \dots & 0 \\ \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ 0 & \dots & 0 & 0 & \dots & H_{n_c} \end{bmatrix}_{(u,c^*)} \begin{bmatrix} \delta \mathbf{x}_1 \\ \vdots \\ \delta \mathbf{x}_{n_c} \\ \text{---} \\ \delta \mathbf{x}_{n_c+1} \\ \vdots \\ \delta \mathbf{x}_{n_x} \end{bmatrix}$$

If \mathbf{x}^* is an ESE then by definition, in the limit, as $t \rightarrow \infty$, $\mathbf{x}(t)$ must asymptotically approach \mathbf{x}^* . This means that the eigenvalues of the matrix in (15) must have non-positive real parts (note that zero eigenvalues are allowed since higher order terms in the expansion can provide for stability). Since the matrix in (15) is in block upper triangular form, this condition on the eigenvalues implies that the

matrices in (7) and (8) must have non-positive eigenvalues. Furthermore if (7) and (8) have eigenvalues with negative real parts, then \mathbf{x}^* will be locally asymptotically stable. If the system is asymptotically stable, then it will also be ecologically stable since any solution to (1) which starts in $\mathbf{O} \cap \mathcal{B}$, will remain in \mathbf{O} for all future time (Goh, 1980).