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An ESS Maximum Principle for Matrix Games

Thomas L. Vincent

Aerospace and Mechanical Engineering, University of Arizona, Tucson, Arizona 85721

and

Ross Cressman

Department of Mathematics, Wilfrid Laurier University, Waterloo, Ontario,
N2L 3C5, Canada

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Previous work has demonstrated that for games defined by differential or difference equations with a continuum of strategies, there exists a *G*-function, related to individual fitness, that must take on a maximum with respect to a virtual variable v whenever v is one of the vectors in the coalition of vectors which make up the evolutionarily stable strategy (ESS). This result, called the ESS maximum principle, is quite useful in determining candidates for an ESS. This principle is reformulated here, so that it may be conveniently applied to matrix games. In particular, we define a matrix game to be one in which fitness is expressed in terms of strategy frequencies and a matrix of expected payoffs. It is shown that the *G*-function in the matrix game setting must again take on a maximum value at all the strategies which make up the ESS coalition vector. The reformulated maximum principle is applicable to both bilinear and nonlinear matrix games. One advantage in employing this principle to solve the traditional bilinear matrix game is that the same *G*-function is used to find both pure and mixed strategy solutions by simply specifying an appropriate strategy space. Furthermore we show how the theory may be used to solve matrix games which are not in the usual bilinear form. We examine in detail two nonlinear matrix games: the game between relatives and the sex ratio game. In both of these games an ESS solution is determined. These examples not only illustrate the usefulness of this approach to finding solutions to an expanded class of matrix games, but aids in understanding the nature of the ESS as well.

1. INTRODUCTION

Conditions for evolutionary stability in continuous games have been developed through the use of the fitness generating functions (see Vincent *et al.*, 1996, and the references by Vincent and co-authors contained therein). Fitness generating functions, called *G*-functions, are used to generate the fitness of any individual in the population dynamic of an ecological system. The simplest case is when the ecological system can be modeled using a single *G*-function (e.g., a single species) where the evolution of any number of individuals of different behavior types (e.g., phenotypes) may be examined in terms of the evolution of the densities of one or more strategy types drawn from a strategy space $\mathcal{U}$. It is shown that, if a coalition vector of strategies $\mathbf{u}_c$ is evolutionarily stable (i.e., if $\mathbf{u}_c$ is an ESS) at an equilibrium point of densities $\mathbf{x}^*$, then the *G*-function must take on a maximum value according to the ESS maximum principle as given in Theorem 1 below.

When applying this theory to matrix games, we need to distinguish between previous results and those obtained here. In particular, we will use the term *matrix(T)-ESS*, (T for traditional) throughout this paper to mean the ESS of a bilinear matrix game according to its traditional definition (Maynard Smith, 1982;

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Hofbauer and Sigmund, 1988; Cressman, 1992) where frequency-dependent payoffs are given by random pairwise interactions. That is, a matrix(T)-ESS is a strategy that satisfies standard static conditions involving expected payoff comparisons. From a dynamic perspective, the most important property of a matrix(T)-ESS is that it corresponds to a monomorphic population that cannot be invaded by a small subpopulation, all of whose members use a single mutant strategy. By contrast, we will use the term *matrix(G)-ESS* (G for general) to mean the ESS of a bilinear matrix game that satisfies Definition 1 below. Heuristically, a matrix(G)-ESS corresponds to a distribution of strategy frequencies (the population may be either monomorphic or polymorphic) that is stable against simultaneous invasion by small subpopulations using any allowable mutant strategies. A matrix(G)-ESS is stable for the specific population dynamic under consideration which may include nonlinear matrix games as well as the traditional bi-linear game. The differences between the two concepts are illustrated in Section 4 below. In certain situations a matrix(T)-ESS and a matrix(G)-ESS are the same; however, there are also situations in which a matrix(G)-ESS does not exist and yet a matrix(T)-ESS does exist and vice versa.

In particular, Vincent *et al.* (1996) point out that, under the standard approach to bilinear matrix games and evolutionary stability, a mixed-strategy matrix(T)-ESS cannot be evolutionarily stable according to Definition 1. The main reason for this, which can be most easily understood in the context of the *G*-function, is that for a mixed-strategy matrix(T)-ESS the *G*-function is flat. That is, it does not take on a proper maximum at such a point. Furthermore it has been shown by Brown and Vincent (1987) that in a bilinear matrix game the mixed-strategy matrix(T)-ESS can always be invaded by more than one mutant using mixed strategies and hence does not have the property of a matrix(G)-ESS.

Since there is an apparent difference between a matrix(T)-ESS and a matrix(G)-ESS, one might conclude that the ESS maximum principle is not relevant for matrix games, suggesting that ESS theory for continuous games must remain separate from that of matrix games. The main purpose of this paper is to emphatically refute this conclusion by developing a corollary to the ESS maximum principle that is directly applicable to evolutionary matrix games and to demonstrate its usefulness with a number of examples of both bilinear and nonlinear matrix games. These examples show that the *G*-function approach, previously developed for continuous games, is equally relevant for matrix games and that the ESS maximum principle can be used to predict the eventual outcome of evolution. Moreover, these methods apply to situations where the matrix game does not have the traditional form of a bilinear payoff.

While the ESS maximum principle can be used to determine an ESS candidate and equilibrium densities in a continuous game, the corollary addresses fundamental questions more traditionally concerned with the evolution of strategy frequencies in matrix games. To this end, Sections 2 and 3 briefly review the theory underlying the ESS maximum principle and show how a corollary follows which is stated in terms of the frequency domain with individual fitness based on random pair-wise interactions between individuals in the population (see Corollary 1 below).

The remaining sections apply the corollary to determine stable frequencies in dynamic evolutionary models that have traditionally been analyzed through their static properties (e.g., games between relatives where interactions are not at random (Section 6) and sex ratio games (Section 7) based on playing the field).

2. THE ESS MAXIMUM PRINCIPLE

In this section we will briefly outline the method and some of the results contained in Vincent *et al.* (1996). In particular, we will consider only the single *G*-function case.

Assume there are a finite but arbitrary number n_s of different strategies (behavioral types) $\mathbf{u} = [\mathbf{u}_1^{\mathrm{T}} \cdots \mathbf{u}_{n_s}^{\mathrm{T}}]^{\mathrm{T}}$ in a population of individuals. The strategies $\mathbf{u}_i$ may be scalars u_i or vectors $\mathbf{u}_i = [u_{i1} \cdots u_{in_u}]^{\mathrm{T}}$ with n_u components. Each strategy $\mathbf{u}_i$ is required to lie in the same subset $\mathscr{U} \subseteq \mathscr{R}^{n_u}$. We will shorten this latter requirement to read $\mathbf{u} \in \mathscr{U}$ (every vector of $\mathbf{u}$ must lie in $\mathscr{U}$). The particular form for $\mathscr{U}$ will be specified later and it will play an important role in clarifying the difference between the standard pure strategy approach to matrix games and the continuous approach which is more natural to the theory presented here.

Let x_i be the density (i.e., the number of individuals) of strategy type $\mathbf{u}_i$ at time t for $i = 1, ..., n_s$ and let $\mathbf{x} = [x_1, ..., x_{n_s}]^{\mathrm{T}}$ be the vector of all such densities. Furthermore, assume that the time rate of change of population density is given by

$$\dot{x}_i = x_i H_i[\mathbf{u}, \mathbf{x}], \tag{1}$$

where H_i is the fitness of individuals x_i using strategies $\mathbf{u}_i$. The individual fitness function $H_i[\mathbf{u}, \mathbf{x}]$ for an individual using strategy type $\mathbf{u}_i$ is assumed to be continuous (it is in fact usually continuously differentiable) in $\mathbf{x}$ in the nonnegative orthant

$$\mathcal{O}^{n_s} = \{\mathbf{x} \in \mathcal{R}^{n_s} \mid \mathbf{x} = [x_1, \ldots, x_{n_s}], x_i \geqslant 0\}$$

and also continuous in $\mathbf{u}$ if $\mathcal{U}$ has a given topology. An immediate consequence of this assumption is that $\mathcal{O}^{n_s}$ is forward invariant under (1) as is $\mathcal{O}^{n_s}_{+} = \{x \in \mathcal{O}^{n_s} \mid x_i > 0\}$ and any boundary orthant (e.g., $\{x \in \mathcal{O}^{n_s} \mid x_1 = 0\}$).

In what follows it is assumed that, for any $\mathbf{u} \in \mathcal{U}$, there exists an equilibrium solution $\mathbf{x}^* \in \mathcal{O}^{n_s}$ satisfying $x_i^*\ H_i[\mathbf{u}, \mathbf{x}^*] = 0$ for $i = 1, \ldots, n_s$. If, for some i, the equilibrium condition is satisfied by the nontrivial solution $H_i[\mathbf{u}, \mathbf{x}^*] = 0$ with $x_i^* > 0$ then the equilibrium solution is called an ecologically feasible equilibrium point or, more simply, an *ecological equilibrium* point. Reorder the i index if necessary so that all nontrivial solutions are listed first. Then, at an ecological equilibrium point, there exists a $\sigma \geqslant 1$ such that the equilibrium solution is given by

$$\begin{aligned} H_i[\mathbf{u}, \mathbf{x}^*] = 0 \text{ with } x_i^* > 0 \qquad & \text{for} \quad i = 1, \ldots, \sigma \\ x_i^* = 0 \qquad & \text{for} \quad i = \sigma + 1, \ldots, n_s. \end{aligned} \tag{2}$$

The strategies corresponding to the non-trivial solutions may be placed into a *coalition vector*

$$\mathbf{u}_c = [\mathbf{u}_1^{\mathrm{T}} \cdots \mathbf{u}_\sigma^{\mathrm{T}}]^{\mathrm{T}}$$

with the remaining strategies placed into a *mutant vector*

$$\mathbf{u}_m = [\mathbf{u}_{\sigma+1}^{\mathrm{T}} \cdots \mathbf{u}_{n_s}^{\mathrm{T}}]^{\mathrm{T}}.$$

For the definition which follows we will require certain properties that are similar to asymptotic stability for the ecological equilibrium point. We cannot assume that $\mathbf{x}^*$ is asymptotically stable at the outset since $\mathbf{x}^*$ will, in general, lie on the boundary of $\mathcal{O}^{n_s}$ and trajectories starting at neighboring points not in $\mathcal{O}^{n_s}$ are of no interest and need not approach $\mathbf{x}^*$. Rather we require that every trajectory starting in a $\mathcal{O}^{n_s} \cap \mathcal{B}$ where $\mathcal{B}$ is an open ball about $\mathbf{x}^*$ remain in $\mathcal{O}^{n_s}$ for all time and converge to $\mathbf{x}^*$ as $t \to \infty$. An ecological equilibrium point which satisfies these properties is called an *ecologically stable equilibrium point* (ESE). If $\mathcal{B}$ can be made arbitrarily large then $\mathbf{x}^*$ is said to be a global ESE; otherwise, it is a local ESE. Note that asymptotic stability of $\mathbf{x}^*$ in $\mathcal{O}^{n_s}$ is a sufficient condition for an ecologically stable equilibrium point.

DEFINITION 1. The vector $\mathbf{u}_c \in \mathcal{U}$ is an **ESS** for the ecological equilibrium point $\mathbf{x}^* \in \mathcal{O}^{n_s}$ if, for any $n_s > \sigma$ and any $\mathbf{u}_m \in \mathcal{U}$, $\mathbf{x}^*$ is an ecologically stable equilibrium point.

Definition 1 incorporates the intuitive concept that an ESS cannot be invaded by mutants. The ESS vector of σ strategy types $\mathbf{u}_c$ is stable against simultaneous invasion by any allowable set of mutant strategies $\mathbf{u}_m$. If $\mathbf{x}^*$ is only a local ESE then the mutants must be rare; otherwise, the mutants need not be rare.

For a given $\mathbf{u}_m \in \mathcal{U}$, an ESS for the ESE x^* is either a stable monomorphic population ($\mathbf{u}_c$ is an ESS coalition with only one strategy vector) or a stable polymorphic population ($\mathbf{u}_c$ is an ESS coalition with more than one strategy vector). However, it is important to note that a population using the ESS requires more than just stability in the population. The essential feature is that an ESS population is stable with respect to strategies used by individuals outside the coalition. An ESS population must be able to maintain itself at x^* subject to continual repeated attacks by any number of other individuals using different mutant strategies $\mathbf{u}_m$.

The ESS maximum principle (Vincent *et al.*, 1996) as given by Theorem 1 below is based on the existence of a fitness G-function defined as follows.

DEFINITION 2. A function $G(\cdot) : \mathcal{U} \times U^{n_s} \times \mathcal{O}^{n_s} \to \mathcal{R}$ is a G-function for (1) if, for every $i = 1, \ldots, n_s$,

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

Note that the G-function is written in terms of a *virtual variable* $\mathbf{v}$ as $G(\mathbf{v}, \mathbf{u}, \mathbf{x})$. Evaluating the G-function using $\mathbf{v} = \mathbf{u}_i$ results in the fitness function for individuals using strategy type $\mathbf{u}_i$.

THEOREM 1 (ESS Maximum Principle). *Let* $G(\mathbf{v}, \mathbf{u}, \mathbf{x})$ *be a G-function for* (1). *If* $\mathbf{u}_c = [\mathbf{u}_1, \ldots, \mathbf{u}_\sigma]$ *is an ESS for the ecological equilibrium point* $\mathbf{x}^* \in \mathcal{O}^{n_s}$, *then* $G(\mathbf{v}, \mathbf{u}, \mathbf{x}^*)|_{\mathbf{v}=\mathbf{u}_i} = 0$ *for* $i = 1, \ldots, \sigma$ *and this is the maximum value of* $G(\mathbf{v}, \mathbf{u}, \mathbf{x}^*)$ *as a function of* $\mathbf{v} \in \mathcal{U}$.

The ESS maximum principle is a necessary condition for an ESS since it was derived by requiring that $\mathbf{x}^*$ be a local ESE. It has a simple geometric interpretation when the strategies are scalars. Suppose that $\mathbf{u}_c$ is an ESS coalition of one with only the one component u_1. If we substitute $\mathbf{u}$ and $\mathbf{x}^*$ into G and plot G as a function of v, its global maximum value must occur at u_1 with a value of zero. If $\mathbf{u}_c$ is an ESS coalition of two (with two components u_1 and u_2) and we substitute $\mathbf{u}$ and $\mathbf{x}^*$ into G and plot G as a function of v, it must have two global maximum values which occur at u_1 and u_2 with a value of zero. Likewise, if $\mathbf{u}_c$ has σ components, plotting $G(v, \mathbf{u}, \mathbf{x}^*)$ verses v will result in σ global maximal points located at each of the strategy points $u_1, \ldots, u_\sigma$ all of which are zero. The same geometric interpretation applies when the strategies are vectors. However, the plotting routine obviously cannot be used if each strategy vector has more than two components.

3. AN ESS MAXIMUM PRINCIPLE FOR FREQUENCY DYNAMICS

Strategy frequency dynamics were introduced by Taylor and Jonker (1978) for the standard payoff matrix model of evolutionary game theory through a strategy density dynamic that can be written in the form of (1). We now develop a model that includes Taylor and Jonker's approach as a special case (see Section 4 below). Specifically, suppose there are n_s different strategies $\mathbf{u} = [\mathbf{u}_1, ..., \mathbf{u}_{n_s}]^{\mathrm{T}}$ in the population and each individual interacts in one pair-wise contest per unit time with a random opponent and receives a payoff through this contest that translates into reproductive success.

Let $E(\mathbf{u}_i, \mathbf{u}_j)$ be the payoff to a $\mathbf{u}_i$ individual when interacting with a $\mathbf{u}_j$ individual. Then

$$H_i[\mathbf{u}, \mathbf{x}] = \sum_{j=1}^{n_s} E(\mathbf{u}_i, \mathbf{u}_j) \frac{x_j}{\sum_{k=1}^{n_s} x_k} \tag{3}$$

is the expected payoff to an individual of strategy type $\mathbf{u}_i$ in a random contest where x_i is the density of strategy $\mathbf{u}_i$. With this matrix form for $H_i[\mathbf{u}, \mathbf{x}]$, the dynamic (1) becomes

$$\dot{x}_i = x_i \sum_{j=1}^{n_s} E(\mathbf{u}_i, \mathbf{u}_j) \frac{x_j}{\sum_{k=1}^{n_s} x_k}. \tag{4}$$

The requirement by the ESS maximum principle in Theorem 1 for an ecological equilibrium (i.e., a nontrivial solution for $\mathbf{x}^*$) cannot be met by (4) under the usual assumption that the payoffs are positive, in which case $G(\mathbf{v}, \mathbf{u}, \mathbf{x})|_{\mathbf{v}=\mathbf{u}_i}$ cannot equal zero for $i = 1, ..., \sigma$ since $G(\mathbf{v}, \mathbf{u}, \mathbf{x})|_{\mathbf{v}=\mathbf{u}_i} = H_i[\mathbf{u}, \mathbf{x}] > 0$. The standard way to avoid this difficulty (used, for example, by Taylor and Jonker, 1978 for bilinear matrix games) is to express the dynamic in terms of the frequencies

$$p_i \triangleq \frac{x_i}{N},$$

where

$$N = \sum_{k=1}^{n_s} x_k$$

is the total population number. In terms of these variables, (4) may be written as the following equivalent system

$$\begin{aligned} \dot{p}_i &= p_i \left[\sum_{j=1}^{n_s} E(\mathbf{u}_i, \mathbf{u}_j)\, p_j - \mathbf{p}^{\mathrm{T}} \mathbf{E}(\mathbf{u})\, \mathbf{p} \right] \\ \dot{N} &= N \mathbf{p}^{\mathrm{T}} \mathbf{E}(\mathbf{u})\, \mathbf{p}, \end{aligned} \tag{5}$$

where $\mathbf{E}(\mathbf{u})$ is the $n_s \times n_s$ matrix whose components are $E(\mathbf{u}_i, \mathbf{u}_j)$ and the frequency vector $\mathbf{p} = [p_1 \cdots p_{n_s}]^{\mathrm{T}}$ lies in the frequency space defined by

$$\Delta^{n_s} \triangleq \left\{ (p_1, ..., p_{n_s}) \,\middle|\, \sum_{i=1}^{n_s} p_i = 1, p_i \geqslant 0 \right\}.$$

Note that the p_i equations are decoupled from N and a nontrivial equilibrium solution is possible for $\mathbf{p}^*$. Thus, while a nontrivial solution need not exist for N, if we are not interested in population number, we may simply ignore this equation. The advantage with this approach is that the ESS maximum principle may now be applied directly to (5) by letting p_i play the role of x_i in the theorem. We will take this approach in what follows.

A more convenient matrix form for (5) is

$$\begin{aligned} \dot{p}_i &= p_i [\mathbf{e}(\mathbf{u}_i) - \mathbf{p}]^{\mathrm{T}}\, \mathbf{E}(\mathbf{u})\, \mathbf{p} \\ &= p_i H_i(\mathbf{u}, \mathbf{p}), \end{aligned} \tag{6}$$

where $\mathbf{e}(\mathbf{u}_i) \in \Delta^{n_s}$ is the ith unit coordinate vector $[0 \cdots 0\ 1\ 0 \cdots 0]^{\mathrm{T}}$ with 1 in the ith component in accord with the $\mathbf{u}_i$ strategy. In fact, each $\mathbf{p}^* = \mathbf{e}(\mathbf{u}_i)$ is a nontrivial equilibrium solution of (5). It follows from (6) that

$$G(\mathbf{v}, \mathbf{u}, \mathbf{p}) = [\mathbf{e}(\mathbf{v}) - \mathbf{p}]^{\mathrm{T}}\, \mathbf{E}(\mathbf{u})\, \mathbf{p} \tag{7}$$

is the relevant G-function for strategy frequency dynamics. In terms of this G-function we have the following corollary to the ESS maximum principle.

COROLLARY 1 (ESS maximum principle for frequencies). *Let* $G(\mathbf{v}, \mathbf{u}, \mathbf{p})$ *be the G-function for* (6) *as given by* (7). *If* $\mathbf{u}_c = [\mathbf{u}_1, ..., \mathbf{u}_\sigma]$ *is an ESS for the ecological equilibrium point* $\mathbf{p}^* \in \Delta^{n_s}$, *then* $G(\mathbf{v}, \mathbf{u}, \mathbf{p}^*)|_{\mathbf{v}=\mathbf{u}_i} = 0$ *for* $i = 1, ..., \sigma$ *and this is the maximum value of* $G(\mathbf{v}, \mathbf{u}, \mathbf{p}^*)$ *as a function of* $\mathbf{v} \in \mathcal{U}$.

This corollary follows directly from the maximum principle under the notation change indicated. It is important to emphasize that the above principle applies whenever individual fitness is given by (3) for any functions $E(\mathbf{u}_i, \mathbf{u}_j)$ whether these result from random pairwise interactions or not. Such possibilities are considered in Sections 5, 6, and 7.

In what follows, we are especially interested in the case where the ESS is a coalition of one (i.e., $\sigma = 1$). For this situation it is possible to state a stronger result provided that $G(\mathbf{v}, \mathbf{u}, \mathbf{p})$ takes on a proper maximum with respect to $\mathbf{v}$ (i.e., $G(\mathbf{v}, \mathbf{u}, \mathbf{p}^*) < 0$ for all $\mathbf{v} \neq \mathbf{u}_1$ which lie in the set $\mathscr{U}$).

Corollary 2 (Sufficient condition for an ESS). *Given a matrix game defined by* (6), *if* $\sigma = 1$ (*i.e.*, $\mathbf{p}^* = [1\ 0\ \cdots\ 0]^{\mathrm{T}}$) *and* $G(\mathbf{v}, \mathbf{u}, \mathbf{p}^*)|_{\mathbf{v}=\mathbf{u}_1} = 0$ *is a proper maximum of* $G(\mathbf{v}, \mathbf{u}, \mathbf{p}^*)$, *then* $\mathbf{u}_1$ *is an ESS.*

Corollary 2 follows from the fact that under the conditions given, $\mathbf{p}^*$ is a local ecologically stable equilibrium point for any $n_s > 1$. This can be seen by linearizing (6) about the equilibrium $\mathbf{p}^*$ to obtain an upper triangular matrix (Vincent *et al.*, 1996) whose main diagonal entries are

$$-E(\mathbf{u}_1, \mathbf{u}_1),\ G(\mathbf{v}, \mathbf{u}, \mathbf{p}^*)|_{\mathbf{v}=\mathbf{u}_2}, \ldots, G(\mathbf{v}, \mathbf{u}, \mathbf{p}^*)|_{\mathbf{v}=\mathbf{u}_{ns}}.$$

The first term is not relevant for determining stability in the frequency domain since p_1 (as well as all other frequencies) are restricted to lie in Δ^{n_s}. After imposing this constraint, the remaining terms are the eigenvalues for the linearized system. Since $\mathbf{u}_1$ is a proper maximum, all the remaining terms are negative and so $\mathbf{p}^*$ is asymptotically stable.

We will now use the corollaries to examine the standard matrix game and demonstrate problems associated with a mixed strategy solution. We first sort out the potentially confusing distinction between a matrix game played using mixed strategies and the same game played with pure strategies. We do not need two theories to do this. The essential difference between the two games lies in the definition of the strategy set $\mathscr{U}$ so that the ESS vector for both games may be sought using Corollaries 1 and 2. This unification of the pure and mixed strategy models represents one of the major advantages in using the ESS maximum principle to solve matrix games.

4. BILINEAR MATRIX GAMES

The standard mixed-strategy evolutionary model (Cressman, 1992) associated with an $n_u \times n_u$ matrix game assumes that

$$E(\mathbf{u}_i, \mathbf{u}_j) = \mathbf{u}_i^{\mathrm{T}}\ \mathbf{M}\mathbf{u}_j,$$

where $\mathbf{u}_i$ and $\mathbf{u}_j$ are mixed strategies defined in the continuous strategy space

$$\mathscr{U}_c = \left\{ \mathbf{u}_i \in \mathscr{R}^{n_u} \,\middle|\, 0 \leqslant u_{ij} \leqslant 1\ \forall j = 1, \ldots, n_u \text{ and } \sum_{j=1}^{n_u} u_{ij} = 1 \right\}$$

and $\mathbf{M}$ is an $n_u \times n_u$ payoff matrix of constants

$$\mathbf{M} = \begin{bmatrix} m_{11} & \cdots & m_{1n_u} \\ \vdots & \ddots & \vdots \\ m_{n_u 1} & \cdots & m_{n_u n_u} \end{bmatrix}$$

The usual interpretation of the strategies is that they are probabilities associated with choosing a row or column. For example, in a 2×2 matrix game, if player i has the strategy $\mathbf{u}_i = [.25\ \ .75]^{\mathrm{T}}$ then, over many contests, this player is choosing row one 25 % of the time and row two 75 % of the time. On the other hand, player j with the strategy $\mathbf{u}_j = [0\ \ 1]$ plays column two in every contest. This game is bilinear in the strategies since $E(\mathbf{u}_i, \mathbf{u}_j)$ is linear in the components of the strategy vectors $\mathbf{u}_i$ and $\mathbf{u}_j$.

A common, more restricted version of the game is based on the model of Taylor and Jonker (1978). In this case, the strategy choices are restricted to only "pure" strategies. That is, the components of the strategy vector can only take on the values 0 or 1. The discrete strategy space for the pure strategy version of this matrix game is the n_u-element space defined by

$$\mathscr{U}_p = \left\{ u_i \in \mathscr{R}^{n_u} \,\middle|\, u_{ij} \in \{0, 1\}\ \forall j = 1, \ldots, n_u \right.$$
$$\left. \text{and } \sum_{j=1}^{n_u} u_{ij} = 1 \right\}$$

Moreover, the frequency dynamic (6) is now the replicator dynamic (Hofbauer and Sigmund, 1988)

$$\dot{p}_i = p_i \left(\sum_{k=1}^{n_u} m_{ik} p_k - \sum_{j,k=1}^{n_u} p_j m_{ik} p_k \right) \tag{8}$$

with respect to the payoff matrix $\mathbf{M}$. This well-known frequency dynamic on Δ^{n_u} is the original matrix game dynamic proposed by Taylor and Jonker (1978) as the continuous-time approximation to a nonoverlapping generation model of a single haploid species where an individual's expected payoff is equal to its number of offspring, all of whom inherit the identical strategy of their parent.

4.1. *Using Corollary* 1 *to Solve the* 2×2 *Game*

The basic approach for solving any evolutionary stability problem using the ESS maximum principle is to first examine if there exists an ESS coalition of one. In this case, $\mathbf{p}^* = [1 \quad 0 \cdots 0]^{\mathrm{T}}$ so that, from (7),

$$G^* \triangleq G(\mathbf{v}, \mathbf{u}, \mathbf{p}^*) = E(\mathbf{v}, \mathbf{u}_1) - E(\mathbf{u}_1, \mathbf{u}_1). \qquad (9)$$

If this G^* function takes on a proper maximum with respect to $\mathbf{v}$ at $\mathbf{u}_1$, then $\mathbf{u}_1$ is a matrix(G)-ESS by Corollary 2 (recall that, for bilinear matrix games, a matrix(G)-ESS is defined here as one that satisfies Definition 1 with $\mathbf{x}^*$ replaced by $\mathbf{p}^*$). Furthermore, if $\mathbf{p}^*$ is a global ecologically stable equilibrium point (for any $n_s > 1$), then one need look no further since, by definition, there cannot exist an ESS coalition of two or more strategy vectors. If conditions are such that G^* does not take on a proper maximum with respect to $\mathbf{v}$ at $\mathbf{u}_1$, then one must look for an ESS coalition of two. In seeking an ESS coalition of two, $\mathbf{p}^* = [p_1^* \; p_2^* \; \cdots \; 0]^{\mathrm{T}}$ so that

$$G^* \triangleq G(\mathbf{v}, \mathbf{u}, \mathbf{p}^*) = E(\mathbf{v}, \mathbf{u}_1)\, p_1^* + E(\mathbf{v}, \mathbf{u}_2)\, p_2^* - (\mathbf{p}^*)^{\mathrm{T}}\, \mathbf{E}(\mathbf{u})\, \mathbf{p}^* \qquad (10)$$

Similar arguments can now be used to see if an ESS coalition of two exists. If not, one can then seek an ESS coalition of three, etc.

We will now demonstrate this procedure for finding the matrix(G)-ESS vector in the 2×2 bilinear game using the two different strategy sets $\mathscr{U}_p$ and $\mathscr{U}_c$.

4.1.1. *Pure strategies—coalition of one.* If an ESS coalition of one exists for the pure strategy case, it is given by either $\mathbf{u}_1 = [0 \;\; 1]^{\mathrm{T}}$ or $\mathbf{u}_1 = [1 \;\; 0]^{\mathrm{T}}$. We will examine if these solutions satisfy the ESS maximum principle by first substituting $\mathbf{u}_1 = [1 \;\; 0]^{\mathrm{T}}$ into (9) to obtain

$$G^* = v_1 m_{11} + v_2 m_{21} - m_{11}\,.$$

There are only two points to check. Clearly when $\mathbf{v} = \mathbf{u}_1$, $G^* = 0$ and when $\mathbf{v} = [0 \;\; 1]^{\mathrm{T}}$, $G^* = m_{21} - m_{11}$. Thus, $\mathbf{u}_1$ satisfies Corollary 1 if and only if $m_{21} - m_{11} \leqslant 0$. Furthermore, G^* takes on a proper maximum at $\mathbf{u}_1$ if and only if

$$m_{21} - m_{11} < 0.$$

That is, by Corollaries 1 and 2, $m_{21} - m_{11} < 0$ implies $\mathbf{u}_1 = [1 \;\; 0]^{\mathrm{T}}$ is a matrix(G)-ESS.

In order to obtain a complete characterization of a matrix(G)-ESS in this situation, we examine in detail the frequency dynamic (6) when mutants are introduced. There is only one possible mutant strategy; namely, $\mathbf{u}_2 = [0 \;\; 1]^{\mathrm{T}}$. Although the stability conditions for $p^* = [1 \;\; 0]^{\mathrm{T}}$ are well known in this case from the theory of bilinear matrix games, we will develop them here from first principles to illustrate the connection between a matrix(G)-ESS and a matrix(T)-ESS.

From either (6) or (8), and using $p_2 = 1 - p_1$, we obtain

$$\begin{aligned} \dot{p}_1 &= p_1\{[1 \quad 0] - [p_1 \quad p_2]\} \begin{bmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{bmatrix} \begin{bmatrix} p_1 \\ p_2 \end{bmatrix} \\ &= p_1 p_2 [1 \quad -1] \begin{bmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{bmatrix} \begin{bmatrix} p_1 \\ p_2 \end{bmatrix} \\ &= -p_1 p_2 [p_1(m_{21} - m_{11}) + p_2(m_{22} - m_{12})] \end{aligned}$$

For ecological stability, we need $\dot{p}_1 > 0$ for p_1 less than but sufficiently close to 1. Thus, $\mathbf{p}^*$ is ecologically stable if and only if either

$$m_{21} - m_{11} < 0 \qquad (11)$$

or

$$m_{21} - m_{11} = 0 \text{ and } m_{22} - m_{12} < 0. \qquad (12)$$

It follows from (11) that, when G^* takes on a proper maximum, $\mathbf{p}^*$ is ecologically stable. This is the basis of the proof of Corollary 2. However, it follows from (12) that ecological stability is also possible without G^* taking on a proper maximum. That is, Corollary 1 along with (12) is a sufficient condition for $\mathbf{u}_1 = [1 \quad 0]^{\mathrm{T}}$ to be an ESS. Moreover, it is well known that conditions (11) and (12) are exactly the same conditions for $\mathbf{u}_1 = [1 \;\; 0]^{\mathrm{T}}$ to be a matrix(T)-ESS for the 2×2 matrix $\mathbf{M}$ (Maynard Smith, 1982). We thus arrive at the conclusion that $\mathbf{u}_1$ is a matrix(G)-ESS if and only if it is a matrix(T)-ESS. It also follows that there can be payoff matrices $\mathbf{M}$ for which $\mathbf{u}_1$ satisfies Corollary 1 but $\mathbf{u}_1$ is not a matrix(G)-ESS and that this can only occur when G^* is identically zero as a function of $\mathbf{v}$.

A similar analysis shows the second case, $\mathbf{u}_1 = [0 \;\; 1]^{\mathrm{T}}$, is an ESS coalition of one if and only if either

$$m_{12} - m_{22} < 0$$

or

$$m_{12} - m_{22} = 0 \qquad \text{and} \qquad m_{11} - m_{21} < 0.$$

In particular, $[0 \;\; 1]^{\mathrm{T}}$ is a matrix(G)-ESS if and only if it is a matrix(T)-ESS.

4.1.2. *Pure strategies—coalition of two.* In this case, the only possible solution is the coalition $\mathbf{u}_1 = [1 \quad 0]^{\mathrm{T}}$, $\mathbf{u}_2 = [0 \quad 1]^{\mathrm{T}}$. From (10), the G^* function reduces to

$$G^* = [v_1 \quad v_2] \begin{bmatrix} m_{11} \\ m_{21} \end{bmatrix} p_1^* + [v_1 \quad v_2]$$

$$\begin{bmatrix} m_{12} \\ m_{22} \end{bmatrix} p_2^* - (\mathbf{p}^*)^{\mathrm{T}} \mathbf{M}\mathbf{p}^*.$$

From the equilibrium requirements that $G^*(\mathbf{v}, \mathbf{u}, \mathbf{p}^*) = 0$ at $\mathbf{v} = \mathbf{u}_1$ and $\mathbf{v} = \mathbf{u}_2$,

$$m_{11} p_1^* + m_{12} p_2^* - (\mathbf{p}^*)^{\mathrm{T}} \mathbf{M}\mathbf{p}^* = 0$$

and

$$m_{21} p_1^* + m_{22} p_2^* - (\mathbf{p}^*)^{\mathrm{T}} \mathbf{M}\mathbf{p}^* = 0.$$

Solving these equations for p_1^* and p_2^* yields

$$p_1^* = \frac{m_{22} - m_{12}}{m_{11} + m_{22} - m_{12} - m_{21}} = \frac{a}{a+b}$$

$$p_2^* = \frac{m_{11} - m_{21}}{m_{11} + m_{22} - m_{12} - m_{21}} = \frac{b}{a+b}$$

where

$$a = m_{22} - m_{12}$$

$$b = m_{11} - m_{21}.$$

Thus an ecological equilibrium will exist if and only if a and b are both positive or both negative (i.e., if and only if $ab > 0$). These requirements also guarantee that the ESS maximum principle is satisfied trivially since, in this case, G^* is a zero maximum with respect to $\mathbf{v}$ at both $\mathbf{u}_1$ and $\mathbf{u}_2$ (i.e., G^* is identically zero as a function of $\mathbf{v}$). However, an analysis of the dynamic shows $\mathbf{p}^*$ is ecologically stable if and only if a and b are both negative—the exact conditions for $\mathbf{p}^*$ to be a matrix(T)-ESS (Maynard Smith, 1982). That is, $\mathbf{u}_c = [\mathbf{u}_1, \mathbf{u}_2]$ is a matrix(G)-ESS coalition of two if and only if $\mathbf{p}^*$ is a matrix(T)-ESS. It is again clear that there are payoff matrices $\mathbf{M}$ for which $\mathbf{u}_c$ satisfies Corollary 1 but $\mathbf{u}_c$ is not a matrix(G)-ESS and in this case G^* is identically zero as a function of $\mathbf{v}$.

4.1.3. *Mixed strategies—coalition of one.* Suppose $\mathbf{u}_1 = [u_1 \quad 1 - u_1]^{\mathrm{T}}$ is an ESS coalition of one in mixed strategies (i.e., when $\mathcal{U} = \mathcal{U}_c$). Then $\mathbf{p}^* = [1 \quad 0]^{\mathrm{T}}$ and

$$G^* \triangleq G(v, u_1, \mathbf{p}^*) = [v - u_1 \quad u_1 - v] \begin{bmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{bmatrix} \begin{bmatrix} u_1 \\ 1 - u_1 \end{bmatrix}$$

$$= (v - u_1)[(a+b)\, u_1 - a].$$

Since the gradient is given by

$$\left. \frac{\partial G^*}{\partial v} \right|_{v = u_1} = (a+b)\, u_1 - a$$

and $0 \leqslant u_1 \leqslant 1$, it follows that the necessary condition for G^* to take on a maximum with respect to v at u_1 results in

$$u_1 = \begin{cases} 1 & \text{if} \quad (a+b) - a > 0 \quad (\text{i.e., if } b > 0) \\ 0 & \text{if} \quad a > 0 \\ \dfrac{a}{a+b} & \text{if} \quad ab > 0 \end{cases} \tag{13}$$

While the necessary conditions of Corollary 1 are satisfied by any of the three cases in (13), when we plot G^* as a function of v, it is discovered that only for the $u_1 = 1$ or $u_1 = 0$ case does G^* take on a proper maximum with respect to v. With $u_1 = a/(a+b)$, the plot of G^* is flat at zero for all values of v. This suggests that there may not be an ESS coalition of one solution for the third case. In fact, it has been shown (Brown and Vincent, 1987) that not only is there no ESS coalition of one when $u_1 = a/(a+b)$, but there is never an ESS coalition of two or more in this case.

In summary, for 2 × 2 bilinear matrix games, the only matrix(G)-ESS's for the mixed-strategy model are pure strategy coalitions of one that correspond to a matrix(T)-ESS. On the other hand, for the pure-strategy model, $\mathbf{u}_c$ is a matrix(G)-ESS if and only if $\mathbf{p}^*$ is a matrix(T)-ESS.

There are related results for $n_u \times n_u$ bilinear matrix games. For the mixed-strategy model, only matrix(G)-ESS coalitions of one are possible and these must be pure-strategy matrix(T)-ESS's. For the pure-strategy model, a matrix(T)-ESS with σ positive components corresponds to a matrix(G)-ESS coalition of σ. However, other ESS coalitions emerge when $n_u > 2$ since the static matrix(T)-ESS criteria does not completely characterize asymptotic stability for the frequency dynamic (8) (see Taylor and Jonker, 1978).

5. NONLINEAR MATRIX GAMES

In the previous section we applied the continuous G-function method and ESS maximum principle to the traditional bilinear matrix games of evolutionary game theory. We found that the underlying linearities can produce a flat G^*-function at solutions that satisfy Corollary 1. This means that Corollary 2 will often not be satisfied for coalitions of one and additional analysis is required to determine whether the system is ecologically stable or not. However, our analysis is in no way restricted to bilinear matrix games. Specifically, the above linearities that produce flat G^*-functions can be eliminated in (5) by relaxing the assumption that the elements of the matrix $\mathbf{M}$ need be constants or that the strategies need be interpreted as probabilities. Rather the components of $\mathbf{M}$ may be functions of strategy and/or $\mathscr{U}$ need not be restricted to either $\mathscr{U}_c$ or $\mathscr{U}_p$. For these nonlinear matrix games, application of the ESS maximum principle will yield interior candidate solutions that are, more often, proper extrema of the G-function yielding results more akin to those obtained with the original applications of the G-function method (Vincent *et al.*, 1993).

The following example, chosen for mathematical clarity, illustrates the above discussion. We change the strategy set of a well-known bilinear matrix game (with an interior matrix(T)-ESS–flat G^*-function) to include a nonlinearity. Applying Corollary 1 results in an interior solution with a proper maximum which is now an ESS coalition of one.

In order to illustrate the usefulness for more realistic applications of the tools developed here, additional biologically interesting examples are given in Sections 6 and 7. These latter examples are formulated as matrix games where the components of $\mathbf{M}$ are nonlinear functions of strategy.

5.1. *A Simple Nonlinear Example*

Consider a 2×2 game with a constant matrix $\mathbf{M}$ as used above but with the constraint set defined by

$$\mathscr{U} = \{\mathbf{u}_i \in \mathscr{R}^2 \mid 0 \leqslant u_{ij} \leqslant 1 \ \forall \ j = 1, 2 \text{ and } u_{i1}^2 + u_{i2} = 1\}.$$

Note that in the bilinear game $\mathscr{U}_c$ is the straight line segment from $[1 \ \ 0]$ to $[0 \ \ 1]$. In this game $\mathscr{U}$ is a convex curve from $[1 \ \ 0]$ to $[0 \ \ 1]$.

Let us first examine an ESS coalition of one. Using the G-function as defined by (7), we again obtain (9) which reduces to

$$G^* = v_1 m_{11} u_{11} + v_1 m_{12} u_{12} + v_2 m_{21} u_{11} + v_2 m_{22} u_{12} - E(\mathbf{u}_1, \mathbf{u}_1). \tag{14}$$

From the constraints

$$v_1^2 + v_2 = 1$$
$$u_{11}^2 + u_{12} = 1$$

we can eliminate v_2 and u_{12} to obtain

$$G^* = v_1 m_{11} u_{11} - v_1 m_{12} u_{11}^2 + v_1 m_{12} - m_{21} u_{11} v_1^2 + m_{21} u_{11} + m_{22} v_1^2 u_{11}^2 - m_{22} v_1^2 - m_{22} u_{11}^2 + m_{22} - E(\mathbf{u}_1, \mathbf{u}_1). \tag{15}$$

Thus

$$\frac{\partial G^*}{\partial v_1} = m_{11} u_{11} - m_{12} u_{11}^2 + m_{12} - 2m_{21} u_{11} v_1 + 2m_{22} v_1 u_{11}^2 - 2m_{22} v_1$$

and replacing v_1 with u_{11} yields

$$\left.\frac{\partial G^*}{\partial v_1}\right|_{v_1 = u_{11}} = m_{11} u_{11} - m_{12} u_{11}^2 + m_{12} - 2m_{21} u_{11}^2 + 2m_{22} u_{11}^3 - 2m_{22} u_{11}.$$

If an ESS coalition of one exists in the interior of $\mathscr{U}$, we may find it by setting this derivative equal to zero. For an explicit example, consider the "game of chicken" matrix

$$M = \begin{bmatrix} 0 & 15 \\ 5 & 10 \end{bmatrix}.$$

In this case, setting $\frac{\partial G^*}{\partial v_1}|_{v_1 = u_{11}} = 0$ results in the solutions $u_{11} = -0.87444,\ 0.54201,\ 1.5824$. Thus, $\mathbf{u}_1^*$ with components

$$u_{11} = 0.54201, \ u_{12} = 0.70623$$

is the only candidate ESS coalition of one in the interior of $\mathscr{U}$. We can check to see if this solution represents a proper maximum for G^* by substituting this value of $\mathbf{u}_1$ into (15) to obtain

$$G^*|_{u_{11} = 0.54201,\, u_{12} = 0.70623} = -9.7723 v_1^2 + 10.593 v_1 + 9.7723 - 12.643.$$

A plot of this quadratic function (Fig. 1) yields a proper maximum for G^* at $v_1 = 0.54201$ with the maximum value of zero.

In this case, $\mathbf{p}^* = [1 \ \ 0 \ \cdots \ 0]^{\mathrm{T}}$ is an ecologically stable equilibrium for all possible mutant strategies and hence $\mathbf{u}_1^*$ is an ESS. Compare this result with the same bilinear matrix game played on the strategy set $\mathscr{U}_c$. In that case, we obtain the matrix(T)-ESS $u_{11} = 0.5, \ \ u_{12} = 0.5$ which

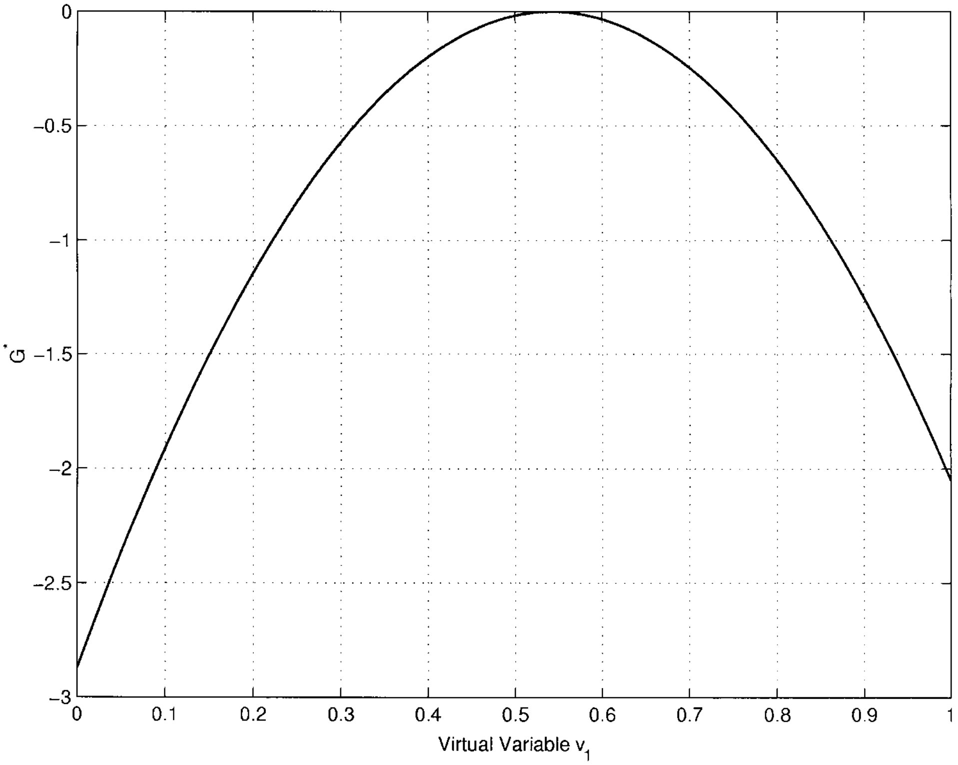

FIG. 1. The G^* function takes on a proper maximum at the ESS solution.

is not a proper maximum point of the relevant function G^* and not a matrix(G)-ESS with respect to all possible mutant strategies.

6. GAMES BETWEEN RELATIVES

In this section, we again assume that there are a finite number n_u of pure strategies and that individuals can be using any mixed strategy in $\mathcal{U}_c$ in their pair-wise contests. However, contests are not at random in that an individual using strategy $\mathbf{u} \in \mathcal{U}_c$ is more likely to meet an opponent using the same strategy (called a game between relatives) than would be the case under random pairs. The static version of the model considered here originated (Grafen, 1979, and Hines and Maynard Smith, 1979) as a means to incorporate Hamilton's (1964) concept of relatedness in kin selection into an inclusive fitness function as opposed to a fitness function based explicitly on the underlying genetics. It is then assumed that the rate that games occur between relatives reflects the degree of relatedness.

Specifically, in place of (3), suppose the individual fitness of someone using strategy $\mathbf{u}_i$ is

$$H_i[\mathbf{u}, \mathbf{x}] = \alpha \mathbf{u}_i^{\mathrm{T}} \mathbf{M} \mathbf{u}_i + (1-\alpha)\, \mathbf{u}_i^{\mathrm{T}} \mathbf{M} \frac{\sum_{j=1}^{n_s} x_j \mathbf{u}_j}{\sum_{j=1}^{n_s} x_j}$$

where $\mathbf{M}$ is a payoff matrix of constants and $0 < \alpha < 1$ is the strategy-independent rate that games occur between relatives. In terms of frequency

$$H_i[\mathbf{u}, \mathbf{p}] = \alpha \mathbf{u}_i^{\mathrm{T}} \mathbf{M} \mathbf{u}_i + (1-\alpha)\, \mathbf{u}_i^{\mathrm{T}} \mathbf{M} \sum_{j=1}^{n_s} p_j \mathbf{u}_j - \sum_{j=1}^{n_s} p_j \mathbf{u}_j^{\mathrm{T}} \mathbf{M} \sum_{j=1}^{n_s} p_j \mathbf{u}_j.$$

This model has been investigated by Hines and Maynard Smith (1979) from the frequency perspective (see also Grafen, 1979, and Taylor, 1989 for the case $n = 2$) without explicit consideration of the underlying dynamic. In our terminology, these references found ESS coalitions of one through static fitness comparisons similar to those defining a matrix(T)-ESS.

The corresponding G-function for the frequency dynamic model is

$$G(\mathbf{v}, \mathbf{u}, \mathbf{p}) = \alpha \mathbf{v}^{\mathrm{T}}\mathbf{M}\mathbf{v} + (1-\alpha)\, \mathbf{v}^{\mathrm{T}}\mathbf{M} \sum_{j=1}^{n_s} p_j \mathbf{u}_j - \sum_{j=1}^{n_s} p_j \mathbf{u}_j^{\mathrm{T}} \mathbf{M} \sum_{j=1}^{n_s} p_j \mathbf{u}_j. \tag{16}$$

We will now seek an ESS coalition of one, $\mathbf{u}_1$, using Corollary 1. In this case it is necessary that

$$G(\mathbf{v}, \mathbf{u}, \mathbf{p}^*) = \alpha \mathbf{v}^{\mathrm{T}}\mathbf{M}\mathbf{v} + (1-\alpha)\, \mathbf{v}^{\mathrm{T}}\mathbf{M}\mathbf{u}_1 - \mathbf{u}_1^{\mathrm{T}}\mathbf{M}\mathbf{u}_1$$

take on a maximum with respect to $\mathbf{v}$ at $\mathbf{u}_1$. Since the maximum value is zero, it follows that for all $\mathbf{v} \in \mathscr{U}_c$

$$\alpha \mathbf{v}^{\mathrm{T}}\mathbf{M}\mathbf{v} + (1-\alpha)\, \mathbf{v}^{\mathrm{T}}\, \mathbf{M}\mathbf{u}_1 - \mathbf{u}_1^{\mathrm{T}}\mathbf{M}\mathbf{u}_1 \leqslant 0. \tag{17}$$

Thus

$$(\mathbf{u}_1 - \mathbf{v})^{\mathrm{T}}\, \mathbf{M}\mathbf{u}_1 + \boldsymbol{\alpha} \mathbf{v}^{\mathrm{T}}\, \mathbf{M}(\mathbf{u}_1 - \mathbf{v}) \geqslant 0$$

which is equivalent to

$$(\mathbf{u}_1 - \mathbf{v})^{\mathrm{T}}\, \mathbf{M}\mathbf{u}_1 + \boldsymbol{\alpha} \mathbf{v}^{\mathrm{T}}\, \mathbf{M}(\mathbf{u}_1 - \mathbf{v}) + [\alpha \mathbf{u}_1^{\mathrm{T}}\mathbf{M}(\mathbf{u}_1 - \mathbf{v}) - \alpha \mathbf{u}_1^{\mathrm{T}}\, \mathbf{M}(\mathbf{u}_1 - \mathbf{v})] \geqslant 0$$

$$(\mathbf{u}_1 - \mathbf{v})^{\mathrm{T}}(\mathbf{M} + \alpha \mathbf{M}^{\mathrm{T}})\, \mathbf{u}_1 - \alpha(\mathbf{u}_1 - \mathbf{v})^{\mathrm{T}}\, \mathbf{M}(\mathbf{u}_1 - \mathbf{v}) \geqslant 0.$$

It follows that (17) can be rewritten as

$$(\mathbf{u}_1 - \mathbf{v})^{\mathrm{T}}\, (\mathbf{M} + \alpha \mathbf{M}^{\mathrm{T}})\, \mathbf{u}_1 \geqslant \alpha(\mathbf{u}_1 - \mathbf{v})^{\mathrm{T}}\, \mathbf{M}(\mathbf{u}_1 - \mathbf{v}). \tag{18}$$

Suppose that $\mathbf{u}_1$ lies in the interior of $\mathscr{U}_c$. Unless

$$(\mathbf{u}_1 - \mathbf{v})^{\mathrm{T}}\, (\mathbf{M} + \alpha \mathbf{M}^{\mathrm{T}})\, \mathbf{u}_1 = 0$$

for all $\mathbf{v} \in \mathscr{U}_c$ it would always be possible to find a $\mathbf{v} \in \mathscr{U}_c$ such that $\mathbf{u}_1 - \mathbf{v}$ would result in a negative value for the left hand side of (18). This would violate the inequality since by making the length of $\mathbf{u}_1 - \mathbf{v}$ arbitrarily small, the quadratic nature of the right hand side of (18) would result in its value being greater than the left hand side. Thus

$$(1+\alpha)(\mathbf{u}_1 - \mathbf{v})^{\mathrm{T}}\, \mathbf{M}(\mathbf{u}_1 - \mathbf{v}) = (\mathbf{u}_1 - \mathbf{v})^{\mathrm{T}}\, (\mathbf{M} + \alpha \mathbf{M}^{\mathrm{T}})(\mathbf{u}_1 - \mathbf{v}) \leqslant 0.$$

In fact, this last inequality must be proper or else there is a continuum of equilibrium points through $\mathbf{u}_1$ in the "direction" $\mathbf{v}$ which contradicts that $\mathbf{u}_1$ is an ESS. This shows that $\mathbf{u}_1$ is a matrix(T)-ESS for the adjusted payoff matrix $\mathbf{M} + \alpha \mathbf{M}^{\mathrm{T}}$.

Theorem 2. *Suppose* $0 < \alpha < 1$ *is fixed and* $\mathbf{u}_1$ *is in the interior of* $\mathscr{U}_c$. *Then* $\mathbf{u}_1$ *is an ESS for the game against relatives with payoff matrix* $\mathbf{M}$ *if and only if* $\mathbf{u}_1$ *is a matrix-(T)-ESS for the matrix* $\mathbf{M} + \alpha \mathbf{M}^{\mathrm{T}}$.

Proof. The "only if" direction is proved above. For the other direction, assume $\mathbf{u}_1$ is a matrix ESS of $\mathbf{M} + \alpha \mathbf{M}^{\mathrm{T}}$. For a fixed set of mutant strategies $\mathbf{u}_2, \ldots, \mathbf{u}_{n_s}$ in Δ^{n_u}, we have $G(\mathbf{u}_i, \mathbf{u}_1, \mathbf{p}^*) < G(\mathbf{u}_1, \mathbf{u}_1, \mathbf{p}^*)$ for $2 \leqslant i \leqslant n_s$ by the above analysis. Thus, by Corollary 2, $\mathbf{u}_1$ is an ESS for the strategy frequency dynamic. ▮

Let us apply the above result to the 2×2 payoff matrix $M = \left[\begin{smallmatrix} a & b \\ c & d \end{smallmatrix}\right]$. An interior ESS must be a matrix(T)-ESS of $\mathbf{M} + \alpha \mathbf{M}^{\mathrm{T}} = \left[\begin{smallmatrix} (1+\alpha)a & b+\alpha c \\ c+\alpha b & (1+\alpha)d \end{smallmatrix}\right]$ and so the first component of $\mathbf{u}_1$ is given by

$$\frac{b - d + \alpha(c-d)}{(1+\alpha)(b+c-a-d)}$$

which must be between 0 and 1 and the denominator must be positive (see Taylor, 1989). In this case, the ecological equilibrium point $\mathbf{p}^* = [1\ \ 0 \cdots 0]^{\mathrm{T}}$ is a global ESE. Therefore, we may conclude that there is a unique global ESS coalition of one in the interior of $\mathscr{U}_c$ if and only if $c + \alpha b > (1+\alpha)\, a$ and $b + \alpha c > (1+\alpha)\, d$.

The analysis of pure strategy ESS's is not so straightforward. If $(1+\alpha)\, a > c + \alpha b$, then $\mathbf{u}_1 = (1, 0)$ is a matrix(T)-ESS of $\mathbf{M} + \alpha \mathbf{M}^{\mathrm{T}}$. On the other hand, it is only an ESS coalition of one if we also have the inequality $a > \alpha d + (1-\alpha)\, c$ that results from considering mutants of the form $\mathbf{v} = (0, 1)$. However, if $\mathbf{u}_1 = (1, 0)$ is a matrix(T)-ESS of $\mathbf{M} + \alpha \mathbf{M}^{\mathrm{T}}$ but not an ESS coalition of one, then $\mathbf{u}_1 = (0, 1)$ is also a matrix(T)-ESS of $\mathbf{M} + \alpha \mathbf{M}^{\mathrm{T}}$ that is automatically an ESS coalition of one. Thus, for two-strategy games between relatives, there is always at least one ESS coalition of one.

7. SEX RATIO GAME

We will use an elementary (nongenetic) model to explain why the number of males and females are approximately equal in most animal populations. It is assumed that the sex ratio of offspring is determined by their mother and that a female's fitness is measured by the expected number of grandchildren. The strategy of females of type i is specified by $\mathbf{u}_i = [u_{i1}\ \ u_{i2}]^{\mathrm{T}}$ where u_{i1} are the number of male children and u_{i2} are the number of female children. Thus $k_i = u_{i1} + u_{i2}$ is the total number of her children. Under random mating, each male is assumed to mate with $\bar{r}_{\text{sex}}$ females where $\bar{r}_{\text{sex}}$ is the current sex ratio (total number of females/total number of males) of the population as a whole. In this case the expected number of grandchildren from a female of type i is

$$k_i u_{i2} + \bar{k}\bar{r}_{\text{sex}} u_{i1},$$

where $\bar{k}$ is the average number of children per female in the population as a whole. In the special case of only two strategy types, i and j, with i in small numbers and j in large numbers, the sex ratio may be approximated by $\bar{r}_{\text{sex}} = \frac{u_{j2}}{u_{j1}}$ and $\bar{k}$ may be approximated by k_j. In this case the expected number of grandchildren from a female of type i competing in a population of females of type j may be written as (Maynard Smith, 1982; Cressman, 1992)

$$E(\mathbf{u}_i, \mathbf{u}_j) = k_i u_{i2} + k_j \frac{u_{j2}}{u_{j1}} u_{i1} \tag{19}$$

which, in nonlinear matrix form, is

$$E(\mathbf{u}_i, \mathbf{u}_j) = [u_{i1} \;\; u_{i2}] \begin{bmatrix} 0 & k_j/u_{j1} \\ k_i/u_{j1} & 0 \end{bmatrix} \begin{bmatrix} u_{j1} \\ u_{j2} \end{bmatrix}.$$

The above assumption for $\bar{r}_{\text{sex}}$ and $\bar{k}$ allows us to put this game into a matrix game format. While these assumptions are not valid when there are many different types in the population away from equilibrium conditions, they will be valid when examining the conditions for an ESS coalition of one near equilibrium. Since the ESS maximum principle is applied at equilibrium and since the ESS of interest will turn out to be a coalition of one, we will continue our analysis using this expected payoff matrix. It should be noted that, if this problem is formulated without the above assumptions, it may still be solved using the ESS maximum principle, albeit as a continuous game rather than a nonlinear matrix game.

7.1. *The Politically Correct Solution*

If the cost of producing a male or female child is the same, then the number of children produced will simply depend on the total resources available to each female. If we assume these resources to be the same for all types it follows that $k_i = k_j = k$. The strategy set in this case may be written as

$$\mathcal{U} = \{\mathbf{u}_i \in \mathcal{R}^2 \mid 0 \leqslant u_{ij} \leqslant k \;\forall\; j = 1, 2 \text{ and } u_{i1} + u_{i2} = k\}.$$

From (19), the expected payoff in this case becomes

$$E(\mathbf{u}_i, \mathbf{u}_j) = k\left[u_{i2} + \frac{u_{j2}}{u_{j1}} u_{i1}\right].$$

Assuming an ESS coalition of one we have from (9)

$$G^* = E(\mathbf{v}, \mathbf{u}_1) - E(\mathbf{u}_1, \mathbf{u}_1)$$

$$G^* = k\left[v_2 + \frac{u_{12}}{u_{11}} v_1\right] - E(\mathbf{u}_1, \mathbf{u}_1).$$

Using the constraints to eliminate v_2 and u_{12} we have

$$G^* = k\left[k - v_1 + \frac{k - u_{11}}{u_{11}} v_1\right] - E(\mathbf{u}_1, \mathbf{u}_1).$$

A necessary condition for G^* to take on a maximum with respect to v_1 in the interior of $\mathcal{U}$ is given by

$$\left.\frac{\partial G^*}{\partial v_1}\right|_{v_1 = u_{11}} = -1 + \frac{k - u_{11}}{u_{11}} = 0$$

which implies $u_{11} = k/2$. That is, half of the offspring should be males.

Although the result is the expected one that $\bar{r}_{\text{sex}} = 1$, it has the same properties as a matrix(T)-ESS result rather than an ESS result since

$$G(v_1, u_{11}, \mathbf{p}^*)|_{u_{11} = k/2} = k^2 - E(\mathbf{u}_1, \mathbf{u}_1)$$

does not depend on v_1 and so G^* has no proper maximum when $\mathbf{u}_1 = [\frac{k}{2} \; \frac{k}{2}]^{\mathrm{T}}$. Thus, it is unclear from the above analysis whether each female will have the same number of sons as daughters or whether this is only the average behavior of the female population. This problem may be avoided if the constraint set $\mathcal{U}$ is modified so that the components of the strategy vector are not restricted to lie on a straight line. In fact, this possibility is considered in the literature on sex ratio games as a special case of resource allocation models where the allocation decision is how many sons and how many daughters to produce (see p. 44 of Maynard Smith, 1982). We consider an elementary nongenetic version of this situation in the following section.

7.2. *Other Possible Solutions*

If the cost of producing females is different from the cost of producing males, then a relationship must exist between the two such as $u_{i2} = f(u_{i1})$. If we again assume the resources available for producing offspring is the same for all types, there will be an upper limit, k, to the total number of children produced when they are all males. That is the strategy set for this case is

$$\mathcal{U} = \{\mathbf{u}_i \in \mathcal{R}^2 \mid 0 \leqslant u_{i1} \leqslant k \text{ and } u_{i2} = f(u_{i1})\},$$

where the total number of children produced is given by

$$k_i = u_{i1} + u_{i2} = u_{i1} + f(u_{i1}).$$

Clearly $f(u_{i1})$ must satisfy the requirement that $f(k) = 0$. Note that we would return to the politically correct strategy set if we took $f(u_{i1}) = k - u_{i1}$.

In order to simulate a convex curve, we will use an arc of a circle

$$u_{i2} = f(u_{i1}) = \sqrt{(k^2 - u_{i1}^2)}\,. \qquad (20)$$

In this case k children will be produced if they are either all females or all males. A female who uses a mixed strategy will produce a greater number of children with the maximum number corresponding to $u_{i1} = \sqrt{2}\,\frac{k}{2}$.

From (19) the expected payoff in this case is

$$E(\mathbf{u}_i, \mathbf{u}_j) = [u_{i1} + f(u_{i1})]\, f(u_{i1}) + \left[u_{j1} + f(u_{j1}) \right] \frac{f(u_{j1})}{u_{j1}}\, u_{i1}.$$

Assuming an ESS coalition of one we have from (9)

$$G^* = [v_1 + f(v_1)]\, f(v_1) + [u_{11} + f(u_{11})]\, \frac{f(u_{11})}{u_{11}}\, v_1 - E(\mathbf{u}_1, \mathbf{u}_1).$$

Thus

$$\frac{\partial G^*}{\partial v_1} = \left[1 - \frac{v_1}{f(v_1)} \right] f(v_1) - [v_1 + f(v_1)]\, \frac{v_1}{f(v_1)} + [u_{11} + f(u_{11})]\, \frac{f(u_{11})}{u_{11}}$$

which reduces to

$$\frac{\partial G^*}{\partial v_1} = f(v_1) - 2v_1 - \frac{v_1^2}{f(v_1)} + f(u_{11}) + \frac{f^2(u_{11})}{u_{11}}.$$

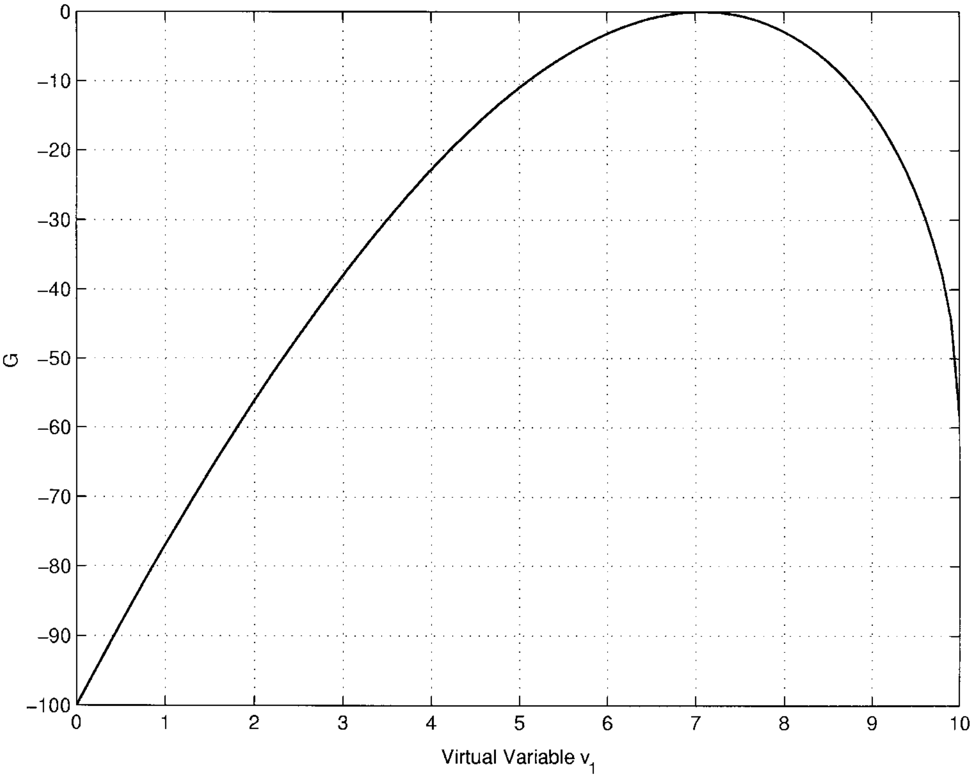

FIG. 2. The ESS produces the maximum number of children.

We again seek an interior solution for v_1 from

$$\left.\frac{\partial G^*}{\partial v_1}\right|_{v_1=u_{11}} = 2f(u_{11}) - 2u_{11} - \frac{u_{11}^2}{f(u_{11})} + \frac{[f(u_{11})]^2}{u_{11}} = 0$$

that has the solution

$$u_{11} = \sqrt{2}\,\frac{k}{2}.$$

This is the same value for u_{11} which produces the maximum number of children. To see if this is a proper maximum we plot G^* as a function of v_1. Choosing $k = 10$ we obtain the results shown in Fig. 2. Thus, by Corollary 2, u_{11} corresponds to an ESS coalition of one. Furthermore, simulation may be used to demonstrate that this solution is in fact a globally ecologically stable equilibrium and so it is the unique ESS.

It follows from (20) that $u_{12} = u_{11}$. Thus, in this case, the ESS is again the politically correct solution of producing the same number of males and females. However, this result differs from the previous case in that this solution is now an ESS. The reason that we get the same result is because of the symmetry in the trade-off curve between males and females. Seeking an ESS with a nonsymmetric trade-off can yield other solutions.

8. SUMMARY

We have done some housecleaning here by demonstrating that the ESS maximum principle, originally developed to determine the ESS vector and the resulting stable equilibrium densities in differential and difference equation models, is also applicable for the determination of the ESS vector and the evolution of strategy frequencies in a matrix game setting. Both continuous games and matrix games are brought under the aegis of the ESS maximum principle through the introduction of two new corollaries in Section 3. Our principle aim is one of unification and to bring the *G*-function approach to researchers in matrix game theory. We have demonstrated that by doing so, not only do we have a better understanding of the difference between an ESS solution and the traditional matrix(T)-ESS solution, but now, matrix games may be readily extended from the traditional bilinear matrix game to include nonlinear matrix games.

We demonstrated in Section 4 that the new corollaries can be used to deal with both standard models of evolutionary matrix game theory; namely, the pure strategy frequency dynamic where each individual must play one of the n_u pure strategies and the mixed strategy frequency dynamic where individuals can randomize their strategies. It is shown that, for 2 × 2 payoff matrices, all solutions which satisfy the ESS maximum principle (whether given by coalitions of one or two strategies) that are evolutionarily stable must correspond to strategy frequencies in the matrix(T)-ESS. However, in the mixed strategy model, it is shown that any ESS coalition must be a coalition of one which consists of a single pure strategy.

Section 5 extends the matrix game model to situations where the set of individual strategies (i.e., the strategy space) is not constrained to be mixtures of pure strategies. Section 6 shows that the solutions obtained in the literature from static fitness comparisons for games between relatives are actually dynamically stable since they correspond to ESS coalitions of one. Similarly, the elementary models of stable sex ratios in Section 7 also correspond to ESS coalitions of one. Together, Sections 6 and 7 illustrate the relevance of our approach to biological models that are concerned with the frequency of individual behavioral types in the population. First, coalitions that satisfy the ESS maximum principle (Corollary 1) are the only candidates for stable equilibrium outcomes of the evolutionary dynamics. Furthermore, if a coalition of one yields a proper maximum (Corollary 2), then all individuals are expected to adopt this strategy in the long run.

For the most part, this paper restricts attention to applications of the ESS maximum principle when the strategy space is one dimensional. In this case, the techniques for determining ESS coalitions of one are closely related to those used in inclusive fitness arguments (e.g., Taylor, 1996). However, the general ESS maximum principle allows for the possibility that stable coalitions of two or more strategy types can be present in the population. We intend to pursue such possibilities in the frequency domain through future research.

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