

Evolutionarily Stable Strategies and Game Dynamics

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ABSTRACT

We consider a class of matrix games in which successful strategies are rewarded by high reproductive rates, so become more likely to participate in subsequent playings of the game. Thus, over time, the strategy mix should evolve to some type of optimal or stable state. Maynard Smith and Price (1973) have introduced the concept of ESS (evolutionarily stable strategy) to describe a stable state of the game. We attempt to model the dynamics of the game both in the continuous case, with a system of non-linear first-order differential equations, and in the discrete case, with a system of non-linear difference equations. Using this model, we look at the notions of stability and asymptotic behavior. Our notion of stable equilibrium for the continuous dynamic includes, but is somewhat more general than, the notion of ESS.

1. INTRODUCTION

Over the past 5 years there has been much work in applying concepts of game theory to model various kinds of animal conflict. In particular the definition of ESS (evolutionarily stable strategy) of Maynard Smith and Price [4] seems to have provided a good notion of stable equilibrium, and most models that have appeared have contained one or more ESSs. Frequently, statements have been made about the behavior of a game-theoretic model away from an ESS, and sometimes simulation studies have been done to track this behavior. But, to our knowledge, there has been no systematic attempt to produce a notion of dynamic which might apply to the type of games being studied, and to relate the notion of stable equilibrium for this dynamic to the notion of ESS.

In Sec. 2 we consider a general class of games (which includes the linear games usually studied), and provide a general definition of ESS. In Sec. 3

we introduce a notion of dynamic for both the continuous (overlapping generations) and the discrete case. Our main theorem is that under a non-degeneracy condition, an ESS is always stable for the continuous dynamic. This is not however true for the discrete dynamic, essentially because of an overshoot phenomenon. Finally we give an example of a dynamically stable equilibrium point which is not an ESS.

2. EVOLUTIONARILY STABLE STATES

Suppose we have a population of individuals who are playing a game in competition with one another. There are n possible *pure strategies* available, numbered 1 to n , and at each instant, every individual is using one of these strategies. For each strategy i let s_i be the proportion of individuals who are, at that moment, using strategy i . The probability vector $s = (s_1, s_2, \dots, s_n)$ is called the *state vector* of the population. We assume that the payoff per unit time to an individual using strategy i is a function $F(i|s)$ of the state s of the population. We refer to $F(i|s)$ as the *fitness* of i in state s .

The basic idea is this: the more fit a strategy is at any moment, the more likely it is to be employed in the future. The mechanism behind this is either that individuals tend to switch to strategies that are doing well, or that individuals bear offspring who tend to use the same strategies as their parents, and the fitter the individual, the more numerous his offspring. In any case, as time goes on, the strategy mix s may change. A dynamic game theory will look at how the state vector s moves with time, and will look for equilibrium states and examine their stability.

Indeed, let $K = \{p : \sum p_i = 1, p_i \geq 0\}$ be the *state space* of the population. That is, each element $p \in K$ represents a possible strategy mix. A state p in K is called an *equilibrium state* if the fitnesses $F(i|p)$ are equal for all pure strategies i actually used by individuals in a population in state p . We let $\text{supp}(p)$, the *support* of p , denote this set of pure strategies. That is, $\text{supp}(p) = \{i : p_i \neq 0\}$. An equilibrium state, if undisturbed, should persist, since all existing strategies are equally fit. However, in real life, an equilibrium state will almost surely be disturbed, so that we are only interested in it if the system, once disturbed, returns to the equilibrium state. If this is the case, the equilibrium is said to be *stable*.

If q is in K , let us define $F(q|p) = \sum q_i F(i|p)$. We can think of $F(q|p)$ as the average fitness of a group of individuals playing the game against members of a population in state p , when a proportion q_i of the group uses strategy i . If we let e_i denote the state of a population using strategy i only, then $F(e_i|p) = F(i|p)$. Observe that if p is an equilibrium state, then $F(q|p) = F(p|p)$ whenever $\text{supp}(q)$ is contained in $\text{supp}(p)$.

When should an equilibrium state p be stable? Maynard-Smith and Price [4] have provided a way of answering this question. Their idea is very simple

in that it uses no more machinery than we have already developed, and requires no further assumptions. It is probably for this reason that it has appeared so much in the literature recently. They propose that p should be stable if whenever a small subpopulation switches to state q , its average fitness in the perturbed state will be less than the average fitness of the remaining population. This idea motivates the following definition.

DEFINITION [4]

A state p is called an *ESS (evolutionarily stable state)* if for every state $q \neq p$, if we let $\bar{p} = (1 - \epsilon)p + \epsilon q$ (the perturbed state), then $F(q|\bar{p}) < F(p|\bar{p})$ for sufficiently small $\epsilon > 0$.

We remark that ϵ in this definition measures the proportion of players in the q -group. Observe that an ESS is certainly an equilibrium state. Indeed, letting q be the pure state e_i (concentrated at i) and letting ϵ approach zero, we have $F(i|p) \leq F(p|p)$. If i is in $\text{supp}(p)$, this implies that $F(i|p) = F(p|p)$, since the p -average of the numbers $F(i|p)$ equals $F(p|p)$.

Suppose p is an equilibrium point. Define the matrix A by the formula

$$a_{ij} = \frac{\partial}{\partial p_j} F(i|p).$$

Take $q \neq p$, and set $\bar{p} = (1 - \epsilon)p + \epsilon q$. Expanding $F(q|\bar{p})$ and $F(p|\bar{p})$ about p and subtracting yields

$$F(q|\bar{p}) - F(p|\bar{p}) = F(q|p) - F(p|p) + \epsilon[(q-p)A(q-p)] + o(\epsilon). \quad (1)$$

Thus the 1st-order advantage of the q -group over the p -group is given by the formula

$$F(q|p) - F(p|p) + \epsilon[(q-p)A(q-p)].$$

If p is an ESS, then for every q in K this should be non-positive if ϵ is sufficiently small. Therefore, we must have $F(q|p) - F(p|p) \leq 0$ for every q in K .

We will now introduce a non-degeneracy condition, which ensures that the 1st-order advantage of the q -group over the p -group is strictly negative for sufficiently small ϵ . First of all, if i is not in $\text{supp}(p)$, we will require that $F(i|p) < F(p|p)$. Strategies that do not occur in an ESS are, if they emerge, strictly less fit than the strategies that do occur. Secondly, if i is in $\text{supp}(p)$, then, as we have seen, $F(i|p) = F(p|p)$, and so $F(q|p) = F(p|p)$ whenever $\text{supp}(q) \subset \text{supp}(p)$. That is, if the members of the q -group restrict themselves to strategies already used by the p -group, the average fitness of the q -group in encounters with the p -group is precisely equal to the average fitness of

the p -group in encounters with itself. Thus, to get a strictly negative 1st-order advantage of the q -group over the p -group we must have $(q-p)A(q-p) < 0$ whenever $\text{supp}(q) \subset \text{supp}(p)$ and $q \neq p$. Equivalently, putting $x = q - p$, so that $x \neq 0$, $\sum x_i = 0$, and $\text{supp}(x) \subset \text{supp}(p)$, then we must have $xAx < 0$.

DEFINITION

An equilibrium point p is a *regular ESS* if $F(i|p) < F(p|p)$ whenever $i \notin \text{supp}(p)$, and $xAx < 0$ whenever $\text{supp}(x) \subset \text{supp}(p)$, $x \neq 0$, and $\sum x_i = 0$.

It is easy to check, using (1) and the discussion following it, that a regular ESS is an ESS. Generically, every ESS is regular. That is, in a mathematically precise sense, nearly every fitness function $F(q|p)$ is such that every ESS is regular. In particular, if \bar{F} is a fitness function for which ESSs are not all regular, then there is a fitness function F as close to \bar{F} as may be required, for which they are. Therefore, since in any model of a conflict the fitness function provides only an approximation to the real fitness, we may always assume it to be such that all ESSs are regular.

There are at least two reasons for working with regular ESSs. The definition of regular ESS provides what is in effect a simple computational scheme for checking whether an equilibrium point is a regular ESS. Details can be found in [2]. Secondly, certain theorems which we expect to be true about ESSs may fail in the absence of regularity. Our main dynamic-stability theorem in Sec. 3 is such a theorem.

An important class of games are the *linear games*, so called because for every i , $F(i|p)$ is linear in p . For such games there is a matrix A , called the *payoff matrix*, for which $F(i|p) = a_i p$ and $F(q|p) = qAp$, where a_i is the i th row of A . For a linear game, Eq. (1) holds with $o(\epsilon) = 0$ (A being the payoff matrix), and so if p is an ESS, it follows that $xAx < 0$ whenever $\text{supp}(x) \subset \text{supp}(p)$, $x \neq 0$, and $\sum x_i = 0$. This result was first published by Haigh [2]. Thus, for linear games, an ESS is regular if $a_i p < pAp$ whenever $i \notin \text{supp}(p)$. In particular, for a linear game, an ESS with full support is always regular.

3. GAME DYNAMICS

In order to discuss stability, we must now define a dynamic for the game. There are undoubtedly many ways to do this, each related to certain hypotheses about the population. We will assume a population of haploid individuals, each using the same pure strategy throughout its lifetime, and producing offspring using the parent's strategy. Then the change in the population's strategy mix is determined by the rate at which the users of each strategy reproduce. The simplest hypothesis is that of exponential growth or decay. So let us denote by n_i the number of i -strategists in the population and by $N = \sum n_i$ the total number of individuals. Then the state

of the population is $s = (s_1, \dots, s_n)$, where $s_i = n_i/N$ is the proportion of i -strategists, and $\dot{n}_i = r_i n_i$, where r_i is the current growth rate of n_i . It follows that $\dot{N} = \bar{r}N$, where $\bar{r} = \sum s_i r_i$ is the average growth rate. If we differentiate $s_i = n_i/N$, we get $\dot{s}_i = s_i(r_i - \bar{r})$. This should tell us how s moves in the state space K .

To put this into our game framework, let us suppose that the fitness $F(i|s)$ of a strategy is an estimate of the growth rate r_i . In terms of our reproductive model, this means we must choose our fitnesses so that in time Δt each individual gives rise to $F(i|s)\Delta t$ additional individuals. Then our dynamic equation becomes

$$\dot{s}_i = s_i [F(i|s) - F(s|s)]. \tag{2}$$

Now suppose we have discrete generations. We interpret r_i as the number of new individuals each individual produces in unit time. Thus if an individual simply dies without offspring, this corresponds to $r_i = -1$. Otherwise $r_i > -1$. Letting \hat{n}_i denote the new value of n_i , we have the difference equation $\hat{n}_i = n_i(r_i + 1)$. We calculate $\hat{s}_i = s_i(r_i + 1)/(\bar{r} + 1)$. Setting $r_i = F(i|s)$ we have

$$\hat{s}_i = s_i \frac{F(i|s) + 1}{F(s|s) + 1}, \tag{3}$$

$$\Delta s_i = s_i \frac{F(i|s) - F(s|s)}{F(s|s) + 1}. \tag{4}$$

The difference equation (3) is the one most convenient to work with, but the equation (4) for the increment $\Delta s_i = \hat{s}_i - s_i$ allows us to compare the continuous (2) and the discrete dynamics. We observe that if we plot a trajectory of s using (4), we approximate an integral curve of the continuous dynamic (2). The approximation improves with increasing $F(s|s) + 1$. We will return to this point. Let us also remark that the state space K is, as expected, invariant under both (2) and (3).

In Sec. 2 we defined the notion of equilibrium point for the game. We also have a notion of equilibrium point for (2) ($\dot{p} = 0$) and for (3) ($\hat{p} = p$). All three notions are easily seen to coincide. We will now look at how the three notions of stability relate.

If p is an equilibrium point, we call it *stable* if every trajectory that begins near p converges towards p . To examine the stability of p for the continuous dynamic we linearize the system (2) about p . That is, for $s \in K$ we let $x = s - p$. Then $\dot{x}_i = \dot{s}_i$, and so (2) becomes $\dot{x}_i = (x_i + p_i)[F(i|x + p) - F(x + p|x + p)]$. Collecting only those terms on the right-hand side that are linear in x gives a system of the form $\dot{x} = Bx$. This is the linearization of (2)

about p . We say that p is *strictly stable* (against perturbations in $\sum s_i = 1$) if the eigenvalues of the matrix B belonging to the invariant subspace $\sum x_i = 0$ have strictly negative real part. A standard theorem in differential equations asserts that p is stable for the system (2) if it is strictly stable. We can do the same thing for the discrete dynamic (3) to get the linearization $\hat{x} = Cx$. In this case we say p is *strictly stable* (against perturbations in $\sum s_i = 1$) if the eigenvalues of C belonging to $\sum x_i = 0$ have modulus strictly less than one. As before, strict stability implies stability.

THEOREM

If p is a regular ESS, then p is a strictly stable equilibrium point of the continuous dynamical system (2), restricted to K .

The proof of this theorem will be given in Sec. 4. It follows from this theorem that, for the continuous dynamic, a regular ESS is always a stable state. In fact, it will be shown in a remark following the proof that a regular ESS is globally stable in a continuous linear game. This means that even after a large perturbation the population will return to p , provided the perturbation does not eliminate entirely any strategy that was used before the perturbation.

For the discrete dynamic the corresponding result is false. That is, for a discrete dynamic, an ESS need not be a stable equilibrium. To see why we might expect this, consider the linear game with three pure strategies and payoff matrix

$$A = \begin{bmatrix} -\epsilon & 1 & -1 \\ -1 & -\epsilon & 1 \\ 1 & -1 & -\epsilon \end{bmatrix}$$

It is not hard to show that $p = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ is a regular ESS if $\epsilon > 0$. The continuous dynamic for this linear game is

$$\dot{x}_i = (x_i + p_i) [a_i(x + p) - (x + p)A(x + p)].$$

Since $a_i p = p A p$, the linearization about p is given by $\dot{x}_i = p_i(a_i x - x A p - p A x)$. Since $\sum x_i = 0$ this simplifies further to give the equations $\dot{x}_i = p_i a_i x$. This system has matrix $A/3$. The eigenvalues corresponding to the subspace $\sum x_i = 0$ are $-\epsilon/3 \pm i/\sqrt{3}$. As ϵ gets close to zero from above we get close to a situation where both eigenvalues are imaginary. This implies that the trajectories of the continuous dynamic (2) are almost closed orbits, rather like the picture in Fig. 2 for the case $\alpha = 3$ (however, these figures refer to a different example). Now the discrete dynamic (3) is equivalent to a numerical approximation of the continuous dynamic. We would expect a numerical approximation to diverge outward from a (nearly) closed orbit. This

error would accumulate, and for sufficiently small $\epsilon > 0$ we would expect, after a single cycle about p , to be outside rather than inside our starting point. Actually it is not hard to show by direct calculation that for all $\epsilon > 0$, p fails to be strictly stable for the discrete dynamic.

The converse of the theorem is also not true. That is, a strictly stable equilibrium point of the continuous dynamic need not be an ESS. To see this, consider the linear game with three pure strategies and payoff matrix

$$A = \begin{bmatrix} 2 & 1 & 5 \\ 5 & \alpha & 0 \\ 1 & 4 & 3 \end{bmatrix}$$

with parameter α . The game has an equilibrium point in the interior of the state space K (a triangle) if $-8 < \alpha < 8.5$. As α moves from -8 to 8.5 , these equilibrium points trace out a straight line from $(3, 1, 0)/4$ on one edge to $(0, 2, 3)/5$ on another (see Fig. 1). It can be shown that this equilibrium point is an ESS if and only if $\alpha < 0$. However, it is strictly stable for (2) if and only if $\alpha < 3$. If $\alpha = 3$ the equilibrium point is neutrally stable, and can be shown to be in fact stable by looking at higher-order terms. From this fact, one can use a standard argument (which only works in the plane) to show that for sufficiently small $\epsilon > 0$, the case $\alpha = 3 + \epsilon$ must have a stable limit cycle surrounding the unstable equilibrium point. In Fig. 2 we have plotted sample trajectories for the dynamical system (2) for various values of α .

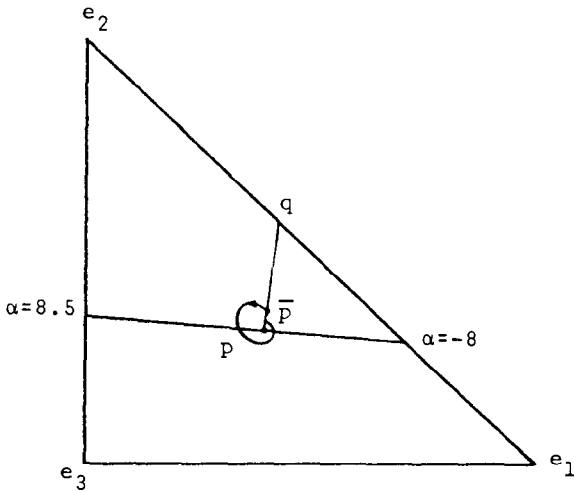


FIG. 1. The line of equilibrium points corresponding to various values of α . The point p is the equilibrium point for the case $\alpha = 1$. It is dynamically stable, but it is not an ESS.

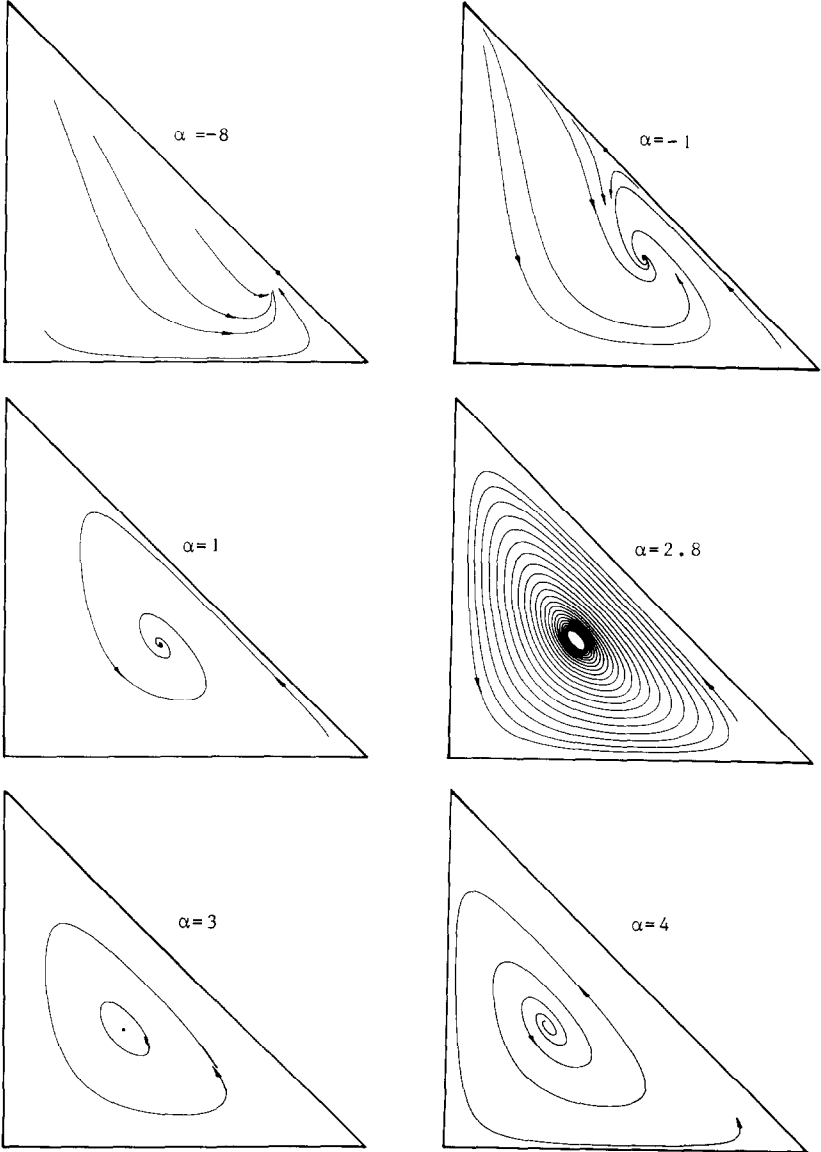


FIG. 2.

Let us try to explain, using this example, why the notions of ESS and strict stability do not coincide. It is important to seek such an explanation, because the result is at first counterintuitive. In doing so, we hope to clarify the biological significance of the notion of ESS.

Before we embark on this explanation, let us point out that there are two different ways of regarding games of this type. Suppose there are three pure strategies. Then we can imagine that there are three types of players in the population, types 1, 2, and 3, and a player of type i always uses strategy i . A population in state p is simply one in which the proportion of players of type i is p_i . On the other hand we can imagine that mixed strategies are available to each player. A player might decide to play strategy 1 with a certain probability, strategy 2 with another probability, and strategy 3 the rest of the time. In this case, to get the state p of the population we let p_i be the overall proportion of times that i is played at that time. Which interpretation is most suitable will depend on the nature of the game and the strategies being considered. In our mathematical treatment we do not distinguish between the two interpretations. But for the purpose of the following heuristic discussion let us use the first interpretation. Every player is one of three possible types, and the proportions p_i may change because of differential fitness.

Take the case $\alpha = 1$. Then $p = (15, 11, 9)/35$ is the equilibrium point. Let us demonstrate that this is not an ESS. Take $q = (18, 17, 0)/35$ as the perturbing state and set $\bar{p} = (1 - \epsilon)p + \epsilon q$. Let us write down the fitness of each type of player. Note that $Ap = (86, 86, 86)/35$ and $Aq = (53, 107, 86)/35$. Then

$$F(1|\bar{p}) = (1 - \epsilon)86 + \epsilon 53 = (86 - 33\epsilon)/35,$$

$$F(2|\bar{p}) = (1 - \epsilon)86 + \epsilon 107 = (86 + 21\epsilon)/35,$$

$$F(3|\bar{p}) = (1 - \epsilon)86 + \epsilon 86 = 86/35.$$

Taking p and q averages,

$$F(p|\bar{p}) = 86/35 - 0.22\epsilon,$$

$$F(q|\bar{p}) = 86/35 - 0.19\epsilon.$$

Thus $F(p|\bar{p}) < F(q|\bar{p})$ for any $\epsilon > 0$. That is, in the perturbed population \bar{p} , the q -group has higher average fitness than the p -group, and this implies that p is not an ESS.

But notice that the q -group is composed of two types of players, type 1 and type 2, and these types do not have equal fitness. Indeed $F(2|\bar{p})$ is much greater than $F(1|\bar{p})$. The effect of this fitness difference will be to move the population, not towards q , but sideways towards e_2 (the pure state

with only type-2 players). As the state changes from \bar{p} , the direction in which the population moves changes. The result of this continual change is to make the state rotate around p (see Fig. 1) and encounter the line pq again at a point closer to p than \bar{p} is. As this behavior continues the state converges to p . Thus p is stable.

Could the q -group have taken advantage of their greater than average fitness? Only if they shared this fitness in such a way as to preserve the “ q -ness” of the group. In this case, this would require a transfer of fitness from type-2 individuals to type-1 individuals, so that the ratio of type 1 to type 2 would remain at 18:17. This measure of concerted action on their part would certainly alter the dynamics and would presumably move the overall state away from \bar{p} in the direction of q . Just what would ultimately happen would depend upon what assumptions we wanted to make about the possibility of other forms of concerted action. Indeed we would really need a new kind of game theory to handle these problems. [The experience of the social scientists is that it is very difficult to build a satisfactory theory of games which allows for cooperative behavior between players.]

What then is the significance of the notion of ESS? Let us use heuristic language at this point. If in the future it appears to be biologically important to make the following ideas precise, then more work can be done in this direction. If p is an ESS, then p is stable not only in the every-man-for-himself game, but also in the game where fitness exchange between different types is allowed. If p is not an ESS, then either it is unstable in the every-man-for-himself game (e.g. $\alpha = 4$) or it is stable in this game ($\alpha = 1$). In the latter case it will always be vulnerable to some concerted action on the part of a deviant subgroup.

It would appear that if we are not going to permit fitness exchanges between different strategies, then the correct notion of stable equilibrium is not ESS, but our notion of strict stability. However, we can see at least four reasons why the notion of ESS will be the one that continues to be used in practice. First, it is easy to use and work with, and can be readily generalized to the case of infinitely many strategies (for example, the continuum of strategies in [5]). Secondly, our notion of dynamic stability required us to make an assumption about the way in which fitness is translated into growth, and hence relative growth of the different p . We chose the simplest exponential model, but others may lead to different notions of stability. The definition of ESS does not require these assumptions. Thirdly, the games that have arisen in the biological literature seem to have enough ESSs to account for our observations. Only if we were to find a real game which seemed to persist in a state which was not an ESS, would we be inclined to look for stable equilibrium points of a suitable system of differential equations. Fourthly, many of the games which have arisen in

the literature have only 2 pure strategies. In this case, as is easily seen, strict stability and ESS are equivalent.

4. PROOF OF THE THEOREM

We may suppose that $\text{supp}(p) = \{1, 2, \dots, k\}$. Let A be the matrix defined by

$$a_{ij} = \frac{\partial}{\partial p_j} F(i|p),$$

and let a_i denote its i th row. Since $F(i|p) - F(p|p) = 0$ when $1 \leq i \leq k$, and since $p_i = 0$ when $i > k$, the linearization of (2) about p is given by the equations

$$\dot{x}_i = p_i \left(a_i x - pAx - \sum_j x_j F(j|p) \right), \quad 1 \leq i \leq k, \tag{5}$$

$$\dot{x}_i = x_i [F(i|p) - F(p|p)], \quad i > k. \tag{6}$$

Now the $F(i|p)$ are all equal to $F(p|p)$ for $1 \leq i \leq k$, so that (5) can be written

$$\dot{x}_i = p_i \left(a_i x - pAx - \sum_{j=k+1}^n x_j [F(j|p) - F(p|p)] \right), \tag{7}$$

using the fact that $\sum x_j = 0$. Thus the entire system can be written

$$x = Bx = \begin{bmatrix} G & H \\ 0 & R \end{bmatrix} x, \tag{8}$$

where G is the $k \times k$ matrix with entries $g_{ij} = p_i [a_{ij} - (pA)_j]$, and R is diagonal with entries $r_{ii} = F(i|p) - F(p|p)$. The numbers r_{ii} are all < 0 by our regularity assumption.

Now, for any matrix D , let $D^{(j)}$ be the matrix obtained from D by subtracting column j from every column and omitting the j th row and column. If the subspace $\sum x_j = 0$ is invariant under D , then the eigenvalues of D which belong to this subspace are just the eigenvalues of $D^{(j)}$ for any j . This is because $D^{(j)}$ gives the same transformation as D on the subspace $\sum x_i = 0$ provided, when using $D^{(j)}$, we omit the j th entry of all our vectors.

Returning to our proof, it is enough to show that the eigenvalues of $B^{(k)}$ have negative real part. Now we can write

$$B^{(k)} = \begin{bmatrix} G^{(k)} & K \\ 0 & R \end{bmatrix},$$

so that we will be finished if we can show that the eigenvalues of $G^{(k)}$ have negative real part. The simplest way to do this is to think of the dynamical system $\dot{x} = Gx$ on R^k . Let $V(x) = \sum_1^k x_i^2 / 2 p_i$. We will show that in the subspace $\sum_1^k x_i = 0$, $V(x)$ decreases along trajectories of this dynamical system. Indeed

$$\begin{aligned} \dot{V}(x) &= \sum_1^k \frac{x_i \dot{x}_i}{p_i} = \sum_{i=1}^k x_i \sum_{j=1}^k \frac{g_{ij} x_j}{p_i} \\ &= \sum_{i,j=1}^k x_i a_{ij} x_j - \left(\sum_1^k x_i \right) \left(\sum_1^k (pA)_j \right) = \sum_{i,j} x_i a_{ij} x_j < 0, \end{aligned}$$

using the regularity of p and the fact that $\sum x_i = 0$. We call $V(x)$ a Lyapounov function for G in the subspace $\sum x_i = 0$. It follows that the eigenvalues of $G^{(k)}$ have negative real part [3, (6.5)].

The proof appears awkward, but it seems to be unavoidably so. The problem is that the block-triangular form of B does not fit nicely with the subspace $\sum x_i = 0$. However, if p has full support, then $B = G$ and we need only work with the Lyapounov function.

This completes the proof of the theorem. A slightly different argument, using the Lyapounov function

$$F(x) = \frac{\left(1 + \frac{x_1}{p_1}\right) \cdots \left(1 + \frac{x_n}{p_n}\right)}{\left(n + \frac{x_1}{p_1} + \cdots + \frac{x_n}{p_n}\right)^n}$$

shows that a regular ESS in a linear game is globally stable.

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