A Note on Evolutionary Stable Strategies and Game Dynamics

In 1974 J. Maynard Smith introduced the fundamental notion of an evolutionarily stable strategy (ESS) in order to explain the evolution of genetically determined social behaviour within a single animal species. If the possible pure strategies for contests within a species are $1, 2, \ldots, n$, and if $A = (a_{ij})$ is the payoff matrix, then a_{ij} is the payoff for the pure strategy i played against the pure strategy j; $\sum_j a_{ij}q_j$ is the payoff for the pure strategy i against the mixed strategy given by a probability vector $q = (q_1, \ldots, q_n)$; and

$$pAq = \sum_{i,j} p_i a_{ij} q_j$$

the payoff for strategy $p = (p_1, \ldots, p_n)$ played against q. Let

$$S_n = \{x = (x_1, \ldots, x_n) : \sum_j x_j = 1, \quad x_i \geq 0 \quad \text{for } i = 1, \ldots, n\}$$

be the simplex of all possible strategies.

D1: (Maynard Smith, 1974) A state $p \in S_n$ is called an ESS if for all $q \neq p$ either $pAp > qAp$ or $pAp = qAp$ and $pAq > qAq$.

In Taylor & Jonker (1978) the authors used the fact that the payoff, in animal contests, corresponds "by definition" to the rate of increase. This suggests for the investigation of the evolution of behaviour the dynamical model given by

$$\dot{x}_i/x_i = \sum_j a_{ij} x_j.$$

With this equation, however, the strategies $(x_1, \ldots, x_n)$ don't remain on the simplex. But since only the differences in payoff are relevant for the game, one may consider

$$\dot{x}_i/x_i = \sum_j a_{ij} x_j - A,$$

where the function A is chosen in such a way that $\sum_i \dot{x}_i = 0$ whenever

$\sum_i x_i = 1$. This leads to the equation

$$\dot{x}_i = x_i\Big(\sum_j a_{ij}x_j - \sum_{i,j} x_i a_{ij}x_j\Big) \quad i = 1, \ldots, n \tag{1}$$

on the (invariant) simplex S_n.

Having derived this equation, Taylor & Jonker proceed to show, as their main result, that if p is an ESS satisfying a mild regularity condition, then p is an equilibrium state for (1) which is strictly stable (i.e. all eigenvalues have strictly negative real part). The converse is not valid.

In this note, we give a simple characterization of ESS which implies immediately that every ESS is an equilibrium state for (1) which is asymptotically stable (all orbits near p converge to p). Thus both the hypothesis and the result are slightly weaker than in Taylor & Jonker (1978). We begin by reformulating D1.

D2: A state $p \in S_n$ is called an ESS if for all $q \in S_n$ one has

$$pA((1-\varepsilon)p + \varepsilon q) > qA((1-\varepsilon)p + \varepsilon q) \tag{2}$$

provided $\varepsilon > 0$ is sufficiently small.

The equivalence of the two definitions is easily seen since (2) means

$$(1-\varepsilon)(pAp - qAp) + \varepsilon(pAq - qAq) > 0.$$

The interpretation of D2 is easy: if a mutation in a population with strategy p introduces a small population with strategy q, then the p-population fares better than the q-population against the new (mixed) population $(1-\varepsilon)p + \varepsilon q$. D2 then is equivalent to
D3: A state $p \in S_n$ is called an ESS if

$$pAx > xAx$$

for all $x \in S_n$, $x \neq p$, in a sufficiently small neighbourhood of p.

This follows by multiplying (2) by ε and adding $(1-\varepsilon)pA((1-\varepsilon)p + \varepsilon q)$ on both sides.

Let us now use the fact that p is the unique maximum of the function

$$P : (x_1, \ldots, x_n) \to \prod_i x_i^{p_i}$$

on S_n, since the Lagrange multiplier must be equal to

$$\partial P/\partial x_i = P(P_i/x_i),$$

which implies that the x_i must be proportional (and hence equal) to the p_i, at the maximum. The time derivative of P along the orbits of (1) is

$$\dot{P} = \sum_i \partial P / \partial x_i \cdot x_i = P \sum_i p_i \left(\sum_j a_{ij} x_j - \sum_{i,j} x_i a_{ij} x_j \right)$$

$$= P(pAx - xAx).$$

Hence D3 is equivalent to having $\dot{P}(x) > 0$ for all $x \neq p$ in a small neighbourhood of p. Thus
D4: A state $p \in S_n$ is an ESS if

$$V = \prod_i p_i^{p_i} - \prod_i x_i^{p_i}$$

is a strict local Ljapunov function at p for (1).

As a corollary of D4, one obtains that every ESS is asymptotically stable.

As an example, we mention that for the case of the "4-hypercycle", where

$$A = \begin{bmatrix} 0 & k_1 & 0 & 0 \\ 0 & 0 & k_2 & 0 \\ 0 & 0 & 0 & k_3 \\ k_4 & 0 & 0 & 0 \end{bmatrix}$$

(with $k_i > 0$) the unique equilibrium in the interior of S_n is always globally stable; the function V is a Ljapunov function if all k_i are equal, but it is never a strict Ljapunov function. For the "3-hypercycle", the equilibrium is again always a global attractor, but V is a (strict) Ljapunov function if the three constants $\sqrt{k_1}, \sqrt{k_2}$ and $\sqrt{k_3}$ satisfy the (strict) triangle inequality.

These examples imply that not every asymptotically stable equilibrium is an ESS, and that (as noted already by Haigh in an appendix to Maynard Smith (1974) even for $n = 3$ there need not be an ESS at all. Another example is given by

$$A = \begin{bmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{bmatrix}$$

(which corresponds to the game of scissors-paper-stone which is treated by a different ecological model in May & Leonard (1975). Here $p = (1/3, 1/3, 1/3)$ and $\dot{P} = 0$ on S_3 (every orbit in the interior is periodic).

Since there is nothing special about the Ljapunov function V, it could be that under certain circumstances it would be more appropriate to study asymptotically stable equilibria of (1), rather than ESS.

Let us mention finally that equation (1), and relatives of it, have been investigated in Eigen (1971), Eigen & Schuster (1978) and Schuster, Sigmund, Wolff & Hofbauer (1978) in the context of self organization of macromolecules. It seems interesting that the same equation (1) plays a certain role at the two very ends, so to speak, of evolution, namely prebiotic evolution and evolution of animal behaviour.

Recently we learned that Zeeman had already obtained a proof that every ESS is an attractor. His result has not been published yet. We would like to thank Professors Maynard Smith and Zeeman for helpful advice and making unpublished material available to us.

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