On the Definition of an Evolutionarily Stable Strategy

G. T. Vickers

Department of Applied and Computational Mathematics

and

C. Cannings

Department of Probability and Statistics, University of Sheffield, Sheffield S10 2TN, U.K.

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An ESS must be able to withstand invasion by a small group. It is shown that there are (at least) two possible mathematical interpretations of this statement. In some important applications the two definitions of an ESS are equivalent, but this is not generally the case and a simple example is given to illustrate this. In the weaker form, not favoured here, an ESS may not withstand some infinitely small invasions, but in the stronger form the ESS is certain to survive all invasions up to a fixed fraction of the population. Also, when a pay-off matrix is used to define a dynamic, the stronger definition is the more convenient.

The motivation of the definition of an evolutionarily stable strategy (ESS) as originally formulated by Maynard Smith & Price (1973), and more formally by Maynard Smith (1974), is that a population playing the ESS should be able to withstand a small, invading group. The assumption that an invading group be small is a reflection of the low rates of mutation and migration to which large populations are usually subject. Riley (1979) has explored aspects of ESSs in finite populations where the invasion (even if by a single individual) may be appreciable. The purpose of this note is to draw attention to a feature of the ESS definition which is ambiguous and to argue for the stricter of the two interpretations.

Following Maynard Smith (1974), suppose that the original population is playing strategy $p$ ($p$ may either specify a probability vector over a countable set of pure strategies, or a density over a continuous set, or a mixture) and an invading group plays $q$. Note that the ESS definition will not require a specification of whether individuals within the population are playing pure strategies or mixtures; only the ensemble of strategies is considered. Let $E(p, q)$ be the expected pay-off to a $p$-player against a $q$-player. Then saying that a population playing $p$ can resist invasion by $q$ is equivalent to requiring that

$$E(p, (1 - \epsilon)p + \epsilon q) > E(q, (1 - \epsilon)p + \epsilon q),$$

where $\epsilon$ is the proportion of $q$-players in the composite population. Now there are two ways of interpreting the requirement that (1) should hold for all small, positive $\epsilon$. 

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Definition 1

The strategy \( p \) is an ESS if, for any strategy \( q \) different from \( p \), there is an \( \varepsilon_0 \) such that (1) holds whenever

\[
0 < \varepsilon < \varepsilon_0.
\]

Definition 2

The strategy \( p \) is an ESS if there is an \( \varepsilon_0 \) such that (1) holds whenever

\[
0 < \varepsilon < \varepsilon_0
\]

for all strategies \( q \) different from \( p \).

The formulation of Maynard Smith (1974) was essentially definition 1 and from this he derived an equivalent statement:

Definition 3

The strategy \( p \) is an ESS if, for any strategy \( q \) different from \( p \), either (i) \( E(p, p) > E(q, p) \) or (ii) \( E(p, p) = E(q, p) \) and \( E(p, q) > E(q, q) \).

Definitions 1 and 3 are equivalent, while definition 2 is more restrictive. An ESS under definition 2 is necessarily an ESS under definitions 1 and 3. That the converse is not true can be seen from the following simple example.

Suppose pure strategies are available labelled 1, 2, \ldots, i.e. we have a countable strategy space. Let the pay-off of the \( i \)th pure strategy against the \( j \)th pure strategy be \( a_{ij} \) where the infinite matrix \( A = (a_{ij}) \) is given by

\[
A = \begin{bmatrix}
0 & -1 & -1 & -1 & \\
-\frac{1}{2} & 0 & \\
-\frac{1}{3} & 0 & \\
\frac{1}{4} & 0 & \\
\ldots & & & &
\end{bmatrix}.
\]

Now under definition 1 or 3

\( p \equiv \) (play pure strategy 1 always)

is clearly an ESS since

\[
E(p, p) = 0 > E(q, p) \quad \forall q \neq p.
\]

However, with

\( q \equiv \) (play pure strategy \( k \) always), \( k \neq 1 \),

the difference between the two sides of (1) is

\[
E(p - q, (1 - \varepsilon)p + \varepsilon q) = (1 - \varepsilon)/k - \varepsilon.
\]

Now for any fixed \( \varepsilon_0 \), this expression is negative for sufficiently large \( k \). A continuous analogue of this example is easily constructed by taking the strategy space as \([1, \infty)\) with pay-offs \(-1/x\) for \( x \neq 1 \) against 1, 0 for \( x \) against \( x \) and \(-1\) for 1 against \( x \neq 1 \).
Cases where the definitions are equivalent

Suppose \( p \) is an ESS under definition 1 or 3. Then the space of strategies \( q \neq p \) can be partitioned into three subsets:

(a) \( q \) such that \( E(p, p) = E(q, p) \) and hence
\[
E(p, q) > E(q, q),
\]
(b) \( q \) such that \( E(p, p) > E(q, p) \) and \( E(p, q) < E(q, q) \)
and
(c) \( q \) such that \( E(p, p) > E(q, p) \) and \( E(p, q) \geq E(q, q) \).

Now for \( q \) satisfying (a) or (c) condition (1) is satisfied for any \( \varepsilon \). It is only strategies for which (b) holds which need to be examined. Clearly, if this set is empty then the definitions are equivalent. An important situation in which this is true is when the ESS \( p \) (as per definition 3) contains every possible pure strategy to be played, for then (a) holds for all \( q \). Another case in which there are no strategies satisfying (b) is given by the following result.

**Theorem 1**

For the War of Attrition (Bishop & Cannings, 1978) the definitions are equivalent. Here the strategy space may be discrete or continuous i.e. \( \{1, 2, \ldots, n\} \) or \( \{1, 2, \ldots\} \) or \( [0, a] \) or \( [0, \infty) \).

**Proof**

It is shown in Bishop & Cannings (1978) that if \( r \) and \( s \) are any two strategies then
\[
T(r, s) = E(r, r) - E(r, s) - E(s, r) + E(s, s) \leq 0.
\]
Accordingly, the set defined by (b) is empty. (The case with strategy space \([0, \infty)\) also has an ESS which contains all strategies and so could have been excluded without reference to \( T(r, s) \).)

The next theorem shows that even if the set described by (b) is not empty the definitions may still be equivalent.

**Theorem 2**

If the real \( n \times n \) matrix \( A \) has an ESS \( p \) according to definition 1 then \( p \) is also an ESS of \( A \) with definition 2.

**Proof**

There is no loss of generality in supposing that every element of \( A \) is positive. Let \( \nu \) be the largest element of \( A \). Let \( Q \) be the set of all probability vectors which satisfy (b) above, then
\[
q \in Q \Rightarrow (p - q)^T A (p - q) > 0.
\]
and
\[
(p - q)^T A p > 0.
\]
It is required to show the existence of $\varepsilon_0$ with

$$\frac{(p-q)^TAp}{(p-q)^TA(p-q)} \geq \varepsilon_0 > 0 \quad \forall q \in Q.$$ 

Let

$$(Ap)_i = \lambda, \quad i \in S$$

$$(Ap)_i \leq \lambda - \mu < \lambda \quad i \in T$$

where

$$S \cup T = \{1, 2, \ldots, n\}.$$ 

Then $p_i = 0$ for $i \in T$. If $T$ is empty then so is $Q$ and there is nothing to prove. For any $q \in Q$ set

$$q = t + s,$$

where

$$t_i = 0 \quad \forall i \in T \quad \text{and} \quad s_i = 0 \quad \forall i \in S,$$

and let

$$\sum_{i=1}^{n} s_i = \gamma, \quad \sum_{i=1}^{n} t_i = 1 - \gamma.$$ 

If $\gamma = 0$ then $q^TAp = \lambda = p^TAp$ and $q \notin Q$. Hence $\gamma$ is positive. Also

$$(p-q)^TAp = (p-t)^TAp - s^TAp = \gamma \lambda - \sum_{i \in T} s_i(Ap)_i.$$ 

Thus

$$\gamma \lambda > (p-q)^TAp \geq \gamma \lambda - (\lambda - \mu) \gamma = \mu \gamma.$$ 

Now let

$$r = (1 - \gamma)p - t$$

then

$$\sum_{i=1}^{n} r_i = 0 \quad \text{and} \quad r_i = 0 = p_i \quad \forall i \in T.$$ 

Thus

$$r^TAr < 0.$$ 

Also

$$(p-q)^TA(p-q) = r^TAr + (\gamma p - s)^TAr + (p - q)^TAs$$

$$< \sum_{i=1}^{n} \sum_{j=1}^{n} ((\gamma p_i + s_j)\nu[(1 - \gamma)p_j + t_j] + (p_i + q_i)\nu(\gamma p_j + s_j))$$

$$= 4\gamma(1 - \gamma)\nu + 4\gamma \nu$$

$$< 8\gamma \nu.$$
Thus
\[
\frac{(p-q)^T A p}{(p-q)^T A (p-q)} > \frac{\mu}{8 v} \quad \forall q \in Q
\]
and since this bound is independent of \( q \), the proof is complete.

We claim that definition 2 is the more reasonable. This choice is based on both biological and mathematical considerations. From the evolutionary biology viewpoint it is required that a population playing an ESS should be able to withstand a small contingent of invaders. But as the example shows, the size of this contingent may have to be vanishingly small in the case of definition 1. In the case of definition 2 we know that the population can withstand invasion up to a fraction \( \epsilon_0 \). Indeed, the maximum value of \( \epsilon_0 \) may be of interest in some situations. Riley (1979) in considering a finite population of size \( N \) implicitly requires \( \epsilon_0 \) to be at least \( 1/N \) (although his main point was of a somewhat different nature).

From the mathematical viewpoint, it is easier to work with the second definition. For example, following Taylor & Jonker (1978) we may introduce a dynamic
\[
\dot{p}_i = p_i \{(A p_i) - p^T A p\}, \quad 1 \leq i \leq n,
\]
for a population of pure strategists whose reproductive success is proportional to their pay-off. Using definition 2, Hofbauer et al. (1979) prove that an ESS is always locally stable. The more difficult result, that this conclusion is still true for definition 1, is shown by Zeeman (1980).

REFERENCES