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Evolutionary and Continuous Stability

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A strategy in a population game is evolutionarily stable if, when adopted by large enough a majority in the population, it becomes advantageous against any mutant strategy. It is said to be continuously stable if, when the majority slightly deviates from it, some reduction of this deviation becomes individually advantageous. This definition is meaningful if a continuum of (pure) strategies is available to each individual in the population. For that case, a necessary and a sufficient condition for an evolutionary stable strategy being a continuously stable strategy is analyzed.

1. Introduction

The concept of evolutionary stability (Maynard Smith & Price, 1973; Maynard Smith, 1972, 1974, 1976) stems from two basic assumptions. First, any phenotypic pattern, say strategy or a distribution of strategies (say, a mixed strategy) which is established in the population is never fully fixed. At best, erratic, small deviations from it are always maintained in the population by forces of second order. The second assumption, taken over by the evolutionary stable strategy theory is that in many cases, even if the genetical (or cultural) basis for a given pattern is not known, there are reasons to believe that natural selection operates to increase some relatively simple individual payment function which is at least probabilistically affected by the pattern in question. Viability, or maybe fertility, are good candidates for such a "payment function". Thus, a natural question is whether the assumed forces of natural selection are likely to amplify or decrease the inevitable small deviations from a given strategy, once it has been accepted as a consensus in a population.

Of the two assumptions, the validity of the second one has been both challenged and defended (at least as a useful approximation) by many authors (see Barlow & Silverberg, 1980, and many references there. See also Eshel, 1982; Eshel & Feldman, 1981). It is not the intention of this work to investigate this question further. Instead, it concerns a possible

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qualitative difference between the very meaning of evolutionary stability in cases where a finite (or discrete) set of pure strategies is available for the individual and its meaning in cases wherein a continuum of pure strategies is available. In the first situation any deviation from a so-called "consensus strategy", small as this deviation may be, can only result from some substantial change on the part of a certain "abberant" minority. A strategy which, when adopted by a large enough majority, is advantageous against any minority-strategy has therefore been called by Maynard Smith & Price (1973) an evolutionarily stable strategy (ESS). However, in cases where a continuum of pure strategies is available for the individual, small deviations of the population from any consensus strategy may also correspond to small continuous shifts of the entire population or a large majority within it.

For small deviations of this sort, an additional question to be asked is whether natural selection will then favor individual strategies which are slightly closer to the ESS or whether on the contrary, it will favor some further deviation away from the ESS.

In a previous study (Eshel & Motro, 1981), the concept of evolutionarily stable strategies has been employed in order to predict a stable level of mutual help among relatives which are both dependent and compete with each other. It has been shown that in some situations, more than one evolutionarily stable level of mutual help can exist (see also Eshel & Cohen, 1975).

We found, moreover, that for some, but not necessarily for all ESSs of the model, if a large enough majority of the population chooses a strategy close enough to the ESS, then only those mutant strategies which are even closer to the ESS will be selectively advantageous. For other ESSs, the opposite was proven true; any small deviation of the entire population from the ESS creates a selective advantage for those mutant strategies that deviate slightly further apart from the ESS. We call ESSs of the first kind *continuously stable strategies* (CSS).

The objective of this work is to develop a general concept of continuous stability and to find simple analytic conditions for it. Some hypothetical examples are studied in order to illustrate the suggested difference between the two levels of evolutionary stability and their possible meaning for continuous strategies.

2. CSS and ESS—Definition and Analysis of Basic Properties

Following Maynard Smith & Price we assume a large population in which the reproductive success or any other relevant payment function $v(x, y)$ of the individual depends both on his own strategy, x, and on the strategy y, pure or mixed, of a random individual which he is expected to encounter.

Because of their interest in strategies which are "immune to invasion by any mutant strategy", Maynard Smith & Price were concerned with the following question.

(i) If x is the *exact* strategy being chosen by a large enough majority in the population, say $1-\varepsilon$, will the expected payment it yields to its chooser (when encountered by a random opponent in this specific population) be at least as high as the expected payment yielded by any alternative strategy $y \neq x$ (pure or mixed) chosen by the minority?

If the answer to this question is positive, x is called ESS. Assuming random encounters with additive effect (which is another tacit assumption often made into ESS arguments. See, for example, Eshel & Cavalli Sforza, 1981). The requirement for ESS turns out to be written more conveniently, as follows:

A strategy x is an ESS if for any alternative strategy y, either (Maynard Smith, 1974; Bishop & Cannings, 1976)

$$v(x, x) > v(y, x) \tag{1}$$

or

$$v(x, x) = v(y, x) \text{ and } u(x, y) > v(y, y). \tag{2}$$

Concentrating on pure continuous strategies, we are also interested in the question:

(ii) If a large enough majority of the population prefers a strategy y which is sufficiently close to x (say $|x-y| < \delta$), will it be advantageous for each individual in this population to choose a strategy closer to, rather than further apart from x?

It is shown in the next two sections that a positive answer to (i) does not guarantee a positive answer to (ii) (It trivially does in the case of a discrete set of pure strategies). Yet with a negative answer to (ii) natural selection, if favoring individual reproductive success (a necessary condition for the use of ESS arguments) is likely to amplify continuously any small deviation of the entire population from the ESS.

We therefore distinguish between ESSs which provide a positive answer to (ii) and those which do not.

Definition: an ESS x is said to be continuously stable (CSS) if there is a value $\varepsilon > 0$ such that for any strategy y in an ε vicinity of x there is a positive value $\delta > 0$ such that for any strategy u at a δ vicinity of y, $v(u, y) > v(y, y)$ if and only $|u-x| < |y-x|$.

This condition, stronger than ESS, guarantees a positive answer to (ii) but it is not easy to work with. We now develop more convenient equivalent conditions for continuous stability.

3. CSS and ESS—Analysis of the One Dimensional Situation

We concentrate on situations in which the individual (pure) strategy x is determined by a single continuous parameter (time, length, weight etc.). We assume, for convenience that the payment function $v(x, y)$ has all continuous second derivatives. An immediate necessary condition for a strategy $\hat{x}$ being an ESS is

$$\left\{\frac{\partial}{\partial y} v(y, \hat{x})\right\}_{y=\hat{x}} = 0 \tag{3}$$

and

$$\left\{\frac{\partial^2}{\partial y^2} v(y, \hat{x})\right\}_{y=\hat{x}} \leq 0. \tag{4}$$

We now prove:

Theorem 1

(i) *A necessary condition for an* ESS x *being a* CSS *is that at the point* $x = y = \hat{x}$

$$\frac{\partial^2 v}{\partial x\, \partial y} + \frac{\partial^2 v}{\partial x^2} \leq 0. \tag{5}$$

(ii) A sufficient condition for an ESS $\hat{x}$ being a CSS is that both equations (4) and (5) hold as strict inequalities.

Proof.

Let $\hat{x}$ be any ESS then we know equation (3) holds. Thus from the continuity of the second order derivative it follows that a positive value $\varepsilon > 0$ exists so that for all θ with $|\theta| < \varepsilon$.

$$\left.\frac{\partial v(x, \hat{x}+\theta)}{\partial x}\right\}_{x=\hat{x}+\theta} = \left\{\left(\theta \frac{\partial}{\partial x} + \theta \frac{\partial}{\partial y}\right)\left(\frac{\partial v(x, y)}{\partial x}\right)\right\}_{x=y=\hat{x}} + o(\theta). \tag{6}$$

$$= \theta\left\{\frac{\partial^2 v(s, y)}{\partial x^2} + \frac{\partial^2 v(s, y)}{\partial x\, \partial y}\right\}_{x=y=\hat{x}} + o(\theta)$$

(i) Suppose equation (5) does not hold, namely $\{\partial^2 v/\partial x^2 + \partial^2 v/\partial x \partial y\}_{x=y=\hat{x}} > 0$, and consider a strategy y with $\hat{x} - \varepsilon < y < \hat{x}$. From equation (6) we then know that $\partial v/\partial x\}_{x=y} < 0$.

This means that a positive value $\delta = \delta(y) > 0$ exists so that for $y - \delta < u < y$, $v(u, y) > v(y, y)$ while for $y < u < y + \delta$, $v(u, y) < v(y, y)$. Thus, if the entire population chooses a strategy y, slightly smaller than $\hat{x}$ ($\hat{x} - \varepsilon < y < \hat{x}$) then a slight modification from the population consensus y (i.e. a strategy u with $|u - y| < \delta$) becomes advantageous if and only if $u < y$, i.e. further apart from the ESS $\hat{x}$. Hence $\hat{x}$ is not a CSS. (The same is shown for a strategy $\hat{x} < y < \hat{x} + \varepsilon$.)

(ii) Assume both equations (4) and (5) hold as strict inequalities. From equation (6) it follows that for $y < \hat{x}$, and x sufficiently small close to y

$$v(x, y) > v(y, y) \text{ if } y < x < \hat{x}$$

and

$$v(x, y) < v(y, y) \text{ if } x < y < \hat{x}$$

while for $y > \hat{x}$ we get

$$v(x, y) > v(y, y) \text{ if } \hat{x} < x < y$$

$$v(x, y) > v(y, y) \text{ if } \hat{x} < y < x.$$

Thus $\hat{x}$ is a CSS.

For some biological purposes the following analysis of continuous stability is more explanatory.

Let $\hat{x}$ be any ESS. From equation (3), the continuity of $\partial^2 v/\partial x^2$ and $\partial^2 v/\partial x\,\partial y$ and by the implicit function theorem it follows that a continuous function $u(y)$ exists at least in the vicinity of $\hat{x}$ so that

$$\left.\frac{\partial v(u, y)}{\partial u}\right\}_{u=u(y)} = 0. \qquad (7)$$

Assuming, further, that equation (6) holds as a strict inequality, then from the continuity of $\partial^2 v/\partial x^2$ (as a function of x and y) it also follows that at least at the vicinity $|y - \hat{x}| < \varepsilon$ of $\hat{x}$, $\partial^2 v/\partial x\, \partial y\}_{x=u(y)} < 0$, and $x = u(y)$ is a local maximum of $v(x, y)$, i.e., $u(y)$ is the individually optimal strategy when the entire population chooses y. Indeed, an intersection $y = u(y)$ of the curve $u(y)$ with the main diagonal $y = x$ means that as a public consensus $y = u(y)$ is also individually optimal, hence ESS.

Theorem 2

An ESS $\hat{x}$ is a CSS if and only if the curve $y = u(x)$ intersect the main diagonal $y = x$ from above.

Proof

From the implicit function theorem it follows that $u(x)$ is differentiable at $x = \hat{x}$ and

$$u'(x) = \frac{\left.\dfrac{\partial^2 v(x, \hat{x})}{\partial x^2}\right\}_{x=\hat{x}}}{\left.\dfrac{\partial^2 v(x, y)}{\partial x\, \partial y}\right\}_{x=y=\hat{x}}}. \tag{8}$$

Theorem 2 thus follows immediately from Theorem 1.

In some cases, unique, globally optimal strategy $u(x)$ exists for any strategy x accepted by the population (e.g. Eshel & Motro, 1981). The ESSs of the population game are, then, all the intersection $x = u(x)$ of the curve $u(x)$ of optimal behavior with the main diagonal. The CSSs of the game are then all the points in which $u(x)$ intersects the main diagonal from above.

4. Examples

Like most examples used in the theory of ESS the following refers to situations in which neither the genetic basis for a commonly observed trait, nor its exact effect on the individual fitness can be safely measured. (Indeed, when these can be measured, more rigorous methods are recommended.) Instead, plausible (but obviously oversimplifying) assumptions are used to illustrate some basic properties of evolutionary stability in continuous cases.

Example 1. *Gregarious behavior versus spacial optimization*

Gregarious behavior of either one sex or both is quite common in nature. On many occasions, choosing a location close to other members of the population may be advantageous in decreasing the predation probability (Hamilton, 1971; Eshel, 1978), or in increasing the probability of mating (many references). In other situations, having a specific trait close to that of other individuals of the population may have the same advantageous effect on the carrier.

Indeed, different choices of a location (or a trait) may also have a direct effect on the individual's fitness. Thus, the fitness of an individual with a choice x depends both on the special property of the location x and on some average distance $|x - y|$ or more conveniently $(x - y)^2$ of this location from those of other individuals of the population. Thus, if a location (or trait) y is accepted as a population consensus, then

$$v(x, y) = \phi(x, (x - y)^2). \tag{9}$$

where $\phi(x, u)$ is a decreasing function of u. We set

$$\phi(x, 0) = \phi(x) \tag{10}$$

for the population payment function (i.e. the payment function shared by all individuals in a population accepting x as a consensus).

If the choice of locations (or traits) is limited to a finite or a discrete set of possible alternatives $x = x_1, x_2, x_3, \ldots,$ then it is quite possible that

$$V(x_i, x_i) = \phi(x_i) > \operatorname*{Min}_{j \neq i} \phi(x_j, (x_i - x_j)^2 \tag{11}$$

and x_i is an ESS even if it does not maximize the population payment function $\phi(x)$. With rather plausible choices of ϕ it is possible, moreover, that equation (11) holds for any choice x_i and any strategy is then, an ESS. For example, if the x_i mean the strategy "chose the island i for your mating location" and if this strategy is accepted by the entire population, then any individual which will exclusively choose a "better" island will not have many offspring.

As we now see, the situation is different when x can be chosen over a continuum and each individual can shift in an infinitesimal way. Assuming, further, that $\phi(x, d)$ has continuous second derivatives, than on the diagonal $x = y$ we have

$$\frac{\partial v}{\partial x} = \phi'(x)$$

$$\frac{\partial^2 v}{\partial^2 x^2} = \phi''(x) + 2\frac{\partial}{\partial u}\phi(x, u)$$

$$\frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial x \partial y} = \phi''(x).$$

Hence, the CSS are in this case, exactly those points at which $\phi(x)$ achieves a local maximum. Possible other ESSs are also the points of inflection and some minima. These are unstable in the sense that if a large enough majority of the population even slightly deviates from them, some further deviation will become individually advantageous.

Even with very little knowledge about the exact configuration of $\phi(x, u)$, one qualitative difference between the discrete and the continuous cases can be drawn. While evolutionary "blind allies" are likely to occur in the first case, they are less likely to occur in the latter, when the route of evolution can follow a sequence of infinitesimal changes.

Example 2. Evolutionarily stable investment in a competitive trait

Assume that in order to successfully reproduce, each individual (say, a male) in the population should first survive and then win a random number X of contests with other members of the population $P(X=k)=P_k$, $k=0, 1, 2, \ldots$. The probability that a random individual wins a contest depends (among other factors) on the difference $x-y$ between his investment in a certain "competitive" trait, and that of his opponent. We denote this probability by $\psi(x-y)$ where ψ is an increasing function with

$$\psi(x-y)=1-\psi(y-x). \tag{12}$$

(Exactly one of the two participants of a contest wins.) A candidate for a competitive trait may be the length of a horn, extra body weight, etc. Indeed, an investment x in any such a trait is likely to affect the probability that the investor survives other, non-competitive situations. We call this probability $\phi(x)$ and we assume for convenience that both $\phi(x)$ and $\psi(u)$ have continuous second derivatives. In this case, it follows from equation (12) that

$$\psi''(0)=0. \tag{13}$$

We are interested in the possible stability of a given amount of investment y as a population-consensus. If such a consensus is accepted, then, indeed, the winning probability of a single individual with investment x will be $\psi(x-y)$ in a single contest, $[\psi(x-y)]^n$ in n successive contests, and

$$\sum_{k=0}^{\infty} P_k[\psi(x-y)]^k = F(\psi(x-y)) \tag{14}$$

in a random number X of contests, where

$$F(s)=\sum P_k s^k = Es^X \tag{15}$$

is the probability generating function of the random number of contests. The probability that this individual will successfully reproduce is, therefore

$$V(x,y)=\phi(x)F(\psi(x-y)). \tag{16}$$

By differentiating with respect to x at $x=y$ and employing equation (3) we get

$$\frac{\phi'(y)}{\phi(y)}=-\psi'(0)\frac{F'(\frac{1}{2})}{F(\frac{1}{2})} \tag{17}$$

as a necessary condition for ESS (this immediately implies $\phi'(y)<0$ so that an ESS is always a superoptimal strategy for non-competitive criteria).

Employing equations (4), (16) and (17) the condition for ESS becomes

$$\frac{\phi''(y)}{\phi'(y)} < \frac{F''(\frac{1}{2})}{F'(\frac{1}{2})}\psi'(0) + 2\frac{\phi'(y)}{\phi(y)}, \tag{18}$$

while the condition (5) for CSS is

$$\frac{\phi''(y)}{\phi'(y)} < \frac{\phi'(y)}{\phi(y)}. \tag{19}$$

In the special case where the number of contest per individual has a Poisson distribution with expectation λ, $F(s) = e^{\lambda(s-1)}$ and the condition (17) becomes

$$\frac{\phi'(y)}{\phi(y)} = -\lambda\psi'(0).$$

In this case, the condition (18) for ESS and the condition (19) for CSS are equivalent

$$\frac{\phi''(y)}{\phi(y)} > -\lambda\psi'(0).$$

However, if the number of contests is fixed, say N, then $F(s) = s^N$, equation (17) becomes

$$\frac{\phi'(y)}{\phi(y)} = -2N\psi'(0).$$

(Note that in the case of a Poisson distribution an expectation of $\lambda = 2N$ rather than $\lambda = N$ is needed to create the same effect on the ESS.)

The condition (18) for ESS is then

$$\frac{\phi''(y)}{\phi'(y)} > -2(N+1)\psi'(0).$$

While the condition (19) for CSS is strictly stronger

$$\frac{\phi''(y)}{\phi''(y)} > -2N\psi'(0).$$

The difference between the two conditions is easily manifested if we think of the simplest unimodal function

$$\phi(x) = \frac{1}{1+(x-\mu)^2}$$

with μ being the non-competitive optimum. In this case, equation (17) has no solution if $2N\psi'(0) > 1$ and two solutions if $2N\psi'(0) < 1$. Denote $2N\psi'(0) = \rho$, these two solutions are

$$y_1 = \frac{1 - \sqrt{1-\rho^2}}{2\rho} + \mu$$

$$y_2 = \frac{1 + \sqrt{1-\rho^2}}{2\rho} + \mu$$

both being larger than the non-competitive optimum and both satisfying the criterion (18) for ESS. However, only the smaller one also satisfies the condition (19) for CSS.

Note that as $\rho \to 0$ (i.e. the expected advantage in winning probability due to individual increase of investment is small) the CSS tends to the noncompetitive optimum μ, as being expected from a decent optimum. The other ESS does not.

Example 3. *Warning coloration as ESS*

Warning coloration can help a potential prey only if it is recognizable as a group marker. Thus as in example 1, its advantage depends on its resemblance (or closeness) to the color of other individuals in the population. A model very much like that of gregarious behavior (example 1) can be developed. It is possible, however, that the probability of an individual being recognized as belonging to a given group is not only a decreasing function of its distance from the group, but also an increasing function of its conspicuousness. If, in addition, a cryptic individual has higher probability to escape by simply not being noticed by a predator, an equally likely model can assume that the escape probability of an individual of conspicuous x is given by:

$$v(x, y) = 1 - \phi_1(x)[1 - \phi_2(x)\psi(x-y)^2]$$

where ϕ_1 and ϕ_2 are both increasing with the individual's conspicuousness x. More specifically, $\phi_1(x)$ is the probability that the individual will be noticed, $\phi_2(x)$ is the probability that if noticed, its special pattern will be noticed, $\psi(x-y)^2$ is the probability that it will be recognized as resembling y.

Especially if $\phi_1(x) = \alpha\phi_2(x)$, $\alpha > 0$, an analysis based on equations (3)–(5) indicates that the CSSs may be either the extreme conspicuousness, the extreme cryptiness or both. Other ESSs may exist, but they are not CSS.

Example 4. *An example from economy—adaptation of prices to demand*

Let n competing sellers offer the same good to a given public. If the amount offered by the ith seller is x_i $(i = 1, 2, \ldots, n)$, then his net profit is $x_i\phi(\sum_{k=1}^n x_k)$, where ϕ, namely the demand function, is decreasing and convex.

It is not difficult to see that all pure Nash solutions $\underset{\sim}{x}=(x_1, x_2, \ldots, x_n)$ of the n-seller's conflict, if it exists, satisfy $x_1=x_2=\cdots=x_n=x$ say, with

$$x=-\frac{\phi(nx)}{\phi'(nx)} \tag{20}$$

$$x^2\leq 2\frac{\phi(nx)}{\phi''(nx)}. \tag{21}$$

The concepts of ESS and CSS are meaningful, in this case, if the "population" of potential sellers is much larger than n, and if the situation of random n of them competing on the same market is common. A consensus, accepted by the population of sellers about how to behave in such a situation has a *Nash property* if no single seller can increase its expected gain by exclusively behaving in a different way. The seller's consensus has the *ESS* property if, when accepted by a large enough majority of potential sellers, it will remain individually optimal (this requirement is stronger than the Nash property but weaker than a strict Nash property). Finally, an ESS value x has the *CSS* property if when a consensus y, close enough to it, is accepted by a large enough majority of potential sellers, small deviations from y will be advantageous for the individual seller if and only if in the direction of x. Note that if y is accepted as a consensus among sellers, the expected payment for an individual who attempts to sell x units is $x\phi((n-1)y+x)$. Thus, by using equations (5) we know that a strategy x, satisfying equation (20) is a CSS if and only if

$$x^2<\frac{n+1}{n}\frac{\phi(nx)}{\phi''(nx)}. \tag{22}$$

This condition is indeed stronger than condition (21) (which is equivalent to equation (4)) even in its sharp version. Thus the properties of ESS or a strict Nash solution do not imply that of CSS.

If $\ln\phi(u)$ is a concave function (i.e., if the demand is decreasing with price faster than exponentially), then

$$\frac{\partial^2}{\partial x^2}\ln V(x_1y)=\frac{1}{x^2}+\frac{\partial^2}{\partial x^2}\ln\phi((n-1)+x)<0$$

for all x and y. Therefore, for any value x, accepted as a population consensus, there is a unique value $y^*=y^*(x)$ which strictly and globally maximizes the individual payment $v(y, x)$.

Using the theorem of the implicit functions it is not difficult to show that $y^*(0)>0$ and $y^*(x)<x$ for a sufficiently large x.

Any solution of the equation $y^*(x)=x$ is a strict Nash solution (and, therefore, an ESS). But only solutions at which the curve $y=y^*(x)$ intersect the main diagonal $y=x$ from above is CSS (theorem 2). As we see, there is always one such a solution (provided $\ln \phi(u)$ is concave). But it is not difficult to produce analytic examples with any number of strict Nash solutions $x=y^*(x)$ (see, for comparison, Eshel & Motro, 1981). In this case, only part of the solution can be CSSs. Any solution x^* which is not CSS must appear between CSS solutions, say $\underset{\sim}{x}<x^*<\bar{x}$, so that for a population consensus $x<x<\bar{x}$ larger than the "solution" x^*, $Y^*(x)>x$ and any individual will gain by even increasing his individual price. The opposite is true if $\underset{\sim}{x}<x<x^*$. Hence, a consensus on such Nash solution x^* (through strict Nash solution and ESS) is not likely to evolve. More likely, the seller's population will move to either $\underset{\sim}{x}$ or $\bar{x}$.

To summarize, in the case of continuous strategies it is possible that small deviation of the entire population from an ESS makes it advantageous for each individual to move a little further from the ESS. In other cases, any small deviations of the entire population from an ESS will make it advantageous for each individual in the population to move a little closer to the ESS. ESSs of the latter sort are called continuously stable strategies.

A necessary and almost sufficient condition for an ESS being a CSS is that $\partial^2 V/\partial x\,\partial y+\partial^2 V/\partial x^2\leq 0$ where $V(x, y)$ is expected payment for an individual choosing a strategy x when encountered by an individual choosing a strategy y.

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