J. Math. Biol. 46, 445–459 (2003)
Digital Object Identifier (DOI):
10.1007/s00285-002-0194-2

Mathematical Biology

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Evolutionary and dynamic stability in continuous population games

Received: 9 July 2002 / Revised version: 12 November 2002 /

Abstract. Asymptotic stability under the replicator dynamics over a continuum of pure strategies is shown to crucially depend on the choice of topology over the space of mixed population strategies, namely probability measures over the real line. Thus, Strong Uninvadability, proved by Bomze (1990) to be a sufficient condition for asymptotic stability under the topology of variational distance between probability measures, implies convergence to fixation over a pure strategy x^* only when starting from a population strategy which assigns to x^* a probability sufficiently close to one. It does not imply convergence to x^* when starting from a distribution of small deviations from x^*, regardless of how small these deviations are. It is, therefore, suggested that when a metric space of pure strategies is involved, another topology, hence another stability condition, may prove more relevant to the process of natural selection. Concentrating on the case of a one dimensional continuous quantitative trait, we resort to the natural Maximum Shift Topology in which an ε-vicinity of the fixation on a pure strategy x^* consists of all mixed population strategies with support which includes x^* and is in the ε-neighborhood of x^*. Under this topology, a relatively simple necessary and sufficient condition for replicator asymptotic stability, namely Continuous Replicator Stability (CRSS), is demonstrated. This condition is closely related to the static stability condition of Neighbor Invadability (Apaloo 1997), and slightly stronger than the condition of Continuous Stability (Eshel and Motro 1981).

1. Introduction

An Evolutionarily Stable Strategy, ESS, has been originally defined for symmetric two-person games (Maynard Smith and Price 1973. See also Hamilton 1967) as a strategy that, once almost fixed in the population, is strictly advantageous over any single mutant strategy when in sufficiently low frequency. Of a wider use is the equivalent definition (Bishop and Cannings 1976. Maynard Smith 1982): A strategy X is an ESS if it is both a best response to itself and, in case there is another best response to it, say Y, then X is a better response to Y than Y itself. It was further shown (Taylor and Jonkers 1978) that an ESS as a population state in a finite population game, in which individuals are limited to the choice of pure

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Key words or phrases: CSS – ESS – NIS – Strong uninvadability – Weak topology – Replicator dynamics – Long-term evolution – Continuous population games – Continuous replicator stability – Asymptotic stability

strategies, is locally asymptotically stable in the corresponding replicator dynamics with the natural Euclidean topology. As it has been established, however, in a bulk of later works (Bomze and Pötscher 1989, Bomze 1990, Bomze 1991, Bomze and van Damme 1992. See also Weibull 1995, Hofbauer and Sigmund 1998), further requirements are needed to guarantee that an ESS would be asymptotically stable in the replicator dynamics of a population game with infinitely many individual strategies, especially in the case of infinitely many *pure* strategies.

In the latter case, the state of the population at any given moment is naturally characterized by a probability measure μ over some σ-field on the set of pure strategies. Sticking to the commonly used terminology, we refer to μ as to the *population strategy* at that moment. Since general (mixed) *individual strategies* (to be distinguished from population strategies) are, all the same, characterized by probability measures over the same σ-field, the same notation $V(\mu,\eta)$ is generally used for both the payoff of a μ-player against an η-player, and the expected payoff of a μ-player in a linear population game with a population strategy η. However, the very definition of asymptotic stability, in this case, crucially depends on the choice of topology over the appropriate space of probability measures.

In the articles mentioned above, asymptotic stability was analyzed for the metric topology determined by the variational norm $\|\mu\| = \sup\limits_{\|f\|_\infty \leq 1, f \in c} \left|\int f d\mu\right|$ (e.g. Bomze 1990). Employing this topology (with some plausible regularity assumptions), a sufficient condition for the replicator asymptotic stability of a population strategy μ was shown by Bomze to be the requirement of *Strong Uninvadability*, namely the existence of a positive value $\varepsilon > 0$ such that for any strategy η with $0 < \|\eta - \mu\| < \varepsilon$, $V(\mu,\eta) > V(\eta,\eta)$. Note, however, that the variational metric assumes no structure over the set of *pure strategies*, assigning a fixed distance 2 between any two of them. As a special case, the variational distance of a strategy μ from the fixation on a pure strategy x^*, say δ_{x^*}, is readily given by $\|\mu - \delta_{x^*}\| = \int |\mu - \delta_{x^*}|\,(dx) = 2[1-\mu(\{x^*\})]$, hence the only strategies μ which are ε-close to δ_{x^*} in this metric are those assigning probability $\mu(\{x^*\}) \geq 1 - \varepsilon/2$ to the *exact* value of x^*.

Concentrating on the case of a quantitative trait with a continuum of pure strategies, we shall see, thus, that x^* may be Strongly Uninvadable, while for any neighborhood U of x^* there is a population strategy μ with $\mathbf{supp}\mu \in U$, such that starting from μ, the replicator dynamics would converge rather to a point in $\mathbf{supp}\mu$, which is the furthest possible from x^*. This makes Strong Uninvadability incompatible with the static stability concepts of a *Continuously Stable Strategy, CSS* (Eshel and Motro 1981) and *Neighbor Invader Strategy, NIS* (Apaloo 1997), defined for a pure trait in a continuum.

Continuous Stability adds to the simple ESS condition, an extra requirement (independent of that of ESS) that a value $\varepsilon > 0$ exists such that if the entire population deviates from x^* to $x^* + \theta$ where $0 < |\theta| < \varepsilon$, then mutations of a sufficiently small effect would be advantageous if and only if in the direction of x^*. Neighbor Invadability requires that in such a situation, a back mutation to x^* itself would be favorable. As we shall see, this is a slightly stronger requirement than continuous stability. Identifying pure strategies with points in $\mathbf{R}$ and, thus, representing a general (mixed) strategy by a distribution function on $\mathbf{R}$, we see that both these concepts correspond to the *maximal shift topology*, determined by the distance $d(F, G) = \Delta(F, G) + \Delta(G, F)$ between any two strategies F and G, given by

$$\Delta(F, G) = \mathbf{Inf}\,\{\varepsilon \geq 0 : \forall s \in \mathbf{R},\, F(s-\varepsilon) \leq G(s) \leq F(s+\varepsilon)\}\,, \qquad (1.1)$$

and in which the ε-vicinity of the fixation δ_{x^*} on x^* consists of all probability distributions with support in the ε-neighborhood of x^*.

In order to unify the two approaches and, at the same time, to generalize the concepts of CSS and NIS to mixed strategies, it was suggested by Öechssler and Riedel (2002) that a more general stability condition should be based on the *weak topology*, determined by the (asymmetric) distance

$$d_w(F, G) = \mathbf{Inf}\,\{\varepsilon \geq 0 : \forall s,\, F(s-\varepsilon) - \varepsilon \leq G(s) \leq F(s+\varepsilon) + \varepsilon\}\,. \qquad (1.2)$$

In this topology, a distribution function F is ε-close to the fixation δ_{x^*} if it assigns probability of at least $1 - 2\varepsilon$ to the ε*-neighborhood* of x^* on the real line, not necessarily to $\{x^*\}$ itself. Based on this topology, Öechssler and Riedel have suggested the stability criterion of *Evolutionary Robustness (ER)* of a general strategy F, requiring (much analogously to the requirement of Strong Uninvadability in the case of the variational distance) that a positive value $\varepsilon > 0$ exists, such that for any strategy $G \neq F$ in the weak-topology-ε-vicinity of F,

$$V(F, G) > V(G, G). \qquad (1.3)$$

It was further conjectured by Öechssler and Riedel that ER is a sufficient condition for asymptotic stability in the weak topology. At the moment, however, it seems difficult not only to establish this conjecture, but even to demonstrate a non trivial mixed ER strategy.

In the present work we restrict our attention to replicator fixation stability under the maximal shift topology (1.1) over probability distributions on the real line. Under this topology, a relatively simple necessary condition for fixation-stability is demonstrated, namely *Continuous Replicator Stability, CRSS*, which is, indeed, a necessary condition for fixation stability under the weak topology. Moreover, by replacing weak inequalities by strict ones, this condition become sufficient. Continuous Replicator Stability is shown to be almost, but not quite, equivalent to the combination of static stability conditions of ESS and NIS, namely to ESNIS (Apaloo 1997); and it is slightly stronger than the static stability condition of a CSS, which shown to be necessary and sufficient for *long term stability* of x^* (Eshel et al. 1997). It is shown that none of these closely related stability criteria imply, nor is implied by the condition of Strong Uninvadability. They are all implied, though, by Evolution Robustness.

2. One difficulty and three approaches to fixation-stability in continuous population game dynamics

Concentrating on a population game with a continuum of pure strategies, referred to as a *continuous population game*, we identify pure strategies with points on $\mathbf{R}$

with the Borel σ-algebra. We characterize a general strategy by the one dimensional (cumulative) distribution function F, with $V(F, G)$ being the payoff of an F-strategist when playing against a G-strategist. We denote by H_x the distribution function corresponding to the point-distribution δ_x, namely

$$H_x(u) = \begin{cases} 0 & \text{if } u < x \\ 1 & \text{if } u \geq x \end{cases} \quad \text{for all } -\infty < x < \infty.$$

We further denote by $v(x, y) = V(H_x, H_y)$ the restriction of this function to pure strategies, assuming that all partial derivatives of $v(x, y)$ up to the third degree exist and are continuous. Assuming, further, a linear payoff for mixed strategies, we know that

$$V(G, F) = \iint v(x, y)dG(x)dF(y). \tag{2.1}$$

As a special case, if F is a population strategy, then the expected payoff of an x-strategist in this population is

$$V(H_x, F) = \int v(x, y)dF(y). \tag{2.2}$$

Assume now that all individuals in the population are pure strategists, each reproducing offspring equal to itself with a rate equal to its current payoff, and that a per capita death rate, average to the per capita birth rate, keeps the total population size normalized. For any $t \geq 0$, the distribution F_t, given F_0, is then determined by the continuous-state replicator dynamics

$$\frac{\partial}{\partial t} F_t(x) = \int_{-\infty}^{x} [V(H_u, F_t) - V(F_t, F_t)]dF_t(u), \tag{2.3}$$

whenever (2.3) has a solution and whenever this solution is unique. In the case of continuous distributions with densities $f_t = F_t'$, this can be written, more conveniently as:

$$\frac{\partial}{\partial t} f_t(x) = f_t(x)[V(H_x, F_t) - V(F_t, F_t)].$$

Unfortunately, there is a serious difficulty concerning the very concept of local asymptotic stability of a pure strategy x^* under the replicator dynamics defined by (2.3), with either the *weak topology* (1.2) or the *maximal shift topology* (1.1). Naturally, one would indeed like to consider conditions under which, for some $\varepsilon > 0$ and for all F_0 with $\mathbf{supp}F_0 \in (x^* - \varepsilon, x^* + \varepsilon)$, the dynamics (2.3) would converge (say weakly) to H_{x^*}. Note, though, that $\mathbf{supp}F_t$ is an invariant of the dynamics (2.3) (Bomze 1991). Consequently, these dynamics only allow convergence to H_{x^*} from probability distributions F_0 such that $\int_U dF_0(x) > 0$ for any neighborhood U of x^*, a requirement which is not implied by $\mathbf{supp}F_0 \in (x^* - \varepsilon, x^* + \varepsilon)$. This is not surprising, given that the replicator dynamics allows only for changes in the frequencies of pure strategies, *already existing in the population*. The requirement that $\int_U dF_0(x) > 0$ for any neighborhood U of x^*, is therefore, equivalent to the classic restraint of *genetic availability* as pre-requisite for evolutionary change.

One way to resolve this difficulty is to superimpose on (2.3) small perturbations due to rare mutations (e.g. Turelli 1984, Bürger 1989, Bomze and Bürger 1995, Bürger and Bomze 1996). Applying this approach to natural populations requires, though, a population size which is sufficiently large as to guarantee, each generation anew, a steady (though with a rate tending to zero) flux of all sort of relevant mutations.

As being argued elsewhere (Eshel 1991, 1996; see also Hemmerstein 1996, Metz et al. 1996, Geritz et al. 1998, Diekmann et al. 2002), we believe (though this is, indeed, an open subject for a debate) that advantageous mutations occur very rarely, one at a time, even in populations which, for other aspects, are large enough as to justify the mathematically convenient assumption of an infinite size. Under this assumption, a distinction was made (Eshel 1991, 1996) between the process of *short-term evolution*, concerning deterministic changes in the frequencies of existing genotypes, and the stochastic process of *long-term evolution*, in which random mutations, introduced, one at a time, into a population close to short-term stable equilibrium, may or may not be rejected by natural selection, initiating a new process of short-term evolution in the latter case. *Long-term fixation-stability* of x^* is, then, defined as convergence of the long-term process to x^* in probability as close to one as desired, when starting from a sufficiently small neighborhood of x^* (e.g. Eshel et al. 1997, 1998, Eshel and Feldman 2001). While the dynamics (2.3) falls, according to this approach, under the category of a short-term process, it was shown that the long-term convergence to x^* does not require any assumption about the genetic availability of x^*.

Finally, sticking to the replicator dynamics (2.3), a third, mathematically straightforward, approach is to ignore whatsoever all sorts of mutations, thus to restrict our discussion to those initial probability-measures that apply *positive probability weight to any small neighborhood of* x^*, thus allowing convergence to x^*, if favored by natural selection. This corresponds to the alternative, empiricist approach, regarding *observed* genetic availability as pre-requisite for evolutionary change (e.g. Lewontin 1974).

Resorting to either the weak or the maximal shift topology, we were not able to characterize conditions for fixation-stability under the first approach. We shall see, though, that, quite surprisingly, at least the latter two approaches lead to somehow different conditions for fixation-stability, corresponding to different time scales of the evolutionary process, the short-term, deterministic one, characterized by changes in the frequencies of the existing genotypes, and the long-term, stochastic one, allowing new mutations to renew the short-term process each time anew.

Thus, on one hand it was already shown (Eshel et al. 1997) that a necessary condition for the long-term fixation stability of a pure strategy x^* under the assumption of small effect mutations (given that any mutation with effect less than a sufficiently small value $\varepsilon > 0$ is possible in the long run) is that the appropriate first and second derivatives v_x^*, v_{xx}^* and v_{xy}^* of $v(x, y)$ at $x = y = x^*$ would satisfy the following three requirements:

$$v_x^* = 0 \tag{2.4}$$

$$v_{xx}^* \leq 0 \tag{2.5}$$

$$v_{xx}^* + v_{xy}^* \leq 0, \tag{2.6}$$

regardless of the distribution of the mutations; a sufficient condition for it being (2.4) with a strict inequality version of (2.5)–(2.6). Quite interestingly, this is equivalent to the static stability requirement of *CSS* (Eshel 1982).

On the other hand, assuming the replicator dynamics (2.3) without mutations but restricting our attention to probability distributions F_0 such that $\int_U dF_0(x) > 0$ for any neighborhood U of x^*, we shall see now that a somehow stronger necessary and almost sufficient stability condition is required, in which (2.6) is to be replaced by the inequality $v_{xx}^* + 2v_{xy}^* \leq 0$, which, together with (2.4) and (2.5), is equivalent to the requirement of the NIS condition (Apaloo 1997).

3. Fixation stability under the continuous-state replicator dynamic

Notation 1. $D_\epsilon(x^*) = \{F : d(F, H_{x^*}) < \varepsilon, x^* \in \sup dF\}$ *where the distance* $d(F, G)$ *of the distribution* F *from the distribution* G *is given by* (*1,1*).

$D_\epsilon(x^*)$ is the set of all strategies with support in the ε-neighborhood of x^*, with x^* itself within this support. The requirement that $x^* \in \sup dF$ means that x^* is *genetically available* when starting from a distribution F of (pure) individual strategies in the population.

Definition 2. *The pure strategy* x^* *is said to be a* ***Continuously Replicator Stable Strategy****, say* ***CRSS****, if there exists a positive value* $\varepsilon > 0$ *such that for any initial population strategy* $F_0 \in D_\epsilon(x^*)$*, the replicator dynamics* (*2.3*) *converges weakly* (*i.e. almost anywhere*) *to* H_{x^*}

Note, though, that since the replicator dynamics (2.3) is characterized by a set $\{F_t\}_{t\geq 0}$ of distribution functions with equally bounded support, its weak convergence to H_{x^*} is equivalent to its convergence in second moment to H_{x^*}, namely to $\lim \int (x - x^*)^2 dF_t(x) = 0$.

Employing the Taylor expansion of $v(x, y)$ around $x = y = x^*$ and denote $v(x^*, x^*) = v^*$, (2.1) becomes:

$$\begin{aligned} V(G, F) = \int [&v^* + (x - x^*)v_x^* + (y - x^*)v_y^* + \frac{1}{2}(x - x^*)^2 v_{xx}^* \\ &+ (x - x^*)(y - x^*)v_{xy}^* + \frac{1}{2}(y - x^*)^2 v_{yy}^*]dG(x)dF(y) + o(\varepsilon^2) \\ = v^* &+ (EX - x^*)v_x^* + (EY - x^*)v_y^* + \frac{1}{2}E(X - x^*)^2 v_{xx}^* \\ &+ (EX - x^*)(EY - x^*)v_{xy}^* + \frac{1}{2}E(Y - x^*)^2 v_{yy}^* + o(\varepsilon^2), \end{aligned} \tag{3.1}$$

where the derivatives are taken at $x = y = x^*$, and X and Y are random variables, distributed G and F respectively.

In the same way, (2.2) yields:

$$V(H_x, F) = v + (x - x^*)v_x + (EY - x^*)v_y + \frac{1}{2}(x - x^*)^2 v_{xx} \\ +(x - x^*)(EY - x^*)v_{xy} + \frac{1}{2}E(Y - x^*)^2 v_{yy} + o(\varepsilon^2). \quad (3.2)$$

Inserting (3.1) and (3.2) into (2.3), we get:

$$\frac{\partial}{\partial t}F_t(x) = \int_{-\infty}^{x} \{(u - EX_t)v_x^* + \frac{1}{2}[(u - x^*)^2 - E(X_t - x^*)^2]v_{xx}^* \\ +(u - EX_t)(EX_t - x^*)v_{xy}^*\}dF_t(u) + o(\varepsilon^2), \quad (3.3)$$

where X_t is a random variable, distributed F_t.

Theorem 3. (*a*) *A necessary condition for the Continuous Replicator Stability of x^* is given by* (*2.4*)–(*2.5*) *and*

$$v_{xx}^* + 2v_{xy}^* \leq 0. \quad (3.4)$$

(*b*) (*2.4*) *with the strict version of* (*2.5*) *and* (*3.4*) *is sufficient for the Continuous Replicator Stability of x^*.*

Note that, given (2.5), the requirement (3.4) is stronger than the CSS requirement (2.6).

Proof. (a) It is easy to see that the requirements (2.4)–(2.5) are necessary for the replicator-stability of x^* against any mutation of a sufficiently small effect, when in a sufficiently small frequency (e.g. Eshel et al. 1997). Let us, thus, choose for F_0 the discrete distribution function which attributes the probabilities $p_0(x^*) = 1 - h_0 > 0$ and $p_0(x^* + \theta) = h_0 > 0$ to the points x^* and $x^* + \theta$ respectively, where $0 < \theta < \varepsilon$, indeed $F_0 \in D_\epsilon(x^*)$. But starting from F_0, we know that a second moment convergence to H_{x^*} does not occur unless both (2.4) and (2.5) are satisfied, in which case x^* cannot be CRSS.

Let us assume now that (2.4)–(2.5) does, but (3.4) does not hold at x^*. We show that in this case, for any given $\varepsilon > 0$, there is a distribution $F_0 \in D_\epsilon(x^*)$, starting from which, second moment convergence to H_{x^*} does not occur. For this we choose a discrete distribution function F_0, attributing the probabilities $p_0(x^*) = h_0 > 0$ and $p_0(x^* + \theta) = 1 - h_0 > 0$ to the points x^* and $x^* + \theta$ respectively, where $0 < \theta < \varepsilon$. The (discrete) replicator dynamics $\{F_t\}$ is then given by probabilities $p_t(x^*) = h_t$ and $p_t(x^* + \theta) = 1 - h_t$ for any $t \geq 0$. Given (2.4), namely $v_x = 0$, the discrete version of (3.3) readily yields

$$\frac{\partial}{\partial t}h_t = -\frac{h_t}{2}[v_{xx}^* VarX_t + (v_{xx} + 2v_{xy}^*)(EX_t - x^*)^2] + o(\varepsilon^2).$$

Having then $EX_t = x^* + (1 - h_t)\theta$ and $VarX_t = h_t(1 - h_t)\theta^2$, this becomes:

$$\frac{\partial}{\partial t}h_t = -\theta^2 \frac{h_t(1 - h_t)}{2}[v_{xx}^* h_t + (v_{xx}^* + 2v_{xy}^*)(1 - h_t)] + o(\varepsilon^2). \quad (3.5)$$

But having assumed that (3.4) does not hold, we know that $v_{xx} + 2v_{xy} > 0$. For a sufficiently small h_t, (3.5) thus yields $\frac{\partial}{\partial t}h_t < 0$. Choosing a sufficiently small value of $h_0 > 0$, this can be guaranteed for $t = 0$, hence for all t in some open interval $[0, t_0)$, where $t_0 \geq 0$. This implies $h_{t_0} < h_0$. Thus, by transfinite induction it follows that $h_t < h_0$ and $\frac{\partial}{\partial t}h_t < 0$ for all $t \geq 0$. This implies that the second moment $\int (x - x^*)^2 dF_t(x) = \theta^2(1 - h_t)$ of F_t about x^* can only increase in time, and second moment convergence to x^* is, therefore, impossible.

(b) Let us assume now a strict version of (2.4), (2.5) and (3.4), and show that a value $\varepsilon > 0$ exists, so that for any choice of $F_0 \in D_\epsilon(x^*)$, $\lim \int (x - x^*)^2 dF_t(x) = 0$.

In a previous article (Eshel et al. 1997) it was shown that for any point x^* at which $v_x^* = v_x(x^*, x^*) = 0$ and $v_{xx}^* = v_{xx}(x^*, x^*) \neq 0$, there is a value $\varepsilon > 0$ such that, starting from any distribution function $F_0 \in D_\epsilon(x^*)$, the replicator dynamics (2.3) weakly converges either to a single point or to a pair of points in $\sup pF_0$. Since the dynamics is restricted to a bounded support, this implies convergence in second moment as well. For this value of ε, let us assume that, starting from some $F_0 \in D_\epsilon(x^*)$, the random variable X_t, distributed F_t, does not converge in second moment to x^*. Since X_t then converges to another discrete distribution, we know that $\lim_{t\to\infty} E(X_t - x^*)^2 > 0$. But since $E(X_t - x^*)^2 = VarX_t + (EX_t - x^*)^2$, this means that $\lim_{t\to\infty} VarX_t > 0$, or $\lim_{t\to\infty} (EX_t - x^*)^2 > 0$. From the strict version of (2.5) and (3.4) it, therefore, follows that there is a positive value $R > 0$ such that for some $t_0 > 0$ and for all $t \geq t_0$, $v_{xx}^* VarX_t + (v_{xx}^* + 2v_{xy}^*)(EX_t - x^*)^2 < -R$. But with equality (2.4), (3.3) can readily be written as:

$$
\begin{aligned}
&\frac{\partial}{\partial t}F_t(x)\\
&= \int_{-\infty}^{x} \left\{ \frac{1}{2}[(u - x^*)^2 - E(X_t - x^*)^2]v_{xx}^* + (u - EX_t)(EX_t - x^*)v_{xy}^* \right\} dF_t(x)\\
&\quad + o(\varepsilon^2) = -\frac{1}{2}\int_{-\infty}^{x} \left\{ v_{xx}^* VarX_t + (v_{xx}^* + 2v_{xy}^*)(EX_t - x^*)^2 \right.\\
&\qquad \left. -(x^* - u)\big[(x^* - u)v_{xx}^* - 2(EX_t - x^*)v_{xy}^*\big] \right\} dF_t(x) + o(\varepsilon^2).
\end{aligned}
$$

Denote $L(u, EX_t) = [(x^* - u)v_{xx}^* - 2(EX_t - x^*)v_{xy}^*]$, this can be written as:

$$
\begin{aligned}
\frac{\partial}{\partial t}F_t(x) = \frac{1}{2}\int_{-\infty}^{x} &\{(x^* - u)L(u, EX_t) - v_{xx}^* VarX_t\\
&- (v_{xx}^* + 2v_{xy}^*)(EX_t - x^*)^2\} dF_t(u) + o(\varepsilon^2). \qquad (3.6)
\end{aligned}
$$

But for $F_t \in D_\epsilon(x^*)$, $|L(u, EX)| < \varepsilon v_{xx}^*$, hence for a sufficiently small value $h > 0$ and for all $|u - x^*| < h$, $|(x^* - u)L(u, EX)| < \frac{R}{2}$. Recalling that $v_{xx}^* VarX_t + (v_{xx}^* + 2v_{xy}^*)(EX_t - x^*)^2 < -R$, it follows that for all such u,

$$
(x^* - u)L(u, EX_t) - [v_{xx} VarX_t + (v_{xx} + 2v_{xy})(EX_t - x^*)^2] \geq \frac{R}{2}.
$$

From this and (3.6) it follows that:

$$\frac{\partial}{\partial t}[F_t(x^*+h) - F_t(x^*-h)] = \frac{\partial}{\partial t}\int_{x^*-h}^{x^*+h} dF_t(u) \geq \frac{R}{4}\int_{x^*-h}^{x^*+h} dF_t(u)$$
$$= \frac{R}{4}[F_t(x^*+h) - F_t(x^*-h)],$$

which implies:

$$F_t(x^*+h) \geq [F_t(x^*+h) - F_t(x^*-h)] \geq e^{\frac{R}{4}t}[F_0(x^*+h) - F_0(x^*-h)]. \tag{3.7}$$

But having $F_0 \in D_\epsilon(x^*)$, thus $x^* \in \sup dF$, we know that $\int_U dF_0(u) > 0$ for any neighborhood U of x^*, hence $[F_0(x^*+h) - F_0(x^*-h)] > 0$. It, therefore, follows from (3.10) that $F_t(x^*+h) \to \infty$ as $t \to \infty$, which is indeed impossible since $F_t(x^*+h) \leq 1$. This completes the proof, leaving $\lim \int (x-x^*)^2 dF_t(x) = 0$ as the only possibility. □

The CRSS condition (2.4), (2.5), (3.4) is necessary but not sufficient for fixation stability under the weak topology (1.2), an obvious additional condition for the latter being the general Uninvadability condition, guaranteeing stability against any deviation of any mutant, when in frequency smaller than some $\varepsilon > 0$. An open question is whether the combination of both is also sufficient for fixation stability in the weak topology.

4. Game theoretical interpretation of continuous replicator stability and related concepts

4.1. CRSS and NIS

Employing the Taylor expansion of $v(y, y) - v(x^*, y)$ as a function of y around x^*, together with the requirement (2.4), we get:

$$v(y, y) - v\left(x^*, y\right) = \frac{1}{2}(y - x^*)^2(v^*_{xx} + 2v^*_{xy}) + o(y - x^*)^2. \tag{4.1}$$

The combination of conditions (2.4) and (3.4) is thus necessary and, as a strict inequality, sufficient for the requirement that for any y in some ε-neighborhood of x^*, $v(y, y) - v(x^*, y) < 0$, which is exactly the NIS requirement for x^* (Apaloo 1997). At the same time, the combination of conditions (2.4) and (2.5) is necessary and, as a strict inequality, sufficient for the requirement of Evolutionary Stability against mutations of sufficiently small effect, say Limited Evolutionary Stability. This means that, except, maybe, for the case where either (2.4) or (2.5) holds as an equality, CRSS is equivalent to the combination of NIS and Limited Evolutionary Stability. The following example indicates, however, that in the most general case, a pure strategy can be both ESS and NIS, but not CRSS.

Example . Let $v(x, y) = (x - y)^4 - 2x^4$. Having $v(0, 0) = 0$ and for all $x \neq 0$, $v(x, 0) = -x^4 < 0$, we know that $x^* = 0$ is an ESS. Moreover, for any $y \neq 0$, $v(y, y) = -2y^4 < y^4 = v(0, y)$, hence $x^* = 0$ is also a NIS. Consider now the replicator dynamics $F_t = p_t \delta_{-h} + (1 - 2p_t)\delta_0 + p_t \delta_h$, $(t \geq 0)$, as determined by (2.3) with $0 < p_0 < 1/2$. Choosing $0 < h < \varepsilon$, F_0 (and all F_t) has a support in the ε-neighborhood of $x^* = 0$. But employing (2.3), one can straightforwardly calculate $\frac{\partial}{\partial t} p_t = p_t(1 - 2p_t)(12p_t - 1)h^4$. Starting from $1/6 < p_0 < 1/2$, p_t is monotone increasing, and the replicator dynamics would, then, carry the distribution F_t away from 0. In this case, the ESS and NIS $x^* = 0$ cannot be asymptotically stable in the maximal shift topology.

4.2. CRSS, NIS and CSS

Denote $f(x) = \{\frac{\partial}{\partial x} v(x, y)|_{y=x}\}$, one can readily get $f^{'}(x^*) = v^*_{xx} + v^*_{xy}$. Employing the Taylor expansion of $f(x) = \frac{\partial}{\partial x}\{v(x, y)|_{y=x}\}$ around $x = x^*$, together with the requirement (2.4), one obtains:

$$\frac{\partial}{\partial x}\{v(x, y)|_{y=x=x^*}\} = (x - x^*)(v^*_{xx} + v^*_{xy}) + o(x - x^*). \tag{4.2}$$

The combination of conditions (2.4) and (2.6) is, thus, necessary and, as a strict inequality, sufficient for the requirement (not guaranteed by the ESS condition) that a positive value $\varepsilon > 0$ exists, such that $\{\frac{\partial}{\partial x} v(x, y)|_{y=x}\}$ is negative for $x^* < x < x^* + \varepsilon$ and positive for $x^* > x > x^* - \varepsilon$. This, in turn, is equivalent to the CSS condition that if the entire population slightly deviates from x^*, then a new mutation of a sufficiently small effect would be favorable if and only if in the direction of x^*, not necessarily to x^* itself (Eshel 1982), a requirement named m-stability by Taylor (1989).

Let us now concentrate on the case where for any pure strategy y there is a unique best response $x = x(y)$, such that

$$v_x(x(y), y) = 0, \tag{4.3}$$

$$v_{xx}(x(y), y) < 0. \tag{4.4}$$

From the definition of $x(y)$ as the unique best response against the pure strategy y, it follows that any real value $y = x(y)$, if it exists, at which $x(y)$ intersects the main diagonal, is a unique best response against itself and hence a pure ESS of the population game. On the other hand, any pure ESS y of the population game, if it exists, must be a best response against itself, hence, from the assumption of the model we know it is a unique best response, thus $y = x(y)$ is an intersection of $x(y)$ with the main diagonal. From (4.3)–(4.4) and the theorem of the implicit functions it follows, further, that $x(y)$ is continuous and differentiable with,

$$\frac{dx}{dy} = -\frac{\frac{d}{dy} v_x(x(y), y)}{\frac{d}{dx} v_x(x(y), y)} = -\frac{v_{xy}(x(y), y)}{v_{xx}(x(y), y)}.$$

At the intersection $(x(y), y) = (x^*, x^*)$, this yields:

$$\frac{dx}{dy} = -\frac{v^*_{xy}}{v^*_{xx}}. \tag{4.5}$$

Recalling that $v_{xx} < 0$, the additional CSS condition (2.6) thus readily becomes:

$$\frac{dx}{dy} \leq 1. \tag{4.6}$$

In the same way it follows from (3.5) that the NIS (or CRSS) condition (3.4) is equivalent to

$$\frac{dx}{dy} \leq \frac{1}{2}. \tag{4.7}$$

Ignoring for the moment the case $dx/dy = 1$, we get:

Corollary. *A CSS is any value, if it exists, at which the curve $x(y)$ intersects the main diagonal $x = y$ from above. A CRSS, which in this case is equivalent to ESNIS (i.e. NIS and ESS, see above), is a value x^* at which the curve $x(y)$ intersects the main diagonal from above* **at a slope smaller than** $arctg\frac{1}{2}$.

Indeed, an intersection from above of the curve $x(y)$ with the main diagonal at x^* (including the case $dx/dy = 1$) means, in this case, that the best response $x(y)$ to a pure strategy y, sufficiently close to x^*, would be in the direction of x^*. An intersection from above *at a slope smaller than* $arctg\frac{1}{2}$ guarantees that, for y sufficiently close to x^*, the best response $x(y)$ would be closer to x^* than to y.

If the best responses to the most extreme strategies are less extreme, namely if the curve $x\ (y)$ starts from above and ends below the main diagonal, then at least one intersection from above is inevitable, hence there must exist at least one CSS (Eshel and Motro 1981). Employing the second part of the corollary, on the other hand, one can easily construct an example in which no CRSS or ESNIS exists under these conditions.

4.3. CRSS, CSS and NIS versus Uninvadability and Strong Uninvadability

As we recall, a strategy μ in a general population game is *Strongly Uninvadable* if a positive value $\varepsilon > 0$ exists such that for any strategy η with $0 < \|\eta - \mu\| < \varepsilon$ in the variational norm, $v(\mu, \eta) > v(\eta, \eta)$. In the special case of a pure strategy x^*, the requirement $\|\delta_{x^*} - \eta\| < \varepsilon$ is equivalent to $\eta = (1 - h)\delta_{x^*} + h\mu$, where μ is any probability measure and $0 < h < \varepsilon$. Strong Uninvadability is, then, readily shown to be equivalent to the existence of a positive value $\varepsilon > 0$ such that for any probability measure μ, essentially different from δ_{x^*} and for any $0 < h < \varepsilon$,

$$V[\delta_{x^*}, (1 - h)\delta_{x^*} + h\mu] > V[\mu, (1 - h)\delta_{x^*} + h\mu], \tag{4.8}$$

which is just the condition for *Uninvadability* (Vickers and Cannings 1987).

Obviously (4.8), being applied to all probability distributions on the real line, cannot possibly be implied by the CRSS condition, which is restricted to some

ε-neighborhood of x^*. On the other hand, the following example indicates that the Uninvadability condition (4.8) (hence, in this case, the Strong Uninvadability condition) does not imply the CRSS condition, nor even the weaker CSS condition:

Example. Define $v(x, y) = -(1-\theta)x^2 - \theta(x-y)^2$. At $x^* = 0$ we get $v_x^* = 0$, $v_{xx}^* = -2$, and $v_{xy}^* = 2\theta$. Consequently $x^* = 0$ is a CSS if $\theta < 1$ and only if $\theta \leq 1$. It is CRSS and NIS if $\theta < 1/2$ and only if $\theta \leq 1/2$. But for any random variable X with distribution function G, one can readily calculate then $V(\delta_0, \delta_0) - V(G, \delta_0) = EX^2$ and $V(G, G) - V(\delta_0, G) = -EX^2 + 2\theta(EX)^2$. The requirement (4.8) for either Uninvadability or Strong Uninvadability is, in this case, that for some $\varepsilon > 0$ and for all random variables X,

$$EX^2 > 2\theta\varepsilon(EX)^2. \tag{4.9}$$

Having $EX^2 > (EX)^2$, it follows that (4.9) is satisfied for any $\varepsilon < 1/2\theta$. The pure strategy $x^* = 0$ is, therefore, Strongly Uninvadable for any value of θ, but it is CRSS only for $\theta \leq 1/2$, and CSS only for $\theta \leq 1$.

We, thus, see, that neither CRSS, CSS or NIS implies, nor is implied by Uninvadability or Strong Uninvadability.

5. Discussion

The replicator dynamics corresponds to the process of *short-term evolution* in large asexual populations, where each individual continuously reproduces copies of itself with differential net success. On the other hand, the concept of ESS (Maynard Smith and Price 1973), as well as related concepts like Unbeatable Strategy (Hamilton 1967), CSS (Eshel and Motro 1981), or NIS (Apaloo 1997), by their very definition, correspond to the stochastic process of *long-term evolution*, where rare mutations, randomly being introduced into the population, may and may not be selected for, thus repeatedly shifting the balance of short-term stable equilibria (Eshel 1991, 1996, Hemmerstein 1996).

As demonstrated by the analysis of multilocus sexual population dynamics, the long-term process of evolution may well lead to stable equilibria which are radically different from those determined by the short-term process, the first but not the latter generally corresponding to local optima (in the case of frequency independent selection) or ESS (in the case of frequency dependent selection. Eshel 1991, 1996, Hemmerstein and Selten 1993, Eshel et al. 1998). The finding that at least when concerning asexual population dynamics on a finite set of individual strategies, the (long-term) ESS condition is sufficient for the (short-term) asymptotic stability under the replicator dynamics (Taylor and Jonkers 1978) is, thus, by no means trivially expected. As we have seen, this finding may not hold even for asexual population dynamics when concerning a continuum of pure strategies. Asymptotic stability, in this case, crucially depends, however, on the choice of topology over the space of mixed strategies.

In the present work, following the static stability concepts of CSS (Eshel and Motro 1981) and NIS (Apaloo 1997), we have adopted the maximal shift topology (1.1), in which the ε-vicinity of the fixation δ_{x^*} on a pure strategy x^* in the space of general (mixed) strategies consists of all mixed strategies with support in the ε-neighborhood of x^*, and for which x^* is genetically available. Under this topology, a necessary and almost sufficient condition for replicator asymptotic stability, called Continuous Replicator Stability, CRSS, has been demonstrated. The conditions for CRSS were shown to be very close, though not quite equivalent to those of NIS (Apaloo 1997), with the additional requirement of limited evolutionary stability against small effect mutations. Recall that a pure strategy x^* is NIS if for any deviation of the entire population to a sufficiently close pure strategy x, a back-mutation to x^* is advantageous. This is a slightly strong variant of Continuous Stability (Eshel and Motro 1981), requiring, in addition to limited evolutionary stability against small effect mutations, that for any monomorphic deviation of the entire population from x^* to a sufficiently close pure strategy x, a back-mutation in the direction of x^*, but not necessarily to x^* itself, is advantageous. The (short term) CRSS condition is, therefore, stronger than the CSS condition, previously proved necessary and sufficient for Long Term Stability (Eshel et al. 1997).

The stability conditions of CRSS, CSS, NIS and ESNIS were shown not to imply, nor to be implied, by the stability conditions of either Uninvadability (Vickers and Cannings 1987) or Strong Uninvadability (Bomze 1990). This is not surprising, given that the latter two, being most generally applicable to any infinite space of strategies, do not take into consideration the specific metric structure of quantitative traits on the continuum, hence the evolutionary fundamental concept of a small quantitative change. All the stability conditions mentioned above are implied, however, by the extremely strong, still to be further studied, condition of Evolutionary Robustness (Öechssler and Riedel 2002).

For closely related approaches to the concept of stability in continuous population games see Taylor (1989), Christiansen (1991), Motro (1994), Matessi and de Pasquale (1996), Metz et al. (1996), Geritz et al. (1998), Dieckmann and Law 1996, Diekmann et al. (2002).

Acknowledgements. We wish to thank Reinhard Bürger, Imanuel Bomze, Odo Diekmann, Jörg Öechssler and Peter Taylor for most helpful remarks on the manuscript. Financial support from the Deutche Forschugsgemeineschft, Graduirtenkollege 629/100, "Quantitative Economics" at the University of Bonn, from the Italian Council for National Research (CNR) and the Department of Mathematics and its Applications at the University of Naples, is gratefully acknowledged.

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