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Evolutionarily stable strategies and short-term selection in Mendelian populations re-visited

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Abstract

This note concerns a one locus, two allele, random mating diploid population, subject to frequency-dependent viability selection. It is already known that in such a population, any evolutionarily stable strategies (ESS), if only accessible by the genotype-to-phenotype mapping, is the phenotypic image of a stable genetic equilibrium (Eshel, I. 1982. Evolutionarily stable strategies and viability selection in Mendelian populations. Theor. Popul. Biol. 22(2), 204–217; Cressman et al. 1996. Evolutionary stability in strategic models of single-locus frequency-dependent viability selection. J. Math. Biol. 34, 707–733). The opposite is not true. We find necessary and sufficient parametric conditions for global convergence to the ESS, but we also demonstrate conditions under which, although a unique, genetically accessible ESS exists, there is another, "non-phenotypic" genetically stable equilibrium.

1. Introduction

A long-time controversy in modern theoretical population biology concerns the legitimacy of evolutionary predictions, made on the mere basis of phenotypic observations (see, e.g. Feldman and Cavalli Sforza, 1981). The concepts of inclusive fitness (Hamilton, 1964, 1972) and evolutionarily stable strategies (ESS) (Maynard Smith and Price, 1973) were suggested specifically for this purpose. A central question within this controversy is whether and under what conditions does frequency-dependent viability selection in random-mating diploid populations lead to stable equilibria that determine an average population strategy which is an ESS.

On one hand, it was shown that under wide conditions, long-term evolution, combining standard selection forces with a slow flux of random mutations, always tends to stabilize an ESS, when it exists (Eshel, 1997; Eshel and Feldman, 2001; Eshel et al., 1998). On the other hand, at least when concerning multilocus genetic systems, this is

generally not true for the short-term evolutionary dynamics of changes in genotype-frequencies without the effect of accumulated new mutations (e.g. Eshel, 1997).

But even in the case of short-term evolution, the situation is different when the relevant phenotypic patterns (strategies) are determined by a single locus. Employing a discrete-time model, and assuming a population game of two pure strategies, it was shown (Eshel, 1982) that any ESS, accessible by a one locus multi-allele genotype-to-phenotype mapping, is phenotypically stable in the sense that it is the image of at least one stable genetic equilibrium (note that an ESS of a population-game with more than two pure strategies may not be stable under discrete-time selection even in asexual population). Employing a continuous-time model, this result was extended by Cressman et al. (1996) to any number of alternative pure strategies, provided the genetic system allows for three alleles at the most. In both cases, what remained to be considered is the question of global convergence to an ESS.

In this note we show that convergence to ESS, even in the case of two allele diploid population, although global under specific parametric conditions, is not always so. For a well-defined range of parameters, for which a mixed

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(hence unique) ESS exists and is accessible by the genotype-to-phenotype mapping, there is also another, "non-phenotypic", genetically stable equilibrium. Being interested in an existence statement (possible local stability of a non-ESS equilibrium when a unique ESS exists and is genetically accessible), we concentrate, for convenience, on the case of weak selection.

2. The problem

Assume an infinite, one locus, two allele, random-mating, diploid population, subject to frequency-dependent viability selection, characterized by the 2×2 payoff matrix

$$\Omega = \begin{pmatrix} v_{11} & v_{12} \\ v_{21} & v_{22} \end{pmatrix},$$

where the payoff is taken to be an additive component of the individual's viability. More specifically, the viability of an individual, playing the strategy i against an opponent playing j, is assumed to be $1 + \varepsilon v_{ij}$, where $\varepsilon > 0$ measures the intensity of selection in respect to the population-game Ω.

Let x_{11}, x_{12}, and x_{22} be the strategies of genotype $A_1 A_1$, $A_1 A_2$, and $A_2 A_2$ respectively, namely the probabilities that any of these genotypes will choose the first pure strategy of the population game. Let p be the frequency of the allele A_1 among newborn offspring in a given generation, and $q = 1 - p$. Assuming Mendelian segregation, the average population strategy is then

$$x(p) = p^2 x_{11} + 2pq x_{12} + q^2 x_{22}$$
$$= (x_{11} - 2x_{12} + x_{22})p^2 + 2(x_{12} - x_{22})p + x_{22}. \quad (1)$$

For any $0 \leqslant x, y \leqslant 1$, denote the payoff of an x-player against a y-player by

$$v(x, y) = v_{11}xy + v_{12}x(1 - y) + v_{21}(1 - x)y + v_{22}(1 - x)(1 - y). \quad (2)$$

The viability of the genotype $A_i A_j$ $(i, j = 1, 2)$ is thus given by

$$\omega_{ij}(p) = \omega_{ij}^{(\varepsilon)}(p) = 1 + \varepsilon v(x_{ij}, x(p)). \quad (3)$$

Employing (1) and (3), the average viability of the population is readily shown to be

$$W(p) = W^{(\varepsilon)}(p) = 1 + \varepsilon v(x(p), x(p)).$$

Following random mating and frequency-dependent viability selection, the frequency of the allele A_1 in the newborn population of the next generation will be

$$p' = p \frac{p\omega_{11}(p) + q\omega_{12}(p)}{W(p)}$$
$$= p \frac{1 + \varepsilon[pv(x_{11}, x(p)) + qv(x_{12}, x(p))]}{1 + \varepsilon v(x(p), x(p))}. \quad (4)$$

In this note, we restrict our analysis to the case

$$v_{11} < v_{21}; \quad v_{22} < v_{12}, \quad (5)$$

where a mixed (hence unique) ESS exists, and is globally stable in the replicator dynamics of asexual population. The ESS is then given by

$$x^* = \frac{v_{12} - v_{22}}{v_{12} - v_{11} + v_{21} - v_{22}}. \quad (6)$$

In order to avoid triviality we assume $x_{11} - 2x_{12} + x_{22} \neq 0$ so that $x(p)$ is a quadratic form of p, obtaining its extremum $\hat{x} = x(\hat{p}) = (x_{11}x_{22} - x_{12}^2)/(x_{11} - 2x_{12} + x_{22})$ at

$$\hat{p} = \frac{x_{22} - x_{12}}{x_{11} - 2x_{12} + x_{22}}. \quad (7)$$

(Note that in the special case $x_{11} - 2x_{12} + x_{22} = 0$ of no penetrance, the average population strategy $x(p)$ becomes a linear function of p, and natural selection then, much like in the case of an asexual population, always shifts $x(p)$ in the direction of the mixed ESS x^*. See the Appendix.)

For the sake of convenience we further concentrate on the case of *weak selection*, in which $\varepsilon > 0$ is small. This is a natural assumption when the outcome of the game Ω is one out of many components that determine the individual's fitness. In such a case, (4) readily yields

$$p' - p = \varepsilon p[pv(x_{11}, x(p)) + qv(x_{12}, x(p)) - v(x(p), x(p))] + o(\varepsilon). \quad (8)$$

Choosing $\frac{1}{\varepsilon}$ as the unit of time, (8) can be written as

$$\frac{p(t + \varepsilon) - p(t)}{\varepsilon} = p[pv(x_{11}, x(p)) + qv(x_{12}, x(p)) - v(x(p), x(p))] + 0(\varepsilon). \quad (9)$$

Letting $\varepsilon \to 0$, the frequency $p(t)$ of the allele A_1 among adults at time t is then given by the ordinary differential equation

$$\dot{p}(t) = p[pv(x_{11}, x(p)) + qv(x_{12}, x(p)) - v(x(p), x(p))].$$

Inserting (1), (2), (6) and (7), the last equality becomes, after straightforward calculations:

$$\dot{p}(t) = p(1 - p)(x_{11} - 2x_{12} + x_{22})(v_{11} - v_{12} - v_{21} + v_{22}) \times (x(p) - x^*)(p - \hat{p}). \quad (10)$$

With the dynamics (10), we are now able to characterize the necessary and sufficient conditions for global convergence to the ESS, if accessible by the genotype-to-phenotype mapping.

3. Analysis of genotypic and phenotypic stability

From (5) it follows that $v_{11} - v_{12} - v_{21} + v_{22} < 0$. Having further assumed that $x_{11} - 2x_{12} + x_{22} \neq 0$, it follows from (10) that the genetic equilibria of the population dynamics are the values $p = 0$, $p = 1$, $p = \hat{p}$ (if within the unit interval), and the solutions p_1^* and p_2^* of the quadratic equation $x(p) = x^*$, if real numbers within the unit interval. The stable equilibria of the dynamics are those at which the curve of $\dot{p} = f(p)$ intersects the p-axis from above. Without loss of generality one can assume that $x_{11} - 2x_{12} + x_{22} < 0$,

so that the extremum $\hat{x} = x(\hat{p})$ of $x(p) = (x_{11} - 2x_{12} + x_{22})p^2 + 2(x_{12} - x_{22})p + x_{22}$ is a maximum (This can indeed be guaranteed by exchanging the labels of the two pure strategies of the population game). From (10) it then follows that

$$\operatorname{sign}\dot{p} = \operatorname{sign}[x(p) - x^*](p - \hat{p}). \qquad (11)$$

As a result we get:

Proposition 1. *The frequency p of the allele A_1 is time-increasing if $[x(p) - x^*](p - \hat{p}) > 0$, and time-decreasing if $[x(p) - x^*](p - \hat{p}) < 0$. It is at equilibrium when $[x(p) - x^*](p - \hat{p}) = 0$, and at stable equilibrium when the curve of $[x(p) - x^*](p - \hat{p})$ intersects the p-axis from above.*

We can further assume, without loss of generality, that $x_{22} = x(0) \leqslant x(1) = x_{11}$ (It can always be guaranteed by exchanging the labels of the two alleles). This precludes the possibility that the parabola $x(p)$ will obtain its maximum at a value $\hat{p} \leqslant 0$, which leaves us with the two possibilities: Either $\hat{p} \geqslant 1$, or $0 < \hat{p} < 1$. If $\hat{p} \geqslant 1$, we want to distinguish between the following three cases: either $x^* > x(1)$, $x(0) \leqslant x^* \leqslant x(1)$, or $x^* < x(0)$. If $0 < \hat{p} < 1$, then $x(0) \leqslant x(1) < x(\hat{p}) = \hat{x}$, and we want to distinguish between the following four cases: $x^* > \hat{x}$, $x(1) \leqslant x^* \leqslant \hat{x}$, $x(0) < x^* < x(1)$, and $x^* \leqslant x(0)$. Altogether, we have to deal with seven cases:

(I) $\hat{p} \geqslant 1$ and $x^* > x(1)$.
(II) $\hat{p} \geqslant 1$ and $x(0) \leqslant x^* \leqslant x(1)$.
(III) $\hat{p} \geqslant 1$ and $x^* < x(0)$.
(IV) $0 < \hat{p} < 1$ and $x^* > \hat{x}$.
(V) $0 < \hat{p} < 1$ and $x(1) \leqslant x^* \leqslant \hat{x}$.
(VI) $0 < \hat{p} < 1$ and $x(0) < x^* < x(1)$.
(VII) $0 < \hat{p} < 1$ and $x^* \leqslant x(0)$.

In each of the seven cases given above, Proposition 1 provides us with full decomposition of the unit interval into domains of attraction.

In case (I) (see Fig. 1) the ESS x^* is not accessible. Since $\hat{p} \geqslant 1$, the curve $x(p)$ is monotone increasing over the unit interval, hence for all $0 < p < 1$, $x(p) \leqslant x(1) < x^*$. From the additional requirement $p < 1 \leqslant \hat{p}$, we thus get $[x(p) - x^*](p - \hat{p}) > 0$. From Proposition 1, it therefore follows that the value of $p = p(t)$, whatever it is on the open interval $0 < p < 1$, is time-decreasing, hence the genetic equilibrium $p = 1$ is globally stable. The average-population-strategy thus globally converges to the value $x(1)$, which is the closest possible to the (genetically inaccessible) ESS.

In case (II) (see Fig. 2) the ESS x^* is genetically accessible. Again, the curve $x(p)$ is monotone increasing on the unit interval, reaching the value x^* once, at the point $0 \leqslant p_1^* \leqslant 1$. For any point p in the open interval $(0, p_1^*)$ we get $x(p) < x(p_1^*) = x^*$. Given $p < 1 \leqslant \hat{p}$, we get, for any such a point, $[x(p) - x^*](p - \hat{p}) > 0$, and it follows from Proposition 1 that the value of p is time-increasing whenever smaller than p_1^*. In the same way, it is time-
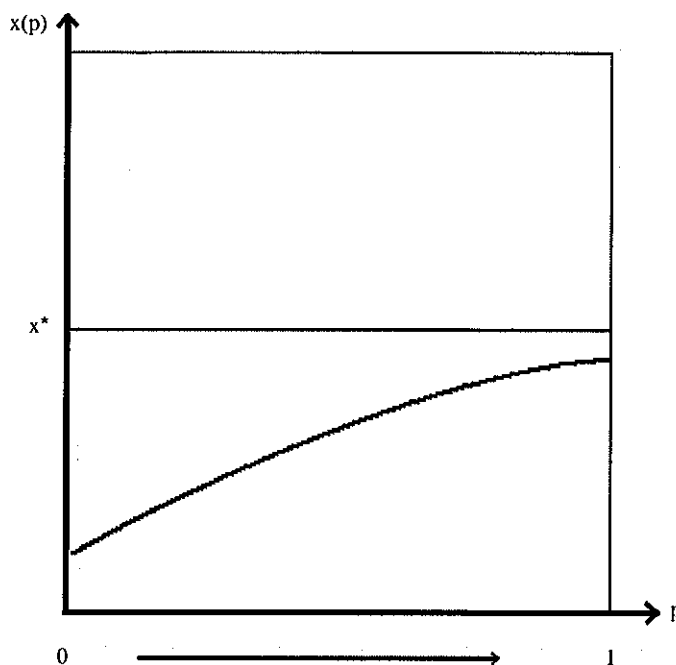

Fig. 1. The ESS x^* is genetically inaccessible. The gene frequency $p = 1$, rendering the average population strategy the closest possible to the ESS, is globally stable (see the text).
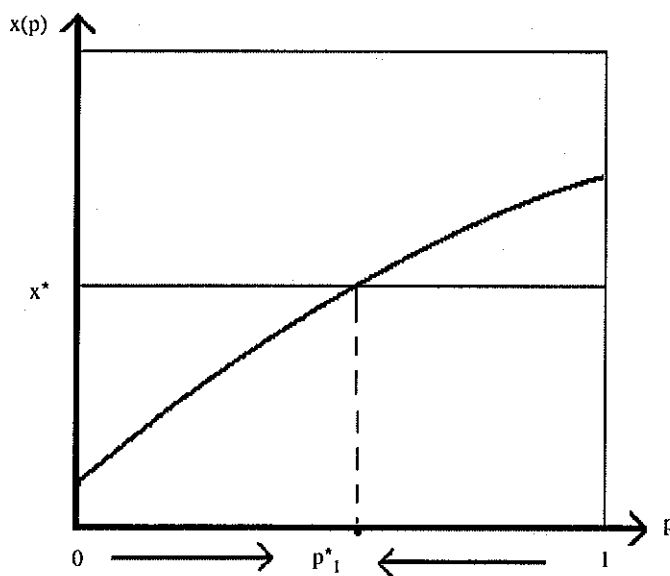

Fig. 2. The ESS x^* is genetically accessible. The gene frequency p_1^*, determining the ESS as average population strategy, is globally stable (see the text).

decreasing whenever larger than p_1^*. It follows that the genetic equilibrium p_1^* is globally stable, and the average-population-strategy thus globally converges to the ESS value $x(p_1^*) = x^*$.

In case (III) (see Fig. 3) the ESS x^* is not accessible. The curve $x(p)$ is still monotone increasing on the unit interval,
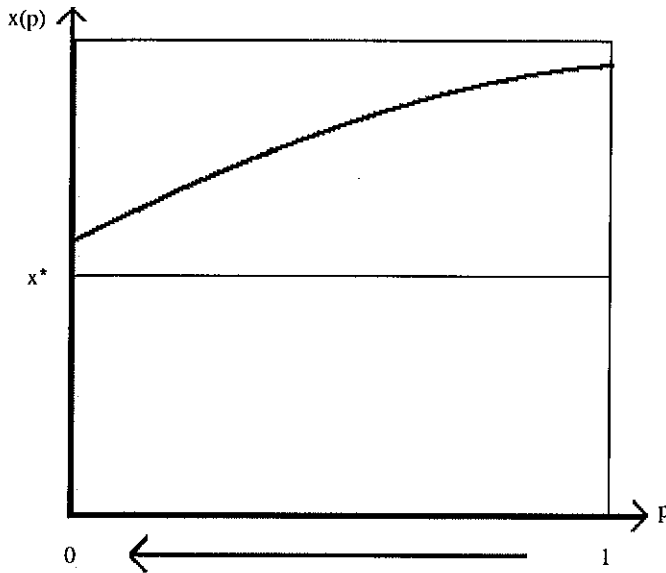
Fig. 3. The ESS x^* is genetically inaccessible. The gene frequency $p = 0$, rendering the average population strategy the closest possible to the ESS, is globally stable (see the text).
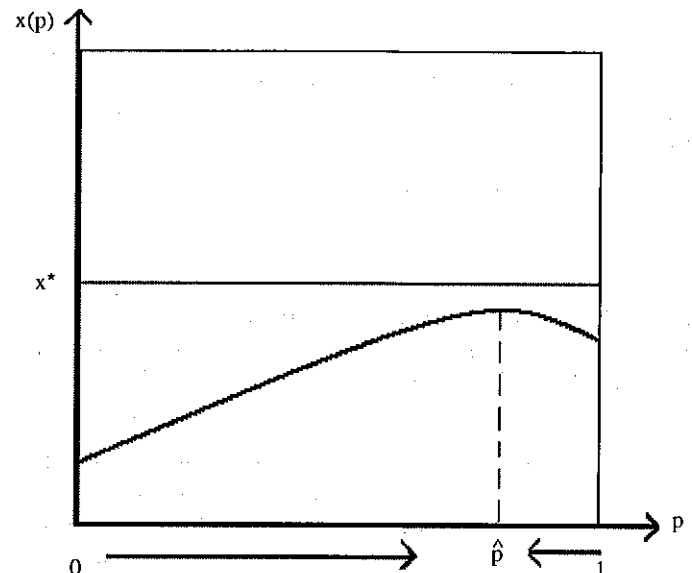

Fig. 4. The ESS x^* is genetically inaccessible. The gene frequency $\hat{p}$, rendering the average population strategy the closest possible to the ESS, is globally stable (see the text).

hence for all $0 < p < 1$, $x(p) > x(0) > x^*$. Given $p < 1 \leqslant \hat{p}$, we know that $[x(p) - x^*](p - \hat{p}) < 0$, and it follows from Proposition 1 that the value of p, whenever it is on the open unit interval, is time-decreasing, hence the genetic equilibrium $p = 0$ is globally stable. The average-population-strategy thus globally converges to the value $x(0)$, which is the closest possible to the (genetically inaccessible) ESS x^*.

In case (IV) (see Fig. 4) the ESS x^* is not accessible. For any p in the unit interval we have $x(p) \leqslant \hat{x} < x^*$, thus for any $p < \hat{p}$ we get $[x(p) - x^*](p - \hat{p}) > 0$ and the value of p is there time-increasing. For the same reason, for $p > \hat{p}$, $[x(p) - x^*](p - \hat{p}) < 0$ and p is there time-decreasing. It follows that the genetic equilibrium $\hat{p}$ is globally stable, and the average-population-strategy thus globally converges to the value $x(\hat{p}) = \hat{x}$, which is the closest possible to the (genetically inaccessible) ESS.

In case (V) (see Fig. 5) the ESS x^* is genetically accessible. The curve $x(p)$ then intersects the constant line $x = x^*$ twice, at $0 \leqslant p_1^* \leqslant \hat{p}$, and at $\hat{p} \leqslant p_2^* \leqslant 1$, with $p_1^* \leqslant p_2^*$. We can then divide the unit interval into four segments:

For $p < p_1^*$ we have $x(p) < x^*$ and $p < \hat{p}$, hence $[x(p) - x^*](p - \hat{p}) > 0$, and the value p is time-increasing when in this interval.

For $p_1^* < p < \hat{p}$ we have $x(p) > x^*$ and $p < \hat{p}$, hence $[x(p) - x^*](p - \hat{p}) < 0$, and the value p is time-decreasing on this interval.

For $\hat{p} < p < p_2^*$ we have $x(p) > x^*$ and $p > \hat{p}$, hence $[x(p) - x^*](p - \hat{p}) > 0$, and the value p is time-increasing on this interval.

For $p_2^* < p < 1$ we have $x(p) < x^*$ and $p > \hat{p}$, hence $[x(p) - x^*](p - \hat{p}) < 0$, and the value p is time-decreasing on this interval.
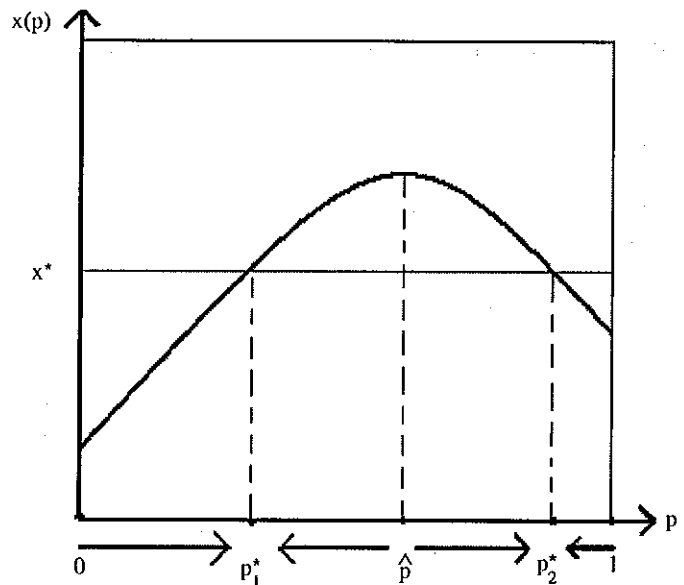

Fig. 5. The ESS x^* is genetically accessible. Both the gene frequencies p_1^* and p_2^*, determining the ESS as the average population strategy, are locally stable, with global phenotypic convergence to the ESS (see the text).

It follows that the genotypic values $p = p_1^*$ and $p = p_2^*$ are both stable. Moreover, their regions of attraction cover the entire open unit interval, hence the ESS value $x^* = x(p_1^*) = x(p_2^*)$ is globally stable in the phenotypic space.

In case (VI) (see Fig. 6) the ESS x^* is, again, genetically accessible. The curve $x(p)$ intersects the constant value x^* once, from below, at $0 < p_1^* < \hat{p}$. We can then divide the unit interval into three non-empty segments:

For $p < p_1^*$ we have $x(p) < x^*$ and $p < \hat{p}$, hence $[x(p) - x^*](p - \hat{p}) > 0$, and the value p is time-increasing on this interval.
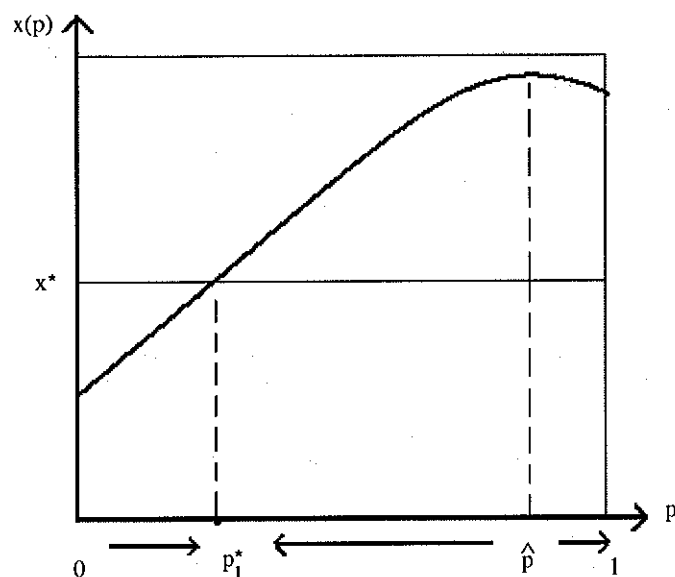
Fig. 6. The ESS x^* is genetically accessible, yet both p_1^* and $p = 1$ are genetically stable. Starting from a gene-frequency larger than $\hat{p}$, the average population strategy converges to the value $x(1)$, which is, locally, the furthest possible from the ESS (see the text).

For $p_1^* < p < \hat{p}$ we have $x(p) > x^*$ and $p < \hat{p}$, hence $[x(p) - x^*](p - \hat{p}) < 0$, and the value p is time-decreasing on this interval.

For $\hat{p} < p < 1$ we have $x(p) > x^*$ and $p > \hat{p}$, hence $[x(p) - x^*](p - \hat{p}) > 0$, and the value p is time-increasing on this interval.

It follows that in this case both the genotypic values $p = p_1^*$ and $p = 1$ are stable, hence the ESS value $x^* = x(p_1^*)$ is phenotypically stable, but not globally so: when starting with a frequency $p > \hat{p}$, the allele A_1 is bound to become fixed in the population, and the average-population-strategy converges to the value $x(1) > x^*$ which is the locally furthest possible from the ESS.

In case (VII) (see Fig. 7) the ESS x^* is not accessible. $x(p) > x^*$ for all $0 \leqslant p \leqslant 1$, hence $[x(p) - x^*](p - \hat{p}) < 0$ for $p < \hat{p}$, and $[x(p) - x^*](p - \hat{p}) > 0$ for $p > \hat{p}$. It follows that in this case there are two stable genetic equilibria, $p = 0$ and $p = 1$, both locally minimizing the distance to the genetically inaccessible ESS x^*.

3.1. Conclusion

We have assumed a one locus, two allele, random-mating, diploid population, subject to a weak frequency-dependent viability-selection due to a two-strategy population-game Ω with a mixed (hence unique) ESS $0 < x^* < 1$. Assuming the most general genotype-to-phenotype mapping within this structure, the ESS x^* may or may not be accessible as an average population strategy. Our analysis thus leads to three results, summarized by the following three propositions:

Proposition 2. *If the ESS x^* is accessible by the genotype-to-phenotype mapping, then the ESS is phenotypically stable*
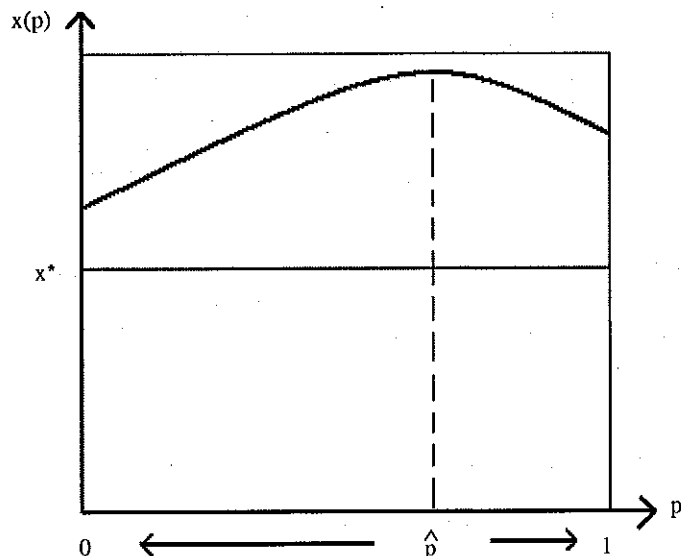

Fig. 7. The ESS x^* is genetically inaccessible. Both the gene frequencies $p = 0$ and 1, rendering the average population strategy, locally, the closest possible to the ESS, are stable (see the text).

in the sense that there is at least one (sometime two) stable genetic equilibrium p^* for which $x(p^*) = x^*$.

Proof. Among the seven cases analyzed above, the ESS is genetically accessible only in cases (II), (V) and (VI). In all the three cases, our analysis indicated the existence of a stable genetic equilibrium p^* for which $x(p^*) = x^*$. ☐

Proposition 3. *The ESS x^*, even if accessible by the genotype-to-phenotype mapping, may not be globally stable: for a well defined, non-empty range of parameters, the dynamics of the population-genetics allows, in addition to a stable genetic equilibrium p^* with $x(p^*) = x^*$, another, "non-phenotypic" stable genetic equilibrium, corresponding to a "non-ESS" average population strategy.*

Proof. In case (VI), analyzed above, the ESS x^* is accessible, but $p = 1$ was shown to be a stable genetic equilibrium with $x(1) \neq x^*$. Employing equalities (6) and (7), one can easily verify that this case corresponds to the non-degenerate range of parameters for which $x_{11} < 2x_{12} > x_{22}$ and $x_{11}(v_{12} - v_{11} + v_{21} - v_{22}) > v_{12} - v_{22} > x_{22}(v_{12} - v_{11} + v_{21} - v_{22})$. ☐

Proposition 4. *If the ESS x^* is inaccessible by the genotype-to-phenotype mapping, then the average population strategies which are locally closest to the ESS are phenotypically stable: The genetic frequencies that determine them are locally stable.*

Proof. This is indicated by the analysis of the cases (I), (III), (IV), and (VII) above, which are those for which the ESS is not accessible by the genotype-to-phenotype mapping. ☐

The results of Propositions 2 and 4 are already known to hold for any number of alleles (Eshel, 1982). The result of Proposition 3 is new, and it can easily be generalized to any number of (specifically chosen) alleles (e.g. assume a two-allele genetic system, corresponding to case VI, and introduce a third allele that is deleterious when the average population strategy is close to either x^* or $x(0)$). Note, though, that a result similar to that of Proposition 3 cannot hold, either in one or in two locus systems, if we allow a small flux of random mutations of all sorts. In this case, long-term convergence to the ESS was shown to occur in probability one (Eshel and Feldman, 2001; Eshel et al., 1998).

Appendix A. The no-penetrance case $x_{11} - 2x_{12} + x_{22} = 0$

One can easily verify that in the case $x_{11} - 2x_{12} + x_{22} = 0$, (1) becomes $x(p) = px_{11} + qx_{22}$, and (4) then yields:

$$\text{sign}[p' - p] = \text{sign}[v(x_{11}, x(p)) - v(x_{12}, x(p))]. \qquad (A.1)$$

But since x^* is a mixed ESS, we know that for any $x \neq x^*$, $v(x, x) < v(x^*, x)$, hence $v(y, x)$ (being a linear function of y) is a decreasing function of y if $x > x^*$, and an increasing function of y if $x < x^*$.

Without loss of generality, assume $x_{11} > x_{12}$ (otherwise just exchange the indexes of the two pure strategies). In this case, if $x(p) > x^*$, then $v(x_{11}, x(p)) < v(x_{12}, x(p))$, and it follows from (A.1) that $p' < p$. In the same way, if $x(p) < x^*$, then $p' > p$. But the assumption $x_{11} > x_{12}$, together

with $x_{11} - 2x_{12} + x_{22} = 0$, implies also $x_{12} > x_{22}$, and it follows from (1) that $x(p)$ is then an increasing function of p. This implies that if $x(p) > x^*$, then (since $p' < p$) $x(p') < x(p)$, and if $x(p) < x^*$, then $x(p') > x(p)$. In either case, natural selection always shifts $x(p)$ in the direction of the mixed ESS, genetically accessible or not.

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