

When will a sexual population evolve to an ESS?

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A diploid, Mendelian population is considered in which m alleles at a single autosomal locus uniquely determine the phenotype of each individual. In the population, a game-theoretical conflict is supposed. If the genetic system is able to uniquely realize the phenotypic evolutionarily stable strategy (ESS) state, then the sexual population will evolve to this ESS.

Keywords: ESS; ESAD; sexual population; phenotypic evolution; one-locus, m -allele system; allele dynamics

1. INTRODUCTION

The notion of an evolutionarily stable strategy (ESS), introduced by Maynard Smith & Price (1973), describes the terminal state of phenotypic evolution. A phenotype frequency vector $q^* \in S_n$ is called an ESS if the following two conditions are satisfied: (i) the equilibrium condition

$$q^* \mathbf{A} q^* \geq q \mathbf{A} q^* \text{ for all } q \in S_n,$$

and (ii) the stability condition

$$\text{if } q \in S_n, q \neq q^* \text{ and } q^* \mathbf{A} q^* = q \mathbf{A} q^*, \text{ then } q^* \mathbf{A} q > q \mathbf{A} q,$$

where $\mathbf{A} \in \mathbf{R}^{n \times n}$ is the phenotypic pay-off matrix. This definition primarily concerns asexual populations. As a matter of fact, the ESS is a purely phenotypic concept.

Maynard Smith (1981) also raised the following question: will a sexual population evolve to an ESS? As an answer he gave both positive and negative examples. This problem has been discussed widely in the literature; for an overview, see Cressman *et al.* (1996), Weissing (1996) and Garay & Varga (1998). Maynard Smith's problem also motivates the main question of this paper. Under what conditions does a sexual population evolve phenotypically to an ESS?

This question was also studied by Cressman *et al.* (1996) for the case when the behavioural phenotypes are genetically and uniquely determined by a one-locus, m allele, panmictic Mendelian model. In the zygote population, a game-theoretical conflict was supposed. Their main result is a sufficient condition for a sexual population to evolve into an ESS. Whereas they obtained this result from the study of allele dynamics, we will start out from the principle of uninvasibility.

2. EVOLUTIONARILY STABLE ALLELE DISTRIBUTION PROVIDING AN ESS

Garay & Varga (1998) defined the concept of an evolutionarily stable allele distribution (ESAD) based on the

uninvasibility principle for a population considered by Cressman *et al.* (1996). ESAD is the counterpart of the phenotypic ESS for allele distributions. For simplicity, the considered locus is supposed to be non-pleiotropic. Now, from Garay & Varga (1998) we briefly recall some definitions, notations and results. The elements of the simplex S_m are considered as allele distributions. For vectors $x, z \in S_m$ we have introduced their dyadic (Kronecker) product as

$$\underline{xz} := (x_1 z_1, x_1 z_2, \dots, x_1 z_m, x_2 z_1, x_2 z_2, \dots, x_2 z_m, \dots, x_m z_1, \dots, x_m z_m).$$

This vector obviously describes the genotype distribution of zygotes, obtained by random mating of two gametes coming from populations with respective allele distributions x and z . This random trial will be called an $x | z$ mating, termed inhomogeneous if $x \neq z$. The dyadic product is bilinear and not symmetric.

Let us suppose that each genotype $A_i A_j$ uniquely determines a behavioural phenotype $s_{ij} \in S_n$ (a mixture of n 'pure' phenotypes). Let

$$\mathbf{S} = (s_{11}, s_{12}, \dots, s_{1m}, s_{21}, s_{22}, \dots, s_{2m}, \dots, s_{m1}, s_{m2}, \dots, s_{mm}) \in \mathbf{R}^{n \times m^2}$$

be the matrix composed from the vectors s_{ij} as columns. In \mathbf{S} , two kinds of information are coded: the possible fixed individual phenotypes and the genotype-phenotype correspondence.

Example 1. Consider a two-allele system in which the first (second) pure strategy is the phenotype of the homozygote $A_1 A_1$ ($A_2 A_2$), and A_1 is dominant to A_2 . Then

$$\mathbf{S} = \begin{pmatrix} 1 & 1 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}.$$

\mathbf{S} will also denote the so-called hereditary system function, defined as

$$\mathbf{S}: S_m \times S_m \rightarrow S_n \quad \mathbf{S}x\underline{z}: = \sum_{ij} x_i z_j s_{ij} \in S_n,$$

where $x, z \in S_m$ are allele distributions. The biological meaning of $\mathbf{S}x\underline{z}$ is the phenotype distribution of a zygote population resulting from an $x | z$ mating. In case of a homogeneous $x | x$ mating, $\mathbf{S}x\underline{x}$ provides the phenotype distribution of a sexual population in a Hardy–Weinberg genetic equilibrium. In Mendelian populations, obviously $\mathbf{S}x\underline{z} = \mathbf{S}z\underline{x}$, for all $x, z \in S_m$.

Now we recall the definition of ESAD in phenotypic form.

Definition 1. An allele distribution $p^* \in S_m$ is called an ESAD if for all $p \in S_m, p \neq p^*$ there exists $\epsilon_p > 0$ such that, for all $0 < \epsilon < \epsilon_p$, we have

$$(\mathbf{S}p^*x)\mathbf{A}(\mathbf{S}x\underline{x}) > (\mathbf{S}p\underline{x})\mathbf{A}(\mathbf{S}x\underline{x}), \tag{1}$$

where $x = (1 - \epsilon)p^* + \epsilon p$.

The biological meaning of the ESAD is as follows: the average fitness of a zygote subpopulation resulting from an inhomogeneous $p^* | x$ mating is greater than that of a zygote subpopulation coming from a $p | x$ mating, provided both subpopulations play against the whole zygote population obtained by an $x | x$ mating. (Here x is the perturbed allele distribution.)

The formalization used in inequality (1) seems biologically very natural from the following considerations. First, a selection with pay-off matrix \mathbf{A} is carried out at zygote level. Second, the dyadic product is appropriate to handle both the inhomogeneous and the homogeneous matings. Third, the matrix \mathbf{S} codes the hereditary system. Furthermore, the formalism of inequality (1) will also be used in the formulation of the main result of this paper.

From the viewpoint of the dynamical theory of evolution, the ESAD is an analogue of the concept of ESS, as we have the following.

Theorem 1. Any ESAD is an asymptotically stable equilibrium point of the replicator dynamics of the alleles. (For a proof, see Appendix A.)

This theorem has been proved in Garay & Varga (1998) for an interior ESAD; for a non-interior ESAD, the Lyapunov function technique used in Hofbauer & Sigmund (1988) applies without difficulty.

Now we turn to the main problem of our paper: when will an ESS correspond to the phenotypic image of an ESAD? For this, two sufficient conditions will be given below.

Proposition 1. Let us suppose that for some ESS $q^* \in S_n$, the hereditary system function \mathbf{S} satisfies the following two conditions: (i) there exists $p^* \in S_m$, with $\mathbf{S}p^*p^* = q^*$, and (ii) if $p \in S_m, p \neq p^*$, then $\mathbf{S}pp^* \neq q^*$. Then p^* is an ESAD. (For a proof, see Appendix A.)

The above condition (i) posed on the hereditary system means that it is able to realize the ESS phenotypically at a Hardy–Weinberg equilibrium. Condition (ii) requires that the phenotype distribution of zygotes resulting from an inhomogeneous $p^* | p$ mating is not the ESS q^* .

Remark 1. A geometrical reformulation of conditions (i) and (ii) may be the following. Denote by $\mathbf{F} \in \mathbf{R}^{n \times m}$ an $n \times m$ matrix satisfying $\mathbf{S}pp^* = \mathbf{F}p$ for all $p \in S_m$, and let M be the (convex) cone generated by the vectors pointing from p^* into S_m :

$$M := \{z \in \mathbf{R}^m \mid \exists \lambda_0 \in \mathbf{R}^+, \forall \lambda \in]0, \lambda_0[. p^* + \lambda z \in S_m\}.$$

It is easy to see that conditions (i) and (ii) are satisfied simultaneously if and only if the transversality condition $\text{Ker}\mathbf{F} \cap M = \{0\}$ is fulfilled.

The above condition is closely related to the linear independence condition of theorem 4.1 in Cressman *et al.* (1996). In the case of an interior ESS, both conditions are equivalent. A slight difference between them is illustrated by the following.

Example 2. Let us suppose that $e_1 \in S_3$ is a pure ESS, and consider the following hereditary system (genotype–phenotype correspondence): $A_1A_1 \rightarrow e_1$, $A_2A_2 \rightarrow e_2$, $A_3A_3 \rightarrow e_3$ and $A_iA_j \rightarrow e_1 (i \neq j)$. Then we easily obtain that

$$\mathbf{F} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 1 & 1 \end{pmatrix},$$

and proposition 1 applies: $\text{Ker}\mathbf{F}$ consists of the multiples of the vector $(0, 1, -1)$. Clearly, $\text{Ker}\mathbf{F} \cap M = \{0\}$, implying that the population containing only A_1 alleles is at an ESAD. Therefore, by theorem 1 the sexual population evolves into the ESS.

Based on proposition 1, another type of uniqueness is required in the following.

Theorem 2. Let us suppose that for some ESS $q^* \in S_n$, the hereditary system function \mathbf{S} satisfies the following conditions: there exists a unique $p^* \in S_m$ with $\mathbf{S}p^*p^* = q^*$. Then p^* is an ESAD. (For a proof, see Appendix A.)

The above uniqueness condition means that only one allele distribution is able to realize the ESS phenotypically at a Hardy–Weinberg equilibrium.

Remark 2. Either proposition 1, or theorem 2 combined with theorem 1, guarantee that, according to the replicator dynamics of the alleles, the sexual population evolves phenotypically to an ESS.

3. CONCLUSION

The Darwinian principle of uninvadability turned out to be very insightful. It led to concepts of ESS and ESAD, also making it possible to describe the phenotypic evolution of a sexual population in a rather simple way.

Our results, and those of Cressman *et al.* (1996), enable us to reformulate Cressman *et al.*'s conjecture in our different mathematical context: if the hereditary system is able to realize the ESS phenotypically, then the sexual population necessarily evolves to an allele distribution that provides this ESS phenotypically. The intuitive background of this conjecture is the following. Consider a population that is in a genetical equilibrium but not an ESS. It follows that a subpopulation that is not only in a genetical equilibrium, but is also an ESS, will have an average fitness greater than that of the whole population. This seems to imply (local) asymptotic stability of an evolutionarily stable state. A proof of the above conjecture needs a thorough analysis of the case of genetic redundancy (meaning a multiple genetic realization of the ESS).

APPENDIX A

Proof of theorem 1. Let us follow the proof of the theorem in 16.4 of Hofbauer & Sigmund (1988). There it is shown that the function

$$P(x) = \prod_{i=1}^m x_i^{p_i^*} \quad (x \in S_m)$$

has a strict maximum at the point p^* . Hence, $P - P(p^*)$ is negative definite with respect to p^* .

Let $x \in S_n, x \neq p^*$ be such that $x_i > 0$ for all i with $p_i^* > 0$. Then $P(x) > 0$. Denote by f the right-hand side of the above dynamics. Then, setting $0 \log 0 = 0 \log \infty = 0$, for the derivative $D(P - P(p^*))$ with respect to this dynamics we have $D(P - P(p^*)) = DP$, and

$$\begin{aligned} \frac{DP(x)}{P(x)} &= \langle (\log \circ P)'(x), f(x) \rangle \\ &= \sum_{i=1}^m p_i^* \log'(x_i) x_i [(\mathbf{S}e_i x) \mathbf{A}(\mathbf{S}xx) - (\mathbf{S}xx) \mathbf{A}(\mathbf{S}xx)] \\ &= (\mathbf{S}p^* x) \mathbf{A}(\mathbf{S}xx) - (\mathbf{S}xx) \mathbf{A}(\mathbf{S}xx). \end{aligned}$$

Because p^* is an ESAD, by theorem 2 of Garay & Varga (1998),

$$(\mathbf{S}p^* x) \mathbf{A}(\mathbf{S}xx) - (\mathbf{S}xx) \mathbf{A}(\mathbf{S}xx) > 0,$$

provided $x \in S_m$ belongs to a certain neighbourhood of p^* and $p^* \neq x$. This means that $P - P(p^*)$ is a strict local Lyapunov function of the replicator dynamics. ■

Proof of proposition 1. We shall use the following equalities based on the bilinearity of the dyadic product: if $p, p^* \in S_m$ and $x = (1 - \epsilon)p^* + \epsilon p$ with some $\epsilon \in]0, 1[$, then

$$\begin{aligned} xx &= (1 - \epsilon)p^* x + \epsilon p x = p^* x + \epsilon(p - p^*)x \\ &= p^* p^* + \epsilon p^*(p - p^*) + \epsilon(p - p^*)p^* + \epsilon^2(p - p^*)(p - p^*). \end{aligned} \quad (\text{A1})$$

1. Let us suppose that in the equilibrium condition the inequality is strict:

$$q^* \mathbf{A}q^* > q \mathbf{A}q^* \quad \text{for all } q \in S_n, q \neq q^*.$$

(This means that q^* is a pure ESS.) Then by the conditions (i) and (ii) of proposition 1, p^* is an ESAD. By using equality (A2) it is easy to see that inequality (1) can be written in the following form:

$$\begin{aligned} &[\mathbf{S}(p^* - p)p^*] \mathbf{A}[\mathbf{S}p^* p^*] \\ &+ \epsilon[\mathbf{S}(p^* - p)p^*] \mathbf{A}[\mathbf{S}(p^*(p - p^*) + (p - p^*)p^*)] \\ &+ \epsilon[\mathbf{S}(p^* - p)(p - p^*)] \mathbf{A}[\mathbf{S}p^* p^*] \\ &+ \epsilon^2[\mathbf{S}(p^* - p)p^*] \mathbf{A}[\mathbf{S}(p - p^*)(p - p^*)] \\ &+ \epsilon^2[\mathbf{S}(p^* - p)(p - p^*)] \mathbf{A}[\mathbf{S}(p^*(p - p^*) + (p - p^*)p^*)] \\ &+ \epsilon^3[\mathbf{S}(p^* - p)(p - p^*)] \mathbf{A}[\mathbf{S}(p - p^*)(p - p^*)] > 0. \end{aligned} \quad (\text{A2})$$

Hence, ϵ_p can be chosen with the property required in the definition of ESAD.

2. Now, let us suppose that

$$q^* \mathbf{A}q^* = q \mathbf{A}q^* \quad \text{for all } q \in S_n,$$

and

$$q^* \mathbf{A}q > q \mathbf{A}q \quad \text{for all } q \in S_n, q \neq q^*.$$

(This means that q^* is an interior ESS.) In the literature the following reformulation is well-known (see Haigh 1975): q^* is an interior ESS if and only if

$$\mathbf{A}q^* = \lambda \mathbf{1} \quad \text{with some } \lambda \in \mathbf{R}, \text{ where } \mathbf{1} = (1, 1, 1, \dots, 1) \in \mathbf{R}^n, \quad (\text{A3})$$

and

$$\xi \mathbf{A} \xi < 0 \quad \text{for all } \xi \in \mathbf{R}^n \text{ with } \xi \neq \mathbf{0} \text{ and } \sum_i \xi_i = 0. \quad (\text{A4})$$

Using equation (A1) it is easily seen that inequality (1) is equivalent to the following two conditions:

$$[\mathbf{S}(p^* - p)x] \mathbf{A}[\mathbf{S}p^* x] \geq 0, \quad (\text{A5})$$

and if equality holds for some $p \neq p^*$ in relation (A5), then

$$[\mathbf{S}(p^* - p)x] \mathbf{A}[\mathbf{S}(p^* - p)x] < 0. \quad (\text{A6})$$

Obviously, the sum of the coordinates of the n -dimensional vector $\mathbf{S}(p^* - p)p^*$ is zero. Thus, because q^* is an interior ESS, statement (A4) implies inequality (A6). Therefore, it is enough to consider condition (A5), which reads

$$(1 - \epsilon)[\mathbf{S}(p - p^*)x] \mathbf{A}[\mathbf{S}p^* p^*] + \epsilon[\mathbf{S}(p - p^*)x] \mathbf{A}[\mathbf{S}p^* p] < 0. \quad (\text{A7})$$

Because $\mathbf{S}p^* p^* = q^*$ is an interior ESS, from statement (A3) the first member in equation (A7) is zero. Furthermore, $\epsilon > 0$, so the inequality

$$[\mathbf{S}(p - p^*)] \mathbf{A}[\mathbf{S}p^* p] < 0 \quad (\text{A8})$$

also holds. Inequality (A8) is equivalent to the following two conditions:

$$[\mathbf{S}(p - p^*)p^*] \mathbf{A}[\mathbf{S}p^* p] \leq 0, \quad (\text{A9})$$

and if equality holds for some $p \in S_m, p \neq p^*$ in condition (A9), then

$$[\mathbf{S}(p - p^*)p] \mathbf{A}[\mathbf{S}p^* p] < 0. \quad (\text{A10})$$

Because for a Mendelian population we have $\mathbf{S}p p^* = \mathbf{S}p^* p$, by the stability condition of the definition of an ESS, in relation (A9) a strict inequality holds. Hence, ϵ_p can be chosen with the required property.

3. Finally, suppose that for the considered ESS, in the equilibrium condition equality holds only for the vectors q of a proper subset of the simplex. This subset is a face of the simplex containing q^* in its interior. Then the reasoning of case 2 applies within this face. For the complement of this face case 1 can be applied. ■

In the proof of theorem 2 we use the following.

Remark 3. Let $\mathbf{F} \in \mathbf{R}^{n \times m}$ denote a matrix for which $\mathbf{S}p p^* = \mathbf{F}p$ for all $p \in S_m$. An easy calculation shows that

$$\text{Ker } \mathbf{F} \subset T := \{\xi \in \mathbf{R}^m \mid \sum_i \xi_i = 0\}.$$

Proof of theorem 2. If $\text{Ker}\mathbf{F} = \{0\}$, then proposition 1 implies our assertion. Suppose that $\text{Ker}\mathbf{F} \neq \{0\}$. Then for any $\xi \in \text{Ker}\mathbf{F}$ with $p: = (p^* + \xi) \in S_n$, from remark 3 we easily obtain

$$\mathbf{F}p = \mathbf{S}p^* = q^*. \quad (\text{A11})$$

Let us now follow the scheme of the proof of proposition 1.

1. Suppose that p^* is a pure ESS. Then by relation (A11) the first and second members in inequality (A2) are equal to zero. Because the population is Mendelian and q^* is a pure ESS, from equation (A11) for the third member of equation (A2) we get

$$\begin{aligned} [\mathbf{S}(p^* - p)(p - p^*)]\mathbf{A}[\mathbf{S}p^*p^*] &= [\mathbf{S}p^*p - p^*p]\mathbf{A}[\mathbf{S}p^*p^*] \\ &= [\mathbf{S}p^*p^* - p^*p]\mathbf{A}[\mathbf{S}p^*p^*] > 0, \end{aligned}$$

implying the existence of the required ϵ_p .

2. Suppose now that q^* is an interior ESS. Then relation (A11) implies that equality holds in both (A9) and (A10). Therefore, we have equality in relation (A5) too.

Thus, inequality (A6) implies that with some $\epsilon_p > 0$, the requirement of the definition of an ESAD is satisfied.

3. In the case when q^* belongs to a subsimplex, a combination of the above two reasonings applies. ■

REFERENCES

- Cressman, R., Hofbauer, J. & Hines, W. G. S. 1996 Evolutionary stability in strategic models of single-locus frequency-dependent viability selection. *J. Math. Biol.* **34**, 707–733.
- Garay, J. & Varga, Z. 1998 Evolutionarily stable allele distributions. *J. Theor. Biol.* (In the press.)
- Haigh, J. 1975 Game theory and evolution. *Adv. Appl. Prob.* **7**, 8–11.
- Hofbauer, J. & Sigmund, K. 1988 *The theory of evolution and dynamical systems*. Cambridge University Press.
- Maynard Smith, J. 1981 Will a sexual population evolve to an ESS? *Am. Nat.* **117**, 1015–1018.
- Maynard Smith, J. & Price, G. R. 1973 The logic of animal conflict. *Nature* **246**, 15–18.
- Weissing, F. J. 1996 Genetic versus phenotypic models of evolution: can genetics be neglected in long-term perspective? *J. Math. Biol.* **34**, 533–555.