Evolutionarily Stable Strategies
and Viability Selection in Mendelian Populations

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For various genetical structures, including haploid and diploid, one-locus n-alleles, and n-locus additive viability random mating models, natural selection resulting from intrapopulation conflicts between random individuals leads to exactly those genetical equilibria which determine a mixture of strategies evolutionarily stable according to the game theory definition of Maynard Smith and Price (1973).

1. INTRODUCTION

The concept of evolutionarily stable strategy (ESS) has been introduced by Maynard Smith and Price (1973) to characterize a strategy with the property that when adopted by a large enough majority in the population becomes the choice for each individual in that population, in the sense that it then maximizes the expected *fitness* or *survival* of its chooser. Once such a strategy has been established, it seems likely to be stable in a parthenogenetical population (Maynard Smith, 1974, 1976). A crucial question to be settled is whether natural selection, operating within the framework of known genetical structures does lead to the establishment and stabilization of ESSs, or strategies close to them (Lloyd, 1977; Maynard Smith, 1981). Concentrating on the simplest ESS problem of two alternative strategies in a population, this study is conducted under a wider assumption on the possible genetical basis for the choice of a strategy by a given individual. Indeed, a strategy in this sense may not necessarily be a behavioral pattern. It may be any phenotypic trait which affects the outcome of a conflict between individuals in the population.

For a class of genetical structures, namely locally adaptive ones, it is shown that all stable equilibria maintained by the system determine either fixation or mixture of strategies which are ESSs. The class of locally adaptive systems, for which this result holds, is shown to include all one-

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locus n-alleles, random mating viability models of a diploid population, but also other structures of genetic transmission of strategies. With some restriction on the intensity of the selection forces within this class of genetic structures it is shown further that any ESS corresponds to some stable equilibrium.

2. Evolutionary Stability and Convergence of Genotype Frequencies

Consider a large population in which any individual can choose one out of n strategies, say $S_1,...,S_n$. Let $x_j \geqslant 0$ be the proportion of individuals choosing the strategy S_j before selection ($j = 1,..., n$); and assume that the result of a given encounter confers an incremental or decremental fitness (say, viability) of v_{ij} to an individual following the strategy S_i, whose opponent practises the strategy $S_j(i,j = 1, 2,..., n)$. Thus, $V = \|v_{ij}\|$ can be construed as a population game matrix. Assuming random encounter between individuals in the population (for different assumptions see Cavalli-Sforza and Eshel, 1982), the expected change in fitness of an individual with the strategy S_i due to a random encounter is $\sum_j x_j V_{ij}$. The expected fitness of an individual, choosing the strategy S_i, is, therefore, proportional to

$$u_i(x) = 1 + \theta \sum_j V_{ij}x_j = \sum_j a_{ij}x_j = (Ax)_i, \qquad (2.1)$$

where $\theta > 0$ is up to a scale factor of the expected number of encounters for individuals per generation and we use the abbreviation $a_{ij} = 1 + \theta V_{ij}$.

If an individual employs a mixed strategy $y = (y_1,..., y_n)$, where y_i is the probability of him choosing the strategy S_i while population strategy is x his expected fitness is

$$V(x, y) = \sum_i y_i u_i(x) = \sum_{ij} y_i a_{ij}x_j = yAx. \qquad (2.2)$$

Within this framework, the formal definition of ESS suggested by Maynard Smith (1974) and further refined by Bishop and Cannings (1976) is as follows:

A strategy y is an ESS if for any strategy $x \neq y$,

$$V(y, y) \geqslant V(x, y) \qquad (2.3)$$

and if (2.3) holds as an equality, then

$$V(y, x) > V(x, x). \qquad (2.4)$$

Condition (2.3) guarantees that the strategy x will not be advantageous

when adopted by a single deviant individual. Condition (2.4) guarantees that if the strategy x is not disadvantageous at that stage, it will become disadvantageous when slightly accumulated. A version of the Nash theorem for symmetric games guarantees the existence of a strategy x satisfying (2.3) (namely, a symmetric *Nash solution* of the population game). There is no guarantee that an ESS exists for a given population game. In this work we see, however, that an ESS always exists in a 2×2 population game.

We now assume that the choice of a given strategy by an individual in a population depends, at least in a probabilistic way, on the genotype of the individual. We concentrate on the simplest situation where $k = 2$, i.e., each individual has exactly two possible strategies, S_1 and S_2, but there are m genotypes, $B_1, B_2,..., B_m$. Let p_i be the frequency of the genotype B_i among juveniles at a given generation and let h_i be the probability that an individual of genotype B_i will choose the strategy S_1.

The frequency of individuals choosing the strategy S_1 in the population will then be

$$x = x(\mathbf{p}) = \sum_{i=1}^{n} p_i h_i. \tag{2.5}$$

For convenience we speak of population strategy $0 \leqslant x \leqslant 1$ when we mean that fraction x of the population adopts strategy S_1 and the remaining fraction $1 - x$ uses strategy S_2.

The average fitness $u_1(x)$ of an individual choosing strategy S_1 where a proportion x in the population adopts strategy S_1 in this population is given by (2.1) and the fitness of the genotype B_i in this situation is

$$w_i = w_i(x) = h_i u_1(x) + (1 - h_i) u_2(x). \tag{2.6}$$

Assuming mating according to some given rule, appropriate segregation (depending on the structure of genotypes $B_1,..., B_m$) and natural selection with the frequency-dependent coefficient (2.6), one can calculate the frequencies $p'_1,..., p'_n$ of the relevant genotypes in the next generation.

For example, in a one-locus random mating diploid model with n alleles, if h_{ij} is the probability that an individual of genotype $A_i A_j$ will choose the strategy S_1, $p_1,..., p_n$ are the allelic frequencies at a given generation, then by the Hardy–Weinberg law,

$$x = \sum_{ij} p_i p_j h_{ij}. \tag{2.7}$$

(Note that both the p_i's and x are measured before selection.) After selection and random mating we, therefore, have

$$p'_i = \frac{p_i \sum_j p_j w_{ij}(x)}{\sum_{kj} p_k p_j w_{kj}(x)}, \tag{2.8}$$

where, following (2.6), the $w_{ij}(x)$ are given by $w_{ij}(x) = h_{ij}u_1(x) + (1 - h_{ij})u_2(x)$. At this point, a traditional population geneticist would focus on the stable fixed points $\hat{\mathbf{p}}$ of transformation (2.8). An animal-conflict-oriented population biologist would emphasize the population strategy

$$\hat{x} = \hat{x}(\mathbf{p}) = \sum_{i=1}^{n} h_i\, p_i \tag{2.9}$$

coresponding to each stable equilibrium. Sometimes, information about the population strategy $\hat{x} = x(\hat{p})$ is much easier to obtain than direct information about $\hat{p}$. Moreover, the population strategies $\hat{x}(\hat{p})$, corresponding to the stable genetical equilibria, do not depend on the specific genetical system except for the obvious restriction on the range of possible strategies allowed by the system, namely,

$$\lambda \leqslant \hat{x} \leqslant \mu \qquad (0 \leqslant \lambda < \mu \leqslant 1) \tag{2.10}$$

where

$$\lambda = \min_{\mathbf{p} \in \Delta^n} \sum_{ij} p_i h_{ij}\, p_j \tag{2.11}$$

$$\mu = \max_{\mathbf{p} \in \Delta^n} \sum_{ij} p_i h_{ij}\, p_j \tag{2.12}$$

and Δ^n is the space of probability n-vectors.

A relevant ESS value should therefore, be defined in terms of the game matrix $\|V_{ij}\|$ and restriction (2.10) on the choice of strategies.

Following Bishop and Cannings, we have

DEFINITION. A strategy $\lambda \leqslant x \leqslant \mu$ is an ESS of the population game $\|V_{ij}\|$ with the restriction $\lambda \leqslant y \leqslant \mu$ on the choice of a strategy y (namely, an ESS of the *restricted game*) if for any $y \neq x$ with that *restriction*, conditions (2.3)–(2.4) hold.

Our objective now is to determine a structure under which the population strategies (2.9), determined by the stable genetical equilibria will be the ESSs of the restricted population game.

3. LOCALLY ADAPTIVE SYSTEMS

In order to emphasize the main concepts and methods it is convenient to describe the dynamics of the two-strategy population game in a general setting which includes the examples of (2.8)..

Consider a 2×2 population game $\|V_{ij}\|$. To avoid degeneracies, we assume

$$V_{11} - V_{12} - V_{21} + V_{22} \neq 0. \qquad (3.1)$$

Generally, consider that the proportion x of individuals in the population choosing the strategy S_1 may depend on a number of parameters $p_1, ..., p_n$, with the vector $\mathbf{p} = (p_1, ..., p_n)$ belonging to some compact set (e.g., $\mathbf{p}$ are probability vectors belonging to the simplex).

In a formal way

$$x = \phi(\mathbf{p}). \qquad (3.2)$$

For technical convenience, we assume that ϕ has all continuous derivatives and that these derivatives are not all identically zero on any open set of ϕ.

Finally, it is assumed that the parameters P_i $(i = 1, ..., n)$ change over successive generations to the new values p_i' determined by the parameters $\mathbf{p}$ of the first generation and the values $u_1(x)$ and $u_2(x)$, the game matrix corresponding to the population strategy $x(\mathbf{p})$ (cf. (2.1)): Formally,

$$p_i' = f_i(\mathbf{p}, u_1, u_2) = f_i(\mathbf{p}, u_1(\phi(\mathbf{p})), u_2(\phi(\mathbf{p})))]$$
$$= F_i(p), \qquad \text{say} \quad (i = 1, 2, ..., n). \qquad (3.3)$$

The frequency of individuals choosing the strategy S_1 in the next generation is, therefore,

$$x' = \phi(\mathbf{p}'). \qquad (3.4)$$

We are interested in a structure for which iteration of (3.3) converges to a stable vector $\hat{\mathbf{p}}$, the induced population strategy $\phi(\hat{p})$ of which is always an ESS of the restricted game. We show that this structure includes the one-locus n-allele random mating diploid system as a special case.

DEFINITION. The system (3.2)–(3.3) associated with the game matrix $\|a_{ij}\|$ and possibly with the restriction $\lambda \leqslant x \leqslant \mu$ on the choice of strategies is called a locally adaptive system with respect to the (restricted) game if for all $\mathbf{p} \in \Gamma$ i.e., $\mathbf{p}$ is a strictly positive frequency vector with $\lambda < x = \phi(\mathbf{p}) < \mu$,

$$\begin{aligned} x' > x \qquad & \text{if} \quad u_1(x) > u_2(x) \\ x' < x \qquad & \text{if} \quad u_1(x) < u_2(x) \end{aligned} \qquad (3.5)$$

or equivalently

$$\text{sign}\{\phi(\mathbf{p}') - \phi(\mathbf{p})\} = \text{sign}\{u_1(\phi(\mathbf{p})) - u_2(\phi(\mathbf{p}))\}. \qquad (3.6)$$

In this case, the transformation (3.3) is also said to be locally adaptive. This means that at any step the change $p \to p'$ in the population parameters results in an increase in the frequency of individuals practising the strategy that was advantageous at the time of the change. Note, however, that in the context of frequency-dependent selection, imposed by the viability game $\|a_{ij}\|$ on a given genetical structure, the condition (3.5) for local adaptivity of the system does not imply an increase in the average fitness $xu_1(x) + (1 - x) u_2(x)$ of the population, since $u_1(x)$ and $u_2(x)$ also change with x.

From arguments of continuity, it follows that for any adaptive system, inequality (3.5) holds, at least in a weak sense, at the boundaries $x = \lambda$ or $x = \mu$, and also

$$x' = x \qquad \text{if} \quad u_1(x) = u_2(x). \tag{3.7}$$

EXAMPLE 1. *A one-locus haploid model.* $p_1,...,p_n$ are the frequencies of the types $A_1,..., A_n$ in the population. h_i is the probability that an individual of type A_i $(i = 1, 2,..., n)$ will choose the strategy S_1. This is the only difference between types, thus we assume $h_i \neq h_j$ for all $i \neq j$. In this example, for any probability vector $\mathbf{p} \in S^n$

$$x = \phi(\mathbf{p}) = \sum_{i=1}^{n} p_i h_i, \tag{3.8}$$

which is obviously differentiable and, with the h_i being different from one another, nonconstant on an open set. We further set

$$\lambda = \min_{i=1,...,n} h_i, \qquad \mu = \max_{i=1,..., n} h_i, \tag{3.9}$$

and

$$f_i(\mathbf{p}, u_1, u_2) = \frac{p_i w_i}{\sum_j p_j w_j} \tag{3.10}$$

where

$$w_j = w_j(x) = h_j u_1(x) + (1 - h_j) u_2(x). \tag{3.11}$$

From (3.8) and (3.10) we obtain

$$x' = \phi(\mathbf{p}) = \frac{\sum h_i w_i p_i}{\sum w_i p_i}. \tag{3.12}$$

Hence, employing (3.8),

$$x' - x = \phi(\mathbf{p}') - \phi(\mathbf{p}) = \frac{\sum w_i h_i p_i - \sum w_i p_i \sum h_i p_i}{\sum w_i p_i}.$$

With (3.11), we have

$$x' - x = \left(\sum p_i w_i\right)^{-1} (u_1 - u_2)\left[\sum_i p_i h^2 - \left(\sum_i p_i h_i\right)^2\right], \quad (3.13)$$

But $\sum p_i h_i^2 > (\sum p_i h_i)^2$ unless the $h_i - s$ are identical, and condition (3.5) for local adaptiveness of the haploid system with respect to any game of individual survival is satisfied.

EXAMPLE 2. *A one-locus, random mating diploid model.* $(p_i,..., p_n) \in S^n$ are the frequencies of alleles in the population. As shown in the previous section

$$x = \phi(\mathbf{p}) = \sum_{ij} p_i p_j h_{ij}. \quad (3.14)$$

λ and μ are given by (2.11) and (2.12), respectively,

$$p_i' = \frac{p_i \sum_i p_j w_{ij}(x)}{\sum_{jk} p_j p_k w_{jk}(x)} \quad (3.15)$$

where

$$w_{ij} = h_{ij} u_1 + (1 - h_{ij}) u_2 = u_2 + (u_1 - u_2) h_{ij}. \quad (3.16)$$

But for any given symmetric matrix $\|w_{ij}\|$ of positive values and p_i' $(i = 1, 2,..., n)$ as determined in (3.15) we know (Kingman, 1961) that

$$\sum_{ij} p_i' p_j' w_{ij} \geqslant \sum_{ij} p_i p_j w_{ij} \quad (3.17)$$

with equality only if $\mathbf{p}' = \mathbf{p}$.

Inserting (3.16) into (3.17), one obtains

$$u_2 + (u_1 - u_2) \sum_{ij} p_i' p_j' h_{ij} \geqslant u_2 + (u_1 - u_2) \sum_{ij} p_i p_j h_{ij}$$

or

$$(u_1 - u_2)(x' - x) \geqslant 0 \quad (3.18)$$

with equality only at equilibrium. This proves condition (3.5) for local adaptivity in respect to games of individual viability.

EXAMPLE 3. *A multilocus, multiallele nonepistatic additive viability model of a randomly mated diploid population.* $B_i,..., B_m$ are the various genotypes allowed by the model; $p_1,..., p_m$ are their relative frequencies in a

given generation. $h_1,..., h_n$ are the probabilities of their choosing the first strategy. $x = \sum p_i h_i$ is, therefore, the population strategy and

$$w_i = w_i(x) = u_2 + (u_1 - u_2) h_i$$

is the viability of the genotype B_i. If the probability h_i is a sum of probabilistic effects, each being determined at a different locus, then the viability $w_i(x)$, determined by h_i and the population strategy, is, at any given generation, additive as well. In this case, we know (Ewens 1969) that with recombination, ransom mating, and selection, the new frequencies p_i' will satisfy the inequality

$$\sum p_i' w_i \geqslant \sum p_i w_i$$

with equality only at equilibrium (the w_i's are those of the previous generation). Again, this inequality is equivalent to

$$(u_1 - u_2)\left(\sum p_i' h_i - \sum p_i h_i\right) = (u_1 - u_2)(x' - x) > 0. \qquad (3.19)$$

Hence, the multilocus, nonepistatic additive model is shown to be locally adaptive with respect to any give of individual survival.

4. STABLE FIXED POINTS OF AN ADAPTIVE SYSTEM AND ESS

THEOREM 1.   *If $\hat{p} \in \text{Int } \Gamma$ (i.e., if $p_i > 0$, $i = 1, 2,..., n$) is a stable polymorphic equilibrium of the locally adaptive transformation (3.3), then $y = \phi(p)$ is an ESS of the game.*

In order to prove this theorem we need the following lemmas about ESS.

LEMMA 1.   *A strategy y satisfy $\lambda \leqslant y \leqslant \mu$ (i.e., a mixture $(y, 1-y)$) is an ESS of the population game if for all $x \neq y$ (within the restrictions $\lambda \leqslant x \leqslant \mu$ of the game)*

$$(y - x)[u_1(y) - u_2(y)] \geqslant 0 \qquad (4.1)$$

and in the case of equality in (4.1)

$$(y - x)[u_1(x) - u_2(x)] > 0. \qquad (4.2)$$

LEMMA 2. (i) *If the edge strategy $y = \lambda$ is an ESS, then at least for some $\varepsilon > 0$ and for all $\lambda < x < \lambda + \varepsilon$,*

$$u_1(x) < u_2(x). \tag{4.3}$$

(ii) *If the edge strategy is not an ESS, then for all $\varepsilon > 0$ there exist at least one $\lambda < x < \lambda + \varepsilon$.*

$$u_1(x) > u_2(x). \tag{4.4}$$

LEMMA 3. (i) *If $\lambda < y < \mu$ is an ESS, then $u_1(y) = u_2(y)$ and (4.2) holds.*

(ii) *If $\lambda < y < \mu$ is not an ESS, then either $u_1(y) \neq u_2(y)$ or $u_1(y) = u_2(y)$ and*

$$(y - x)[u_1(x) - u_2(x)] < 0 \qquad \text{for all} \quad x \neq y. \tag{4.5}$$

LEMMA 4. *For any $\lambda \leqslant y \leqslant \mu$: (i) If $u_1(y) = u_2(y)$ and if for all $0 < |x - y| < \varepsilon$ ($\varepsilon > 0$ small enough), $(x - y)[u_1(x) - u_2(x)] < 0$, then y is an ESS.*

(ii) *If y is an ESS, then $(x - y)[u_1(x) - u_2(x)] < 0$ for all $0 < |x - y| < \varepsilon$.*

The proofs of these lemmas are given in the Appendix.

Proof of Theorem 1. That $\hat{\mathbf{p}}$ is a stable equilibrium of the transformation F, means that for some vicinity S of $\hat{\mathbf{p}}$, $\mathbf{p}^{(n)} = \mathbf{F}^{(n)}(\mathbf{p}^{(0)}) \to \hat{\mathbf{p}}$ for all $\mathbf{p}^0 \in S$. From the continuity of ϕ, $x_n = \phi(\mathbf{p}^{(n)}) \to y = \phi(\hat{\mathbf{p}})$. But from the assumption that ϕ is not constant on any open set we know that for some $p^{(0)} \in S$, $x_0 = \phi(\mathbf{p}^0) \neq y$. For any $\varepsilon > 0$, there is, therefore, n such that $|x_{n+1} - y| < |x_n - y| < \varepsilon$. If $x_n > y$, then $x_{n+1} < x_n$ and, from (3.5), we therefore know that $u_1(x_n) < u_2(x_n)$. If $x_n < y$, then $x_{n+1} > x_n$ and therefore $u_1(x_n) > u_2(x_n)$. In both cases, $(x_n - y)[u_1(x_n) - u_2(x_n)] < 0$. Moreover, since $y = \phi(\hat{\mathbf{p}}) = \phi(F(\hat{p}))$, it follows from (3.5) that $u_1(y) = u_2(y)$. Hence, it follows from Lemma 4 that y is an ESS. ∎

Next is the opposite question: Are all ESSs of the population game stable with respect to the transformation determined by the genetical structure?

DEFINITION. A population strategy x ($\lambda \leqslant x \leqslant \mu$) is said to be stably maintained by the transformation (3.3) if, when the initial population state ϕ determines a population strategy $\phi(\mathbf{P})$ close to x, then the iteration of (3.3) results with convergence of the population strategy to x. In a formal way:

A population strategy $\lambda \leqslant x \leqslant \mu$ is said to be stably maintained by the transformation (3.3) if for small enough $\varepsilon > 0$ and for all $\mathbf{p} \in \Gamma$ for which $|\phi(\mathbf{p}) - x| < \varepsilon$

$$|\phi(\mathbf{F}^{(n)}(\mathbf{p})) - x| \to 0. \tag{4.6}$$

DEFINITION. The transformation F is said to maintain a protected mixture of strategies if neither of the edge strategies is stably maintained by it.

THEOREM 2. (i) *If an edge strategy of a restricted game is an* ESS, *then it is stably maintained by all locally adaptive transformations corresponding to the game.*

(ii) *If a substantially mixed* ESS $\lambda < y < \mu$ *exists, then a protected mixture of strategies is maintained by any locally adaptive transformation* F *corresponding to the population game. Moreover, in this case* F *either stably maintains the mixed strategy* y *or it allows for initially increasing fluctuations around it.*

Proof. (i) Let $y = \lambda$ be an ESS. From Lemma 2 we know that for $\lambda < x < \lambda + \varepsilon$, $u_1(x) < u_2(x)$. Hence, if $\phi(\mathbf{p}) = x$, (3.5) implies that

$$x' = \phi(\mathbf{p}') = \phi(\mathbf{F}(\mathbf{p})) < x. \tag{4.7}$$

Convergence of the sequence $\phi(\mathbf{F}^{(n)}(\mathbf{p}))$ to λ is immediately implied by (4.7) and the continuity of ϕ and F.

(ii) Suppose $\lambda < y < \mu$ is an ESS. From Lemma 3 it follows that

$$(y - \lambda)[u_1(\lambda) - u_2(\lambda)] > 0.$$

Hence, $u_1(\lambda) > u_2(\lambda)$ and for x close enough to λ, say $0 < |x - \lambda| < \varepsilon$, $u_1(x) > u_2(x)$.

From this and from the local adaptivity property (3.3) of F it follows that for any $\mathbf{p} \in \Gamma$ with $0 < |\phi(\mathbf{p}) - \lambda| < \varepsilon$, $\phi(\mathbf{F}(\mathbf{p})) > \phi(\mathbf{p})$; thus $|\phi(\mathbf{F}(\mathbf{p})) - \lambda| > |\phi(\mathbf{p}) - \lambda|$ and the edge strategy λ is not stably maintained. In the same way, $y = \mu$ is also not stably maintained by F; thus, F maintains a protected polymorphism.

Moreover, Lemma 3 and (3.5) also implies that if $\lambda < y < \mu$ is an ESS, then for any $\mathbf{p} \in \Gamma$,

$$\text{sign}(y - x) = \text{sign}(x' - x). \tag{4.8}$$

This means that x' is either closer to y than x or, in the case of very

strong selection forces, it is further apart on the other side of y. Thus, the locally adaptive system either stably maintains the ESS value y or it allows fluctuations around it. ∎

5. DISCUSSION

The Darwinian theory of evolution concerns long-run changes in phenotypes in a population due to natural selection. However, long lasting phenotypic changes may reflect changes in the distribution of genotypes in a population. And quite generally, it is impossible to understand and predict the effect of natural selection on a given trait without a knowledge of the mechanism, genetical or other, by which this trait is transmitted from generation to generation. This partly explains the fact that changes in genotypic frequencies became the focus of modern studies in population biology. Another reason, quite attractive to quantitatively oriented scientists, is the possibility of drawing rigorous results about the changes in genotype frequencies once the selection forces operating on a given genetical structure are known.

Unfortunately, the genetical basis for evolutionary changes in phenotypic traits which are of a direct interest to students of natural history is rarely, if ever, known. Even less so are the exact selection forces operating on them (e.g., Lewontin, 1974).

An alternative approach to the study of this sort of trait attempts to avoid complications stemming from the specific nature of one genetical structure or another. Instead, intuitively understood criteria of phenotype optimization are suggested, with the basic asumption that despite technical counterexamples, accumulated through years of population genetic research, the basic Darwinian relation between adaptation and natural selection must lead to some sort of local optimization, at least as a workable approximation. Thus, instead of dealing with many technical, unmeasurable, and presumably insignificant details, it is preferable to ignore them in order to obtain simple qualitative results which are at least easy to interpret. The crucial question is under what circumstances the technical details being ignored are, indeed, insignificant.

This can be settled only by a comparison between results, obtained by the intuitive model with those achieved under a sufficiently general family of rigorous models. It should be kept in mind, though, that the very concept of a "sufficiently general" family of rigorous models cannot, in itself, be determined in a rigorous way; and no family of models is general enough as to provide us with more than a sample information about the validity of a given criteriona in the much wider context of the theory of evolution.

One of the two perhaps most important examples involves the concept of

evolutionarily stable strategies (ESS), suggested by Maynard Smith and Price (1973). The question here is, what is the relevance of results drawn by methods of game theory to the actual laws of natural selection in population genetics theory. At least in one case, namely, that of selection for optimal spread of seeds, interesting results drawn by pure methods of ESS (Hamilton and May, 1977) were fully verified by a rigorous analysis of both haploid and diploid populations (Motro, 1982a, b). In other cases, such as parent offspring conflict (Trivers, 1974) the result of a rigorous analysis of genetical models seems less in agreement with the ESS model of local optimality (e.g., Feldman and Eshel, 1982).

The present work is an attempt to develop a theoretical basis for comparison between ESSs of a given population game and the strategies which are determined by exact genetical structures.

The selective value of a strategy (or phenotype) affecting the outcome of intrapopulation conflicts is, by definition, frequency dependent. When conflicts occur with random encounters between individuals in the population (though not necessarily only then), the selective value of a strategy is additively frequency dependent. In this study we concentrate on the case of two alternative strategies (phenotypes), the choice (or manifestation) of each depending, at least statistically, on the individual's genotype, or maybe on some other inherited character of it.

For those genetical structures which obey Fisher's fundamental law of natural selection (including all one locus random mating viability models) it is shown that natural selection due to intrapopulation conflicts between random individuals stabilizes only those genetical equilibria which determine evolutionarily stable mixtures of strategies according to the game theory definition of Maynard Smith and Price. Moreover, with some further assumption, precluding fluctuations, any ESS of the appropriate population game is stably mainained by the genetical structure.

It is now well established, however, that Fisher's fundamental law, connecting adaptation and natural selection in the intuitively Darwinian way is mathematically false for almost all multilocus genetical systems (e.g., Karlin, 1975). These cast serious limitations on our ability to predict any precise adaptive pattern, at all (cf. Maynard Smith, 1978; Lewontin 1974. It is, therefore, not the intention of this study to claim that exact ESS values are, indeed, predicted to be found in natural populations. Instead it is shown that the game theory argument of ESS is mathematically equivalent in result to rigorous analysis of the specific models studied here and, thus, can legitimately replace them.

APPENDIX

Proof of Lemma 1.   *Y* is an ESS if and only if for all $x \neq y$, $V(y, y) \geqslant V(x, y)$ and if in the case of equality $V(y, x) > V(x, x)$.

In the case of two competing strategies, condition (4.1) is written as

$$y u_1(y) + (1 - y) u_2(y) \geqslant x u_1(y) + (1 - x) u_2(y)$$

and (4.2) becomes

$$y u_1(x) + (1 - y) u_2(x) \geqslant x u_1(x) + (1 - x) u_2(x).$$

Thus, (4.1) and (4.2) immediately follow.

Proof of Lemma 2.   (i)   Suppose $y = \lambda$ is an ESS. Condition (4.1) can then be written as

$$u_1(\lambda) - u_2(\lambda) \leqslant 0.$$

If $u_1(\lambda) - u_2(\lambda) < 0$, it follows from the continuity of u_1 and u_2 that (4.3) holds for at least $\lambda < x < \lambda + \varepsilon$. If, on the other hand, $u_1(\lambda) - u_2(\lambda) = 0$, (4.2) means that $u_1(x) - u_2(x) < 0$ for all $\lambda < x \leqslant \mu$.

(ii)   Suppose $y = \lambda$ is not an ESS. In this case, either (4.1) is not true, or it holds as an equality and (4.4) results from the continuity of u_1 and u_2, If (4.1) holds as an equality, (4.2) means that for all $\lambda < x \leqslant \mu$, $u_1(x) - u_2(x) \geqslant 0$. But in this case,

$$u_1(x) - u_2(x) = u_1(\lambda) - u_2(\lambda) + (a_{11} - a_{12} - a_{21} + a_{22})(x - \lambda)$$
$$= \theta(V_{11} - V_{12} - V_{21} - V_{22})(x - \lambda) \geqslant 0$$

and from (3.1) it follows that $V_{11} - V_{12} - V_{21} + V_{22} > 0$ (it can be neither zero nor negative); hence (4.4) must hold for all $x > \lambda$.

Proof of Lemma 3.   (i) is immediate from (4.1) and (4.2). Also, if y is not an ESS and $u_1(y) = u_2(y)$, (4.6) holds at least as a weak inequality. As in the proof of Lemma 1, the sharp version of (4.6) is implied from (3.1).

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