

Evolutionary Stability: One Concept, Several Meanings*

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Received July 19, 1989

Several definitions of evolutionary stability (evolutionarily stable strategy—ESS, continuously stable strategy—CSS, evolutionary genetic stability—EGS, evolutionarily stable state—ES state) are presented in a unifying framework. © 1990 Academic Press, Inc.

INTRODUCTION

Fifteen years ago, A. Jacquard (1975) published a paper in *Theoretical Population Biology* entitled "Inbreeding: One word, several meanings," which was motivated by a proliferation of definitions for inbreeding that had created confusion. The concept of evolutionary stability has come to the same point. Since its introduction in 1973 by J. Maynard Smith and G. R. Price (1973), the notion of evolutionary stability has proliferated in many directions from game dynamic perspectives to sex ratio evolution theory, not to mention general frequency- and density-dependent selection, including kin selection in exact population genetic models. Several papers in *Theoretical Population Biology* have contributed to the development of the concept and the introduction of definitions. In this paper, we try to unify the theory and terminology.

1. EVOLUTIONARILY STABLE STRATEGY

It is from a game-theoretic approach to animal conflicts that Maynard Smith and Price (1973) introduced the notion of evolutionary stability. In a contest with an opponent, an individual chooses a behavior according to

* Research supported in part by Natural Sciences and Engineering Research Council of Canada.

some *strategy* \mathbf{s} , which is defined as a probability distribution on a given set of possible behaviors. It will be assumed throughout this section unless stated otherwise that the set of possible behaviors is finite, that is, the game is *finite*. With possible behaviors numerated from 1 to N , a strategy reduces to an N -dimensional frequency vector

$$\mathbf{s} = (s_1, \dots, s_N), s_i \geq 0 \quad \text{for } i = 1, \dots, N, \sum_{i=1}^N s_i = 1,$$

where s_i is the probability of adopting behavior i ($i = 1, \dots, N$). A strategy that consists of adopting a single behavior i with probability 1, also denoted i , is called a *pure strategy*. Any other strategy is called a *mixed strategy*.

The expected *payoff* to an \mathbf{s} -strategist against an \mathbf{s}^* -strategist is denoted $A(\mathbf{s}, \mathbf{s}^*)$. In a *linear game*, the payoff function $A(\mathbf{s}, \mathbf{s}^*)$ is bilinear with respect to \mathbf{s} and \mathbf{s}^* . This is the case, for instance, if two opponents choose their behavior according to their strategy independently of one another. This will be assumed throughout this section. In particular, a linear game with possible behaviors numerated from 1 to N has a payoff function in the form

$$A(\mathbf{s}, \mathbf{s}^*) = \sum_{i,j=1}^N s_i a_{ij} s_j^* = \mathbf{s}^T A \mathbf{s}^* \quad (\text{T for transpose}),$$

where $a_{ij} = A(i, j)$ is the expected payoff to an individual adopting behavior i against an opponent adopting behavior j ($i, j = 1, \dots, N$) and the matrix

$$A = \|a_{ij}\|_{i,j=1}^N$$

is the *payoff matrix*.

An *evolutionarily stable strategy* (ESS) is defined as a strategy \mathbf{s}^* such that for every strategy $\mathbf{s} \neq \mathbf{s}^*$

$$\begin{aligned} &\text{either } A(\mathbf{s}^*, \mathbf{s}^*) > A(\mathbf{s}, \mathbf{s}^*) \\ &\text{or } A(\mathbf{s}^*, \mathbf{s}^*) = A(\mathbf{s}, \mathbf{s}^*) \\ &\text{and } A(\mathbf{s}^*, \mathbf{s}) > A(\mathbf{s}, \mathbf{s}). \end{aligned} \quad (\text{I})$$

This definition guarantees that the mean payoff to \mathbf{s}^* -strategists always exceeds the mean payoff to \mathbf{s} -strategists in an infinite population consisting of a large enough majority of \mathbf{s}^* -strategists (called *residents*) and a minority of \mathbf{s} -strategists (called *mutants*) for every $\mathbf{s} \neq \mathbf{s}^*$ if pairwise contests

occur at random in the population. Indeed, the mean payoffs in such a population with a proportion $1-\varepsilon$ of \mathbf{s}^* -strategists and ε of \mathbf{s} -strategists are

$$(1-\varepsilon)A(\mathbf{s}, \mathbf{s}^*) + \varepsilon A(\mathbf{s}, \mathbf{s}) = A(\mathbf{s}, \bar{\mathbf{s}})$$

$$(1-\varepsilon)A(\mathbf{s}^*, \mathbf{s}^*) + \varepsilon A(\mathbf{s}^*, \mathbf{s}) = A(\mathbf{s}^*, \bar{\mathbf{s}}),$$

where $\bar{\mathbf{s}} = (1-\varepsilon)\mathbf{s}^* + \varepsilon\mathbf{s}$, and we have for $\mathbf{s} \neq \mathbf{s}^*$ and $\varepsilon > 0$ small enough

$$A(\mathbf{s}^*, \bar{\mathbf{s}}) > A(\mathbf{s}, \bar{\mathbf{s}}) \quad (\text{II})$$

if and only if (I) holds (Maynard Smith, 1974). Moreover, since we have

$$A(\bar{\mathbf{s}}, \bar{\mathbf{s}}) = (1-\varepsilon)A(\mathbf{s}^*, \bar{\mathbf{s}}) + \varepsilon A(\mathbf{s}, \bar{\mathbf{s}}),$$

an equivalent condition is

$$A(\mathbf{s}, \bar{\mathbf{s}}) < A(\bar{\mathbf{s}}, \bar{\mathbf{s}}) \quad (\text{III})$$

for $\bar{\mathbf{s}} \neq \mathbf{s}^*$ close enough to \mathbf{s}^* , or alternatively (Hofbauer *et al.*, 1979)

$$A(\mathbf{s}^*, \bar{\mathbf{s}}) > A(\bar{\mathbf{s}}, \bar{\mathbf{s}}) \quad (\text{IV})$$

for $\bar{\mathbf{s}} \neq \mathbf{s}^*$ close enough to \mathbf{s}^* .

The meaning of (III) and (IV) is that the mean payoff to \mathbf{s}^* -strategists exceeds the mean payoff in the population which exceeds the mean payoff to \mathbf{s} -strategists for $\mathbf{s} \neq \mathbf{s}^*$ if the mean strategy $\bar{\mathbf{s}}$ in the population is close enough to \mathbf{s}^* . Moreover, (I) compels

$$A(\mathbf{s}, \mathbf{s}^*) \leq A(\mathbf{s}^*, \mathbf{s}^*) \quad (\text{Va})$$

for every strategy \mathbf{s} ; in particular

$$A(i, \mathbf{s}^*) \leq A(\mathbf{s}^*, \mathbf{s}^*)$$

for every pure strategy i . Let $I(\mathbf{s}^*)$ be the set of i for which

$$A(i, \mathbf{s}^*) = A(\mathbf{s}^*, \mathbf{s}^*).$$

Necessarily, $I(\mathbf{s}^*)$ contains the support of \mathbf{s}^* , denoted $\text{supp}(\mathbf{s}^*)$, which is the set of i for which $s_i^* > 0$. With (Va) in force, \mathbf{s}^* is an ESS if and only if (Haigh, 1975)

$$\begin{aligned} & A(\mathbf{s} - \mathbf{s}^*, \mathbf{s} - \mathbf{s}^*) \\ &= A(\mathbf{s}, \mathbf{s}) - A(\mathbf{s}^*, \mathbf{s}) - A(\mathbf{s}, \mathbf{s}^*) + A(\mathbf{s}^*, \mathbf{s}^*) \\ &< 0 \end{aligned} \quad (\text{Vb})$$

for all $\mathbf{s} \neq \mathbf{s}^*$ with $\text{supp}(\mathbf{s})$ contained in $I(\mathbf{s}^*)$. If $I(\mathbf{s}^*)$ contains a single pure strategy, necessarily \mathbf{s}^* , we have a strict inequality in (Va) for all $\mathbf{s} \neq \mathbf{s}^*$ and this is a sufficient condition for \mathbf{s}^* to be an ESS.

In the case of an *infinite game* with a continuum of pure strategies, a mixed strategy may be a density function but conditions (I)–(V) are still equivalent for an ESS if the game is linear and $\text{supp}(\mathbf{s})$ is defined for almost all pure strategies with respect to \mathbf{s} . In the war of attrition in which the contestant who is prepared to continue the contest longer receives a gain V ($V/2$ in case of a tie) and each contestant pays a cost equal to the duration of the contest, we have the kernel

$$A(x, y) = \begin{cases} V - y & \text{for } x > y \geq 0 \\ \frac{V}{2} - y & \text{for } x = y \geq 0 \\ -x & \text{for } y > x \geq 0 \end{cases}$$

which gives the payoff to a contestant prepared to continue a fixed time x against an opponent prepared to continue a fixed time y ($x, y \geq 0$). The density function

$$\mathbf{s}^*(x) = \frac{1}{V} e^{-x/V} \quad \text{for } x \geq 0$$

is the unique ESS (Maynard Smith, 1974; Bishop and Cannings, 1976).

2. CONTINUOUSLY STABLE STRATEGY

Evolutionary stability can be defined directly from contests between a rare mutant population and a resident population without any linearity assumption on the payoff function. In such a case, conditions (III) and (IV) are not equivalent and must be considered separately.

Let $E(\mathbf{m}, \mathbf{r})$ be the mean payoff per individual to a mutant population with mean strategy \mathbf{m} (*m-population*) when introduced in infinitesimal frequency into an infinite resident population with mean strategy \mathbf{r} (*r-population*). Assuming N -dimensional frequency vectors as strategies and a payoff function $E(\mathbf{m}, \mathbf{r})$ with partial derivatives of high enough order we have the expansion

$$\begin{aligned} E(\mathbf{m}, \mathbf{r}) &= E(\mathbf{r}, \mathbf{r}) + (\mathbf{m} - \mathbf{r})^T \mathbf{F}(\mathbf{r}) \\ &\quad + \frac{1}{2} (\mathbf{m} - \mathbf{r})^T \mathbf{B}(\mathbf{r}) (\mathbf{m} - \mathbf{r}) \\ &\quad + \text{higher order terms,} \end{aligned}$$

where

$$F_i(\mathbf{r}) = \frac{\partial E}{\partial m_i}(\mathbf{r}, \mathbf{r}) \quad \text{for } i = 1, \dots, N$$

and

$$B(\mathbf{r}) = \left\| \frac{\partial^2 E}{\partial m_i \partial m_j}(\mathbf{r}, \mathbf{r}) \right\|_{i,j=1}^N.$$

By analogy with (III) and (IV), we may look for a resident strategy \mathbf{r}^* such that

$$E(\mathbf{m}, \mathbf{r}^*) < E(\mathbf{r}^*, \mathbf{r}^*) \quad (\text{VI})$$

for every mutant strategy $\mathbf{m} \neq \mathbf{r}^*$ close enough to \mathbf{r}^* , which defines \mathbf{r}^* -stability, or a mutant strategy \mathbf{m}^* such that

$$E(\mathbf{m}^*, \mathbf{r}) > E(\mathbf{r}, \mathbf{r}) \quad (\text{VII})$$

for every resident strategy $\mathbf{r} \neq \mathbf{m}^*$ close enough to \mathbf{m}^* , which defines \mathbf{m}^* -stability.

A necessary (sufficient) condition for (VI) is:

$$\begin{aligned} &F_i(\mathbf{r}^*) \leq c \text{ for all } i, \text{ with } = \text{ for } i \text{ in } \text{supp}(\mathbf{r}^*); \\ &(\mathbf{m} - \mathbf{r}^*)^T B(\mathbf{r}^*)(\mathbf{m} - \mathbf{r}^*) \leq 0 \text{ (} < 0 \text{ for sufficiency)} \\ &\text{for all } \mathbf{m} \neq \mathbf{r}^* \text{ with } \text{supp}(\mathbf{m}) \text{ in } \mathcal{S}(\mathbf{r}^*) = \{i: F_i(\mathbf{r}^*) = c\}, \\ &\text{where } c \text{ is a constant (see, e.g., Thomas, 1984).} \end{aligned}$$

The above condition is also necessary (sufficient) for the weaker condition

$$E(\mathbf{m}, \mathbf{r}) < E(\mathbf{r}, \mathbf{r}), \quad (\text{VI}')$$

where $\mathbf{r} = \mathbf{r}^* + t(\mathbf{m} - \mathbf{r}^*)$ for \mathbf{m} close enough to \mathbf{r}^* and $t > 0$ small enough, which defines \mathbf{r} -stability.

A necessary (sufficient) condition for (VII) is:

$$\begin{aligned} &F_i(\mathbf{m}^*) \leq c \text{ for all } i, \text{ with } = \text{ for } i \text{ in } \text{supp}(\mathbf{m}^*); \\ &(\mathbf{m}^* - \mathbf{r})^T [A(\mathbf{m}^*) + \frac{1}{2}B(\mathbf{m}^*)](\mathbf{m}^* - \mathbf{r}) \leq 0 \text{ (} < 0 \text{ for sufficiency)} \\ &\text{for all } \mathbf{r} \neq \mathbf{m}^* \text{ with } \text{supp}(\mathbf{r}) \text{ in } \mathcal{S}(\mathbf{m}^*), \text{ where} \\ &A(\mathbf{m}^*) = \left\| \frac{\partial^2 E}{\partial m_i \partial r_j}(\mathbf{m}^*, \mathbf{m}^*) \right\|_{i,j=1}^N. \end{aligned}$$

Assuming (VI') for $\mathbf{r}^* = \mathbf{m}^*$, the weaker condition with $[A(\mathbf{m}^*) + B(\mathbf{m}^*)]$ in place of $[A(\mathbf{m}^*) + B(\mathbf{m}^*)/2]$ above is necessary (sufficient) for

$$E(\mathbf{r} + t(\mathbf{m}^* - \mathbf{r}), \mathbf{r}) \begin{cases} > E(\mathbf{r}, \mathbf{r}) & \text{if } t > 0 \\ < E(\mathbf{r}, \mathbf{r}) & \text{if } t < 0 \end{cases} \quad (\text{VII}')$$

for $\mathbf{r} \neq \mathbf{m}^*$ close enough to \mathbf{m}^* and $|t|$ small enough, which defines \mathbf{m} -stability.

With the change of variables $\mathbf{m} = \mathbf{r} + \delta$, we have

$$A(\mathbf{m}^*) + B(\mathbf{m}^*) = \left\| \frac{\partial^2 E}{\partial \delta_i \partial r_j}(\mathbf{m}^*, \mathbf{m}^*) \right\|_{i,j=1}^N$$

in the necessary (sufficient) condition for \mathbf{m} -stability.

In the case where $E(\mathbf{m}, \mathbf{r})$ is linear with respect to \mathbf{m} , we have

$$E(\mathbf{m}, \mathbf{r}) = \mathbf{m}^T \mathbf{F}(\mathbf{r}),$$

where $\mathbf{F}(\mathbf{r}) = (F_1(\mathbf{r}), \dots, F_N(\mathbf{r}))$ and $F_i(\mathbf{r})$ is the mean payoff to the pure strategy i ($i = 1, \dots, N$). In this case, if (VII') holds, then it holds for all t . Moreover, (VII') and (VI') with $\mathbf{m}^* = \mathbf{r}^*$ are equivalent to each other and both equivalent to

$$E(\mathbf{r}^*, \mathbf{r}^* + t(\mathbf{m} - \mathbf{r}^*)) > E(\mathbf{m}, \mathbf{r}^* + t(\mathbf{m} - \mathbf{r}^*))$$

for $\mathbf{m} \neq \mathbf{r}^*$ close enough to \mathbf{r}^* and $t > 0$ small enough. A necessary (sufficient) condition for both (VII') and (VI') with $\mathbf{m}^* = \mathbf{r}^*$ is then

$$\begin{aligned} F_i(\mathbf{r}^*) &\leq c \text{ for all } i, \text{ with } = \text{ for } i \text{ in } \text{supp}(\mathbf{r}^*); \\ (\mathbf{m} - \mathbf{r}^*)^T A(\mathbf{r}^*)(\mathbf{m} - \mathbf{r}^*) &\leq 0 \text{ (} < 0 \text{ for sufficiency)} \\ \text{for all } \mathbf{m} \neq \mathbf{r}^* \text{ with } \text{supp}(\mathbf{m}) &\text{ in } \mathcal{J}(\mathbf{r}^*), \text{ where} \end{aligned} \quad (\text{VIII})$$

$$A(\mathbf{r}^*) = \left\| \frac{\partial F_i}{\partial r_j}(\mathbf{r}^*) \right\|_{i,j=1}^N.$$

(See, e.g., Taylor and Jonker, 1978.)

The definitions of \mathbf{r} -stability (condition (VI')) and \mathbf{m} -stability (condition (VII')) are multidimensional versions of definitions introduced in Taylor (1989), but with δ -stability called \mathbf{r} -stability for mnemonic reasons. In agreement with a terminology used in Uyenoyama and Bengtsson (1982) and Uyenoyama (1984) in studies on sex ratio evolution and kin selection theory, a *strong* ESS is a resident strategy \mathbf{r}^* satisfying (VI) (\mathbf{r}^* -stability), a *weak* ESS a resident strategy \mathbf{r}^* satisfying (VI') (\mathbf{r} -stability), and an *anti*-ESS a resident strategy \mathbf{r}^* satisfying the converse of (VI') with equality precluded. In all cases, we have actually a *local* ESS.

Finally, generalizing a definition introduced in Eshel (1983), an ESS \mathbf{r}^* is said to be a *continuously stable strategy* (CSS) if (VII'), that is, *m-stability*, holds for $\mathbf{m}^* = \mathbf{r}^*$.

3. RESOURCE ALLOCATION

An N -dimensional *resource allocation vector* is defined as a nonnegative vector

$$\mathbf{r} = (r_1, \dots, r_N), \quad r_i \geq 0 \text{ for } i = 1, \dots, N, \quad \sum_{i=1}^N r_i > 0,$$

where r_i represents the quantity of resources allocated to a function or activity i ($i = 1, \dots, N$). Functions can be partitioned into male and female functions (see, e.g., Charnov, 1982; Taylor, 1984; Charnov and Bull, 1986; Lessard, 1989a).

All the definitions of Section 2 can be extended *mutatis mutandis* to N -dimensional resource allocation vectors as strategies. In that case, the necessary (sufficient) conditions of Section 2 have $c = 0$ if there are no further constraints on resource allocation vectors. With a constraint in the form

$$\sum_{i=1}^N r_i \leq T,$$

where T is an absolute maximum for the total quantity of resources, it suffices to make the change of variables

$$\mathbf{s} = \frac{(r_1, \dots, r_N, T - \sum_{i=1}^N r_i)}{T}$$

and then to apply the conditions of Section 2 without any modification with the new variables as strategies. With a more general constraint in the form (Lessard, 1989a)

$$g(\mathbf{r}) \leq T,$$

where g is strictly and continuously increasing to infinity in each coordinate and $g(\mathbf{0}) = 0$, we can use the change of variables

$$\mathbf{s} = \frac{(r_1, \dots, r_N, [a(\mathbf{r}) - 1] \sum_{i=1}^N r_i)}{a(\mathbf{r}) \sum_{i=1}^N r_i},$$

where $a(\mathbf{r})$ is the unique quantity ≥ 1 such that

$$g(a(\mathbf{r}) \mathbf{r}) = T.$$

The quantity $a(\mathbf{r})$ is such that $a(\mathbf{r})\mathbf{r}$ is on the boundary of the set of all admissible resource allocation vectors determined by $g(\mathbf{r}) \leq T$, called the *resource allocation set*.

4. EVOLUTIONARY GENETIC STABILITY

Typically in population genetic models, the frequencies of types (genotypes, mating types, etc.) carrying a mutant allele near a population equilibrium are related over two successive generations by a recurrence equation of the form

$$\mathbf{x}' = M\mathbf{x} + \text{higher order terms.}$$

If the matrix M is nonnegative and some iterate M^k is positive, which is often the case, there exists a simple positive eigenvalue ρ strictly larger than all other eigenvalues in magnitude with associated left and right positive eigenvectors, \mathbf{u} and \mathbf{v} , such that

$$\frac{M^k}{\rho^k} \rightarrow \mathbf{v}\mathbf{u}^T \quad \text{as } k \rightarrow \infty$$

with $\mathbf{u}^T\mathbf{v} = 1$ and $\mathbf{1}^T\mathbf{v} = 1$ ($\mathbf{1}$ for the unit vector). In the long run near equilibrium, the mutant types will have *relative frequencies* with sum equal to 1 given by \mathbf{v} , *relative reproductive values* with mean equal to 1 given by \mathbf{u} , and *growth rate* $\rho > 0$. There is *invasion (or initial increase in frequency)* of the mutant allele at a geometric rate if and only if

$$\rho > 1.$$

If $\rho = \rho(\mathbf{m}, \mathbf{r})$, where \mathbf{r} is a mean strategy in the population at equilibrium and \mathbf{m} a mean strategy in the mutant population near equilibrium, using \mathbf{v} as the distribution of mutant types, then we can apply the definitions of Section 2 to $\rho(\mathbf{m}, \mathbf{r})$ with $\rho(\mathbf{r}, \mathbf{r}) = 1$ for all \mathbf{r} . (See, e.g., Taylor and Bulmer, 1980; Taylor, 1985.)

In one-locus multiallele models for sex ratio evolution, Eshel and Feldman (1982) obtained a function $\rho(\mathbf{m}, r)$ linear with respect to \mathbf{m} and a population sex ratio strategy $\mathbf{m}^* = \mathbf{r}^*$ —actually, an even sex ratio $(\frac{1}{2}, \frac{1}{2})$ —satisfying the CSS conditions was said to exhibit the *evolutionary genetic stability* (EGS) property. (See Eshel (1985) for EGS of Mendelian population segregation ratio.) In a later study on ESS independent of sex in two-locus systems (Eshel and Feldman, 1984), a multidimensional phenotype strategy \mathbf{r} was said more generally to have the EGS property if

“within a given genetic system ..., a new mutation is favored if and only if it renders the population strategy closer to” \mathbf{r} at least initially after enough generations. (See Lessard (1989a) for multilocus systems in sex-differentiated populations.) The genetic system is of importance since the function ρ is not usually the same from one system to another. In particular, linkage may transform an EGS population strategy into a “genetic anti-ESS” with any mutant allele invading the *population* (see, e.g., Liberman, 1976; Lessard, 1985, 1987).

The EGS property has been studied for several genetic parameters. A *partial* EGS property (actually, \mathbf{m} -stability at viability-analogous Hardy–Weinberg (VAHW) equilibria) in support of a general reduction principle is known to hold for mutation rate, recombination fraction, and migration propensity (Feldman and Liberman, 1986).

An EGS property *over successive attainable equilibria* (EGS property with successive equilibria attainable by successive mutant alleles always closer to the EGS population strategy) has been shown to hold for an even population sex ratio (Karlin and Lessard, 1983, 1986) and a Mendelian population segregation ratio (Lessard, 1985) in one-locus multiallele frameworks.

In general two-sex one-locus multiallele viability models, there may be small fluctuations over successive equilibria before an EGS population strategy is reached, which maximises the product of the male and female mean viabilities (Lessard, 1989a). In such a case, we have an EGS property *over sequences of equilibria*. When there is convergence according to this scheme, we say that we have an *evolutionarily attractive* population strategy (Lessard, 1984).

5. EVOLUTIONARILY STABLE STATE

It remains to see whether an ESS as mean strategy can be maintained in a population. Is an ESS, as a mean strategy, at a population equilibrium restored following small perturbations on the equilibrium frequencies of individual strategies? If the answer is yes, we have an *evolutionarily stable* (ES) *state*. Two kinds of perturbations must be considered: perturbations on frequencies of individual strategies already represented at equilibrium for *internal stability* and small initial frequencies of mutant individual strategies for *external stability*. Internal stability has a meaning only in *polymorphic populations* with two or more individual strategies represented at equilibrium.

In order to study evolutionary stability in polymorphic populations, we consider N -dimensional frequency vectors as strategies, we interpret $E(\mathbf{m}, \mathbf{r})$

of Section 2 as the reproductive rate of an \mathbf{m} -strategist in a population with mean strategy \mathbf{r} and we assume

$$\mathbf{E}(\mathbf{m}, \mathbf{r}) = \mathbf{m}^T \mathbf{F}(\mathbf{r})$$

such that $\mathbf{E}(\mathbf{r}, \mathbf{r})$ is the mean reproductive value in the population. Let \mathbf{r}^* satisfy the ESS sufficient condition (VIII). For haplotypes adopting pure strategies $1, \dots, N$ in relative frequencies p_1, \dots, p_N in an infinite population, we have the dynamical equations

$$\dot{p}_i = p_i [\mathbf{E}(i, \mathbf{p}) - \mathbf{E}(\mathbf{p}, \mathbf{p})] \quad \text{for } i = 1, \dots, N,$$

where $\mathbf{p} = (p_1, \dots, p_n)$. Then the equilibrium point $\mathbf{p} = \mathbf{r}^*$ is an ES state (Taylor and Jonker, 1978; Hofbauer *et al.*, 1979; Zeeman, 1980). For haplotypes adopting mixed strategies $\mathbf{s}_1, \dots, \mathbf{s}_n$ in relative frequencies p_1, \dots, p_n in an infinite population, we have

$$\dot{p}_i = p_i [\mathbf{E}(\mathbf{s}_i, \bar{\mathbf{s}}) - \mathbf{E}(\bar{\mathbf{s}}, \bar{\mathbf{s}})] \quad \text{for } i = 1, \dots, n,$$

where

$$\bar{\mathbf{s}} = \sum_{i=1}^n p_i \mathbf{s}_i.$$

In this case, the *equilibrium manifold* $\bar{\mathbf{s}} = \mathbf{r}^*$, when it exists, appears to be an ES state. (See, e.g., Hines (1980, 1982) and Zeeman (1981) for proofs under generic conditions; see Lessard (1989b) for a more general proof). In diploid random mating populations with alleles A_1, \dots, A_n at one locus, we have

$$\mathbf{s}_i = \sum_{j=1}^n p_j \mathbf{s}_{ij},$$

where \mathbf{s}_{ij} is the strategy adopted by an individual of genotype $A_i A_j$ ($i, j = 1, \dots, n$). Again, the equilibrium manifold $\bar{\mathbf{s}} = \mathbf{r}^*$ appears to be an ES state when it exists (Lessard, 1984; Cressman and Hines, 1984; Thomas, 1985a, b; Cressman, 1988a; Hofbauer and Sigmund, 1988). A general proof extending Lessard (1989b) confirms this fact.

6. CONCLUDING REMARKS

Conditions for a population state to be evolutionarily stable in frequency-dependent selection models, as in Section 5, can be extended to frequency- and density-dependent selection models (see, e.g., Cressman, 1988b; Lessard, 1989b). This is particularly relevant for resource allocation models.

Often in sex-differentiated selection models and kin selection models, it is not sufficient that the mean strategy be equal to an ESS for a population equilibrium to exist and further conditions are required (see, e.g., Karlin and Lessard, 1983).

In general, if payoff depends on the whole distribution of strategies (pure or mixed) in a population rather than just the mean strategy, then we must look for an ESS that is a distribution of strategies (pure or mixed). (See, e.g., Akin, 1982.)

For further discussion on ESS theory, we recommend Maynard Smith (1982) and Hines (1987).

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