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INITIAL INCREASE OF NEW MUTANTS AND SOME CONTINUITY PROPERTIES OF ESS IN TWO-LOCUS SYSTEMS

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In a random mating, diploid population with viability determined by the genotype at two or more linked loci, natural selection does not guarantee an increase in the average viability of the population. Since it was first pointed out by Moran (1964), this apparent contradiction to the Darwin-Fisher-Wright expectation has been shown to occur in most multilocus nonadditive fitness regimes (Ewens 1969; Karlin 1975). As a result, even in a constant environment, it cannot be generally true that natural selection on genotypes distributed among phenotypes operates to maximize the average individual adaptation to the environment, i.e., to produce an optimal population strategy.

When selection is considered to be frequency dependent, as in the models leading to the theory of evolutionary stable strategies (Maynard Smith and Price 1973), it is far from obvious that average fitness should be locally maximized when more than a single locus is involved. In this case, unlike that with a single gene, for a random set of genotypes and randomly chosen parameters relating these genotypes to the phenotypes, genetic equilibria are most unlikely to determine an ESS distribution of phenotypes. (See, e.g., Lessard 1984. Of course, one can question whether such parameters are indeed distributed at random.)

The long-term effects of natural selection should not be considered in the context of changes in frequencies of a fixed set of genotypes. Even if nonneutral mutations occur at random, they do not succeed at random so that the set of extant genotypes in a population should not be regarded as random. As has been demonstrated for the sex ratio (Eshel and Feldman 1982) for the Mendelian segregation ratio under unlinked control (Eshel 1985), and for a one-locus two-phenotype frequency-dependent system (Lessard 1984), criteria for success of new mutations may be different from and easier to interpret for genotypes than are the rules governing frequency changes of a given fixed set of genotypes.

We know very little about the range of possible new mutations that may affect the course of evolution of a given phenotype. For this reason we call "long-term aspects of natural selection" those genetic criteria for the success of new mutations which can be interpreted in purely phenotypic terms.

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We first determine a compact average fitness condition for the initial increase from a stable equilibrium of a new mutant allele at one of two multiple-allelic loci. No new analytic tools are required for this, but we can use the characterization to address a phenotypic question, namely, the properties of new phenotypes (or strategies) determined by the genetic system and the distribution of phenotypes (or strategies) which is immune to invasion, when stability is measured in terms of immunity to any new mutant allele.

A GENERAL CONDITION FOR INITIAL INCREASE OF A MUTANT ALLELE IN A GENERAL TWO-LOCUS VIABILITY MODEL

Let $A_1, A_2, \ldots, A_n$ and $B_1, B_2, \ldots, B_m$ be the alleles segregating at two linked loci with recombination fraction r. The viability of the genotype A_iB_j/A_kB_ℓ is $w_{ijk\ell}$ $(i,k = 1,2, \ldots n; j,\ell = 1,2, \ldots m)$, with

$$w_{ijk\ell} = w_{i\ell kj} = w_{kji\ell} = w_{k\ell ij}. \tag{1}$$

The frequency of the chromosome A_iB_j after selection and recombination is denoted x_{ij}. With random mating the average viability of newborn offspring is

$$\bar{W} = \sum_{ijk\ell} w_{ijk\ell} x_{ij} x_{k\ell}. \tag{2}$$

After random mating, segregation, selection, and recombination the frequency of A_iB_j in the next generation is

$$x'_{ij} = (\bar{W})^{-1}\left\{r\sum_{k\ell} w_{ijk\ell} x_{i\ell} x_{kj} + (1 - r)\sum_{k\ell} w_{ijk\ell} x_{ij} x_{k\ell}\right\}. \tag{3}$$

We denote the equilibrium frequencies of $\{A_iB_j\}$ by $\{x^*_{ij}\}$. Clearly $\{x^*_{ij}\}$ solves (3) with the prime deleted from the left side. This is true for frequency-independent as well as for frequency-dependent selection. In the latter case $w_{ijk\ell}$ should be interpreted as functions of $\mathbf{x} = (x_{11}, x_{12}, \ldots, x_{nm})$.

Now suppose that a new allele A_{n+1} at the A-locus appears in low frequency near the equilibrium $\{x^*_{ij}\}$:

$$x_{n+1,j} = \epsilon_j; \qquad \sum_j \epsilon_j = \epsilon > 0, \; |x_{ij} - x^*_{ij}| < \epsilon \qquad (i \neq n + 1) \tag{4}$$

where ϵ is small. If (in the case of frequency-dependent selection) $w_{ijk\ell}$ are continuous functions of $\mathbf{x}$ (with frequency-independent selection included as a special case) then, neglecting terms of smaller order than ϵ,

$$\bar{W}^*\epsilon'_j = \epsilon_j \sum_{k=1}^{n}\sum_{\ell=1}^{m} w_{n+1,jk\ell} x^*_{k\ell} + r\sum_{k=1}^{n}\sum_{\ell=1}^{m} w_{n+1,jk\ell}(\epsilon_\ell x^*_{kj} - \epsilon_j x^*_{k\ell}) \tag{5}$$

$$j = 1,2, \ldots m.$$

In the case of frequency-dependent selection $w_{ijk\ell}$ stands for the selection coefficient evaluated at $\{x^*_{ij}\}$. The perturbations in the selection coefficients away

from their equilibrium values in this case will be multiplied by ϵ's and yield quantities which may be neglected in (5). The linear approximation (5) may be written

$$\boldsymbol{\epsilon}' = \mathbf{A}\boldsymbol{\epsilon} \tag{6}$$

where the matrix $\mathbf{A} = \|\partial\epsilon_j'/\partial\epsilon_\ell\|$ and

$$\begin{aligned} \overline{W}\frac{\partial\epsilon_j'}{\partial\epsilon_j} &= (1-r)\sum_{k\ell} w_{n+1,jk\ell}x_{k\ell}^* + r\sum_k w_{n+1,jkj}x_{kj}^* \\ \overline{W}\frac{\partial\epsilon_j'}{\partial\epsilon_\ell} &= r\sum_k w_{n+1,jk\ell}x_{kj}^* \qquad (\ell \neq j). \end{aligned} \tag{7}$$

Let λ be the leading eigenvalue of $\mathbf{A}$ and $\mathbf{u} = (u_1, u_2, \ldots, u_m)$ the corresponding right eigenvector of $\mathbf{A}$ normalized so that $\Sigma_i u_i = 1$. From the Frobenius theorem we know that λ is a positive real number and that $\mathbf{u}$ is a unique positive vector.

We now claim *Proposition 1:*

$$\lambda = (\overline{W})^{-1}\sum_{j=1}^m u_j \sum_{k=1}^n \sum_{\ell=1}^m w_{n+1,jk\ell}x_{kl}^*. \tag{8}$$

To see this, write for $j = 1,2, \ldots m$,

$$\lambda u_j = \sum_{\ell=1}^m u_\ell \frac{\partial\epsilon_j'}{\partial\epsilon_\ell}. \tag{9}$$

Substituting from (7) and summing over j in (9) we obtain

$$\begin{aligned} \lambda &= \lambda\sum_j u_j \\ &= (1-r)(\overline{W})^{-1}\sum_{j=1}^m\sum_{k=1}^n\sum_{\ell=1}^m u_j w_{n+1,jk\ell}x_{k\ell}^* \\ &\quad + r(\overline{W})^{-1}\sum_{j=1}^m\sum_{k=1}^n\sum_{\ell=1}^m u_\ell w_{n+1,jk\ell}x_{kj}^*. \end{aligned} \tag{10}$$

The indices j and ℓ can be interchanged and, using (1), (10) becomes

$$\lambda = (\overline{W})^{-1}\sum_{j=1}^m u_j\sum_{k=1}^n\sum_{\ell=1}^m w_{n+1,jk\ell}x_{k\ell}^*.$$

Now for any vector $\boldsymbol{\epsilon} = (\epsilon_1, \epsilon_2, \ldots, \epsilon_m) \geq 0$ with $\Sigma_{j=1}^m \epsilon_j > 0$

$$\lim_{t\to\infty}\frac{\mathbf{A}^t\boldsymbol{\epsilon}}{\|\mathbf{A}^t\boldsymbol{\epsilon}\|} = \mathbf{u}, \qquad \text{with norm } \|\mathbf{z}\| = \sum_i |z_i|. \tag{11}$$

From (8) and (11) the proportions u_j can be viewed as the weights assigned to $A_{n+1}B_j$ among the carriers of A_{n+1} in a sufficiently small neighborhood of $\{x_{ij}^*\}$ so that the linear approximation is valid. (Note that the u_j are independent of the values ϵ_j characteristic of the mutant chromosomes since the stability of the

original equilibrium is independent of ϵ_j.) With this interpretation of $\mathbf{u}$ it follows from (8) that a mutant allele at one locus of a randomly mating two-locus system under viability selection will succeed in the population if its average marginal viability is greater than that of the resident population (i.e., if $\lambda > 1$), the average being a weighted average with weights corresponding to $\mathbf{u}$. Clearly, under these conditions $\lambda > 1$ and $\{x_{ij}^*\}$ is locally unstable to the invasion of $\mathbf{A}_{n+1}$.

SOME TWO-LOCUS DYNAMICS OF ESS

Our point of departure is Maynard Smith's construction of a population viability game and the general definition of an ESS. Let $\alpha_1, \alpha_2, \ldots, \alpha_r$ be the alternative (pure) strategies of an individual in the population. An individual is said to have the (mixed) strategy $\mathbf{h} = (h_1, h_2, \ldots, h_r)$ with $\Sigma_{i=1}^r h_i = 1$ and $h_i > 0$ $(i = 1, 2, \ldots, r)$, if it chooses the pure strategy α_i with probability h_i $(i = 1, 2, \ldots, r)$.

Now suppose that there are s types in the population with p_j the proportion of individuals of type j, all of whom have strategy $\mathbf{h}^{(j)}$. The population strategy is then defined as

$$\mathbf{y} = \sum_{j=1}^{s} p_j \mathbf{h}^{(j)}. \tag{12}$$

The component y_ℓ of $\mathbf{y}$ is the probability that a randomly chosen individual in the population will choose the pure strategy α_ℓ $(\ell = 1, 2, \ldots, r)$. We make the crucial assumption that encounters occur at random between the members of the population. (For other assumptions, see Eshel and Cavalli-Sforza [1982] and Cavalli-Sforza and Feldman [1983]). Under these conditions y_j can equally well be regarded as the probability that one's randomly chosen opponent will choose the pure strategy α_j $(j = 1, 2, \ldots, r)$.

Suppose that v_{ij} is the expected payoff for an individual who chooses the pure strategy α_i on encountering an opponent with pure strategy α_j; here payoff is measured as viability. The matrix $\|v_{ij}\|$ defines the population game. From (12), the expected payoff for an α_i-strategy individual playing against a randomly chosen opponent from a $\mathbf{y}$-strategy population is $\Sigma_{j=1}^r y_j v_{ij}$. The expected payoff to an individual with mixed strategy $\mathbf{h}$ is

$$v(\mathbf{h}, \mathbf{y}) = \sum_{i=1}^{r} \sum_{j=1}^{r} h_i y_j v_{ij}. \tag{13}$$

A population strategy $\mathbf{y}^*$ is ESS if for all $\mathbf{h} \neq \mathbf{y}^*$

$$v(\mathbf{y}^*, \mathbf{y}^*) \geq v(\mathbf{h}, \mathbf{y}^*), \tag{14}$$

and in the case of equality in (14)

$$v(\mathbf{y}^*, \mathbf{h}) > v(\mathbf{h}, \mathbf{h}) \tag{15}$$

(Maynard Smith 1974; Bishop and Cannings 1976). Equivalently, suppose that a sufficiently small minority in the population, ϵ, chooses a strategy $\mathbf{h}$ different from

the ESS population strategy $\mathbf{y}^*$. Then the population strategy becomes $(1 - \epsilon)\,\mathbf{y}^* + \epsilon\mathbf{h}$ and

$$\begin{aligned} v[\mathbf{h}, (1 - \epsilon)\,\mathbf{y}^* + \epsilon\mathbf{h}] &= \epsilon\, v(\mathbf{h}, \mathbf{h}) + (1 - \epsilon)\, v(\mathbf{h}, \mathbf{y}^*) \\ &< \epsilon\, v(\mathbf{y}^*\, \mathbf{h}) + (1 - \epsilon)\, v(\mathbf{y}^*, \mathbf{y}^*) \qquad (16) \\ &= v[\mathbf{y}^*, (1 - \epsilon)\,\mathbf{y}^* + \epsilon\mathbf{h}] \end{aligned}$$

(see, e.g., Taylor and Jonker 1978; Hofbauer et al. 1979). That is, in playing against a random opponent from a population sufficiently close to an ESS strategy, the minority strategy $\mathbf{h}$ receives a smaller payoff.

Our ultimate objective is to obtain some information about the dynamic properties of ESS in two-locus genetic models. To this end we proceed with some more general continuity features of ESS. Suppose that $\hat{\mathbf{y}}$ is a population strategy determined by a distribution of types in the population (e.g., by some genetic equilibrium), and let $\hat{\mathbf{y}}$ be close to an ESS $\mathbf{y}^*$. That is, for a given small $\delta > 0$, $\|\hat{\mathbf{y}} - \mathbf{y}^*\| < \delta$ with Euclidean norm $\|\cdot\|$. In this case there is a positive ϵ $(0 < \epsilon < \delta)$ and a strategy $\mathbf{k} \neq \mathbf{y}^*$, within the r-dimensional simplex of strategies, such that

$$\hat{\mathbf{y}} = \epsilon\,\mathbf{k} + (1 - \epsilon)\,\mathbf{y}^*. \qquad (17)$$

Since $\mathbf{y}^*$ is an ESS it follows from (16) that

$$\begin{aligned} v(\mathbf{k}, \hat{\mathbf{y}}) &= v[\mathbf{k}, (1 - \epsilon)\,\mathbf{y}^* + \epsilon\,\mathbf{k}] \\ &< v[\mathbf{y}^*, (1 - \epsilon)\mathbf{y}^* + \epsilon\,\mathbf{k}] = v(\mathbf{y}^*, \hat{\mathbf{y}}). \end{aligned}$$

Further, using (17) and (13) we have

$$\begin{aligned} v(\hat{\mathbf{y}}, \hat{\mathbf{y}}) &= v[(1 - \epsilon)\,\mathbf{y}^* + \epsilon\,\mathbf{k}, \hat{\mathbf{y}}] \\ &= (1 - \epsilon)\, v(\mathbf{y}^*, \hat{\mathbf{y}}) + \epsilon\, v(\mathbf{k}, \hat{\mathbf{y}}) \qquad (18) \\ &< v(\mathbf{y}^*, \hat{\mathbf{y}}) \end{aligned}$$

(Hofbauer et al. 1979). In other words if $\hat{\mathbf{y}}$ is sufficiently close to $\mathbf{y}^*$, then $\mathbf{y}^*$ is a better strategy against $\hat{\mathbf{y}}$ than is $\hat{\mathbf{y}}$.

This line of reasoning can be used to show *Proposition 2:* Let $\hat{\mathbf{y}}$ be a population strategy close enough to an ESS $\mathbf{y}^*$. A proportion of a mutant strategy $\mathbf{h}$ in the exact direction of $\mathbf{y}^*$ or beyond, i.e., such that

$$\mathbf{h} - \hat{\mathbf{y}} = c(\mathbf{y}^* - \hat{\mathbf{y}}) \qquad (19)$$

for some $c > 0$, is advantageous over $\hat{\mathbf{y}}$ when $\mathbf{h}$ is sufficiently rare. A mutant strategy in the opposite direction under the same conditions, i.e.,

$$\mathbf{h} - \hat{\mathbf{y}} = -c(\mathbf{y}^* - \hat{\mathbf{y}}) \qquad (19')$$

is inferior to the population strategy $\hat{\mathbf{y}}$.

To see this note that if $\mathbf{h} = (1 - c)\,\hat{\mathbf{y}} + c\mathbf{y}^*$ then

$$v(\mathbf{h}, \hat{\mathbf{y}}) = (1 - c)\, v(\hat{\mathbf{y}}, \hat{\mathbf{y}}) + c\, v(\mathbf{y}^*, \hat{\mathbf{y}})$$

and, from (18) with $c > 0$ we have $v(\mathbf{h}, \hat{\mathbf{y}}) > v(\hat{\mathbf{y}}, \hat{\mathbf{y}})$. In other words, $\mathbf{h}$ is better than

the original population strategy $\hat{\mathbf{y}}$ against $\hat{\mathbf{y}}$. By continuity, it follows that $\mathbf{h}$ is also better than $\hat{\mathbf{y}}$ against any new population strategy consisting of a large enough proportion of $\hat{\mathbf{y}}$ and a small enough proportion of $\mathbf{h}$.

In the two-strategy case ($r = 2$) any deviation from the population strategy can be expressed as one of (19) and (19′). In this case we have *Proposition 2′:* In a two-strategy game, if a population strategy $\hat{\mathbf{y}}$ is sufficiently close to an ESS $\mathbf{y}^*$, then a sufficiently rare new mutant strategy is superior to the $\hat{\mathbf{y}}$ if and only if it is in the direction of $\mathbf{y}^*$, or beyond.

When $r > 2$, deviation from the population strategy is multidimensional and the direction of this deviation must be clarified. However, a stronger version of Proposition 2 may be obtained. We require the *Definition:* Let $\mathbf{y}^{(1)}$ and $\mathbf{y}^{(2)}$ be any strategies (mixed or pure). A strategy $\mathbf{y}^{(3)}$ is said to deviate from $\mathbf{y}^{(1)}$ in the approximate direction of $\mathbf{y}^{(2)}$ if the zero-sum vector $\mathbf{y}^{(3)} - \mathbf{y}^{(1)}$ falls within some sharp cone around the direction of the deviation $\mathbf{y}^{(2)} - \mathbf{y}^{(1)}$. $\mathbf{y}^{(3)}$ is said to be in approximately the opposite direction to $\mathbf{y}^{(2)}$ if it falls within the adjacent cone around $-[\mathbf{y}^{(2)} - \mathbf{y}^{(1)}]$. Clearly $\mathbf{y}^{(3)}$ deviates from $\mathbf{y}^{(1)}$ in the approximate direction of $\mathbf{y}^{(2)}$ if and only if for an arbitrary strategy $\mathbf{y}$ we can write

$$\mathbf{y}^{(3)} - \mathbf{y}^{(1)} = \alpha[\mathbf{y}^{(2)} - \mathbf{y}^{(1)}] + \beta[\mathbf{y} - \mathbf{y}^{(1)}] \tag{20}$$

where $\alpha, \beta > 0$ and β/α is bounded from above. This enables us to show *Proposition 3:* Let $\hat{\mathbf{y}}$ be a population strategy sufficiently close to an ESS $\mathbf{y}^*$. Then a mutant strategy $\mathbf{h}$ in small enough frequency will be advantageous against $\hat{\mathbf{y}}$ if it is in the approximate direction of $\mathbf{y}^*$, and disadvantageous against $\mathbf{y}^*$ if it is in approximately the opposite direction.

To see this refer to (18) from which it follows that there is a value $0 < \theta < 1$ such that

$$v(\hat{\mathbf{y}}, \hat{\mathbf{y}}) = \theta\, v(\mathbf{y}^*, \hat{\mathbf{y}}). \tag{21}$$

If a mutant strategy $\mathbf{h}$ deviates from $\hat{\mathbf{y}}$ in the approximate direction of $\mathbf{y}^*$ then

$$\mathbf{h} - \hat{\mathbf{y}} = \alpha(\mathbf{y}^* - \hat{\mathbf{y}}) + \xi\,\alpha(\mathbf{y} - \hat{\mathbf{y}}) \tag{22}$$

for some arbitrary $\mathbf{y}$ in the simplex of strategies, $\alpha > 0$ and sufficiently small $\xi > 0$. From (22) it follows that

$$v(\mathbf{h}, \hat{\mathbf{y}}) = (1 - \alpha - \alpha\xi)\, v(\hat{\mathbf{y}}, \hat{\mathbf{y}}) + \alpha\, v(\mathbf{y}^*, \hat{\mathbf{y}}) + \alpha\xi\, v(\mathbf{y}, \hat{\mathbf{y}}).$$

From this and (21) we infer that

$$v(\mathbf{h}, \hat{\mathbf{y}}) > (1 - \alpha - \alpha\xi)\, v(\hat{\mathbf{y}}, \hat{\mathbf{y}}) + \frac{\alpha}{\theta}\, v(\hat{\mathbf{y}}, \hat{\mathbf{y}}).$$

Hence for $0 < \xi < (1 - \theta)/\theta$ we have

$$v(\hat{\mathbf{h}}, \hat{\mathbf{y}}) > v(\hat{\mathbf{y}}, \hat{\mathbf{y}}). \tag{23}$$

In the same way $v(\mathbf{h}, \hat{\mathbf{y}}) < v(\hat{\mathbf{y}}, \hat{\mathbf{y}})$ if $\mathbf{h}$ deviates from $\hat{\mathbf{y}}$ in approximately the opposite direction to $\mathbf{y}^*$. By continuity, it further follows that if $\mathbf{h}$ is sufficiently rare and deviates from $\mathbf{y}^*$ in the approximate direction of $\mathbf{y}^*$ then it is also advantangeous over any mixture of $\hat{\mathbf{y}}$ and $\mathbf{h}$.

These general ESS considerations can be applied to the two-locus genetic situation. Consider a population defined at two genetic loci such that an individual with genotype A_iB_j/A_kB_ℓ ($i, k = 1, 2, \ldots, n; j, \ell = 1, 2, \ldots m$) has the mixed strategy $\mathbf{h}^{(ijk\ell)}$. Let the frequency of the chromosome A_iB_j among newborn offspring (or, equivalently, among adults before encounters occur), be x_{ij}. With random mating the frequencies of the genotypes A_iB_j/A_kB_ℓ at this stage are $2x_{ij}x_{k\ell}$ if $(i, j) \neq (k, \ell)$ and x_{ij}^2 if $(i, j) = (k, \ell)$. From (12) the population strategy is

$$\mathbf{y} = \sum_{ijk\ell} x_{ij}x_{k\ell}\mathbf{h}^{(ijk\ell)}. \tag{24}$$

Using viability as the payoff, i.e., the probability that an individual survives an encounter with a randomly chosen opponent, the payoff to A_iB_j/A_kB_ℓ is

$$w_{ijk\ell} = v[\mathbf{h}^{(ijk\ell)}, \mathbf{y}]. \tag{25}$$

These viabilities substituted into (3) determine the (frequency-dependent) genotype frequency transformation.

Suppose now that $\hat{\mathbf{x}} = \|\hat{x}_{ij}\|$ is a chromosome frequency equilibrium and let the population strategy $\hat{\mathbf{y}}$ (from [24]) determined by this equilibrium be close to an ESS $\mathbf{y}^*$. Assume, further, that a mutant allele A_{n+1} occurs at low frequency in the population. Let $\mathbf{h}^{(n+1,jk\ell)}$ be the strategy of $A_{n+1}B_j/A_kB_\ell$. Its viability will initially be

$$w_{n+1,jk\ell} = v[\mathbf{h}^{(n+1,jk\ell)}, \hat{\mathbf{y}}). \tag{26}$$

By Proposition 1, A_{n+1} will invade the population if

$$\sum_j u_j \sum_{k,\ell} \hat{x}_{k\ell} w_{n+1,jk\ell} > \bar{W}. \tag{27}$$

Now let

$$\tilde{\mathbf{h}} = \sum_j u_j \sum_{k\ell} \hat{x}_{k\ell}\mathbf{h}^{(n+1,jk\ell)} \tag{28}$$

be the appropriately weighted average strategy of individuals carrying A_{n+1}. Then we may rewrite (27) as

$$v(\tilde{\mathbf{h}}, \hat{\mathbf{y}}) > v(\hat{\mathbf{y}}, \hat{\mathbf{y}}), \tag{29}$$

which, together with proposition 2, allows us to state *Proposition 4:* In a two-strategy population viability game in which the individual strategies result from a two-locus genetic system with random mating, suppose that the population strategy, $\hat{\mathbf{y}}$, determined by a genotype frequency equilibrium, is sufficiently close to an ESS $\mathbf{y}^*$ of the game. Then a new mutant allele will invade the population if and only if its appropriately weighted average strategy deviates from the population strategy in the direction of the ESS $\mathbf{y}^*$ (or beyond).

Here by "appropriate weights" we mean the normalized values of the leading right eigenvector of the linear genotypic transformation near the genotype frequency equilibrium. If the population remains long enough within a small vicinity

Δ of the original equilibrium, then the relative frequencies of the mutant chromosomes become as close to the right eigenvector as we please. Hence, if we start from a sufficiently small subneighborhood Δ', then these frequencies can be made as close to the right eigenvector as we wish before the population leaves Δ. The weighted average strategy of the entire population (mutant and nonmutant) will then be closer to the ESS than the original equilibrium population if and only if the appropriately weighted mutant strategy is in the direction of the ESS or beyond. This we may restate as *Proposition 4':* Under the conditions of Proposition 4, a mutant allele will succeed if and only if it renders the population strategy (at least at some initial stage) closer to the ESS.

Proposition 3 allows a corresponding multidimensional result: *Proposition 5.* Suppose that in a general population viability game the individual strategy results from a two-locus genetic system with random mating. If the population strategy $\hat{\mathbf{y}}$ determined by a genotype frequency equilibrium is sufficiently close to an ESS $\mathbf{y}^*$ of the game, then a new mutant will invade the population if its appropriately weighted average strategy deviates from the population strategy in the approximate direction of $\mathbf{y}^*$. It is selected against if its appropriately weighted strategy deviates from the population strategy in the opposite direction.

DISCUSSION

In one-locus multiple-allele genetic systems a new mutant allele will increase (when rare) if its marginal fitness exceeds the average fitness of the resident population (e.g., Kingman 1961). Conditions for initial increase of a mutant at a monomorphic locus linked to another with two alleles were obtained by Bodmer and Felsenstein (1967). These conditions, while algebraically complicated, of course, can be summarized by the more general Proposition 1 above. Proposition 1 shows that a correctly defined marginal average fitness takes the role of the classical one-locus marginal fitness, and illustrates to what extent the increasing mean fitness property might be regarded as being valid for more than one gene. This average uses as weights the leading right eigenvector of the local stability matrix for initial increase, which, of course, may not be easy to evaluate directly.

Propositions 4 and 5 pertain to the long-term stability properties of an ESS strategy in a two-locus genetic system. A continuity property similar to that of Proposition 4 has been shown to hold for the one-to-one sex ratio when sex is determined by an autosomal locus (Eshel and Feldman 1982) and for Mendelian segregation when the segregation ratio is controlled by an unlinked modifier (Eshel 1985). We have termed this property Evolutionary Genetic Stability (EGS) to emphasize that the phenotypic changes result from the accumulation of genetic mutants and the dynamics of the latter are actually what the model depicts.

The concept of EGS applies to a phenotype strategy $\mathbf{x}$ (mixed or pure) within a given genetic system, if, within this system, a new mutation is favored if and only if it renders the population strategy closer to $\mathbf{x}$. That $\mathbf{x}$ is EGS does not necessarily imply that genetic equilibria are those that determine x. For example, the implication is valid in the case of sex ratio determined by an autosomal one-locus system but not valid in the case of a two-locus viability system. The concept of EGS

differs from ESS by the former's independence from arbitrary assumptions about optimization with respect to some "natural" payment function. In at least some specific, well-defined cases the two appear to coincide thereby validating commonsense ESS arguments.

For a two-strategy population viability game determined by a one-locus genetic system, strong results have been shown by Lessard (1984). He showed that a new mutation will invade the system if and only if it initially renders the population strategy closer to the ESS (in the sense of this paper) and further, the population will achieve a new stable equilibrium which determines a population strategy closer (in Euclidean norm) to the ESS. Lessard (1984) called the stronger property for a two-strategy one-locus ESS "evolutionary attractiveness." It has not yet been demonstrated in any other case.

Karlin and Lessard (1983) showed that in the case of sex ratio determined by an autosomal gene, if the one-locus genetic system converges, then it converges to an equilibrium closer to the one-to-one sex ratio ESS than the point of departure. It is important to note, however, that in the two-strategy situation any one-locus genetic equilibrium determines a population strategy which is locally closest to the ESS (Eshel 1982; Lessard 1984). This is not necessarily true for two-locus systems.

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