



LETTER TO THE EDITOR

**Relative Advantage: a Substitute for Mean Fitness in Fisher’s Fundamental Theorem?\***

The notion of Darwinian selection naturally implies the question whether there exists a quantity which increases during the evolution of a population. The first, classical answer to this question was Fisher’s Fundamental Theorem of Natural Selection (1930) stating the following. “*The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time*”. This statement has been the subject of controversy and exegesis for decades. Recently, it has been strongly criticized by Nagylaki (1987, 1989, 1991). On the other hand, much effort has been made to make clear the correct conditions of Fisher’s statement, giving revisited versions of his Fundamental Theorem (see e.g. Price, 1972; Ewens 1989, 1992; Lessard, 1997). Further historical details of this controversy can be traced from the references of the above papers.

The classical Fisher model describes selection on zygotes, in terms of allele frequencies. Denote by  $n$  the number of alleles at a single locus. Let  $\mathbf{A} := (a_{ij})_{n \times n}$  be the fitness matrix where  $a_{ij} > 0$  denotes the fitness of an  $A_i A_j$  zygote. In the *discrete-time* model, for the frequency of allele  $A_i$   $x_i$  as function of time, we have the following replicator equation:

$$x_i(t + 1) = \frac{x_i(t)(\mathbf{A}x(t))_i}{x(t)\mathbf{A}x(t)}. \quad (1)$$

The corresponding *continuous-time* dynamics is obtained in the standard way, replacing  $x_i(t + 1) - x_i(t)$  with  $\dot{x}_i$ , to get

$$\dot{x}_i = \frac{x_i[(\mathbf{A}x)_i - x\mathbf{A}x]}{x\mathbf{A}x}.$$

The latter equation is parallel to that given by Maynard Smith (1982) for phenotypic evolution. Since the omission of the positive denominator  $x\mathbf{A}x$  does not change the qualitative behaviour of the considered dynamics, the following continuous-time *replicator equation* (Hofbauer & Sigmund, 1988) is also generally accepted:

$$\dot{x}_i = x_i[(\mathbf{A}x)_i - x\mathbf{A}x]. \quad (2)$$

Formally, both Fisher’s selection equation and the classical evolutionary game dynamics are particular cases of eqn (2). In this model, the mean fitness of the whole population in state  $x \in S_n$  is defined as  $W(x) = x\mathbf{A}x$ . Fisher’s statement holds for both dynamics (1) and (2): in the course of selection the mean fitness increases. Furthermore, in the continuous-time model the rate of change in the mean fitness is proportional to the variance of the marginal fitnesses of the alleles (see Fisher, 1958; Hofbauer & Sigmund, 1988). In the discrete-time case, this variance provides only a lower estimate for the change in mean fitness (see Lyubich, 1992, p. 313). In the proof of the above results the symmetry of the fitness matrix is crucial.

Evolutionary game theory deals with the frequency-dependent selection in asexual populations, describing its phenotypic evolution

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(Maynard Smith, 1974). In the main body of this paper, we shall consider only symmetric game conflicts which means each individual has the same strategy set and pay-off function (see e.g. Maynard Smith, 1982). In general, there is no biological reason for the pay-off matrix to be symmetric. The case of the symmetric game conflict with symmetric pay-off matrix is called a partnership game (see e.g. Hofbauer & Sigmund, 1998). The game dynamics modelling this process is formally the same as Fisher's equation [see eqn (2)] if  $x_i$  is the relative frequency of the  $i$ th behavioural phenotype in the population, and  $a_{ij}$  stands for the pay-off of an  $i$ -strategist gained from its conflict with a  $j$ -strategist. (Here, without loss of generality, we can also suppose that  $a_{ij} > 0$ .) If the pay-off matrix  $\mathbf{A}$  is symmetric then the above Fisher's theorem also holds.

In this paper, we shall study the following question. What biological quantity other than the mean fitness will increase in the course of the replicator selection? In mathematical terms, this quantity should be a Lyapunov function for the replicator dynamics. Our investigation will be restricted to the case of an interior equilibrium, meaning coexistence of all replicator types.

### Analogue of Fisher's Fundamental Theorem of Natural Selection

Given a rest point of the replicator dynamics,  $p^* \in S_n$ , we recall the concept of *relative advantage* function defined for each population state  $x \in S_n$  as follows:

$$\Phi: S_n \rightarrow \mathbf{R}, \quad \Phi(x) = p^* \mathbf{A}x - x \mathbf{A}x.$$

This notion was introduced in evolutionary game theory (see e.g. Hofbauer & Sigmund, 1990). Quantity  $\Phi$  gives the difference between the fitness of a  $p^*$ -strategist and the mean fitness of the population. The state  $p^*$  is evolutionarily stable if the relative advantage is positive near  $p^*$ . Below we shall use the following (global) characterization of evolutionary stability. A state  $p^* \in \text{int } S_n$  is a totally mixed (or interior) *evolutionarily stable state* (ESS) if and only if it is an equilibrium point, i.e.,

$$(\mathbf{A}p^*)_i = (\mathbf{A}p^*)_j \quad \text{for all } i, j \in 1, \dots, n,$$

and

$$\begin{aligned} \Phi(x) &= p^* \mathbf{A}x - x \mathbf{A}x = (p^* - x) \mathbf{A}(x - p^*) > 0 \\ &(x \in S_n, x \neq p^*) \end{aligned}$$

(see Hofbauer & Sigmund, 1988).

Now we are in position to formulate the following.

**Theorem.** *Let us suppose that the matrix  $\mathbf{A}$  is symmetric. If  $p^* \in \text{int } S_n$  is a totally mixed ESS then*

(i) *the relative advantage function decreases in the course of replicator selection, and*

(ii) *the rate of decrease is proportional to the variance of the marginal fitnesses of the replicators.*

**Proof.** Let  $x$  be the current population state [a solution of the replicator dynamics (2)]. Since  $\mathbf{A}$  is symmetric and  $(\mathbf{A}p^*)_i = (\mathbf{A}p^*)_j$  ( $i, j \in 1, \dots, n$ ), for the composite function  $\Phi \circ x$  we have

$$\begin{aligned} -\frac{1}{2}(\Phi \circ x)' &= \frac{1}{2} \dot{x} [\mathbf{A} + \mathbf{A}^T] x - \frac{1}{2} \dot{x} [\mathbf{A} + \mathbf{A}^T] p^* \\ &= \frac{1}{2} \dot{x} [\mathbf{A} + \mathbf{A}^T] x = \dot{x} \mathbf{A}x. \end{aligned}$$

This means that the rate of change in relative advantage in the course of selection equals the rate of change in mean population fitness. From now on we can proceed as in proof of Fisher's theorem:

$$\begin{aligned} -\frac{1}{2}(\Phi \circ x)' &= \dot{x} \mathbf{A}x = \sum_i x_i [(\mathbf{A}x)_i - x \mathbf{A}x] (\mathbf{A}x)_i \\ &= \sum_i x_i (\mathbf{A}x)_i^2 - [x \mathbf{A}x]^2 \\ &= \sum_i x_i [(\mathbf{A}x)_i - x \mathbf{A}x]^2 \\ &= \text{Var}(\mathbf{A}x) \geq 0, \end{aligned}$$

and the equality holds only at  $p^*$ .  $\square$

In particular, from the definition of the relative advantage of an ESS and the above proof we obtain that  $\Phi$  is a Lyapunov function providing asymptotic stability of the ESS which is a known result (see e.g. Hofbauer & Sigmund, 1988). On the other hand, in the considered symmetric case

(Fisher's selection model and partnership games) the mean population fitness is known to be a Lyapunov function.

**Remark 1.** We note that a counterpart of the Theorem also holds for discrete-time dynamics (1). Indeed,

$$\begin{aligned} \Phi(x(t+1)) - \Phi(x(t)) \\ = x(t)\mathbf{A}x(t) - x(t+1)\mathbf{A}x(t+1). \end{aligned}$$

For the change in relative advantage, instead of statement (ii) of the Theorem, an estimate in terms of variance can be given (see Lyubich, 1992, p. 313).

Similar to Fisher's Fundamental Theorem of Natural Selection, our Theorem holds both for the classical Fisher selection model and for symmetric matrix game dynamics.

**Remark 2.** Consider now the case of a non-symmetric pay-off matrix  $\mathbf{A}$  of a symmetric game conflict. Then we have

$$\begin{aligned} -\frac{1}{2}(\Phi \circ x)' &= \dot{x}[\mathbf{A} + \mathbf{A}^T](x - p^*) \\ &= \dot{x}\mathbf{A}x + \dot{x}\mathbf{A}^T(x - p^*) \\ &= \text{Var}(\mathbf{A}x) + \text{Cov}(\mathbf{A}(x - p^*), \mathbf{A}^T(x - p^*)), \end{aligned}$$

since

$$\begin{aligned} \dot{x}\mathbf{A}^T(x - p^*) &= \sum_{i=1}^n x_i[(\mathbf{A}x)_i - x\mathbf{A}x - (\mathbf{A}p^*)_i \\ &\quad + x\mathbf{A}p^*](\mathbf{A}^T(x - p^*))_i \\ &= \sum_{i=1}^n x_i[(\mathbf{A}(x - p^*))_i \\ &\quad - x\mathbf{A}(x - p^*)](\mathbf{A}^T(x - p^*))_i \\ &= \sum_{i=1}^n x_i(\mathbf{A}(x - p^*))_i(\mathbf{A}^T(x - p^*))_i \\ &\quad - x\mathbf{A}(x - p^*) \sum_{i=1}^n x_i(\mathbf{A}^T(x - p^*))_i \\ &= \text{Cov}(\mathbf{A}(x - p^*), \mathbf{A}^T(x - p^*)). \end{aligned}$$

Therefore, the lack of symmetry of matrix  $\mathbf{A}$  implies that, along with the variance, a covariance term also appears. Thus, the positivity necessary for the proof of statement (i) of our Theorem is not straightforward.

**Remark 3.** Let us consider a symmetric conflict with non-symmetric pay-off matrix

$$\mathbf{A} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}.$$

It is well-known (see e.g. Maynard Smith, 1982) that if  $\alpha := b - a + c - d > 0$  and  $(c - d)/\alpha \in ]0, 1[$  then  $p^* = ((c - d)/\alpha, (d - a)/\alpha)$  is a unique totally mixed ESS. Now, using  $x_1 + x_2 = 1$ , the sum of variance and covariance calculated in Remark 2, in this particular case is

$$\begin{aligned} x_1(1 - x_1)(\alpha x_1 + b - d)(2\alpha(x_1 - p_1^*) \\ + b + c - 2d) \quad (x_1 \in [0, 1]). \end{aligned}$$

For a proof of statement (i) of our Theorem it is enough to see that this quantity is non-positive for  $x$  near  $p^*$  and equals 0 if and only if  $x = p^*$ . Since  $p^*$  is totally mixed, the latter statement holds if and only if  $(\alpha x_1 + b - d)(2\alpha(x_1 - p_1^*) + b + c - 2d)$  ( $x_1 \in [0, 1]$ ) attains a maximum at  $x_1 = p_1^*$ , which is obvious from an elementary calculation. (Actually,  $\Phi$  is a Lyapunov function again.) Summing up, even for a non-symmetric  $2 \times 2$  pay-off matrix, we obtained that the relative advantage of a totally mixed ESS is a quantity being minimized during the selection process.

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