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LETTERS TO THE EDITOR

AN INEQUALITY FROM GENETICS

E. SENETA,* *University of Sydney*

Abstract

A class of fitness matrices whose parameters may be varied to give differing stability structure is shown by Chebyshev's covariance inequality to possess a variance lower bound for the change in mean fitness.

FUNDAMENTAL THEOREM OF NATURAL SELECTION; CHEBYSHEV'S COVARIANCE INEQUALITY

Suppose $W = \{w_{ij}\}_{i,j=1}^{k}$ is a symmetric matrix with non-negative entries (not all zero) and $\boldsymbol{p} = \{p_i\}_{i=1}^{k}$ is a probability vector. Define

$$\bar{w}_i = \sum_j w_{ij} p_j, \qquad \bar{w} = \sum_i \bar{w}_i p_i, \qquad \sigma_G^2 = \sum_i p_i (\bar{w}_i - \bar{w})^2.$$

Assuming $\bar{w} \neq 0$, define an 'updated' probability vector $\boldsymbol{p}' = \{p_i'\}_{i=1}^{k}$ by $p_i' = \bar{w}_i p_i / \bar{w}$, $i = 1, \cdots, k$ and 'updated' $\bar{w}_i'$ and $\bar{w}'$ accordingly. We are concerned with W for which the inequality

$$\delta \overset{\text{def}}{=} \bar{w}' - \bar{w} \geqq \sigma_G^2 / \bar{w} \tag{1}$$

holds for all $\boldsymbol{p}$ which give $\bar{w} > 0$. The significance of this inequality in relation to a mathematical formulation of Fisher's fundamental theorem of natural selection is explained in [2], where it is shown that the 'mean fitness change', δ, is given by

$$\delta = (2\sigma_G^2/\bar{w}) + \boldsymbol{\Delta}^T W \boldsymbol{\Delta} \tag{2}$$

with $\boldsymbol{\Delta} = \boldsymbol{p}' - \boldsymbol{p}$. Since $\boldsymbol{\Delta}^T \mathbf{1} = 0$, it follows that if W has the property that $\boldsymbol{\alpha}^T W \boldsymbol{\alpha} \geqq 0$ for any real $\boldsymbol{\alpha}$ satisfying $\boldsymbol{\alpha}^T \mathbf{1} = 0$, then (1) holds. Indeed the three standard structures of W considered in [2] all satisfy this condition, which ensures that any internal equilibrium point (i.e. a point $\boldsymbol{p}$ such that $\boldsymbol{p} = \boldsymbol{p}' > \mathbf{0}$) is a minimum of the fitness function $\boldsymbol{p}^T W \boldsymbol{p}$ considered as a function of the probability vector $\boldsymbol{p}$, and hence is unstable. On the other hand, the example (due to J. F. C. Kingman and E. Thompson) ([2], [3] where $k = 3$, $w_{11} = 1$, $w_{23} = w_{32} = h > 0$, $w_{ij} = 0$ otherwise, used to show that for appropriately chosen h (1) cannot hold uniformly for all $\boldsymbol{p} > \mathbf{0}$, has a unique internal equilibrium point $\boldsymbol{p} = (h, 1, 1)^T/(h+2)$ which is a saddlepoint of the fitness-function, since $\boldsymbol{\alpha}^T W \boldsymbol{\alpha} = \alpha_1^2 + 2h\alpha_2\alpha_3 = \alpha_1^2 - 2h\alpha_2^2 - 2h\alpha_1\alpha_2$ (since $\alpha_1 + \alpha_2 + \alpha_3 = 0$), and this can be made either positive or negative. The case of general W with $k = 2$ always satisfies $\boldsymbol{\alpha}' W \boldsymbol{\alpha} \geqq 0$ or $\leqq 0$ for $\boldsymbol{\alpha}^T \mathbf{1} = 0$, and always satisfies (1) [2].

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* Postal address: Department of Mathematical Statistics, University of Sydney, NSW 2006, Australia.

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The above results raise a number of questions, a primary one of which is the existence of classes of W satisfying (1) for all $\boldsymbol{p}$ but not necessarily satisfying $\boldsymbol{\alpha}^T W \boldsymbol{\alpha} \geqq 0$ for all $\boldsymbol{\alpha}$ with $\boldsymbol{\alpha}^T \mathbf{1} = 0$. To this end consider for $\beta \geqq 0$, $w_{ii} \geqq 0$, $i = 1, \cdots, k$

$$W = \beta \mathbf{1}\mathbf{1}' + \operatorname{diag}\{w_{ii} - \beta\}. \tag{3}$$

There is an internal equilibrium point (unique), only if $\beta < \min w_{ii}$, or if $\beta > \max w_{ii}$, and $\boldsymbol{\alpha}^T W \boldsymbol{\alpha} = \sum_i \alpha_i^2 (w_{ii} - \beta) \geqq 0$ in the first case and $\leqq 0$ in the second. If W is such that $\min w_{ii} \leqq \beta \leqq \max w_{ii}$, although no internal equilibrium point $\boldsymbol{p}$ exists, it is possible to construct a fixed W such that $\boldsymbol{\alpha}^T W \boldsymbol{\alpha}$ is positive or negative for different choices of $\boldsymbol{\alpha}$ satisfying $\boldsymbol{\alpha}^T \mathbf{1} = 0$. By first noting [2] that in general

$$\delta - (\sigma_G^2 / \bar{w}) = \bar{w}^{-2} \left\{ \sum_{i,j} p_i \bar{w}_i w_{ij} \bar{w}_j p_j - \left(\sum_i p_i \bar{w}_i \right) \left(\sum_i p_i \bar{w}_i^2 \right) \right\} \tag{4}$$

we shall prove that the part in braces is non-negative for all $\boldsymbol{p}$ for the matrix (3), for which

$$\begin{aligned} \bar{w}_i &= w_{ii} p_i + \beta(1 - p_i), \\ &= \beta - p_i(\beta - w_{ii}) \qquad i = 1, \cdots, k. \end{aligned}$$

Then after some simplification the part in braces becomes

$$\begin{aligned} &\beta \left(\sum_i p_i \bar{w}_i \right)^2 + \sum_i (w_{ii} - \beta) p_i^2 \bar{w}_i^2 - \left(\sum_i p_i \bar{w}_i \right) \left(\sum_i p_i \bar{w}_i^2 \right) \\ &= \left(\sum_i p_i \bar{w}_i \right) \left(\beta \sum_i p_i \bar{w}_i - \sum_i p_i \bar{w}_i^2 \right) - \sum_i (\beta - w_{ii}) p_i^2 \bar{w}_i^2 \\ &= \left(\sum_i p_i \bar{w}_i \right) \left(\sum_i p_i^2 \bar{w}_i (\beta - w_{ii}) \right) - \sum_i (\beta - w_{ii}) p_i^2 \bar{w}_i^2 \\ &= \left(\sum_i p_i \bar{w}_i \right) \left(\sum_i p_i \bar{z}_i \right) - \sum_i p_i \bar{w}_i \bar{z}_i \end{aligned} \tag{5}$$

where

$$\bar{z}_i = p_i \bar{w}_i (\beta - w_{ii}) = \bar{w}_i (\beta - \bar{w}_i).$$

Suppose without loss of generality (since only summations are involved) that $\bar{w}_1 \geqq \bar{w}_2 \geqq \cdots \geqq \bar{w}_k$. The function $x(\beta - x)$ is increasing as x increases from 0 to $x = \beta/2$, about which the function is symmetric, and is therefore decreasing thereafter. Thus $\bar{z}_i = \bar{w}_i(\beta - \bar{w}_i)$ is non-decreasing as i increases, so long as $\bar{w}_i \geqq \beta/2$, i.e. so long as $p_i(\beta - w_{ii}) \leqq \beta/2$. Now since $\sum_r^* p_r(\beta - w_{rr}) \leqq \beta$ where $\sum^*$ means summation over any r such that $w_{rr} \leqq \beta$, it follows that there can be at most one r such that $p_r(\beta - w_{rr}) > \beta/2$ i.e. at most, $\bar{w}_k < \beta/2$. Then it follows that $p_{k-1}(\beta - w_{k-1,k-1}) \leqq \beta - p_k(\beta - w_{k,k}) = \bar{w}_k < \beta/2$, so $\bar{w}_{k-1} \geqq \beta - \bar{w}_k > \beta/2$, whence, using the function $x(\beta - x)$, $\bar{w}_{k-1}(\beta - \bar{w}_{k-1}) \leqq (\beta - \bar{w}_k)\bar{w}_k$. Thus we conclude that it is *always* true that $\bar{z}_1 \leqq \bar{z}_2 \leqq \cdots \leqq \bar{z}_k$, and since $\{\bar{w}_i\}$ and $\{\bar{z}_i\}$ vary in opposite directions, it follows from Chebyshev's covariance inequality (e.g. [1], §2.5) that (5) is non-negative.

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