LETTERS TO THE EDITOR

Dear Editor,

Comment on 'Mutations, perturbations and evolutionarily stable strategies'

As part of a study of the role of variability in the theory of evolutionarily stable strategies (ESS), Hines (1982) obtained an approximation to the change in variability from generation to generation of a biological population modelled as in the standard animal conflicts approach of Maynard Smith (1974). The approximation was exact for symmetric distributions, and the error of the approximation was indicated as being 'small for near-symmetric distributions or distributions with small diversity in strategy'. The approximation indicated that variability in the population's strategies would tend to decrease, suggesting eventual convergence in the population to as little diversity as possible, perhaps even to none.

A scaling argment shows that, even with small diversity, decrease in variability need not necessarily hold. We recall that in the language and notation of Hines (1982), individuals of a population engage in contests with randomly selected opponents, each using some strategy s — a probability distribution over a common set of m available tactics or pure strategies. The set of possible strategies form a probability simplex in m-dimensional space. The contests are summarized by payoff matrices V (now more commonly denoted by A). With μ^* denoting the ESS defined below and having the property that for all strategies s, $s^{\mathrm{T}}V\mu^* = \mu^{*\mathrm{T}}V\mu^*$ (if all components of μ^* are positive, as was assumed in the previous paper by Hines and as will be here), the distribution function $F_{n+1}(s)$ for generation $n+1$ can be shown to be generated by that for n by the relationship

$$\begin{aligned} dF_{n+1} &= \alpha_n \boldsymbol{F}(s^{\mathrm{T}}Vt)dF_n \\ &= \alpha_n s^{\mathrm{T}}V\mu_n\, dF_n(s) \end{aligned}$$

where α_n is a normalizing constant which can be expressed as

$$\begin{aligned} \alpha_n &= \mu_n^{\mathrm{T}}V\mu_n^{\mathrm{T}} \\ &= \mu^{*\mathrm{T}}V\mu^* + (\mu_n - \mu^*)^{\mathrm{T}}V(\mu_n - \mu^*) \end{aligned}$$

and where

$$\mu_n = \int_s s\, dF_n(s).$$

With the covariance matrix of strategies in the population at generation n being defined by

$$C_n = \int_s (s-\mu_n)(s-\mu_n)^{\mathrm{T}} dF_n(s),$$

Hines (1982) determined that

$$\mu_{n+1} = \mu_n + \alpha_n C_n V \mu_n$$

and that

$$C_{n+1} = C_n + (\alpha_n C_n V\mu_n)(\mu_n - \mu_{n+1})^{\mathrm{T}} + (\mu_n - \mu_{n+1})(\alpha_n C_n V \mu_n)^{\mathrm{T}}$$
$$+ (\mu_n - \mu_{n+1})(\mu_n - \mu_{n+1})^{\mathrm{T}} + \alpha_n \int_s [(s-\mu_n)(s-\mu_n)^{\mathrm{T}}][(s-\mu_n)^{\mathrm{T}} V\mu_n] dF_n(s).$$

We now modify these results as a preliminary step in exploring their implications. The ESS of a contest described by the payoff matrix V refers to any strategy, say s^*, such that for all other strategies r differing from it, $s^{*\mathrm{T}} V s^* \geqq r^{\mathrm{T}} V s^*$, and for those r leading to exact equality, the additional condition $s^{*\mathrm{T}} V r > r^{\mathrm{T}} V r$. Let μ^* denote such an ESS, and assume that $\mu^* > 0$, component by component. It then follows (as in Hines (1987) for example) that for any covariance matrix of strategies C, $CV\mu^* = 0$, so that

$$\mu_n - \mu_{n+1} = -\alpha_n C_n V(\mu_n - \mu^*)$$

and, with the substitution of this in the above expression for C_{n+1},

$$C_{n+1} = C_n - (\mu_n - \mu_{n+1})(\mu_n - \mu_{n+1})^{\mathrm{T}}$$
$$+ \alpha_n \int_s [(s-\mu_n)(s-\mu_n)^{\mathrm{T}}][(s-\mu_n)^{\mathrm{T}} V(\mu_n - \mu^*)] dF_n(s).$$

The final, third-order term (which is zero for symmetric distributions) in this expression was dropped by Hines to obtain the approximate result cited.

To obtain further insight into this approximation, however, consider an arbitrary distribution over the probability simplex, say F, with mean and covariance matrix μ and C, and consider a related family of distributions $F^{(\varepsilon)}$ which becomes increasingly concentrated at and near μ^* as $\varepsilon \to 0$. Specifically, for S a random vector with distribution function F, let $S^{(\varepsilon)}$ be the related random vector defined by

$$S^{(\varepsilon)} = \mu^* + \varepsilon(S - \mu^*)$$

and let its distribution function be $F^{(\varepsilon)}$. (A referee has noted that this notation is to be interpreted as meaning that $S^{(\varepsilon)}$ has a distribution, such as a normal or a uniform or other distribution, which is more concentrated about μ^* than that of S was; not that $S^{(\varepsilon)}$ is a random vector with a two-point distribution with probability masses $1-\varepsilon$ at μ^* and ε at S.) It is immediate that

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$$\mu^{(\varepsilon)} = \mu^* + \varepsilon(\mu - \mu^*)$$

and that

$$C^{(\varepsilon)} = \varepsilon^2 C.$$

(Although in this model the covariance matrix is of order ε^2, suitable for our present purposes, the covariance matrix under the alternative interpretation is as the referee notes, of order ε.)

As well, in terms of standardized variables,

$$(C^{(\varepsilon)})^{-1/2}(S^{(\varepsilon)} - \mu^{(\varepsilon)}) = C^{-1/2}(S - \mu),$$

so that the standardized forms of S and $S^{(\varepsilon)}$ have the same moments for all $\varepsilon > 0$, and in particular have the same standardized measures of skewness.

For a population with $F^{(\varepsilon)}$ as its distribution in generation 0, and with $\alpha_0^{(\varepsilon)}$ the counterpart to α_0, the mean and variance for generation 1 are given by

$$\mu_1^{(\varepsilon)} = \mu_0^{(\varepsilon)} + \alpha_0^{(\varepsilon)} C_0^{(\varepsilon)} V(\mu_0^{(\varepsilon)} - \mu^*)$$

or

$$\begin{aligned}\mu_1^{(\varepsilon)} - \mu_0^{(\varepsilon)} &= \alpha_0^{(\varepsilon)} C_0^{(\varepsilon)} V(\mu^{(\varepsilon)} - \mu^*)\\ &= \alpha_0^{(\varepsilon)} \varepsilon^2 C_0 V(\mu_0^{(\varepsilon)} - \mu^*).\end{aligned}$$

For μ_0 sufficiently close to μ^* and for ε small, α_0 and $\alpha_0^{(\varepsilon)}$ are both close to $\mu^{*\mathrm{T}} V \mu^*$, and to each other. Therefore,

$$\begin{aligned}C_1^{(\varepsilon)} = C_0^{(\varepsilon)} &- (\mu_0^{(\varepsilon)} - \mu_1^{(\varepsilon)})(\mu_0^{(\varepsilon)} - \mu_1^{(\varepsilon)})^{\mathrm{T}}\\ &+ \alpha_0^{(\varepsilon)} \int_S [(s^{(\varepsilon)} - \mu_0^{(\varepsilon)})(s^{(\varepsilon)} - \mu_0^{(\varepsilon)})^{\mathrm{T}}][(s^{(\varepsilon)} - \mu_0^{(\varepsilon)})^{\mathrm{T}} V(\mu_0^{(\varepsilon)} - \mu^*)] dF_0^{(\varepsilon)}(s),\end{aligned}$$

so that in terms of the unscaled distribution

$$\begin{aligned}C_1^{(\varepsilon)} - C_0^{(\varepsilon)} \simeq &- \varepsilon^6(\mu_0 - \mu_1)(\mu_0 - \mu_1)^{\mathrm{T}}\\ &+ \alpha_0 \varepsilon^4 \int_S [(s - \mu_0)(s - \mu_0)^{\mathrm{T}}][(s - \mu_0)^{\mathrm{T}} V(\mu_0 - \mu^*)] dF_0(s).\end{aligned}$$

For ε small, that final term, involving the third-order central moments of the distribution of S or of $S^{(\varepsilon)}$, dominates if it is not zero. That term can in general be negative definite, positive definite or neither. The presence of any skewness in the distribution of S implies, therefore, that for sufficiently small ε, the effect of that skewness will predominate, determining whether the variability present in the evolving population will increase, decrease, or have some more complex evolution. While the previous analysis by Hines indicates the existence of conditions under which variability of strategies will decrease, it does not establish that such a decrease will in fact occur, or even be necessarily likely. (Again, we note that this demonstration of the importance of a term which appeared

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initially to be comparatively negligible in the limit assumes the interpretation of the definition of $S^{(\varepsilon)}$ previously noted, rather than that commented on by the referee.)

References

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Yours sincerely

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