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EVOLUTIONARILY STABLE STRATEGIES DEPENDING ON POPULATION DENSITY

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ABSTRACT. The concept of evolutionarily stable strategies is extended to include density dependence. Dynamical stability is shown to follow for two-strategy games and for symmetric payoff matrices. It is conjectured that stability also results for general multi-strategy games.

1. The dynamical model. The theory of evolutionarily stable strategies (ESS) has been used primarily to predict long-term outcomes of selection models where an individual's fitness depends on the frequency of strategy-types in the population but not on the total population size (density). The purpose of this paper is to show that suitably-modified ESS concepts remain relevant for stability of more general dynamical models that include both frequency and density dependence.

Suppose each individual in the population uses one of the pure strategies $S_1, \dots, S_n$. Let N_i be the number of S_i-users at time t and $N = \Sigma N_i$ be the density. Then

$$S = [s_1, \dots, s_n],$$

where $s_i = N_i/N$ is a probability vector whose component s_i is the frequency of S_i-users in the population. We refer to S as the mean strategy of the population and to (S, N) as the state of the population at time t.

Assume that the fitness $F_i(S, N)$ of an S_i-individual depends only on the state (S, N), and, furthermore, that this fitness is linear in the components of S. (This linearity can also be obtained by linearizing the dynamics (1.2) about a point.) Then

$$F_i(S, N) = \sum_{k=1}^{n} A_{ik}(N) s_k, \tag{1.1}$$

where we call the $n \times n$ matrix $A(N)$ the density-dependent payoff matrix with entry $A_{ik}(N)$ thought of as the gain (or loss if A_{ik} is negative) in fitness of an S_i-user in a contest against an S_k-user. $F_i(S,N)$ is then the gain in fitness of an S_i-user in a random contest.

The continuous dynamical model results from the assumption that an individual produces offspring using the same strategy at a rate equal to its fitness. That is, $\dot{N}_i = N_i F_i(S,N)$ or, by (1.1),

$$\dot{N}_i = N_i e_i A(N) S, \tag{1.2}$$

where e_i is the unit coordinate vector with 1 in the i^{th} component and $e_i A(N) S$ is the scalar formed by taking the matrix product with S thought of as a column vector.

An elementary calculus exercise yields the equivalent dynamical system

$$\begin{aligned} \dot{N} &= NSA(N)S \\ \dot{s}_i &= s_i(e_i - S)A(N)S. \end{aligned} \tag{1.3}$$

In case $A(N)$ is independent of N, the frequency dynamics $\dot{s}_i$ of (1.3) is the standard density-independent ESS model studied by Taylor and Jonker (1978) among many others [**3**]. There it is shown that an ESS S^* is a locally asymptotically stable equilibrium of the frequency dynamics. But the density dynamics $\dot{N}$ of (1.3) would then follow an exponential curve asymptotically with growth rate $S^* A S^*$, and so it is not meaningful to ask for equilibria of (1.3).

What we are interested in for the rest of this paper is the system (3.1) where there is bona fide dependence of $A(N)$ on N. In particular, we are interested in stability of equilibria of this system.

2. Definition of density dependent ESS. Suppose (S^*, N^*) is an equilibrium of (1.3). Let $A(N^*) = A^*$. From (1.2) we see that $A^* S^*$ must have the i^{th} component zero for every $s_i \neq 0$. Thus, $S^* A^* S^* = 0$ as can be seen directly from the density dynamics of (1.3). Consider the density isocline through (S^*, N^*). This is actually a surface $N = \psi(S)$ of dimension $n-1$. In Figure 1 it is represented as a solid curve since the mean strategy for a two-strategy model is one-dimensional and can be specified by the first component of S between 0 and 1. The dashed frequency isocline $S = \sigma(N)$ is generically one-dimensional with points satisfying $e_i A(N)\sigma(N) = e_j A(N)\sigma(N)$ for all nonzero s_i and s_j.

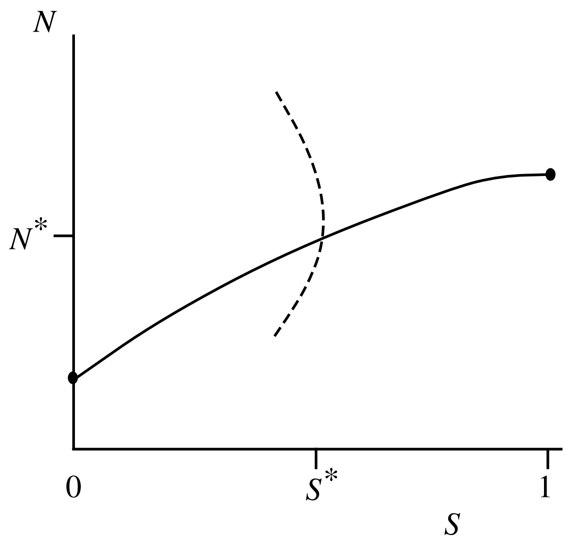

FIGURE 1. Density (solid) and frequency (dashed) isoclines through an equilibrium (S^*, N^*) in the two-strategy model.

DEFINITION . (S^*, N^*) is a DDESS if

(i) $SA^*S^* \le S^*A^*S^*$ for all S;

(ii) $S^*A(\psi(S))S > SA(\psi(S))S$ for all S sufficiently close (but not equal) to S^* for which equality holds in (i).

(iii) $\sigma(N)A(N)\sigma(N)$ is a decreasing function of N near N^*.

The first two conditions are called the frequency conditions while the third is the density condition. If $A(N)$ does not depend on N (i.e., $A(N) = A^*$), the frequency conditions are identical to the ESS conditions [**3**]. In our situation, the right-hand side of the inequalities in (i) and (ii) are both zero. For the two-strategy case, the above definition is the same as that used in [**2**]. The following theorem is a special case of a result proved in the same paper.

THEOREM . *A DDESS is locally asymptotically stable under the dynamics* (1.3) *for the two-strategy model.*

The converse of the above theorem is also true if we ignore the possibility the nonlinear system (1.3) has a linearized eigenvalue with zero real part. Thus, for two-strategy models, the biologically intuitive conditions of a DDESS are equivalent to stability. Practical methods to check these conditions and the connection with two-species population dynamics are elaborated on in [**2**].

3. Multi-strategy density dependent ESS. Suppose (S^*, N^*) is a multi-strategy (i.e., $n > 2$) DDESS and that A^* is a symmetric payoff matrix. The density condition becomes that the derivative of $\sigma(N)A(N)\sigma(N)$ with respect to N is negative at N^*. But $\sigma(N^*) = S^*$, along with A^*S^* and S^*A^* both being zero, implies this derivative is $S^*A'S^*$ where A' is the $n \times n$ matrix of derivatives of $A(N)$ evaluated at N^*. Thus, $\psi(S) < N^*$ for all S sufficiently close (but not equal) to S^*, and this, in turn, implies the second frequency condition is $S^*A^*S > SA^*S$.

To summarize, when A^* is symmetric, (S^*, N^*) is a DDESS if and only if $S^*A'S^* < 0$ and S^* is a density independent ESS for A^*. But these are the exact conditions in [**1**] that are equivalent to stability. That is,

THEOREM . *Assume A^* is symmetric. (S^*, N^*) is a DDESS for the multi-strategy model if and only if it is a locally asymptotically stable equilibrium of the dynamics* (1.3).

Again, the DDESS completely answers the stability problem. Unfortunately, the problem for general nonsymmetric A^* remains open. It is conjectured that the DDESS conditions remain sufficient for stability, and, furthermore, if the dynamics (1.3) is altered to include mixed strategy evolution as in [**2**], then the conditions are also necessary.

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