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Coevolutionary instability of mixed Nash solutions

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1. Introduction

In 1973, Maynard Smith and Price introduced game theory to the study of intraspecific conflicts. The resulting marriage has proved very fruitful of biological models (see Krebs and Davies (1978) for examples). Even simple, biologically intuitive games with a small number of strategies yield evolutionary stable equilibria with an unexpectedly rich mixture of strategy types. Furthermore, in the dynamics of these evolutionary games mathematicians have discovered interestingly complex behavior (see e.g. Bishop and Cannings, 1976; Taylor and Jonker, 1978; Zeeman, 1979).

Here we consider the analogous applications of game theory to conflicts between species (see also Hines (1981)) and examine the dynamics of the resulting coevolutionary games. Our main result, illustrated in detail for 2×2 games, is that no equilibrium of mixed strategies is locally stable. This means that a "coevolutionarily stable situation" is either a vertex equilibrium where each species relies on a single pure strategy, or else it consists of a set of mixed strategies showing no tendency to equilibrium but instead more complicated recurrence, i.e. some sort of cycling of the strategic mixtures.

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2. Coevolutionary processes

We regard the members of a population P as having a choice of strategies indexed by some finite set I. For each choice $i \in I$ there is a payoff A_i which is not constant but will usually depend upon the state of the environment. The state of the population is described by its current distribution of strategies which is a vector $p=\{p_i: i \in I\}$ with $1 \geqslant p_i \geqslant 0$ for all i and $\sum_i p_i = 1$. If the population is in state p then the mean, or average, payoff $A_p = \sum_i p_i A_i$.

For a distribution vector p strategy i is called *active* if $p_i > 0$. The set of active strategies is the support of p, i.e. $\text{supp}(p) = \{i \in I: p_i > 0\}$. p is called *fully mixed*

or *interior* if all strategies are active. At the other extreme, we identify the pure strategy i with the vector δ_i such that $\delta_{ii}=1$ and $\delta_{ij}=0$ for $j\neq i$. So $\text{supp}(\delta_i)=\{i\}$.

If the current generation is in state p then we assume that the weight of strategy i in the next generation will be more or less than p_i according to whether — in the current environment — the payoff A_i is more or less than the mean payoff A_p. Formally, we assume that the transition from the current state to the next state is given by a continuous function (a discrete time dynamical system) satisfying:

$$\text{sgn}(\Delta p_i)=\text{sgn}(A_i-A_p) \qquad (1>p_i>0), \tag{2.1}$$

where the sign of a real number r, sgn(r), is +, 0, or −, according to whether r is positive, zero or negative.

Condition (2.1) is not assumed for extreme values of p_i. If $p_i=0$ then Δp_i cannot be negative as p_i cannot decrease below zero. For behavior on the boundary there are two alternate assumptions. We call the dynamical system *boundary-preserving* if, in addition to (2.1),

$$\Delta p_i=0 \quad (\text{when } p_i=0). \tag{2.2B}$$

This condition means that the pure strategies "breed true". If i is not active in the current population then it cannot appear in subsequent generations.

Alternatively, we call the dynamical system *inward-pointing* if, in addition to (2.1),

$$\text{sgn}(\Delta p_i)=\max(0,\text{sgn}(A_i-A_p)) \quad (\text{when } p_i=0) \tag{2.2I}$$

which means that p_i becomes positive if $A_i>A_p$ but remains at zero if $A_i\leqslant A_p$.

The latter condition should not be confused with the effect of mutation — which we are ignoring. Mutation would instead impose a perturbation on a boundary preserving system (and would override condition (2.1) when p_i is small but positive.

Proposition 1. *In order that p^* be an equilibrium relative to the current environment it is necessary that*

$$A_i=A_{p^*} \quad \textit{for all } i\in\text{supp}(p^*) \tag{2.3}$$

or equivalently, that the payoff for all strategies active for p^* be the same. If the system is boundary-preserving this condition is also sufficient.

If the system is inward pointing it is necessary and sufficient for equilibrium that (2.3) *hold and, in addition,*

$$A_i\leqslant A_{p^*} \quad \textit{for all } i\in I. \tag{2.4}$$

Proof: If $A_i=C$ for all $i\in\text{supp}(p^*)$ then $C=\sum p_i^*C=\sum p_i^*A_i=A_{p^*}$ because the sums are the same whether taken over all i or just over $i\in\text{supp}(p^*)$.

Notice that if $p_i^*=1$ for some i then $p^*=\delta_i$ and $A_i=A_{p^*}$ trivially. Because of the requirement that $1>p_i$ in (2.1), a separate argument — which we leave to the reader — is needed for these pure strategy cases.

Otherwise, $p_i^*<1$ for all i and (2.1) says that $\Delta p_i=0$ for $i\in\text{supp}(p^*)$ if and only if $A_i=A_{p^*}$. (2.2B) says $\Delta p_i=0$ for all inactive i while (2.2I) says that $\Delta p_i=0$ for inactive i if and only if $A_i\leqslant A_{p^*}$.

We need one more game theoretic concept. For $i_1, i_2\in I$ we say that i_1 *dominates* i_2 if $A_{i_1}>A_{i_2}$ for all environmental states.

Lemma 2. *Suppose i_1 dominates i_2. If p^* is an equilibrium, then i_1 and i_2 cannot both be active for p^*, i.e. $p_{i_2}=0$ or $p_{i_1}=0$. If the system is inward pointing then i_2 cannot be active, i.e. $p_{i_2}=0$.*

Proof: If $p^*_{i_2}>0$ and $\Delta p_{i_2}=0$ then $A_{i_1}>A_{i_2}=A_{p^*}$ by domination and (2.3). So by (2.3) again $i_1\notin\text{supp}(p^*)$. If the system is inward pointing the inequality $A_{i_1}>A_{p^*}$ violates (2.4) and so $p^*_{i_2}>0$ contradicts the assumption that p^* is a current equilibrium.

We now apply these preliminaries to two interacting populations P and Q. The strategy choices of P and Q are indexed by finite sets I and J respectively. When an i strategist from P meets a j strategist from Q the payoffs are *constants* A_{ij} and B_{ij} to the P and Q players, respectively. So if the current state of P and Q are given by distributions p and q respectively then the average payoff to an i strategist in P is $A_{iq}\equiv\sum_J A_{ij}q_j$ and the average payoff for the population as a whole is $A_{pq}\equiv\sum_{I,J}p_iA_{ij}q_j$, with similar definitions using B_{ij} for population Q.

We define a *coevolutionary process* for P and Q to be a discrete time dynamical system as above where the state of each population determines the environment of the others. Thus

$$\begin{aligned}&\text{sgn}(\Delta p_i)=\text{sgn}(A_{iq}-A_{pq}) \qquad (1>p_i>0)\\ &\text{sgn}(\Delta q_j)=\text{sgn}(B_{pj}-B_{pq}) \qquad (1>q_j>0).\end{aligned} \tag{2.5}$$

The process is boundary-preserving if, in addition,

$$\begin{aligned}&\Delta p_i=0 \qquad (p_i=0)\\ &\Delta q_j=0 \qquad (q_j=0).\end{aligned} \tag{2.6B}$$

The process is inward pointing if instead

$$\begin{aligned}&\text{sgn}(\Delta p_i)=\max(0,\text{sgn}(A_{iq}-A_{pq})) \qquad (p_i=0)\\ &\text{sgn}(\Delta q_j)=\max(0,\text{sgn}(B_{pj}-B_{pq})) \qquad (q_j=0).\end{aligned} \tag{2.6I}$$

Domination now becomes a finite condition: for $i_1, i_2\in I$, i_1 dominates i_2 if $A_{i_1j}>A_{i_2j}$ for all $j\in J$ and similarly for domination in J. Notice that these conditions are equivalent to the apparently more general: $A_{i_1q}>A_{i_2q}$ for all q.

From Proposition 1 the following is immediate:

Theorem 3. *In order that the pair (p^*, q^*) be an equilibrium for the coevolutionary process it is necessary that*:

$$\begin{aligned}&A_{iq^*}=A_{p^*q^*} \quad \textit{for all } i\in\text{supp}(p^*)\\ &B_{p^*j}=B_{p^*q^*} \quad \textit{for all } j\in\text{supp}(q^*).\end{aligned} \tag{2.7}$$

If the process is boundary preserving these conditions are sufficient as well. If the process is inward pointing it is necessary and sufficient that (2.7) *hold and, in addition*:

$$\begin{aligned}&A_{iq^*}\leqslant A_{p^*q^*} \quad \textit{for all } i\\ &B_{p^*j}\leqslant B_{p^*q^*} \quad \textit{for all } j.\end{aligned} \tag{2.8}$$

A pair satisfying (2.7) and (2.8) is called a *Nash equilibrium.* We will call a pair satisfying (2.7) alone a *weak Nash equilibrium.* Notice that any vertex (δ_i, δ_j) is a weak Nash equilibrium but need not be Nash. On the other hand, the two concepts agree if both p^* and q^* are fully mixed.

Theorem 3 says that once the payoff matrices and boundary behavior are specified the equilibria are determined. They do not depend upon the choice of coevolutionary process.

Nash equilibria always exist. In fact, in our terminology, Nash's proof of this result consists of writing down a particular inward pointing process and applying the Brouwer fixed point theorem.

To illustrate the behavior of coevolutionary processes we specialize to the 2×2 case, i.e. we assume that each population has available two strategies labelled 0 or 1: $I=J=\{0,1\}$. The state of P is described by the real number $p=p_1$ with $0\leqslant p\leqslant 1$ and $p_0=1-p$. Similarly, Q is described by $q=q_1$ with $q_0=1-q$. Notice

$$A_{1q}-A_{pq}=A_{1q}-(pA_{1q}+(1-p)A_{0q})=(1-p)(A_{1q}-A_{0q})$$

whose sign is that of $A_{1q}-A_{0q}=(A_{11}-A_{01})q+(A_{10}-A_{00})(1-q)$ when $0<p<1$. Thus, (2.5) becomes:

$$\begin{aligned}\operatorname{sgn}(\Delta p)&=\operatorname{sgn}(A_{1q}-A_{0q})=\operatorname{sgn}(\alpha_1 q+\alpha_0(1-q)) \qquad (0<p<1)\\ \operatorname{sgn}(\Delta q)&=\operatorname{sgn}(B_{p1}-B_{p0})=\operatorname{sgn}(\beta_1 p+\beta_0(1-p)) \qquad (0<q<1)\end{aligned} \tag{2.9}$$

where

$$\alpha_1=A_{11}-A_{01}, \qquad \alpha_0=A_{10}-A_{00}$$
$$\beta_1=B_{11}-B_{10}, \qquad \beta_0=B_{01}-B_{00}.$$

For the moment we restrict attention to boundary preserving processes and so assume

$$\begin{aligned}\Delta p&=0 \quad \text{when } p=0 \text{ or } 1,\\ \Delta q&=0 \quad \text{when } q=0 \text{ or } 1.\end{aligned} \tag{2.10B}$$

Also, we assume for the moment the following nondegeneracy condition:

$$\text{None of the numbers } \alpha_0, \alpha_1, \beta_0, \beta_1 \text{ vanish.} \tag{2.11}$$

Proposition 4. (a) *If* $\alpha_0, \alpha_1<0$ *then strategy* 0 *dominates strategy* 1 *for* P *and for any* $0<p<1$, $\Delta p<0$. *So* p *decreases monotonically over subsequent generations approaching* 0 *in the limit.*

If $\alpha_0, \alpha_1>0$ *then* 1 *dominates* 0 *for* P *and* 1 *is the limit for all interior initial values.*

(b) *If* $\alpha_0<0<\alpha_1$ *then* $\Delta p=0$ *when* $q=q^*$ *where* $q^*=|\alpha_0/\alpha_1|/(1+|\alpha_0/\alpha_1|)$ *and more generally*

$$\operatorname{sgn}(\Delta p)=\operatorname{sgn}(q-q^*) \text{ for } 0<p<1.$$

If $\alpha_0>0>\alpha_1$ *then* $\operatorname{sgn}(\Delta p)=-\operatorname{sgn}(q-q^*)$.

Proof: Consider the linear function of q: $\alpha_q=\alpha_1 a+\alpha_0(1-q)$. If α_0 and α_1 have like signs then α_q shares this share for all $0\leqslant q\leqslant 1$ and so Δp has this sign for all values of q $(0<p<1)$. Thus the successive values of p form a monotone sequence.

The limiting value must be the p coordinate of an equilibrium and so equals 0 or 1.

On the other hand, if α_0 and α_1 have opposite signs then α_q vanishes at $q = q^*$ and for $q > q^*$ ($q < q^*$) the sign of α_q is that of α_1 (resp. of α_0).

Corollary 5. *Assuming* (2.11), *a nonvertex equilibrium exists if and only if both* α_0, α_1 *and* β_0, β_1 *have unlike signs. There is then a unique, nonvertex equilibrium* (p^*, q^*) *which is fully mixed*:

$$p^* = |\beta_0/\beta_1|/(1+|\beta_0/\beta_1|)$$
$$q^* = |\alpha_0/\alpha_1|/(1+|\alpha_0/\alpha_1|).$$

The behavior of such a 2×2 system falls into one of four categories illustrated by the phase portraits of Figs. 1–4. In Fig. 1 both populations show domination while in Fig. 2 only one does (domination for P is illustrated). In these cases the only equilibria are the vertices. One vertex is a sink attracting every initial position in the interior of the square. The remaining vertices are locally unstable (1 source and 2 saddle points).

Figure 3, which we call the *hyperbolic case*, occurs when there is a fully mixed equilibrium and $\alpha_1 - \alpha_0, \beta_1 - \beta_0$ have like signs. Two vertices are sinks, each attracting initial values from roughly triangular regions separated by an exceptional set of initial points which tend to the saddle point (p^*, q^*). The remaining two vertices are sources.

Figure 4, which we call the *elliptic case*, occurs when there is a fully mixed equilibrium and $\alpha_1 - \alpha_0, \beta_1 - \beta_0$ have unlike signs. No vertex is locally stable as they are all saddles. The interior points orbit around (p^*, q^*). However, as we will see below this interior equilibrium is a source so that nearby orbits spiral outwards. Thus, there are no locally stable equilibria in this case.

Fig. 1. Double domination

$\alpha_0, \alpha_1 < 0$

$\beta_0, \beta_1 < 0$

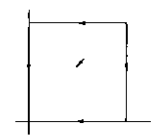


Fig. 2. Single domination

$\alpha_0, \alpha_1 < 0$

$\beta_0 < 0 < \beta_1$

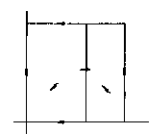


Fig. 3. Hyperbolic case

$\alpha_0 < 0 < \alpha_1$

$\beta_0 < 0 < \beta_1$

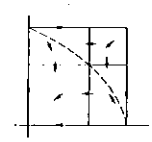
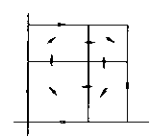


Fig. 4. Elliptic case

$\alpha_0 < 0 < \alpha_1$

$\beta_1 < 0 < \beta_0$



These four robust types are separated by degenerate cases where hypothesis (2.11) does not hold. If $\alpha_0 = \alpha_1 = 0$ then the strategies 0 and 1 are behaviorally indistinguishable for P and $\Delta p = 0$ for all points. On the other hand if only one of α_0, α_1 vanish then P exhibits a weak form of domination. For example, if $\alpha_1 < \alpha_0 = 0$ then $\Delta p < 0$ when $q > 0$ but the entire segment defined by $q = 0$ consists of equilibria.

Finally, if we replace boundary-preserving behavior by the inward pointing assumption the only vertices which are equilibria are the sinks (assuming (2.11)) because only these satisfy the Nash condition (2.8). Thus, for an inward-pointing version of the elliptic case no vertex is an equilibrium and the source (p^*, q^*) is the only equilibrium of the system.

That (p^*, q^*) is a source in the elliptic case is a special case of our main result:

Theorem 6. *A nondegenerate mixed equilibrium is never locally stable with respect to a smooth coevolutionary process.*

By a smooth coevolutionary process we intend a slight sharpening of condition (2.9). So in the 2×2 case we assume that the dynamic is defined by a function $(p, q) \to (f(p, q), g(p, q))$ with

$$\begin{aligned} f(p, q) &= \varphi(p, A_{0q}, A_{1q}) \\ g(p, q) &= \psi(q, B_{p0}, B_{p1}) \end{aligned} \tag{2.12}$$

where φ and ψ are continuously differentiable functions of three real variables satisfying

$$\begin{aligned} &\varphi(p, a, b) = p \\ &\psi(q, a, b) = q \end{aligned} \quad \text{when } a = b \tag{2.13}$$

and

$$\begin{aligned} &\varphi_2 < 0, \varphi_3 < 0 \qquad (0 < p < 1) \\ &\psi_2 < 0, \psi_3 < 0 \qquad (0 < q < 1) \end{aligned} \tag{2.14}$$

where φ_2, φ_3 are the partial derivatives with respect to the second and third variables.

Equation (2.13) means that $f(p, q) = p$ when $A_{0q} = A_{1q}$. (2.14) then implies that $f(p, q) > p$ (or $< p$) if $A_{0q} < A_{1q}$ (resp. $A_{0q} > A_{1q}$). This is condition (2.9) and so explains why we regard (2.13) and (2.14) as the smooth version of (2.9).

Example: Assume that P and Q are randomly mating diploid populations with strategy choices determined by the genotype at one locus with two alleles. Suppose the two alleles for P are P_1 and P_2 and that an individual of genotype $P_\alpha P_\beta$ uses strategy 0 with probability $h_{\alpha\beta}$ $(\alpha, \beta = 1, 2)$. Similarly, an individual of type $Q_\alpha Q_\beta$ uses strategy 0 with probability $k_{\alpha\beta}$ $(\alpha, \beta = 1, 2)$. We assume $h_{11} \geqslant h_{12} \geqslant h_{22}$ with at least one inequality sharp and analogous ordering for the $k_{\alpha\beta}$ probabilities in population Q.

If x is the frequency of allele P_1, the gene frequency, then the strategy frequency p is given by

$$p = h(x) \equiv x^2 h_{11} + 2x(1-x)h_{12} + (1-x)^2 h_{22}. \tag{2.15}$$

The strategy 0 frequency, q, in Q is the analogous function $k(y)$ of the gene frequency, y, of Q_1. Notice that the inequalities assumed about the $h_{\alpha\beta}$'s and $k_{\alpha\beta}$'s make $h(x)$ and $k(y)$ increasing functions with image the interval $[h_{22}, h_{11}]$ and $[k_{22}, k_{11}]$, respectively.

Given frequency q in population Q the viability of $P_\alpha P_\beta$ is:

$$w_{\alpha\beta}(q) = h_{\alpha\beta} A_{0q} + (1 - h_{\alpha\beta}) A_{1q}. \tag{2.16}$$

Hence the frequency x' of P_1 after one round of selection is given by the usual formula:

$$x' = \frac{x[w_{11}(q)x + w_{12}(q)(1-x)]}{x^2 w_{11}(q) + 2x(1-x)w_{12}(q) + (1-x)^2 w_{22}(q)}. \tag{2.17}$$

Notice that by (2.16) the denominator, the mean viability of the population, $\bar{w}(x, q)$ is just the mean payoff $A_{pq} = A_{1q} + p(A_{0q} - A_{1q})$. Substituting (2.16) into (2.17) we define a function $x' = \hat{\varphi}(x, A_{0q}, A_{1q})$. The function φ of (2.12) is obtained by conjugating with the monotone function h, i.e. $p' = h(x')$ and $p = h(x)$ or $x = h^{-1}(p)$.

$$\begin{aligned} \varphi(p, A_{0q}, A_{1q}) &= h[\hat{\varphi}(h^{-1}(p), A_{0q}, A_{1q})]. \\ \psi(q, B_{p0}, B_{p1}) &= k[\hat{\psi}(k^{-1}(q), B_{p0}, B_{p1})] \end{aligned} \tag{2.18}$$

where $\hat{\psi}(y, B_{p0}, B_{p1})$ is defined via the analogues of (2.16) and (2.17).

Conditions (2.13) and (2.14) are easily verified directly and so (2.18) defines a smooth coevolutionary process. (2.19) alone follows from Fisher's Fundamental Theorem which says, in this case, that for fixed q, $\bar{w}(x', q) \geqslant \bar{w}(x, q)$ (with equality only at equilibrium), i.e. $p'(A_{0q} - A_{1q}) \geqslant p(A_{0q} - A_{1q})$. (See for comparison Eshel 1982).

Proof of Theorem 6: Now suppose there is a fully-mixed Nash equilibrium (p^*, q^*). To discuss local stability we linearize at the equilibrium. Our result follows from the discovery that at least one eigenvalue has absolute value greater than 1.

The key fact is that $A_{0q^*} = A_{1q^*}$ and so $f(p, q^*) = p$ for all p. Consequently, $f_p = \partial f/\partial p = 1$ at (p^*, q^*). Similarly, $g_q = \partial g/\partial q = 1$ there. The matrix of the linearization is thus:

$$\begin{pmatrix} 1 & f_q \\ g_p & 1 \end{pmatrix}$$

with eigenvalues

$$\lambda_\pm = 1 \pm \sqrt{f_q g_p}.$$

If $f_p g_q > 0$: The eigenvalues are real and $\lambda_+ > 1$. Because the map preserves orientation of the square the determinant $\lambda_+ \lambda_- > 0$ and so $0 < \lambda_- < 1$. So one eigenvalue is larger than 1.

If $f_p g_q < 0$: The eigenvalues are complex conjugates and $|\lambda_+|^2 = |\lambda_-|^2 = 1 + |f_p g_q| > 1$.

With a bit more analysis we will see that these two possibilities correspond to the hyperbolic and elliptic cases respectively. Furthermore we will see that $f_p g_q = 0$ corresponds to the degenerate cases where (2.11) fails to hold.

Notice that when $a=b$, $-\varphi_2=\varphi_3>0$. To see this differentiate the equation $\varphi(p, a, a)=p$ with respect to a to get $\varphi_2+\varphi_3=0$ and apply (2.14).

$$f_q=\varphi_2(A_{01}-A_{00})+\varphi_3(A_{11}-A_{10})$$
$$=-\varphi_3(A_{01}-A_{00})+\varphi_3(A_{11}-A_{10})=\varphi_3(\alpha_1-\alpha_0).$$

Similarly, $g_p=\psi_3(\beta_1-\beta_0)$ with $\psi_3>0$ and so the sign of $f_q g_p$ is that of $(\alpha_1-\alpha_0)(\beta_1-\beta_0)$. In particular, $f_q g_p=0$ is equivalent to $\alpha_1=\alpha_0$ or $\beta_1=\beta_0$. If $\alpha_1=\alpha_0\neq 0$ there is domination for P and so no fully-mixed equilibrium. If the common value is zero then as described above strategies 0 and 1 are indistinguishable for P and p does not move. Even in this case it is easy to check by looking at phase portraits with β_0, β_1 having unlike nonzero signs that there is no local stability unless $\beta_1=\beta_0=0$ also. So in the 2×2 case there is local stability only in the trivial case where (p, q) never moves.

The general result — which we will just sketch — differs only in various technicalities from the 2×2 case. Now p, q are vectors and $f(p, q)$, $g(p, q)$ are vector functions of vector variables. We assume

$$f(p, q)=\varphi(p, \{A_{iq}\})$$
$$g(p, q)=\psi(q, \{B_{pj}\})$$

with

$$\begin{aligned} p&=\varphi(p, \{a_i\}) \quad \text{(when all } a_i\text{'s are equal)} \\ q&=\psi(q, \{b_j\}) \quad \text{(when all } b_j\text{'s are equal).} \end{aligned} \tag{2.19}$$

The conditions analogous to (2.14) only arise in connection with degeneracy questions as we will see below.

Again, if (p^*, q^*) is a fully mixed equilibrium then differentiating $f(p, q)$ with respect to the p_i's at (p^*, q^*) yields the identity matrix and similarly for differentiating $g(p, q)$ with respect to the q_j's. Thus the matrix of the linearization at (p^*, q^*) is of the block form

$$\begin{pmatrix} 1_I & 0 \\ 0 & 1_J \end{pmatrix}+\begin{pmatrix} 0_I & U \\ V & 0_J \end{pmatrix}$$

where 1_I, 1_J are the $I\times I$ and $J\times J$ identity matrices, 0_I and 0_J are square matrices of zeros. U is the matrix of partials $(\partial f_i/\partial g_j)$ and V is the matrix of partials $(\partial g_j/\partial p_i)$.

Because the left term is the identity, the eigenvalues of the linearization consist of $\{\lambda=1+\mu\}$ where $\{\mu\}$ is the set of eigenvalues of the off diagonal matrix

$$M=\begin{pmatrix} 0 & U \\ V & 0 \end{pmatrix}.$$

Claim: The nonzero eigenvalues of M are exactly the square roots of the nonzero eigenvalues of UV or equivalently the square roots of the nonzero eigenvalues of VU.

To see why this is so, notice first that the square of any eigenvalue of M is an eigenvalue (with the same eigenvector) of

$$M^2 = \begin{pmatrix} UV & 0 \\ 0 & VU \end{pmatrix}.$$

Because this matrix is block diagonal its eigenvalues are those of UV and VU. (These two matrices actually have the same set of nonzero eigenvalues but we won't need that result.)

On the other hand, suppose $UVz = \omega z$ ($\omega \neq 0$) and $\mu^2 = \omega$. It is easy to check directly that the vector

$$\begin{pmatrix} z \\ Vz/\mu \end{pmatrix}$$

is an eigenvector of M with eigenvalue μ.

Now suppose UV or VU has some nonzero eigenvalue ω.

Case 1: If ω is real and positive then $\mu = \sqrt{\omega}$ is an eigenvalue of M and so $\lambda = 1 + \sqrt{\omega}$ is an eigenvalue of the linearization, with $\lambda > 1$.

Case 2: If ω is real and negative then $\mu_\pm = \pm i\sqrt{|\omega|}$ is a conjugate pair of pure imaginary eigenvalues and so $\lambda_\pm = 1 \pm i\sqrt{|\omega|}$ is a conjugate pair for the linearization with $|\lambda_\pm| > 1$.

Case 3: If $\omega_\pm$ is a conjugate pair of complex eigenvalues then the four resulting square roots $\pm\sqrt{\omega_\pm}$ are symmetrically distributed about the origin and contain one conjugate pair, which we label $\mu_\pm$, with positive real part. Then $\lambda_\pm = 1 + \mu_\pm$ is a conjugate pair for the linearization with $|\lambda_\pm| > 1$.

So the only possibility remaining is that all eigenvalues of UV and VU are zero and so all of the eigenvalues of the linearization are exactly 1. This case is degenerate in the sense that given conditions analogous to (2.13) a perturbation of the payoff matrices should eliminate it as a possibility just as weak domination represented the boundary between the four robust types in the 2×2 case.

Corollary 7. *A nondegenerate, locally stable equilibrium for a smooth coevolutionary process can occur only at a vertex. i.e. pure strategies for P and Q. In particular, only a vertex can be a nondegenerate sink.*

Proof: Suppose (p^*, q^*) is an equilibrium and the supports p^* and q^* are $I_0 \subset I$ and $J_0 \subset J$ respectively. If I_0 and J_0 both contain at least two strategies then by restricting to the $I_0 \times J_0$ subgame and applying the previous theorem we see that (p^*, q^*) cannot be locally stable even with respect to perturbations having the same support. If J_0 contains only one strategy, say $J_0 = \{j_0\}$ so that $q^* = \delta_{j_0}$ then p^* is an equilibrium only if all the A_{ij_0}'s are equal. This case is degenerate if I_0 contains more than one strategy. So we are left with the vertex case.

3. Summary and discussion

For an inter population game we have shown, first, that the equilibria depend only upon the payoff matrices of the game and the boundary behavior assumptions

but are independent of the choice of coevolutionary process modelling the dynamics. Secondly, we have seen that — barring degenerate cases — only a Nash equilibrium of pure strategies can be an attracting equilibrium and so only these positions represent biologically observable stationary states. These results overlap with those of Hines (1981). Hines' models are more general in considering the use of mixed strategies by individuals. On the other hand, he restricts attention to a particular dynamical system.

Underlying the mathematics of the failure of stability for mixed equilibria is a simple idea. Suppose (p^*, q^*) is a fully-mixed equilibrium. q^* determines the environment of population P and because p^* is a fully-mixed equilibrium every strategy i for P yields the same payoff. Thus, as long as Q remains at q^* there is no selection pressure tending to hold P at p^* and it is free to drift away. Dynamically, this is the neutral stability of a cone lying on its side as opposed to balanced on its point or resting on its base. Of course, once both P and Q have drifted away from equilibrium the strategies are no longer equivalent and selection pressures begin to move both populations about. But a priori there is no reason that the dynamic behavior should tend to damp out the perturbations and return the system to (p^*, q^*). In fact, our analysis shows the opposite. Small perturbations are intensified and the populations move away from the original equilibrium.

Where then does the system go? In three of the four 2×2 cases the population comes to rest at a pure strategy Nash equilibrium. In the elliptic case there is no such equilibrium. The orbits spiral away from the center but their limiting behavior is uncertain. Do they approach the boundary or some compact set of nonequilibrium strategies in the interior (periodic points or limit cycles)? Unlike the equilibrium behavior, the answers to these questions do depend on the choice of coevolutionary process. For example, in Fig. 4 any map of the square consistent with the directions given by the arrows is a coevolutionary process and any of these outcomes can occur.

In comparing our discrete time results with a continuous time model, Maynard Smith has mentioned that mixed strategy equilibria can be locally stable in the latter case. While true we regard this result as misleading. Consider the differential equation model which generalizes the Taylor–Jonker equations:

$$\begin{aligned} \frac{dp_i}{dt} &= p_i(A_{iq} - A_{pq}) \\ \frac{dq_j}{dt} &= q_j(B_{pj} - B_{pq}) \end{aligned} \tag{3.1}$$

At a fully mixed equilibrium the matrix of linearization is of the form

$$M = \begin{pmatrix} 0_I & U \\ V & 0_J \end{pmatrix}$$

and the proof of Theorem 6 shows that if no eigenvalues with positive real part occur then all the eigenvalues must be zero or pure imaginary. If they are not all zero then the introduction of any lag into the system at all renders the equilibrium unstable (cf. Chapter 2 of May (1973)).

More generally, using the machinery of differential forms it is possible to write down a volume form Ω on the interior $(=\{p: p_i>0$ and $\sum p_i=1\}\times\{q: q_j>0$ and $\sum q_j=1\})$ such that the flow of (3.1) preserves the associated volume or equivalently the vectorfield has zero divergence with respect to Ω. This means that the motion is like that of an incompressible fluid. Stable equilibria can occur but they are never asymptotically stable, i.e. there are no sinks. Perturbations are not intensified but neither are they damped out. In fact there can be no compact set contained in the interior which attracts all nearby orbits. For if A were such an attractor it would have a compact neighborhood U which is mapped to a smaller neighborhood in U by the flow. This is impossible because U has finite volume and this volume is preserved by the flow. Attractors can occur in the boundary — e.g. vertices which are Nash equilibria — because the volume form blows up at the boundary and so neighborhoods of vertices have infinite volume.

References

1. Bishop, R. T., Cannings, C.: Models of animal conflict. Adv. Appl. Prob. **8**, 4: 616–621 (1976)
2. Eshel, I.: Evolutionary stable strategies and natural selection in Mendelian populations. (1982). Theor. Pop. Biol. **21**, 2, 204–217
3. Hines, W. G. S.: Multi-species population models and evolutionary stable strategies. Adv. Appl. Prob. (1981)
4. Krebs, J. R., Davies, N. B.: Behavioral ecology: An evolutionary approach. Sinauer Associates, Sunderland, MA (1978)
5. May, R. M.: Stability and complexity in model ecosystems. Princeton University Press. Princeton, N.J., 1973
6. Maynard Smith, J., Price, G.: The logic of animal conflicts. Nature **246**, 15–18 (1973)
7. Taylor, P., Jonker, L.: Evolutionary stable strategies and game dynamics. Math. Biosci. 40: 145–156 (1978)
8. Zeeman, C.: Population dynamics from game theory. In: Global theory of dynamical systems. Lecture Notes in Mathematics, vol. 819. Berlin–Heidelberg–New York: Springer 1979

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