STABILITY OF MIXED EQUILIBRIA IN INTERACTIONS BETWEEN TWO POPULATIONS*

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ABSTRACT

This paper considers Nash equilibria of a game played by two populations. Stability of the mixed equilibria is discussed for a wide class of differential systems describing the evolutionary dynamics of behavior. The main property of the systems under consideration is that every Nash equilibrium of the game is a fixed point. The paper shows that no mixed equilibrium is linearly asymptotically stable for the autonomous systems of this class. It also establishes that linear instability of the said Nash equilibrium for an autonomous system leads to its Liapunov instability for any corresponding non-autonomous system.

KEYWORDS: *Stability, Interaction, Populations.*

1. INTRODUCTION

This paper discusses the limiting behavior in a wide class of dynamical systems that can be used to describe the evolution of animal or social behavior. The best-known particular instanse of such systems is that of replicator dynamics.

The relationship between stable points or path limits of evolutionary models and solutions of static game theory has been widely discussed (see Bomze, 1988, van Damme, 1987, Hofbauer and Sigmund, 1988, Nachbar 1990, for the surveys of the corresponding results). Under general assumptions, both path limits and stable points correspond to Nash equilibria. The notion of ESS together with strict equilibrium give the sufficient conditions of asymptotic stability for some classes of dynamical models (see Maynard-Smith, 1982, Vasin, 1989). However, these conditions are inapplicable to non-trivial mixed equilibria of asymmetric interactions, in particular, interactions between two populations, since such equilibria are never ESS (Selten, 1980).

As far as the replicator dynamics are concerned, Schuster et al (1981) have shown that for random pair contests of two populations a non-trivial mixed equilibrium is never linearly asymptotically stable, i.e., Re $\lambda \geq 0$ for some eigenvalue λ of the Jacobian at this point. The present paper shows that this proposition is valid for a wide class of continuous evolutionary dynamics. The main property of the systems under consideration is

that every Nash equilibrium of any interaction model is a fixed point of the systems. I call these systems coordinated with equilibrium, or briefly e-coordinated systems. Every monotone system onsidered by Samuelson (1988) or Nachbar (1990) is e-coordinated if its differential operator is smooth. Furthermore, I will show that linear instability (Re $^\lambda$>0) of an equilibrium for an autonomous ε-coordinated system implies its Lyapunov instability for all corresponding non-autonomous systems.

Let us note that Ritzberger and Vogelsberger (1990), and Samuelson and Zhang (1992) establish the more strong proposition for the replicator dynamics and for aggregate monotonic selection dynamics (AMSDs) respectively. They show that only strict equilibria are asymptotically stable in these evolutionary games as applied to n-player normal-form games.

However the present paper considers the essentially wider class of evolutionary dynamics. While any AMSD may be obtained from the replicator dynamics by player-specific reparametrization of time, the class of e-coordinated models includes also any smooth player-and-strategy-specific reparametrization of time in the replicator dynamics (see Section 3).

The remainder of the paper is arranged as follows. The next section defines a general model of interaction between two populations. Section 3 introduces the class of e-coordinated dynamical systems and treats some examples. Section 4 establishes

the theorem on instability of mixed equilibria. Section 5 discusses the stability of equilibria of center-type.

2. THE MODEL OF INTERACTION

Let $X=\{X_1,\ldots,X_m\}$ and $Y=\{Y_1,\ldots,Y_n\}$ be the sets of strategies of two populations. The two populations may be groups either of the same species or of two different species. We assume that in the considered interaction individuals of the first populations come into contact only with the second population and vice versa. At any given time each individual carries out a particular strategy. Let

$$p(t) = (p_1(t),\ldots,p_m(t)) \in \Delta^m = \{p \in \mathbb{R}^m_+ \mid \sum_i p_i = 1\}$$

and $q(t) = (q_1(t),\ldots,q_m(t)) \in \Delta^n$ be frequency distributions of strategies, $M(t)$ and $N(t)$ – the population sizes. The payoff functions $A_i(q(t))$, $i=1,\ldots,m$, and $B_j(p(t))$, $j=1,\ldots,n$, characterize the results of the interaction for all strategies. So we consider the game Γ with the sets of strategies X and Y and the payoff functions $A_i(q)$, $B_j(p)$ as a general model of the interaction between two population.

The reader will recall that a point $(p,q) \in \Delta^m \times \Delta^n$ is Nash equilibrium of Γ iff for any i,j

$$(p_i > 0) \Rightarrow i \in \operatorname*{Argmax}_u A_u(q),$$

$$(1)$$

$$(q_j > 0) \Rightarrow j \in \operatorname*{Argmax}_u B_u(p);$$

the equilibrium is mixed iff for every i,j $p_i(t) < 1$, $q_j(t) < 1$.

It is easy to see that every game with continuous payoff functions has an equilibrium and, moreover, under mild assumptions on the payoff functions' independence the number of positive coordinates for p and q is the same.

The best-studied interaction is random pair contests (Schuster et al., 1981 Bomze, 1986). In this interaction contestants are drawn at random in pairs from the population a_{ij} and b_{ij} are the payoffs to individuals of populations 1 and 2 when the first plays according to strategy X_i and the second according to strategy Y_j. The average payoffs $A_i(q)=\sum_j a_{ij}q_j$, $B_j(p)=\sum_i b_{ij}p_i$ are treated as the payoff functions. In this case, a point (p,q) satisfies (1) if (p,q) is Nash equilibrium of the bimatrix game with matrices A,B. For some other types of interaction, the payoff functions are not linear (see for instance Maynard-Smith, 1982).

We assume further that the functions $A_i(q)$ (resp. $B_j(p)$) are continiously-differentiable on the set Δ^n (resp. Δ^m).

3. THE EVOLUTIONARY MODEL

Let $p(t)$ and $q(t)$ change according to the system

$$\dot{p}_i = c(t, p(0), q(0))\, G_i(p, A(q)), \quad i=1,\ldots,m;$$

$$\dot{q}_j = d(t, p(0), q(0))\, H_j(q, B(p)), \quad j=1,\ldots,n.$$

$$(2)$$

I term this dynamical system e-coordinated if it satisfies the

following conditions:

1) The functions G_i, $i=1,\ldots,m$; H_j, $j=1,\ldots,n$ satisfy the equations

$$G_i(p,A)=0, \quad i=1,\ldots,m;$$

$$H_j(q,B)=0, \quad j=1,\ldots,n,$$

for any distributions $p\in\Delta^m$, $q\in\Delta^n$ and payoff vectors $A=(A_1,\ldots,A_m)$, $B=(B_1,\ldots,B_n)$ such that

$$\forall i \ (p_i>0)\Rightarrow i \in \underset{u}{\mathrm{Argmax}} \ A_u; \quad \forall j \ (q_j>0)\Rightarrow j \in \underset{v}{\mathrm{Argmax}} \ B_v.$$

2) The functions c,d are measurable as functions of t and continiously-differentiable with resp. to $p(0)$, $q(0)$ and the derivatives are bounded uniformly by t. There exist such positive ε_1, ε_2 that for every $t\geq 0$, $p\in\Delta^m$, $q\in\Delta^n$ $\varepsilon_1\leq c(t,p,q)$, $d(t,p,q)\leq\varepsilon_2$.

3) The set $\Delta^m\times\Delta^n$ is the invariant of the system (2). The functions G and H are continiously-differentiable.

Let us note that any system of the form

$$\overset{\bullet}{p}_i=p_i g_i(p)(A_i(q)-\underset{l}{\Sigma}p_l A_l(q)), \quad i=1,\ldots,m,$$

$$\overset{\bullet}{q}_j=q_j h_j(q)(B_j(p)-\underset{l}{\Sigma}q_l B_l(p)), \quad j=1,\ldots,n,$$

with smooth positive functions g,h meets conditions 1), 3). Concrete examples of e-coordinated systems are as follows.

Exampe 1. Non-autonomous replicator dynamics. Let $\mathbf{M}=(M_i=Mp_i,$ $i=1,\ldots,m)$ and $\mathbf{N}=(N_j=Np_j,$ $j=1,\ldots,n)$ be a numerical distribution

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of strategies. Let the functions $F_i^1(M(t), N(t), t)$, $D_i^1(M(t), N(t), t)$, $i=1, \ldots, m$; (resp. F_j^2, D_j^2, $j=1, \ldots, n$) determine the rates of fertility and mortality for the strategies of the population 1 (resp. the population 2).

Children play the same strategies as their parents. For two-sexual species such inheritance may be caused either by learning or by genes linked with sex. Then

$$\dot{M_i} = M_i (F_i^1(M, N, t) - D_i^1(M, N, t)), \quad i=1, \ldots, m;$$

$$\tag{3}$$

$$\dot{N_j} = N_j (F_j^2(M, N, t) - D_j^2(M, N, t)), \quad j=1, \ldots, n.$$

Assume that the functions F_i^L, D_j^L may be expressed in the form

$$F_i^L(M, N, t) = \tilde{c}(M, N, t)\tilde{F}_i^L(q(t)) + \alpha^L(M, N, t);$$

$$D_j^L(M, N, t) = \tilde{c}(M, N, t)\tilde{D}_j^L(q(t)) + \beta^L(M, N, t).$$

Let the initial sizes of the populations be fixed and let us denote by $(M, N)(p(0), q(0), t)$ the solution of the system (3) with initial distributions $p(0)$, $q(0)$. Let

$$A(q) = \tilde{F}^1(q) - \tilde{D}^1(q),$$

$$B(p) = \tilde{F}^2(p) - \tilde{D}^2(p),$$

$$c(p(0), q(0), t) = \tilde{c}((M, N)(p(0), q(0), t), t),$$

$$d(p(0), q(0), t) = \tilde{d}((M, N)(p(0), q(0), t), t).$$

Then the system (3) implies that the distributions $p(t)$, $q(t)$ satisfy the equations

$$\overset{\bullet}{p}_i = c(p(0),q(0),t)p_i(A_i(q)-\underset{k}{\Sigma}p_kA_k(q)), \quad i=1,\ldots,m;$$

(4)

$$\overset{\bullet}{q}_j = d(p(0),q(0),t)q_j(B_j(p)-\underset{u}{\Sigma}q_uB_u(p)), \quad j=1,\ldots,n;$$

This system satisfies the conditions 1) and 3) and is θ-coordinated under general assumptions.

Example 2. The random imitation. Unlike the previous example, every new individual chooses some participant of the same populatuin at random and imitates his strategy. Then the population dynamics are

$$\overset{\bullet}{M}_i = M_i/M \ \underset{k}{\Sigma}M_kF_k^1 - M_iD_i^1, \quad i=1,\ldots,m;$$

$$\overset{\bullet}{N}_j = N_j/N \ \underset{u}{\Sigma}N_uF_u^2 - N_jD_j^2, \quad j=1,\ldots,n.$$

Let the functions F^L, D^L be of the same kind as in Example 1. Then $p(t)$, $q(t)$ satisfy system (1), if we define $A_i(q)=-\tilde{D}_i^1(q)$, $B_j(p)=-\tilde{D}_j^2(p)$.

Example 3. The adaptive imitation. Consider interaction between two populations with the constant sizes and the payoff functions $A_i(q)$, $B_j(p)$. Let $M_i\gamma_{ik}(p(t), A(q(t)))$ (resp. $N_j\nu_{jl}(q(t), B(p(t)))$) be the rate of transition from the strategy X_i to the strategy X_k (resp. from Y_j to Y_i) at the time t. We assume that the functions

ν_{jl}, γ_{ik} are continiously-differentiable. If strategy A_i is better than strategy A_k then the rate of transition from A_i to A_k is lower than the rate of reverse transition: for every p, A $(A_i > A_k)$ $\Rightarrow$ $p_i \gamma_{ik}(p, A) \leq p_k \gamma_{ki}(p, A)$; for every q, B $(B_j > B_l)$ $\Rightarrow$ $q_j \nu_{jl}(q, B) \leq q_l \nu_{lj}(q, B)$. Then $P(t)$, $Q(t)$ change according to the system

$$\dot{p_i} = \sum_{k \neq i} (p_k \gamma_{ki}(p(t), A(q(t))) - p_i \gamma_{ik}(p(t), A(q(t)))), \quad i = 1, \ldots, m;$$

$$\dot{q_j} = \sum_{l \neq j} (q_l \nu_{lj}(q(t), B(p(t))) - q_j \nu_{jl}(q(t), B(p(t)))), \quad j = 1, \ldots, n;$$

Let us note that the system (2) may be reduced to the autonomous one:

$$\dot{p_i} = G_i(p, A(q)), \quad i = 1, \ldots, m,$$

$$\tag{5}$$

$$\dot{q_j} = H_j(q, B(p)), \quad j = 1, \ldots, n,$$

if for any t, $p(0)$, $q(0)$

$$c(p(0), q(0), t) / d(p(0), q(0), t) = \alpha(p(0), q(0)).$$

This case takes place in the interaction between populations of constant sizes, or between individuals of the same species in two different roles; for instance, between "owners" of some resources and "intruders" (see Maynard-Smith, 1982).

4.Stability of mixed equilibria

Consider arbitrary game Γ, θ-coordinated system (2) and the corresponding autonomous system (5). Let us remind that a fixed

point of the system (5) is called a degenerate point if some eigenvalue λ of the Jacobian is equal to 0; the point is a center if for every eigenvalue Re $\lambda=0$, $|\text{Im } \lambda|>0$; the point is a saddle if for some eigenvalue Re $\lambda>0$.

Theorem. *Every mixed equilibrium (P^*,Q^*) is either a degenerate point, or a center, or a saddle of the system (5). In the latter case (P^*,Q^*) is the unstable point of the system (2) for any permissible functions c, d.*

The following lemmas will be used to prove the second part of the theorem.

Lemma 1. *Let $(x,y)(t)=(\bar{x},\bar{y})exp(\lambda t)$ be a solution of the linear system $\dot{x}=Ky$, $\dot{y}=Px$, $x,y \in \Delta^m$, and Re$\lambda>0$; let $a(t)$ be a measurable function, such that for some ε, $\bar{\varepsilon}$ for any t $0<\varepsilon<a(t)<\bar{\varepsilon}<\infty$. Then the system*

$$\dot{x}=Ky, \quad \dot{y}=a(t)Px \qquad (6)$$

has the solution $(\tilde{X},\tilde{Y})(t)=(c(t)\bar{x},d(t)\bar{y})$, where $|c(t)|\geq exp(Re\lambda\varepsilon^{1/2}t)$

Proof. By substitution of $\tilde{X}$, $\tilde{Y}$ to the system (6) one obtains $\dot{c}=\lambda d$, $\dot{d}=a(t)\lambda c$. Hence, $\ddot{c} = a(t)\lambda^2 c$. Let $\lambda=u+iv$, $c(t)-exp(uf(t)+ig(t))$. Then f, g satiafy the system

$$\dot{f}\dot{g}=a(t),$$
$$\ddot{f} =-u\dot{f}^2+a(t)u + v^2a(t)/u(a(t)/\dot{f}^2-1).$$

Let $f(0)=0$, $\dot{f}(0)=\varepsilon^{1/2}$. For every t, if $\dot{f}(t)\leq\varepsilon^{1/2}$, then $\ddot{f}(t)\geq 0$ and if $\dot{f}(t)\geq\bar{\varepsilon}^{1/2}$, then $\ddot{f}\leq 0$. Hence, for every t $\varepsilon^{1/2}\leq\dot{f}(t)\leq\bar{\varepsilon}^{1/2}$,

$$f(t) \geq t\varepsilon^{1/2}, \quad |c(t)| \geq \exp(u\varepsilon^{1/2}t).$$

Lemma 2. *Let the linear system* $\overset{\bullet}{W}=A(t)W$ *have such a solution* $\tilde{W}(t)$, *that for some* $u>0$ *for any* t $|\tilde{W}(t)| \geq \exp(ut)|\tilde{W}(0)|$. *Let* $A(t)$ *be bounded uniformly by* t. *Then the point* 0 *is unstable for the system* $\overset{\bullet}{W}=A(t)W+g_1(t,W)+g_2(t,W(0),W)$ *for any vector-functions* g_1, g_2 *such that* $\|g_1(t,W)\|/\|W\| \to 0$ *as* $\|W\| \to 0$, $\|g_2(t,W(0),W)\| \leq C\|W(0)\| \|W\|^2$ *uniformly by* t.

This proposition is analogous to the well-known theorem of Lyapunov (see, for instance, Rouche et al., theorem 5.8).

Proof of the Theorem. Let $\{i \mid p_i^* > 0\} = \{1, \ldots, r\}$, $\{j \mid q_j^* > 0\} = \{1, \ldots, s\}$ We denote $R=\{2, \ldots, r\}$, $U=\{2, \ldots, s\}$, $S=\{r+1, \ldots, m\}$, $V=\{s+1, \ldots, n\}$; for any vector $W \in \mathbb{R}^m$ and each ordered subset $Q \subset \{i=1, \ldots, m\}$ $W_Q = (W_i, i \in Q)$, $\bar{p}=(p_R, p_S)$, $\bar{q}=(q_U, q_V)$. By the exclusion of the dependent variables $p_1 = 1-p_2-\ldots-p_m$, $q_1 = 1-q_2-\ldots-q_n$ the system (5) is transposed to the form

$$\overset{\bullet}{\bar{p}} = \bar{G}(\bar{p}, A(\bar{q})), \quad \overset{\bullet}{\bar{q}} = \bar{H}(\bar{q}, B(\bar{q})).$$

Let us compute the Jacobian at the point (p^*, q^*). For every $i \in S$, $k \in R$, $j \in V$ for any small enough Δp_k

$$\bar{G}_i(\bar{p}^* + e_j\Delta p_k, A(\bar{q}^*)) \geq 0,$$

$$\bar{H}_j(\bar{q}^*, B(\bar{p}^* + e_k\Delta p_k)) \geq 0,$$

according to the condition 3); here e_k is the corresponding unit vector. Hence, $\partial \bar{G}_i/\partial p_k(\bar{p}^*, \bar{q}^*) = \partial \bar{H}_j/\partial p_k(\bar{p}^*, \bar{q}^*) = 0$. Similarly, for

every $l \in U$, $\partial \bar{H}_j / \partial q_l (p^*, q^*) = \partial \bar{G}_i / \partial q_l (p^*, q^*) = 0$. Now let us show, that for every $i, k \in U$, $j, l \in V$ $\partial \bar{G}_i / \partial p_k (p^*, q^*) = \partial \bar{H}_j / \partial q_l (p^*, q^*) = 0$. Indeed, for any small enough Δp_k the point $(\bar{p}^* + \Delta p_k e_k, \bar{q}^*)$ corresponds to Nash equilibrium of the game Γ' with the payoff functions $A'(\bar{q}) = A(\bar{q})$ and $B'(\bar{p}) = B(\bar{p} - \Delta p_k e_k)$, which are extended in a proper way. Hence, by the condition 1), $\bar{G}_i (\bar{p}^* + e_k \Delta p_k, A(\bar{q}^*)) = 0$. Proof of the second equality is analogous.

Thus, the Jacobian at the point $(\bar{p}^*, \bar{q}^*)$ takes the following block form:

$$
J = \begin{bmatrix}
0 & \dfrac{\partial \bar{G}_R}{\partial p_S} & \dfrac{\partial \bar{G}_R}{\partial q_U} & \dfrac{\partial \bar{G}_R}{\partial q_V} \\[2em]
0 & \dfrac{\partial \bar{G}_S}{\partial p_S} & 0 & \dfrac{\partial \bar{G}_S}{\partial q_V} \\[2em]
\dfrac{\partial \bar{H}_U}{\partial p_R} & \dfrac{\partial \bar{H}_U}{\partial p_S} & 0 & \dfrac{\partial \bar{H}_U}{\partial q_V} \\[2em]
0 & \dfrac{\partial \bar{H}_V}{\partial p_S} & 0 & \dfrac{\partial \bar{H}_V}{\partial q_V}
\end{bmatrix} \quad (\bar{p}^*, \bar{q}^*)
$$

The two blocks of 0's on the diagonal are $(r-1)*(r-1)$ and $(s-1)*(s-1)$ matrices. If $r \neq s$, then $\det J = 0$, i.e. (p^*, q^*) is a degenerate point. Otherwise the characteristic polinomial $f(\lambda)$ of the matrix

$$\bar{J} = \begin{bmatrix} 0 & \dfrac{\partial \bar{G}_R}{\partial q_U} \\ & \\ \dfrac{\partial \bar{H}_U}{\partial p_R} & 0 \end{bmatrix}$$

is even, and either all its eigenvalues are on the imaginari axes or for one of them $Re\ \lambda > 0$.

Now let us consider the latter case and prove the second part of the theorem. We denote $x = \bar{p} - \bar{p}^*$, $y = \bar{q} - q^*$, $W = (x, y)$, $\pi = (\bar{p}, \bar{q})$ and expend the functions c, d, G, H in variable W:

$$c(t, p, q) = c(t, p^*, q^*) + h_1(t, W) \|W\|,$$

$$d(t, p, q) = d(t, p^*, q^*) + h_2(t, W) \|W\|,$$

$$G(q, A(q)) = (\partial G / \partial W)(p^*, q^*)W + h_3(W),$$

$$H(q, B(q)) = (\partial H / \partial W)(p^*, q^*)W + h_4(W),$$

where the functions $h_l(t, W)$, $l = 1, 2$ are bounded uniformly by t, W, $h_l(W) / \|W\| \to 0$ as $\|W\| \to 0$, $l = 3, 4$. By the time change $d\tau = c(t, p^*, q^*)dt$ the system (2) is transposed to the form

$$\dot{x} = (\partial \bar{G} / \partial W)(p^*, q^*)W + g_{11}(t, W) + g_{12}(t, W(0), W);$$

$$(7)$$

$$\dot{y} = \alpha(\tau)(\partial \bar{H} / \partial W)(p^*, q^*)W + g_{21}(t, W) + g_{22}(t, W(0), W);$$

where $\alpha(\tau)=d(t(\tau),p^*,q^*)/c(t(\tau),p^*,q^*)$, $\varepsilon/\bar{\varepsilon}\leq\alpha(\tau)\leq\bar{\varepsilon}/\varepsilon$, and the functions g_{l1},g_{l2} satisfy the conditions of Lemma 2, $l=1,2$. By the assumption the system $d(x_R,y_U)/d\tau=\bar{J}$ (x_R,y_U) has a solution $(\bar{x}_R,\bar{y}_U)\exp(\lambda t)$, Re $\lambda>0$. By Lemma 1 the linearised system

$$\dot{x}=(\partial\bar{G}/\partial W)(p^*,q^*)W,$$

$$\dot{y}=\alpha(\tau)(\partial\bar{H}/\partial W)(p^*,q^*)W$$

has such solution $(\tilde{x}(t),\tilde{y}(t))$ that satisfies

$$\|\tilde{x}_R(\tau)\|\geq\exp(\text{Re }\lambda(\varepsilon/\bar{\varepsilon})^{1/2}\tau)\|\tilde{x}_R(0)\|.$$

Hence, by Lemma 2 the point 0 is unstable for the system (7) as is the point (p^*,q^*) for the initial system (2).

5. DISCUSSION

Schuster et al. (1981) have shown that non-trivial mixed equilibria of pair contests are never linearly asymptotically stable points of the replicator dynamics. The theorem of section 4 establishes the analogous result for arbitrary interaction between two populations for the wide class of autonomous θ-coordinated evolutionary systems. The theorem also shows that for any non-autonomous θ-coordinated system the investigation of the corresponding linearized autonomous system allows us to determine the saddle points which are unstable for the initial system. As for the points of center-type, Schuster et al. have put forward the conjecture: while these points are stable, they are not asymptotically so for the replicator dynamics. This has been

proven for some classes of bimatrix games. This proposition fails in some other autonomous e-coordinated systems (see Hofbauer and Sigmund, 1988), as well as in the non-autonomous replicator dynamics (see Vasin, 1989). But even if a point of center-type is asymptotically stable, the rate of convergence to this point is low. For natural systems, the fluctuation around the point is to be expected in this case.

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