Biol. Cybern. 40, 9–15 (1981)

Biological Cybernetics

Selfregulation of Behaviour in Animal Societies*

II. Games between Two Populations without Selfinteraction

Peter Schuster, Karl Sigmund, Josef Hofbauer, and Robert Wolff

Institut für Theoretische Chemie und Strahlenchemie and Institut für Mathematik der Universität Wien

Abstract. A discussion of the game dynamics for asymmetric contest between two animal populations is presented by means of qualitative analysis.

1. Introduction

In Part I we have only dealt with symmetric contests between equally matched opponents. Asymmetric contests have also received much attention. We refer only to Maynard-Smith and Parker (1976), Dawkins (1976), Parker (1979), Hammerstein (1980), and Schuster and Sigmund (1980).

Typical examples are: the conflicts between intruder and owner, between predator and prey, or between male and female. An example of this last conflict, the so-called "parental investment conflict" (Trivers, 1972) will be briefly discussed in Sect. 7. At first, we shall describe the general form of our models.

2. Differential Equations for Asymmetric Contests without Selfinteraction

Let X and Y be two populations, $X_1, \dots, X_n$ resp. $Y_1, \dots, Y_m$ the pure strategies and $x_1, \dots, x_n$ resp. $y_1, \dots, y_m$ the corresponding frequencies. (The two populations may be two groups of the same species or of two different species.) We assume that individuals of the X-population react only with individuals of the Y-population, and vice versa. This is what we mean by "no selfinteraction".

Let a_{ij} (resp. b_{ij}) be the expected payoff for strategy X_i played against Y_j (resp. Y_i against X_j). Thus we consider the bimatrix game described by the matrices $A=(a_{ij})$ and $B=(b_{ij})$. If $\mathbf{e}_i$ resp. $\mathbf{f}_j$ denotes the i-th (resp. j-th) corner of $\mathbf{S}_n$ (resp. $\mathbf{S}_m$), then $\mathbf{e}_i \cdot A\mathbf{y}$ (resp. $\mathbf{f}_j \cdot B\mathbf{x}$) is the payoff for the pure strategy X_i (resp. Y_j) against strategy $\mathbf{y}=(y_1, \dots, y_m)$ [resp. $\mathbf{x}=(x_1, \dots, x_n)$], and $\mathbf{x} \cdot A\mathbf{y}$ (resp. $\mathbf{y} \cdot B\mathbf{x}$) the payoff for the mixed strategies $\mathbf{x}$ resp. $\mathbf{y}$. The same argument as in Part I leads to the differential equation

$$\begin{aligned} \dot{x} &= x_i(\mathbf{e}_i \cdot A\mathbf{y} - \mathbf{x} \cdot A\mathbf{y}) \qquad i=1, \dots, n \\ \dot{y}_j &= y_j(\mathbf{f}_j \cdot B\mathbf{x} - \mathbf{y} \cdot B\mathbf{x}) \qquad j=1, \dots, m \end{aligned} \tag{36}$$

on the (invariant) state space $\mathbf{S}_n \times \mathbf{S}_m$.

3. Evolutionarily Stable Strategies

For asymmetric games, the notion of ESS seems somewhat poorer than in the symmetric case. In particular, ESS have to be pure. This was proved by Selten (1978) in a game theoretic context considerably more general than the one described here.

In this section, we restrict ourselves to a less sophisticated discussion of evolutionary stability. Let us denote by $(\mathbf{x}, \mathbf{y}) \in \mathbf{S}_n \times \mathbf{S}_m$ the state of two populations engaged in a bimatrix game as described in Sect. 2 and assume that $(\mathbf{p}, \mathbf{q})$ is an evolutionarily stable state. What does this mean? First of all, we obviously should request that $\mathbf{p}$ is a best reply to $\mathbf{q}$ and $\mathbf{q}$ a best reply to $\mathbf{p}$, i.e.

$$\begin{aligned} &\mathbf{p} \cdot A\mathbf{q} \geqq \mathbf{x} \cdot A\mathbf{q} \qquad \forall \mathbf{x} \in \mathbf{S}_n \\ &\mathbf{q} \cdot B\mathbf{p} \geqq \mathbf{y} \cdot B\mathbf{p} \qquad \forall \mathbf{y} \in \mathbf{S}_m . \end{aligned} \tag{37}$$

This just means that $(\mathbf{p}, \mathbf{q})$ is an equilibrium pair (see, e.g., Rauhut et al., 1979). What about the stability of this equilibrium? It is not easy to give a good definition. For symmetric games, if $\mathbf{x}$ and $\mathbf{p}$ are both "best replies" to the ESS $\mathbf{p}$, then $\mathbf{p}$ fares better, against $\mathbf{x}$, than does $\mathbf{x}$. Shall we assume, in the asymmetric case, that $\mathbf{q}$

* This work has been supported financially by the Austrian "Fonds zur Förderung der wissenschaftlichen Forschung" Project Nr. 3502

0340-1200/81/0040/0009/$01.40

fares better, against $\mathbf{p}$, than against $\mathbf{x}$? The biological relevance of this condition seems dubious. Besides, the corresponding inequality

$$\mathbf{q}\cdot B(\mathbf{p}-\mathbf{x})>0 \qquad \forall \mathbf{x}\in \mathbf{S}_n, \qquad \mathbf{x}\neq\mathbf{p}$$

can obviously only be valid if $\mathbf{p}$ is pure.

In some interesting situations, it seems legitimate to consider the total payoff, i.e. the sum of the payoffs of the two populations. The pair of strategies $(\mathbf{p},\mathbf{q})$, then, is a best reply against itself if

$$\mathbf{p}\cdot A\mathbf{q}+\mathbf{q}\cdot B\mathbf{p}\geqq \mathbf{x}\cdot A\mathbf{q}+\mathbf{y}\cdot B\mathbf{p}$$

for all $(\mathbf{x},\mathbf{y})\in \mathbf{S}_n\times\mathbf{S}_m$. This is satisfied if $(\mathbf{p},\mathbf{q})$ is an equilibrium. If $(\mathbf{x},\mathbf{y})$, now, is an alternative best reply against $(\mathbf{p},\mathbf{q})$, then one can postulate as stability condition that $(\mathbf{p},\mathbf{q})$ fares better, against $(\mathbf{x},\mathbf{y})$, than does $(\mathbf{x},\mathbf{y})$ against itself:

$$\mathbf{p}\cdot A\mathbf{y}+\mathbf{q}\cdot B\mathbf{x}>\mathbf{x}\cdot A\mathbf{y}+\mathbf{y}\cdot B\mathbf{x}$$

for all $(\mathbf{x},\mathbf{y})\neq(\mathbf{p},\mathbf{q})$ for which equality holds in (37). This leads to

$$(\mathbf{p}-\mathbf{x})\cdot(A+B^T)(\mathbf{q}-\mathbf{y})<0$$

which, again, can be satisfied only if $\mathbf{p}$ and $\mathbf{q}$ are both pure.

From the point of view of game theory, therefore, equilibria which are not pure seem to have little biological relevance, since they are not evolutionarily stable. We shall see that in the dynamic context of Eq. (36), however, mixed equilibria may be quite important.

4. Invariant Faces

The faces of the state space $\mathbf{S}_n\times\mathbf{S}_m$ (i.e. the products of a face of $\mathbf{S}_n$ with a face of $\mathbf{S}_m$) are all invariant under Eq. (36), and the restriction of (36) to such an invariant face is again an equation of the same type.

Each face is obtained by setting some x_i and y_j equal to 0. We can decompose each such face into its interior and its boundary, which again consists of faces. It is sufficient, therefore, to investigate the restriction of (36) to the following invariant sets:

1) At least one of the population plays only one pure strategy;

2) both populations play properly mixed strategies.

This means

1) $x_i=1$ or $y_j=1$ for some i or j;
2) $x_i>0$ for several i, and $y_j>0$ for several j.

It is clear that one does not lose generality, then, if one investigates the restriction of (36) only for the following two sets

1′) $\mathbf{S}_n\times\{f_1\}$;
2′) interior of $\mathbf{S}_n\times\mathbf{S}_m$.

All other restrictions of type 1) or 2) have the same form as restrictions of type 1′) or 2′).

Case 1′) is easy to deal with. The dynamical system is now described by

$$\dot{x}_i=x_i\left(a_{1i}-\sum_{j=1}^{n}a_{1j}x_j\right) \qquad i=1,\ldots,n \tag{38}$$

together with $(x_1,\ldots,x_n)\in S_n$ and $y_1\equiv 1$. This equation has been described in Eigen and Schuster (1979).

With $a=\max\limits_i a_{1i}$, we obtain $x_i\to 0$ for all i such that $a_{1i}<a$. In the typical case, there exists a unique j with $a_{1j}=a$, and then $x_j\to 1$. If there are several such j, the corresponding x_j still increase to a limit. If $a_{1i}=a_{1j}$, the ratio x_i/x_j remains constant.

Equation (38), then, describes the population X playing against a constant environment. The strategies X_j with highest fitness a_{1j} will be selected.

Case 2′) is more delicate, in general, and will be discussed in the next section.

5. Fixed Points

The fixed points of (36) in the interior of $\mathbf{S}_n\times\mathbf{S}_m$ are the strictly positive solutions of the equations

$$\sum_{j=1}^{m}a_{1j}y_j=\ldots=\sum_{j=1}^{m}a_{nj}y_j \qquad \sum_{j=1}^{m}y_j=1\,, \tag{39}$$

$$\sum_{i=1}^{n}b_{1i}x_i=\ldots=\sum_{i=1}^{n}b_{mi}x_i \qquad \sum_{i=1}^{n}x_j=1\,. \tag{40}$$

If $n>m$ then (39) has a solution only if matrix A satisfies some degeneracy condition, while the solutions of (40) form a linear manifold of dimension $\geqq n-m$. Hence the set of fixed points in the interior of $\mathbf{S}_n\times\mathbf{S}_m$ is either empty (this is the typical case) or it contains an $(n-m)$-dimensional plane. An isolated fixed point can exist only if $n=m$. If it exists, it is unique.

In order to compute the Jacobian at a fixed point, we set

$$x_n=1-x_1-\ldots-x_{n-1} \qquad y_m=1-y_1-\ldots-y_{m-1}\,.$$

Equation (36) becomes

$$\begin{aligned}&\dot{x}_i=x_i\left(\sum_{j=1}^{m-1}a_{ij}y_j+a_{im}(1-y_1-\ldots-y_{m-1})-\mathbf{x}\cdot A\mathbf{y}\right)\\ &i=1,\ldots,n-1\\ &\dot{y}=y_j\left(\sum_{i=1}^{n-1}b_{ji}x_i+b_{jn}(1-x_1-\ldots-x_{n-1})-\mathbf{y}\cdot B\mathbf{x}\right)\\ &j=1,\ldots,m-1\end{aligned} \tag{41}$$

with

$$\mathbf{x}\cdot A\mathbf{y}=\sum_{i=1}^{n-1} x_i$$

$$\cdot(a_{i1}y_1+\ldots+a_{i,m-1}y_{m-1}+a_{im}(1-y_1-\ldots-y_{m-1}))$$

$$+(1-x_1-\ldots-x_{n-1})$$

$$\cdot(a_{n1}y_1+\ldots+a_{n,m-1}y_{m-1}+a_{nm}(1-y_1-\ldots-y_{m-1}))$$

and an analogous expression for $\mathbf{y}\cdot B\mathbf{x}$.

At a fixed point of (36), one obtains

$$\frac{\partial(\dot{x}_i)}{\partial x_j}=x_i\left(-\frac{\partial}{\partial x_j}(\mathbf{x}\cdot A\mathbf{y})\right)=0$$

for $1\leqq i, j\leqq n-1$, since relations (39) imply

$$\frac{\partial}{\partial x_j}(\mathbf{x}\cdot A\mathbf{y})=a_{j1}y_1+\ldots+a_{jm}(1-y_1-\ldots-y_{m-1})$$
$$-[a_{n1}y_1+\ldots+a_{nm}(1-y_1-\ldots-y_{m-1})]=0.$$

Similarly, $\frac{\partial(\dot{y}_j)}{\partial y_i}=0$, and thus the Jacobian at a fixed point of (36) is of the form

$$J=\begin{bmatrix}0 & C\\ D & 0\end{bmatrix},$$

where the two blocks of 0's on the diagonal are $(n-1)\times(n-1)$ resp. $(m-1)\times(m-1)$-matrices. For the characteristic polynomial $p(\lambda)=\det(J-\lambda I)$, one has

$$p(\lambda)=(-1)^{n-m}p(-\lambda)$$

as can be seen by changing sign of the first $n-1$ columns and the last $m-1$ rows of $J-\lambda I$. Also

$$p(\lambda)=\lambda^{|n-m|}f(\lambda),$$

where $f(\lambda)$ is a polynomial of degree $n+m-2-|m-n|$. Indeed, at least $|n-m|$ eigenvalues of J vanish at our fixed point, because the set of fixed points contains an $|m-n|$-dimensional linear manifold. Thus $f(\lambda)$ is an even polynomial. It follows that if λ is a nonvanishing eigenvalue of J, so is $-\lambda$. Hence

Theorem. The fixed points of (36) in the interior of $\mathbf{S}_n\times\mathbf{S}_m$ are neither sinks nor sources. Isolated fixed points, which exist only if $n=m$, are saddles or centers.

In particular, only corners of $\mathbf{S}_n\times\mathbf{S}_m$ can be sinks for (36). This corresponds to the absence of properly mixed ESS, see Sect. 3.

Conjecture. If an isolated fixed point in the interior of $\mathbf{S}_n\times\mathbf{S}_m$ is of center-type (all eigenvalues on the imaginary axis), then it is stable, but not asymptotically stable.

We can prove this conjecture only for $n=2$ (Sect. 6) and check it for higher dimensions under supplementary assumptions (see Sects. 8 and 9).

Just as in the symmetric case (see Part I, 5), time-averages along orbits bounded away from the boundary, and in particular along periodic orbits, satisfy Eqs. (39) and (40) and correspond consequently to interior fixed points of (36), and hence to mixed equilibria of the bimatrix game. Thus even those equilibria which are not evolutionarily stable may be of practical relevance. We shall examplify this in Sect. 7.

6. The Two-Dimensional Case

The case $n=m=2$, treated in Schuster and Sigmund (1980), is quite instructive. Since we may subtract a constant from each columns of A and B, we can assume that all diagonal terms are 0. Thus

$$A=\begin{bmatrix}0 & a_{12}\\ a_{21} & 0\end{bmatrix}\quad B=\begin{bmatrix}0 & b_{12}\\ b_{21} & 0\end{bmatrix}.$$

Since $x_2=1-x$, and $y_2=1-y_1$, it is enough to study the evolution of x_1 and y_1, which we call x and y. Thus (36) reduces to

$$\begin{aligned}\dot{x}&=x(1-x)(a_{12}-(a_{12}+a_{21})y)\\ \dot{y}&=y(1-y)(b_{12}-(b_{12}+b_{21})x)\end{aligned}\tag{42}$$

on the space $\mathbf{Q}_2=\{(x,y):0\leqq x,y\leqq 1\}\cong\mathbf{S}_2\times\mathbf{S}_2$.

If $a_{12}a_{21}\leqq 0$, $\dot{x}$ does not change sign; hence x is either constant or converges to 0 or 1. Similarly if $b_{12}b_{21}\leqq 0$. There remains the case where $a_{12}a_{21}>0$ and $b_{12}b_{21}>0$. There is a unique fixed point, in this case, in the interior of $\mathbf{Q}_2$, namely

$$F=\left(\frac{b_{12}}{b_{12}+b_{21}},\frac{a_{12}}{a_{12}+a_{21}}\right).\tag{43}$$

The Jacobian of (42) at F has eigenvalues $\pm\lambda$, where

$$\lambda^2=\frac{a_{12}a_{21}b_{12}b_{21}}{(a_{12}+a_{21})(b_{12}+b_{21})}.$$

If $a_{12}b_{12}>0$, then F is a saddle. Almost all orbits in the interior of $\mathbf{Q}_2$ will converge to one or the other of two opposite corners. If $a_{12}b_{12}<0$, F is of center type. In this case, all orbits in the interior of $\mathbf{Q}_2$ spiral around F. Indeed, the function

$$V(x,y)=x^{|b_{12}|}(1-x)^{|b_{21}|}y^{|a_{12}|}(1-y)^{|a_{21}|}\tag{44}$$

which vanishes on the boundary of $\mathbf{Q}_2$ and is strictly positive in the interior of $\mathbf{Q}_2$, with F as unique maximum, satisfies

$$\frac{dV}{dt}=\frac{\partial V}{\partial x}\dot{x}+\frac{\partial V}{\partial y}\dot{y}=0$$

as is easily checked, remembering the signs of a_{ij} and b_{ij}. Hence V is constant along the orbits of (42) which are, therefore, periodic: they correspond to constant value curves of V. Clearly

$$\frac{1}{T}\int_0^T x(t)dt=\frac{b_{12}}{b_{12}+b_{21}} \quad \frac{1}{T}\int_0^T y(t)dt=\frac{a_{12}}{a_{12}+a_{21}}, \tag{45}$$

where T is the length of the period.

7. The Dawkins Game

We shall illustrate (42) by an example due to Dawkins (1976), and dealing with an aspect of the battle of sexes:

Male sex cells are much smaller than those of females. At the moment of conception, a mother is already much more committed to her child than the father is. She would have more to lose by the death of the child, in the sense that she would have to invest more to bring a substitute child to the same level. Thus fathers are much more tempted to desert and look for a new mate, leaving the mother in charge of the baby.

The obvious counter-tactic for females would be to force the male to commit himself heavily before copulation. A long engagement period would test the perseverence and fidelity of her mate. More to the point still, his desertion would lead him to another long and arduous courtship. It would be better for him to stay home and invest his resources in the upbringing of his present offspring rather than increase his future one.

Thus a "conspiracy" of coy females would force the males to be faithful.

Among faithful males, however, a fast female would fare better than a coy one, since she would not lose time by a long courtship period. So her genes will spread quicker. After some generations, the population will include a large proportion of fast females. But then, philandering males will have an easy life and many opportunities to spread their genes. Faithful husbands will become rare. Females would do well, then, to be coy. The argument seems to have turned full circle.

Let us assume that the benefit for raising a child successfully is equal to $+a$ for each parent, the total cost for looking after the child is $-b$ and the cost of prolonged courtship is $-c$ $(a,b,c>0)$. Let x be the proportion of faithful males and y the proportion of coy females.

If a faithful male meets a coy female, the payoff for each is $a-c-\frac{b}{2}$. If a faithful male encounters a fast female, both earn $a-\frac{b}{2}$. A philandering male meeting a fast female makes off with $+a$ while the female gets $a-b$. If a philanderer meets a coy female, the payoff for both is 0.

After adding constants to the columns of A and B so that the diagonal terms are 0, we obtain

$$\begin{aligned} a_{12}&=-\frac{b}{2} \quad b_{12}=b-a \\ a_{21}&=c-a+\frac{b}{2} \quad b_{21}=c. \end{aligned} \tag{46}$$

We always have $a_{12}<0$ and $b_{21}>0$. If

$$c+\frac{b}{2}<a<b \tag{47}$$

as in the numerical example given by Dawkins ($a=15$, $b=20$, $c=3$), there exists an equilibrium F in the interior of $\mathbf{Q}_2$, but of course it is not, as claimed by Dawkins (1976), evolutionarily stable. Nevertheless, it is of great interest, as it reflects the time-averages of the endlessly oscillating mixtures of strategies. Indeed, (47) implies that F is of center type. The time-averages, given by (45) as

$$F \doteq \left(\frac{b-a}{b+c-a}, \frac{b}{2(a-c)}\right) \tag{48}$$

are independent of initial conditions. If (47) does not hold, then a pair of pure strategies evolves.

8. Zero Sum Games

Let $(\mathbf{p},\mathbf{q})\in \mathbf{S}_n\times\mathbf{S}_m$ be an equilibrium pair, or optimal, in the sense of (37). Let us define

$$P=\prod x_i^{p_i} \quad Q=\prod y_i^{q_i}.$$

Clearly, we have

$$\dot{P}=P(\mathbf{p}\cdot A\mathbf{y}-\mathbf{x}\cdot A\mathbf{y}) \quad \dot{Q}=Q(\mathbf{q}\cdot B\mathbf{x}-\mathbf{y}\cdot B\mathbf{x}). \tag{49}$$

For zero sum games, which are defined by $B=-A^T$ (the loss of one player is the gain of the other one), optimal strategies correspond to minimax strategies (see Rauhut et al., 1979) and (37) can be written as

$$\mathbf{x}\cdot A\mathbf{q}\leqq\mathbf{p}\cdot A\mathbf{q}\leqq\mathbf{p}\cdot A\mathbf{y} \quad \text{for all} \quad \mathbf{x},\mathbf{y}\in\mathbf{S}_n. \tag{50}$$

Theorem. $(\mathbf{p},\mathbf{q})\in\mathbf{S}_n\times\mathbf{S}_n$ is an optimal pair iff PQ is a constant of motion. In this case $(\mathbf{p},\mathbf{q})$ is stable, but not asymptotically stable, and we have

$$\mathbf{p}=\lim_{T\to\infty}\frac{1}{T}\int_0^T\mathbf{x}(t)dt \quad \mathbf{q}=\lim_{T\to\infty}\frac{1}{T}\int_0^T\mathbf{y}(t)dt,$$

where the time-average is along every orbit in the interior of $\mathbf{S}_n\times\mathbf{S}_n$.

Proof. From (49) with $B=-A^T$, we get

$$(PQ)^{\cdot}=PQ(\mathbf{p}\cdot A\mathbf{y}-\mathbf{x}\cdot A\mathbf{q}). \tag{51}$$

If $PQ \equiv$ const along every orbit, one has

$$\mathbf{p} \cdot A\mathbf{y} = \mathbf{x} \cdot A\mathbf{q}$$

for all $(\mathbf{x}, \mathbf{y})$ in the interior of $\mathbf{S}_n \times \mathbf{S}_n$. This implies (50). Conversely, if $(\mathbf{p}, \mathbf{q})$ is an equilibrium, then $(A\mathbf{q})_i =$ const for all i, and hence $\mathbf{x} \cdot A\mathbf{q} = \mathbf{p} \cdot A\mathbf{q}$ ($=$ value of A), and similarly $\mathbf{p} \cdot A\mathbf{y} = \mathbf{x} \cdot A\mathbf{q}$, which implies $(PQ)^{\cdot} = 0$. This implies that every orbit in the interior remains on a surface of constant value of PQ, and hence cannot converge to the boundary. The rest of the theorem is obvious.

Note that in the zero-sum case, the eigenvalues of the equilibrium $(\mathbf{p}, \mathbf{q})$ are on the imaginary axis. This follows from the theorem in Sect. 5 and the stability of the fixed point, but it is also easy to check it directly.

9. Cyclic Symmetry

An interesting special case is obtained for $n = m$ when both A and B are cyclically symmetric, i.e. such that $a_{ij} = \bar{a}_{j-1}$ and $b_{ij} = \bar{b}_{j-1}$ for $1 \leqq i, j \leqq n$ (indices are counted mod n). By adding the constant

$$-\frac{1}{n}(\bar{a}_0 + \ldots + \bar{a}_{n-1})$$

to each column of A, we may assume that the row sums of A are all 0, and similarly for B.

The eigenvalues of the cyclic matrix A are

$$n\alpha_k = \sum \bar{a}_j \lambda^{jk} \quad \lambda = e^{\frac{2\pi i}{n}} \tag{52}$$

and the eigenvectors are

$$(\lambda^k, \lambda^{2k}, \ldots, \lambda^{nk}) \tag{53}$$

for $k = 0, 1, \ldots, n-1$, as is easy to check. The analogous results holds for B, the eigenvalues are called β_k, the eigenvectors are the same.

Let F denote the fixed point $(\bar{\mathbf{x}}, \bar{\mathbf{y}})$ of Eq. (36) in the interior of $\mathbf{S}_n \times \mathbf{S}_n$. Clearly $\bar{\mathbf{x}} = \bar{\mathbf{y}} = \left(\frac{1}{n}, \ldots, \frac{1}{n}\right)$. Thus $\bar{\mathbf{x}} \cdot A\bar{\mathbf{y}} = 0$. At the point F, therefore

$$\frac{\partial(\dot{x}_i)}{\partial x_j} = -x_i(A\mathbf{y})_k = 0$$

$$\frac{\partial(\dot{x}_i)}{\partial y_j} = x_i(a_{ij} - (x\mathbf{A})_j) = \frac{1}{n} a_{ij}$$

and thus, up to a multiplicative factor $\frac{1}{n}$, the Jacobian of (36) at F is

$$J = \begin{bmatrix} 0 & A \\ B & 0 \end{bmatrix}. \tag{54}$$

The eigenvalues are the zeros of

$$p(\lambda) = \det \begin{bmatrix} -\lambda I & A \\ B & \lambda I \end{bmatrix}.$$

Now since

$$\begin{bmatrix} I & 0 \\ \lambda^{-1}B & I \end{bmatrix} \begin{bmatrix} -\lambda I & A \\ B & -\lambda I \end{bmatrix} = \begin{bmatrix} -\lambda I & A \\ 0 & \lambda^{-1}AB - \lambda I \end{bmatrix}$$

we have

$$p(\lambda) = \det(-\lambda I) \det(\lambda^{-1}AB - \lambda I) = \det(\lambda^2 I - AB).$$

The cyclic matrices A and B have the same eigenvectors (53), hence the eigenvalues of AB are $\alpha_k \beta_k$, $k = 0, \ldots, n$, and hence those of J are $\pm \sqrt{\alpha_k \beta_k}$. It is easy to see that the pair corresponding to $k = 0$ (a pair of zeros) gets eliminated since we consider only the restriction of (36) to $\mathbf{S}_n \times \mathbf{S}_n$.

Theorem. In the case of cyclic symmetry, the eigenvalues of (36) at the interior equilibrium F are $\pm \sqrt{\alpha_k \beta_k}$, $k = 1, \ldots, n-1$.

F is a saddle except iff $\alpha_k \beta_k \leqq 0$ for all k. For $n = 2$, this just means $a_1 b_1 < 0$, a condition we know from Sect. 6. If $n = 3$, it means

$$a_1 b_1 = a_2 b_2 \quad \text{and} \quad a_1 b_2 \leqq 0. \tag{55}$$

In this case, it is easy to check that

$$b_2(\mathbf{x} \cdot A\mathbf{y}) = a_1(\mathbf{y} \cdot B\mathbf{x}) \tag{56}$$

for all $\mathbf{x}, \mathbf{y}$ in the interior of $\mathbf{S}_3$, and that

$$(x_1 x_2 x_3)^{|b_2|} (y_1 y_2 y_3)^{|a_1|}$$

is a constant of motion. Hence in the 3-dimensional cyclic case, if F is not a saddle, then it is stable, but not asymptotically stable.

10. A 3×2-Game

As we saw in Sect. 5, Eq. (36) has in general no fixed point in the interior of $\mathbf{S}_n \times \mathbf{S}_m$, if $n \neq m$. In this case, a consideration of the time-averages as in Part I, 5 shows that some strategies will sometimes be extremely improbable, and likely to be wiped out by random fluctuations.

It is only in degenerate cases that fixed points exists for $n \neq m$. We shall treat one such case for the sake of illustration. Let $n = 3$ and $m = 2$. We may assume without loss of generality that the bottom line of A and B consists of zeros. In order to have fixed points, the first row of A must be a multiple of the second one: this is the degeneracy condition. For example,

$$A = \begin{bmatrix} -1 & 1 \\ -2 & 2 \\ 0 & 0 \end{bmatrix} \quad B = \begin{bmatrix} -2 & 1 & 1 \\ 0 & 0 & 0 \end{bmatrix}$$

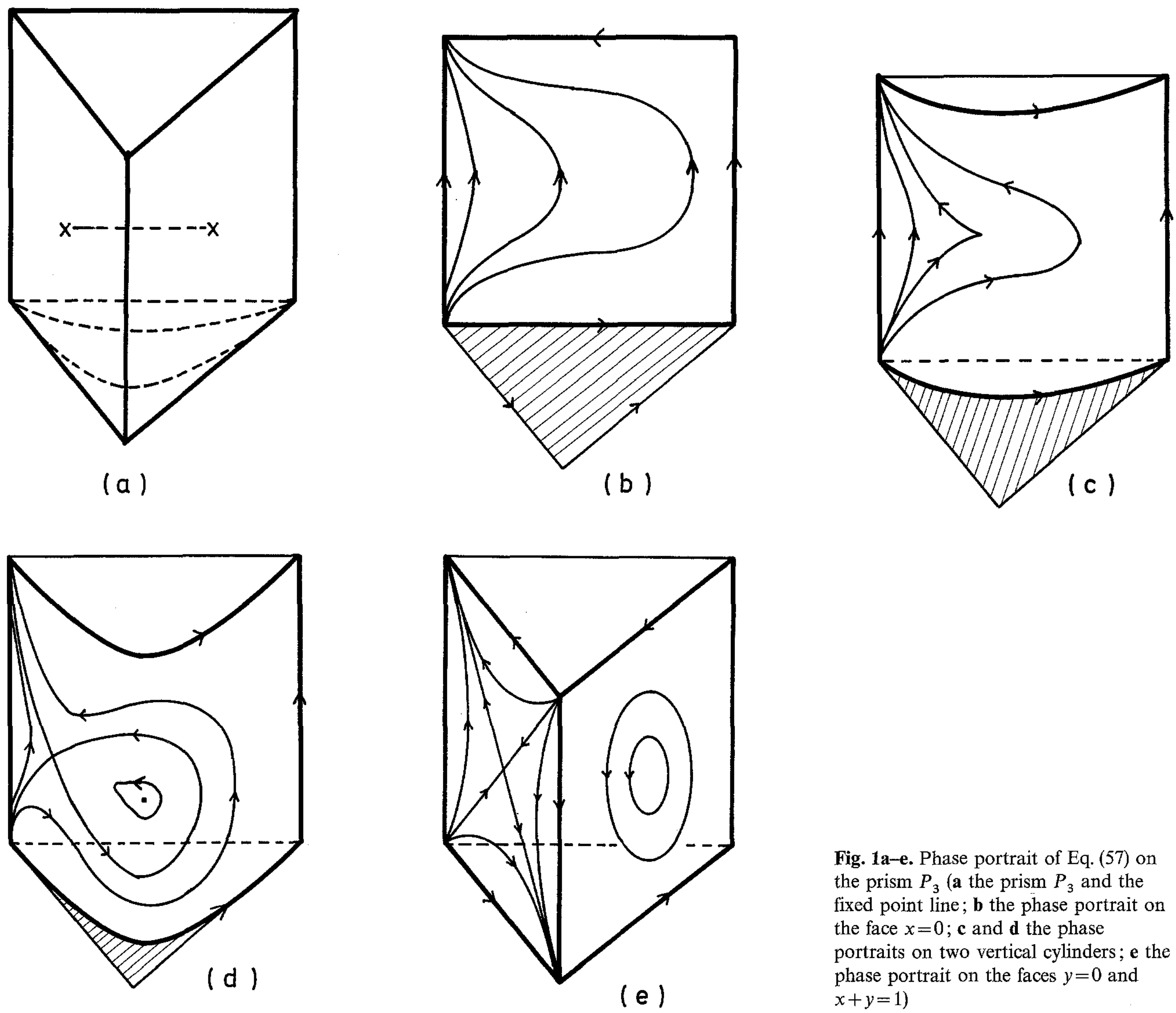

Fig. 1a–e. Phase portrait of Eq. (57) on the prism P_3 (**a** the prism P_3 and the fixed point line; **b** the phase portrait on the face $x=0$; **c** and **d** the phase portraits on two vertical cylinders; **e** the phase portrait on the faces $y=0$ and $x+y=1$)

Setting $x_1=x$, $x_2=y$, and $y_1=z$, we obtain from (36) the equation

$$\begin{aligned}\dot{x}&=x(1-2z)(1-x-2y)\\ \dot{y}&=y(1-2z)(2-x-2y)\\ \dot{z}&=z(1-z)(1-3x)\end{aligned} \tag{57}$$

on the prism $\mathbf{P}_3=\{(x,y,z): 0\leqq x,\ y,z;\ z\leqq 1;\ x+y\leqq 1\}$. The fixed points in the interior of $\mathbf{P}_3$ are those on the line $z=\frac{1}{2}$, $x=\frac{1}{3}$. Their eigenvalues are 0, and $\pm\sqrt{\frac{1}{3}-y}$. Thus on the face $y=0$, we have a saddle, and on the face $x+y=1$, a center.

Note that

$$\frac{dx}{dy}=\frac{x}{y}\frac{1-x-2y}{2-x-2y}. \tag{58}$$

Thus every orbit of (57) satisfies a relation between x and y, corresponding to (58), and independent of z. Their x and y-coordinates are on the solution curves of

$$\begin{aligned}\dot{x}&=x(1-x-2y)\\ \dot{y}&=y(2-x-2y)\end{aligned} \tag{59}$$

an equation of the type (38). The vertical cylinders in $\mathbf{P}_3$ through the solution curves of (59) are invariant for (58). As shown in Fig. 1, as these cylinder sheets curve more and more outward, the phase portrait on them changes drastically. If the sheet intersects the line of fixed points ($z=\frac{1}{2}$, $x=\frac{1}{3}$), a saddle and a center emerge in an unstable configuration similar to the flow of the well-known second order equation $\ddot{q}=\frac{1}{2}(1-q^2)$.

References

Dawkins, R.: The selfish gene. Oxford: Oxford Univ. Press (1976)

Eigen, M., Schuster, P.: The hypercycle – a principle of natural self-organization. Berlin, Heidelberg, New York: Springer 1979

Hammerstein, P.: The role of asymmetries in animal contests. J. Theor. Pop. Biol. (in press) (1980)

Maynard-Smith, J., Parker, G.A.: The logic of asymmetric contests. Anim. Behav. **24**, 159–175 (1976)

Parker, G.A.: Sexual selection and sexual conflict. In: Sexual selection and reproductive competition in the insects. Blum, M.S., Blum, N.A. (eds.), p. 123. New York: Academic Press 1979

Rauhut, R., Schmitz, N., Zachow, E.W.: Spieltheorie. (Teubner Studienbücher.) Stuttgart: Teubner 1979

Schuster, P., Sigmund, K.: Coyness, philandering and stable strategies. Anim. Behav. (in press) (1980)

Selten, R.: A note on evolutionarily stable strategies in asymmetric animal conflicts. Working Papers, Institute of Mathematical Economies, University of Bielefeld 1978

Trivers, R.: Parental investment and sexual selection. In: Sexual selection and the descent of man. Campbell, B. (ed.), p. 128. Chicago: Aldine 1972

Received: July 29, 1980

Prof. Dr. P. Schuster
Institut für Theoretische Chemie
und Strahlenchemie der Universität
Währinger Strasse 17
A-1090 Wien
Austria