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THE DYNAMICS OF ASYMMETRIC GAMES

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FOREWORD

A game dynamical analysis of a simple asymmetric game (two roles with two alternatives each) shows that an interesting class of "semi-stable" heteroclinic cycles leading to a highly unpredictable behaviour can occur in a robust way. Biological examples related to conflicts over ownership and parental investment are analysed.

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The Dynamics of Asymmetric Games

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1. Introduction

Even in the artificial world of 'fair' parlour games and sporting encounters, asymmetries between the contestant's roles are frequent. Some rules are meant to reduce this asymmetry (toss up a coin to decide who moves first; play a return match) but others emphasize it (a draw favours the incumbent champion; the nation organizing the world soccer cup automatically qualifies). In nature, the role of asymmetries is much more pronounced still, and soon after the introduction of game theory in the study of biological contests, a series of papers underlined the special 'logic of asymmetric contests' and drew attention to conflicts with in-built asymmetries like those between owner and intruder, weaker and stronger contestant, male and female, parent and offspring, queen and worker, prey and predator etc ... In Maynard Smith's book on "Evolution and the Theory of Games" (1982), three chapters are devoted to asymmetric games, and a rough census of its list of references seems to show that the majority of conflicts studied by sociobiologists exhibits asymmetries.

In contrast to this, the study of the *dynamics* of asymmetric games has lagged considerably behind that of the symmetric case. Of the few papers, most have investigated the case of separate populations (Taylor (1979), Schuster et. al. (1981)). This is appropriate for coevolutionary games between predator and prey or host and parasite, but hardly so for games between owner and intruder or parent and offspring, where one individual will find itself sometimes in one role and sometimes in the other. It is also plausible that for male-female or worker-queen conflicts, the genetic programs for the two roles are linked. In any case, most of the static game theoretical models assume conditional strategies (for example: if male, be a philanderer; if female, be coy). In the present paper we discuss the corresponding dynamical features.

In section 2 we describe the dynamics in the simplest case (two roles with two alternatives each), in section 3 we apply this to some outstanding examples of asymmetric games in biology (battling spiders, bluffing shrimps and coy birds), and in section 4 we add a recombination term which reduces the dynamic degeneracy. Of special interest are games with cyclic structure, which exhibit a novel type of 'semi-stable' heteroclinic cycle and a 'zip'-like bifurcation from stability to instability along a line of equilibria.

2. The model

In the simplest possible case, there are two roles I and II with two strategies each: $\mathbf{e}_1$ and $\mathbf{e}_2$ for I and $\mathbf{f}_1$ and $\mathbf{f}_2$ for II. Any individual will find itself with probability p in role I and $1-p$ in role II. (This role can change during its life history, e.g. child and parent or owner and intruder, or it can stick for life, like male and female in most cases.) Within the game considered, individuals in one role are assumed to interact only with those in the other role.

The payoff for role I (resp. II) is given by E (resp. F):

$$E = \begin{pmatrix} A & B \\ C & D \end{pmatrix} \qquad F = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

B, for example, is the expected payoff for an $\mathbf{e}_1$-strategist meeting an $\mathbf{f}_2$-player, etc ... Thus we are dealing with bimatrix games.

The population will consist of four 'behavioural' types: $I_1 = \mathbf{e}_1\mathbf{f}_1$ (i.e. play $\mathbf{e}_1$ if in role I and $\mathbf{f}_1$ if in role II), $I_2 = \mathbf{e}_2\mathbf{f}_1$, $I_3 = \mathbf{e}_1\mathbf{f}_2$ and $I_4 = \mathbf{e}_2\mathbf{f}_2$, with frequencies x_1 to x_4, respectively. The state of the population is given by a point in the simlpex

$$S_4 = \{\mathbf{x} = (x_1, \ldots, x_4) : x_i \geq 0, x_1 + \cdots + x_4 = 1\}$$

Let Γ be the sequence of four edges connecting the corners I_1 to I_2 to I_4 to I_3 and back to I_1 again. Each edge connects two types using the same option in one role and different ones in the other. Generally, one of the two alternatives is the better one, and we orient the edge accordingly. This yields essentially to the following orientations of Γ :

*Fig.*1

According to a basic result (Selten 1980), an asymmetric game has no mixed ESS (evolutionarily stable strategy). It is easy to see that type I_j is an ESS if and only if both adjacent edges point towards it. Thus (a) and (b) have one ESS and (c) a pair of opposite ESSs while the cyclic structure of (d) allows no ESS at all. We shall see presently how the dynamics agrees with this static classification.

The payoff for type I_i against I_j is given by $p(1-p)M_{ij}$, with M_{ij} given by the 4×4-matrix

$$M = \begin{pmatrix} A+a & A+b & B+a & B+b \\ C+a & C+b & D+a & D+b \\ A+c & A+d & B+c & B+d \\ C+c & C+d & D+c & D+d \end{pmatrix}.$$

(For example M_{24} is given as follows. With probability $p(1-p)$ the I_2-player is in role I and the I_4-player in role II: the payoff for $\mathbf{e}_2$ against $\mathbf{f}_2$ is D; with the same probability $p(1-p)$ the I_2-player is in role II and the I_4-player in role I, and in this case the I_2-player obtains b; with probability $p^2+(1-p)^2$ both players are in the same role and hence do not interact.)

Thus the game is described now by a single matrix. The payoff is the increment in reproductive value. According to the usual game dynamics (Taylor and Jonker (1978), see also Hofbauer and Sigmund (1988)) we assume that the rate of increase of each type is given by the difference between its payoff and the average payoff in the population. This yields

$$\dot{x}_i = x_i[(M\mathbf{x})_i - \bar{M}] \tag{1}$$

with $\bar{M} = \sum x_i(M\mathbf{x})_i$. (We have divided the right hand side by $p(1-p)$, which corresponds to a change in time scale.) The state space S_4 and its boundary (consisting of the faces where $x_i = 0$) are invariant. From now on we consider only the restriction of (1) to S_4. Subtracting m_{ii} from the i-th column of M does not affect the dynamics. Hence we may use without restriction of generality the matrix

$$M = \begin{pmatrix} 0 & -R & -r & S+s \\ R & 0 & -S-r & s \\ r & -R-s & 0 & S \\ R+r & -s & -S & 0 \end{pmatrix}$$

where $R = C - A$, $S = B - D$, $r = c - a$ and $s = b - d$.

One checks immediately that the ratio $\frac{x_1x_4}{x_2x_3}$ is an invariant of motion, i.e. remains constant under (1). Each equation $x_1x_4 = Kx_2x_3$ (for $K > 0$) defines a saddle-like surface W_K in the interior of the state space S_4. It is bounded by the four edges belonging to Γ.

Of special interest is the case $K = 1$. The surface W_1 corresponds to the Wright-manifold, the surface of linkage zero in the well-known two-locus, two-alleles equation from population genetics. In our setup, $x_1x_4 = x_2x_3$ means that the strategies in role I and role II are independent. W_1 divides S_4 into two halves.

The equilibria of (1) are given by $(M\mathbf{x})_i = \bar{M}$ whenever $x_i > 0$. In intS_4, this means $(M\mathbf{x})_1 = \cdots = (M\mathbf{x})_4$. Together with $x_1 + \cdots + x_4 = 1$, this yields a system of 4 linear equations which is in general of rank 2. The equations $(M\mathbf{x})_2 = (M\mathbf{x})_1$ and $(M\mathbf{x})_2 = (M\mathbf{x})_4$ imply

$$x_1 + x_2 = \frac{S}{R+S} \qquad x_1 + x_3 = \frac{s}{r+s}$$

if the denominators do not vanish. These two equations determine a line of fixed points, which can be written as

$$\begin{aligned} x_i &= m_i + \mu \qquad (i = 1,4) \\ x_i &= m_i - \mu \qquad (i = 2,3) \end{aligned} \tag{2}$$

with

$$\mathbf{m} = \frac{1}{(R+S)(r+s)}(Ss, Sr, Rs, Rr).$$

We note that $\mathbf{m}$ satisfies $m_1 m_4 = m_2 m_3$ and that the line of fixed points given by (2) intersects intS_4 if and only if $\mathbf{m} \in W_1$, i.e. if and only if $RS > 0$ and $rs > 0$. Thus either all of the invariant surfaces W_K $(0 < K < \infty)$ contain a fixed point or none does. The μ-values for which (2) then yields a point in intS_4 are those satisfying

$$-\min(m_1, m_4) < \mu < \min(m_2, m_3).$$

One can compute the Jacobian and hence the eigenvalues of (1) at the interior equilibria. One eigenvalue is always 0, of course. We list now a brief classification and deal subsequently with some biologically relevant examples. Essentially, the arrows of the diagrams in Fig. 1 will correspond to orbits of (1) along the edges of Γ.

(A) No equilibrium in the interior. Then all orbits converge to the boundary, so that the dynamics is reduced to a simple lower dimensional one. Actually, it is easy to check that generically, there exists a single corner of S_4 attracting all interior orbits. This corner corresponds to an ESS, and hence we obtain cases (a) or (b) of Fig. 1. Thus the outcome is fixation of a single type. We call this the case of *global stability*.

(B) A line of equilibria in the interior, and $Rr > 0$. Each equilibrium is a saddle on the corresponding invariant surface. A surface S containing the equilibria and two corners divides S_4 into two parts. In each, there is a corner attracting all orbits, while the orbits in $S \cap S_4$ converge to interior equilibria. This is the case of ***bistability***: up to a set of measure zero, all initial conditions lead to one of two opposite corners. These corners are ESSs. This corresponds to (c) in Fig. 1.

(C) A line of equilibria in the interior, and $Rr < 0$. This is the ***cyclic*** case: I_1 beats I_2, which beats I_4, which beats I_3, which in turn beats I_1 (or the other way round). The Jacobian at the inner equilibria has a pair of complex eigenvalues, which corresponds to a rotational component on the invariant surface W_K.

On W_1, the eigenvalues are purely imaginary. There exists a further invariant of motion, namely

$$S \log(x_1 + x_2) + R \log(x_3 + x_4) - s \log(x_1 + x_3) - r \log(x_2 + x_4)$$

(Actually, this is a Hamiltonian on W_1). Thus W_1 consists of periodic orbits. For $K > 1$ the fixed point is a spiral sink, and for $K \in (0, 1)$ a spiral source (or vice versa), provided $R + S + r + s \neq 0$. Thus if one travels along the line of equilibria, there occurs a degenerate Hopf bifurcation as one crosses W_1: stability changes into instability. This is somewhat similar to the *zip-bifurcation* studied by Farkas (1984) in ecological models although there is no parameter here to move the zip.

We show in the appendix that off W_1, there is no periodic orbit. The edges are orbits converging to one corner as $t \to -\infty$ and to the next one as $t \to +\infty$. Together, they form a heteroclinic cycle. In one half of intS_4, all orbits spiral away from the inner equilibria and towards Γ. In the other half, they spiral away from Γ and towards an interior equilibrium (see Fig. 2).

Fig.2

In the class of *all* dynamical systems, such a behaviour is structurally unstable to a high degree: (a) the saddle connections – orbits leading from one saddle-type equilibrium to an-other – correspond to intersections of stable and unstable manifolds which are not transversal, which is a non-generic situation; (b) the constant of motion foliating the state space into invariant surfaces W_K is nongeneric too; (c) the line of equilibria is a degeneracy, since usually equilibria are isolated; (d) the Hopf bifurcation (which leads to no limit cycle) is also degenerate, since at the critical parameter value $K = 1$ there occurs a constant of motion. Nevertheless, this heteroclinic cycle which is partly attracting and partly repelling occurs in a perfectly robust way within the dynamics of asymmetric games: a small change in parameters will leave the behaviour unaffected.

The outcome is highly unpredictable. In one half of the state space, the evolution tends towards an equilibrium with all four types present. However, this equilibrium is only neutrally stable, as it is imbedded within a line of equilibria. Under random fluctuations, the state will drift along this line and eventually enter the other half of the simplex. There, the dynamics will lead towards Γ. The state will hover close to one corner, then abruptly switch along an edge to the next corner, stay there for a much larger time, switch rapidly (and without exterior cue) to the next one etc ... in a 'cycle' with ever increasing period. Since the state is close to Γ, two or three of the types are present in only a minute amount. Eventually, one of them will be wiped out by a random fluctuation. Then, the cycle is broken and fixation at one of the corners occurs (it is impossible to predict which one). A fortunate sequence of fluctuations (due to mutation or migration for example) can reintroduce some of the missing types, or even all of them; it could even happen that this leads to a state in that half of S_4 where convergence to an interior fixed point occurs, and the whole evolution is repeated again. But basically, the outcome is fixation of a randomly chosen pure type.

3. Examples

(A) Battling spiders

Conflicts between the owner of a territory and an intruder have been analysed by Hammerstein (1981), Maynard Smith (1982), Maynard Smith and Parker (1986) and others, and exemplary field studies of territorial fights of funnel web spiders have been carried out by Riechert (1978). Let role *I* be that of the owner and role *II* that of the intruder. Both contestants have the option to escalate ($\mathbf{e}_1$ resp. $\mathbf{f}_1$) or to stick to ritualized fighting. We denote by $-D$ the cost of an injury and by $-T$ that of a drawn-out ritualized conflict. For the owner, the probability of winning is $\frac{1}{2}$ in a ritual fight and q in an escalated battle. By V_1 and V_2 we denote the value of the territory for the owner resp. for the intruder (they need not be the same). The payoff matrices are

$$E = \begin{pmatrix} qV_1 - (1-q)D & V_1 \\ 0 & \frac{V_1}{2} - T \end{pmatrix}$$

$$F = \begin{pmatrix} (1-q)V_2 - qD & V_2 \\ 0 & \frac{V_2}{2} - T \end{pmatrix}$$

Then $R = (1-q)D - qV_1$, $r = qD - (1-q)V_2$, $S = \frac{V_1}{2} + T > 0$, $s = \frac{V_2}{2} + T > 0$. Interior fixed points exist iff $R > 0$ and $r > 0$. In this case the fixed points are saddles. We have a bistable case with two ESSs (the bourgeois strategy – owner escalates and intruder flees – and the opposite, paradoxical strategy).

(B) Bluffing shrimps

This example has been proposed by Gardner and Morris (1989) to describe the territorial behaviour of a mantis shrimp, which lives and hides in cavities. These crustaceans undergo periodically a stage during which their exoskeleton is renewed. Such newly molten individuals are highly vulnerable to conspecific attacks. Nevertheless, they display sometimes a threatening behaviour towards intruders, leaning out of their cavity and raising their raptorial appendage in a so-called meral spread (a 'bluffing' signal similar to the shaking of a fist). If the intruder is in an intermolt stage, it would win an escalated fight, but does not know the actual state of the owner (P is the probability that it is newly molten).

In the Gardner-Morris example, role I is: owner in a newly molten stage, and role II: intermolt intruder. The owners strategies are $\mathbf{e}_1$ (to flee) and $\mathbf{e}_2$ (to bluff), while the intruders alternatives are $\mathbf{f}_1$ (to attack) or $\mathbf{f}_2$ (to withdraw). If V denotes the value of the territory, $-B$ the cost of bluffing (leaning out of the cavity is not without danger) and $-C$ the cost of losing a fight, the payoff matrices are

$$E = \begin{pmatrix} 0 & 0 \\ -B(1-P) & (V-B)(1-P) \end{pmatrix}$$

$$F = \begin{pmatrix} V(1-P)-CP & V(1-P)-CP \\ V(1-P) & 0 \end{pmatrix}$$

This yields $R = -B(1-P) < 0$, $r = CP > 0$, $S = (B-V)(1-P)$ and $s = V(1-P)-CP$, and hence $R+S+r+s = 0$ – a degenerate case which displays an extra constant of motion (see appendix). If we assume $B < V$ and $CP < V(1-P)$, so that $S < 0$ and $s < 0$, there is a line of fixed points in $\operatorname{int} S_4$. All other orbits in $\operatorname{int} S_4$ are periodic.

(C) Coy birds

A pretty example related to the question of parental investment has been proposed by Dawkins (1976). Some (hypothetical) male birds are faced with the temptation to desert (leaving the female with the task of raising the brood) and to found a new family somewhere else. The counterstrategy of the females is to insist upon a long engagement. It would then be too late in the season, for the male, to start it all over again, and much better to stay and help with the offspring. The two roles are female (I) and male (II); the female can be coy, i.e. insist upon a long engagement before copulation ($\mathbf{e}_1$), or it can be fast ($\mathbf{e}_2$). The male can be a philanderer, i.e. not prepared to put up with a long wait ($\mathbf{f}_1$), or it can be faithful, i.e. willing to accept a long engagement ($\mathbf{f}_2$). If G denotes the increase in fitness (for each parent) corresponding to the successful raising of a brood, $-C$ the cost of parental investment (which can be shared, or borne entirely by the female), and $-E$ the cost inflicted by a long engagement on each partner, then the payoffs are given by

$$E = \begin{pmatrix} 0 & G - \frac{C}{2} - E \\ G - C & G - \frac{C}{2} \end{pmatrix}$$

$$F = \begin{pmatrix} 0 & G \\ G - \frac{C}{2} - E & G - \frac{C}{2} \end{pmatrix}$$

This yields $R = G - C$, $S = -E < 0$, $s = \frac{C}{2} > 0$ and $r = G - \frac{C}{2} - E$. In order to have fixed points in $\operatorname{int} S_4$, we must have $0 < E < G < C < 2(G - C)$. In this case $R + S + r + s = 2(G - E) - C > 0$. The fixed point on W_K is a spiral sink for $K > 1$ and a spiral source for $0 < K < 1$. This is an example with cyclic dynamics.

4. Recombination

In this final section we modify the dynamics (1) by adding recombination:

$$\dot{x}_i = x_i[(M\mathbf{x})_i - \bar{M}] - \varepsilon_i r D. \tag{3}$$

Here $\varepsilon_1 = -\varepsilon_2 = -\varepsilon_3 = \varepsilon_4 = 1$, $r > 0$ is the recombination fraction and $D = x_1x_4 - x_2x_3$ the linkage disequilibrium. This system on S_4 describes a two-locus two-allele model, where the two loci correspond to the two possible roles and the two alleles determine the strategy played in that role, with additive contributions of gametes to fitness.

Then for $Z = \frac{x_1 x_4}{x_2 x_3}$ we have

$$\frac{\dot{Z}}{Z} = \sum_{i=1}^{4} \varepsilon_i \frac{\dot{x}_i}{x_i} = -rD(\sum_{i=1}^{4} \frac{1}{x_i}) = -r(Z-1)x_2x_3(\sum_{i=1}^{4} \frac{1}{x_i})$$

which shows that $Z \to 1$ along all solutions in $\operatorname{int} S_4$. Hence the Wright manifold $W_1 = \{D = 0\} = \{Z = 1\}$ is globally attracting for the system (3), while the other manifolds W_K are no longer invariant.

The dynamics on W_1 is the same as before and its expression can be simplified further: If $x = x_1 + x_3$ denotes the frequency of $\mathbf{e}_1$ and $y = x_1 + x_2$ the frequency of $\mathbf{f}_1$, then on W_1 we have $x_1 = xy$, $x_2 = (1-x)y, \ldots$ and therefore

$$\dot{x} = x(1-x)(S-(R+S)y)$$

$$\dot{y} = y(1-y)(s-(r+s)x).$$

Hence the dynamics on W_1 coincides with the dynamics for bimatrix games introduced by Schuster and Sigmund (1981) and studied further in Schuster et al. (1982) and Hofbauer and Sigmund (1988), ch.17 and 27.

Appendix

Using the transformation $\operatorname{int} S_4 \to \operatorname{int} \mathbb{R}^3_+$, $\mathbf{x} \mapsto \mathbf{y}$, where $y_i = \frac{x_i}{x_4}$, $i = 1, \ldots, 4$ we write the replicator equation (1) as Lotka-Volterra equation

$$\dot{y}_1 = y_1((S+s) - (R+r)y_1 - (R-s)y_2 + (S-r)y_3)$$

$$\dot{y}_2 = y_2(s - ry_1 + sy_2 - ry_3)$$

$$\dot{y}_3 = y_3(S - Ry_1 - Ry_2 + Sy_3).$$

The line of fixed points is given by the equations $ry_1 - sy_2 + ry_3 = s$ and $Ry_1 + Ry_2 - Sy_3 = S$. $H = \log \frac{y_1}{y_2 y_3}$ is an invariant of motion, i.e. $y_1 = Ky_2y_3$ $(K > 0)$ define invariant surfaces $\tilde{W}_K$ in $\operatorname{int} \mathbb{R}^3_+$.

Therefore we can study the dynamics on these surfaces and reduce the system to two dimensions:

$$\begin{aligned}\dot{y}_2 &= y_2(s + sy_2 - ry_3 - rKy_2y_3)\\ \dot{y}_3 &= y_3(S - Ry_2 + Sy_3 - RKy_2y_3).\end{aligned} \tag{A1}$$

For $K = 1$ we obtain

$$\begin{aligned}\dot{y}_2 &= y_2(1 + y_2)(s - ry_3)\\ \dot{y}_3 &= y_3(1 + y_3)(S - Ry_2).\end{aligned}$$

Hence the fixed point on $\tilde{W}_1$ is given by $\mathbf{F} = (\frac{Ss}{Rr}, \frac{S}{R}, \frac{s}{r})$ (from now on $Rr \neq 0$) and the line of fixed points can be written as

$$\begin{aligned}y_1 &= \frac{Ss}{Rr} + (Ss - Rr)\lambda\\ y_2 &= \frac{S}{R} + r(R + S)\lambda\\ y_3 &= \frac{s}{r} + R(r + s)\lambda\end{aligned}$$

This line intersects $\operatorname{int}\mathbb{R}^3_+$ iff $RS > 0$ and $rs > 0$.

The Jacobian of $(A1)$ at the fixed point $\mathbf{F} = (\hat{y}_2, \hat{y}_3)$ is given by

$$J = \begin{pmatrix} (s - rK\hat{y}_3)\hat{y}_2 & -r(1 + K\hat{y}_2)\hat{y}_2\\ -R(1 + K\hat{y}_3)\hat{y}_3 & (S - RK\hat{y}_2)\hat{y}_3 \end{pmatrix}$$

We note that

$$K = \frac{\frac{Ss}{Rr} + (Ss - Rr)\lambda}{\left(\frac{S}{R} + r(R + S)\lambda\right)\left(\frac{s}{r} + R(r + s)\lambda\right)}.$$

A direct computation yields

$$\operatorname{tr} J = Rr(R + S + r + s)\lambda$$

and

$$\det J = -(R + S)(r + s)[Rr(Ss - Rr)\lambda^2 + 2Ss\lambda + \frac{Ss}{Rr}].$$

It is easy to check that $\det J$ does not change its sign along the line of fixed points.

Equation $(A1)$ can be written as

$$\dot{y}_2 = y_2[s(1 + y_2 + y_3 + Ky_2y_3) - (r + s)(1 + Ky_2)y_3]$$
$$\dot{y}_3 = y_3[S(1 + y_2 + y_3 + Ky_2y_3) - (R + S)(1 + Ky_3)y_2]\,.$$

After dividing the right-hand side by $y_2y_3(1 + y_2 + y_3 + Ky_2y_3)$ – which does not change the orbits – we obtain

$$\dot{y}_2 = \frac{s}{y_3} - \frac{(r+s)(1+Ky_2)}{1+y_2+y_3+Ky_2y_3}$$
$$\dot{y}_3 = \frac{S}{y_2} - \frac{(R+S)(1+Ky_3)}{1+y_2+y_3+Ky_2y_3}\,.$$

The divergence of this system is given by $\operatorname{div}(\dot{y}_2, \dot{y}_3) = -\dfrac{(R+S+r+s)(K-1)}{(1+y_2+y_3+Ky_2y_3)^2}$.

If $K = 1$ ($\Leftrightarrow \lambda = 0$) or $R + S + r + s = 0$ (these are the cases for which $\operatorname{tr} J = 0$) the system is divergence-free and hence is Hamiltonian, i.e. of the form $\dot{y}_2 = -\dfrac{\partial H}{\partial y_3}$, $\dot{y}_3 = \dfrac{\partial H}{\partial y_2}$

The Hamilton function H can be easily computed to:

(1) $K = 1$: $H = S\log y_2 - (R+S)\log(1+y_2) - s\log y_3 + (r+s)\log(1+y_3)$

(2) $R + S + r + s = 0$: $H = S\log y_2 - s\log y_3 + (r+s)\log(1+y_2+y_3+Ky_2y_3)^2$

We note, that H is a constant of motion. Therefore the fixed point is either a saddle or surrounded by periodic orbits.

If $K \neq 1$ and $R + S + r + s \neq 0$ then $\operatorname{div}(\dot{y}_2, \dot{y}_3)$ is strictly positive or strictly negative, having the same sign as $\operatorname{tr} J$. Hence – by the Theorem of *Bendixson–Dulac* – there does not exist any periodic orbit on $\tilde{W}_K$.

The following classification of the fixed points in $\operatorname{int} S_4$ characterises also the global dynamics on each surface $\tilde{W}_K$:

If $Rr > 0$ then $\det J < 0$ and all fixed points are saddles.

If $Rr < 0$ then $\det J > 0$ and we obtain:

	$K < 1$	$K = 1$	$K > 1$
$R + S + r + s > 0$	sink	centre	source
$R + S + r + s = 0$	centre	centre	centre
$R + S + r + s < 0$	source	centre	sink

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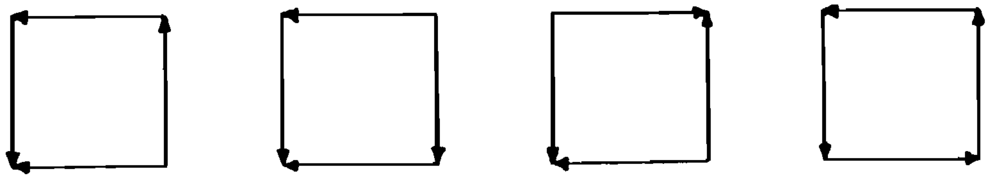
(a) (b) (c) (d)

Figure 1

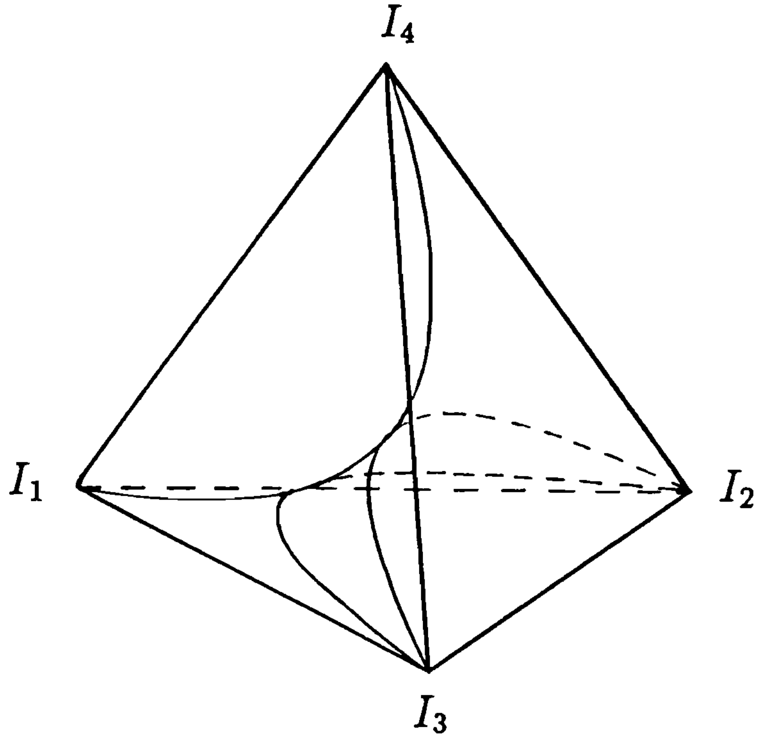

Figure 2