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Biological Cybernetics

Selfregulation of Behaviour in Animal Societies*

III. Games between Two Populations with Selfinteraction

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Abstract. The ordinary differential equation $\dot{x}=x(1-x)\,(a+bx+cy)$ and $\dot{y}=y(1-y)\,(d+ex+fy)$ is classified with the methods of topological dynamics. This equation describes the evolution of strategies in animal contests between two populations.

1. ESS for Two Populations with Selfinteraction

The next situation to consider is obviously that of two populations X and Y interacting with themselves and with each other. The first to define ESS in this case has been Taylor (1979).

Let $x_1, \ldots, x_n$ (resp. $y_1, \ldots, y_m$) be the frequencies of the different X- (resp. Y-) strategies. Let A, B, C, D, be the payoff-matrices describing the interaction of X with itself, of X with Y, of Y with X and of Y with itself. The state $(\mathbf{p},\mathbf{q})\in \mathbf{S}_n \times \mathbf{S}_m$ is again called ESS if

(i) it is a best reply against itself, i.e. for all $(\mathbf{r},\mathbf{s})\neq(\mathbf{p},\mathbf{q})$, one has

$$\mathbf{r}\cdot(A\mathbf{p}+B\mathbf{q})+\mathbf{s}\cdot(C\mathbf{p}+D\mathbf{q})\leqq \mathbf{p}\cdot(A\mathbf{p}+B\mathbf{q})+\mathbf{q}\cdot(C\mathbf{p}+D\mathbf{q})\,; \tag{60}$$

(ii) if $(\mathbf{r},\mathbf{s})$ is an alternative best reply, $(\mathbf{p},\mathbf{q})$ fares better than $(\mathbf{r},\mathbf{s})$ against $(\mathbf{r},\mathbf{s})$. This means that if equality holds in (60), then

$$\mathbf{r}\cdot(A\mathbf{r}+B\mathbf{s})+\mathbf{s}\cdot(C\mathbf{r}+D\mathbf{s})<\mathbf{p}\cdot(A\mathbf{r}+B\mathbf{s})+\mathbf{q}\cdot(C\mathbf{r}+D\mathbf{s}) \tag{61}$$

The corresponding differential equations on $\mathbf{S}_n \times \mathbf{S}_m$ are

$$\begin{aligned} x_i&=x_i(\mathbf{e}_i\cdot A\mathbf{x}+\mathbf{e}_i\cdot B\mathbf{y}-\mathbf{x}\cdot A\mathbf{x}-\mathbf{x}\cdot B\mathbf{y}) \qquad i=1,\ldots,n\\ y_j&=y_j(\mathbf{f}_j\cdot C\mathbf{x}+\mathbf{f}_j\cdot D\mathbf{y}-\mathbf{y}\cdot C\mathbf{x}-\mathbf{y}\cdot D\mathbf{y}) \qquad j=1,\ldots,m, \end{aligned} \tag{62}$$

where $\mathbf{e}_i$ and $\mathbf{f}_j$ are the unit vectors corresponding to the corners of $\mathbf{S}_n$ and $\mathbf{S}_m$ as in Part II.

Again, it is easy to see that $(\mathbf{p},\mathbf{q})$ is an ESS iff the function V defined by

$$(\mathbf{x},\mathbf{y})\rightarrow \prod_{i=1}^{n} x_i^{p_i} \prod_{j=1}^{m} y_j^{q_j}$$

is a strict Ljapunov function. In particular, every ESS is asymptotically stable.

2. Two Strategies for Each Player

In the case $n=m=2$, i.e. if both X and Y have only two strategies, the phase space $\mathbf{S}_2\times\mathbf{S}_2$ is the unit square $\mathbf{Q}_2$ and (62) readily becomes (with $x=x_1$ and $y=y_1$)

$$\begin{aligned} \dot{x}&=x(1-x)(a+bx+cy)\\ \dot{y}&=y(1-y)(d+ex+fy) \end{aligned} \tag{63}$$

for suitable values of the constants a to f.

These equations, which are a generalization of (42, Part II) will be investigated qualitatively in the remainder of this paper. Much of the spirit of this study is due to Zeeman's paper (1979), where he classifies (5, Part I) for $n=3$. In particular, we also omit from our considerations certain degenerate cases, corresponding to values of the parameters $a, \ldots, f$, where bifurcations occur, i.e. where small perturbations lead to drastic changes in behaviour. It will easily be seen that in doing this, we only exclude a set of parameters of measure zero, corresponding to a finite number of algebraic relations. Thus we only consider the cases which are stable in the sense that the phase-portrait remains topologically unchanged under small perturbations of the parameters.

Before proceeding, however, let us recall that equations of type (63) have occured in prominent place in network theories for the nervous system. More pre-

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cisely, the equation

$$\dot{x}_i = x_i(1-x_i)\left(\varepsilon_i + \sum_{j=1}^{n} \alpha_{ij} x_j\right) \tag{64}$$

on the unit cube $\{(x_1, \ldots, x_n) \in \mathbb{R}^n : 0 \leqq x_i \leqq 1\}$ have been studied by Cowan in (1968) and (1970), under the assumption that the matrix (α_{ij}) is skew-symmetric. The variable x_i, here, corresponds to the i-the cell of a neural network: it measures the proportion of time that this cell is "sensitive" to incoming stimuli. Equation (64), then, is a heuristic equation describing a situation where the cells are tonic and the damping is negligible. In this case, Cowan derives a statistical mechanics for the neutral network, using as Hamiltonian the function H:

$$(x_1, \ldots, x_n) \to \sum_i [\log(1 + p_i \exp v_i) - p_i v_i], \tag{65}$$

where $(p_1, \ldots, p_n)$ is the (unique) fixed point in the interior of the cube and

$$v_i = \log \frac{x_i}{(1-x_i)p_i}.$$

It is easily checked that H is indeed a constant of motion.

Note that equations of type (64) in n variables can also be obtained in the usual way, from the game theoretic consideration of n players, interacting with each other, every player having the choice of two strategies. Now let us turn to the two-dimensional case and study (63).

3. General Results: Fixed Points and Straight Lines

Let Φ_1, Φ_2 denote the lines given by

$$\Phi_1 : a + bx + cy = 0$$

$$\Phi_2 : d + ex + fy = 0.$$

In general (63) admits 9 fixed points:

The four corners of the square $F_1 = (0,0)$, $F_2 = (1,0)$, $F_3 = (1,1)$, $F_4 = (0,1)$, then one on each of the limiting lines of the square:

$$F_5 = \{x=0\} \cap \Phi_2 = \left(0, -\frac{d}{f}\right)$$

$$F_6 = \{y=0\} \cap \Phi_1 = \left(-\frac{a}{b}, 0\right)$$

$$F_7 = \{x=1\} \cap \Phi_2 = \left(1, -\frac{d+e}{f}\right)$$

$$F_8 = \{y=1\} \cap \Phi_1 = \left(-\frac{a+c}{b}, 1\right)$$

and finally

$$F = \Phi_1 \cap \Phi_2 = (p, q) = \left(\frac{cd-af}{bf-ec}, \frac{ea-bd}{bf-ec}\right).$$

F as well as $F_5 - F_8$ may be inside or outside of the square.

Linearization around F

The next thing one has to do after knowing the fixed points is to determine the local behaviour of the flow around them.

The Jacobian of (63) is given by $J = \{J_{ij}\}$

$$\begin{aligned} J_{11} &= (1-2x)(a+bx+cy) = bx(1-x) \\ J_{12} &= ey(1-y) \\ J_{21} &\ldots cx(1-x) \\ J_{22} &= (1-2y)(d+ex+fy) + fy(1-y). \end{aligned} \tag{66}$$

At the point F we get

$$J = \begin{bmatrix} bp(1-p) & cp(1-p) \\ eq(1-q) & fq(1-q) \end{bmatrix}.$$

Therefore the eigenvalues are given by

$$\lambda_{1,2} = \tfrac{1}{2}[\mathrm{tr}J \pm ((\mathrm{tr}J)^2 - 4\det J)^{1/2}],$$

where $\mathrm{tr}J = bp(1-p) + fq(1-q)$ is the trace of the Jacobian and $\det J = p(1-p)q(1-q)(bf-ec)$ is the determinant of the Jacobian.

It follows:

$$\begin{aligned} &F \text{ is a saddle} \Leftrightarrow \Delta = bf - ec < 0 \\ &\quad F \text{ is a sink} \Leftrightarrow \Delta > 0 \quad \text{and} \quad \mathrm{tr}J < 0 \\ &\qquad \text{source} \Leftrightarrow \Delta > 0 \quad \text{and} \quad \mathrm{tr}J > 0. \end{aligned} \tag{67}$$

Geometric Interpretation

The sign of the determinant $\Delta = bf - ec$ and hence the type of the fixed point F can be recognized from the geometric position of the lines Φ_1 and Φ_2:

Let us introduce an orientation for lines which do not go through the origin in such a way that the origin

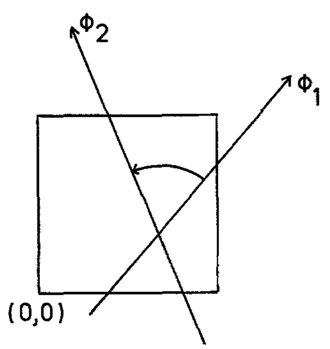


Fig. 1. Orientation for lines. The oriented angle between Φ_1 and Φ_2 determines via (68) the sign of Δ and hence the character of the fixed point F

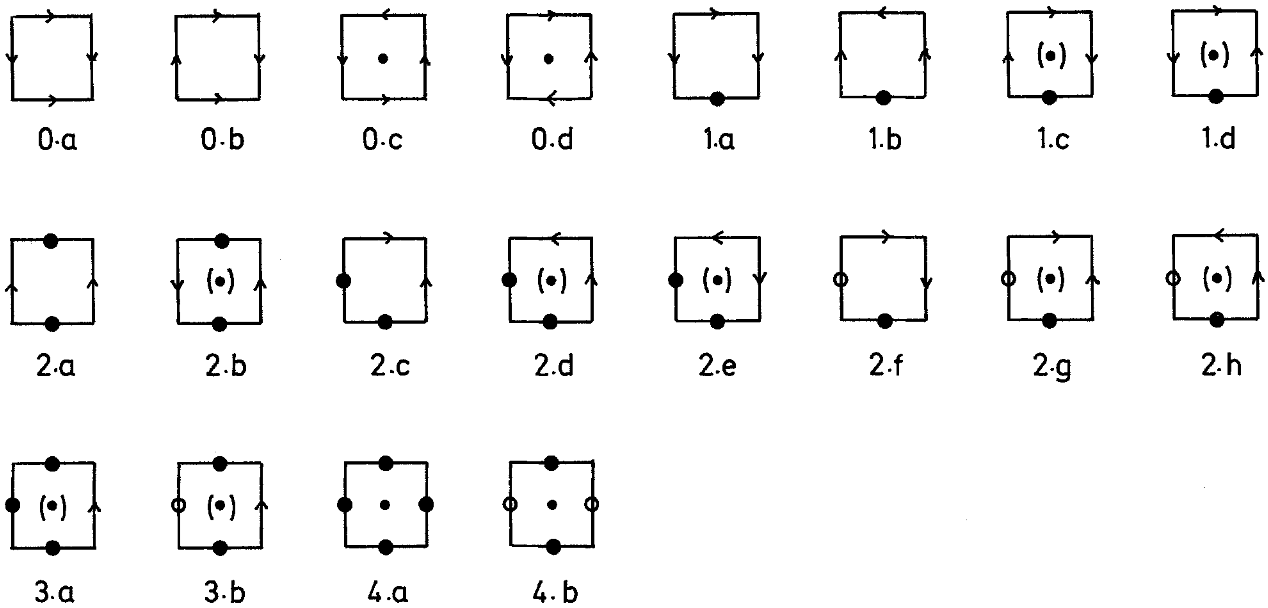


Fig. 2. The 20 stable flows on the boundary. We only put an arrow on the edge if there is no fixed point in the interior of this edge. Otherwise we indicate the fixed point by a solid dot if it is an attractor and by an open dot if it is a repellor for that edge. A dot in the center of the square means that this boundary flow forces the fixed point F to lie inside the square, whereas a dot between brackets says that F may be inside as well as outside the square in this case

lies in the left half plane (Fig. 1). Then basic linear algebra implies

$$0 < \measuredangle(\Phi_1, \Phi_2) < 180° \Leftrightarrow \mathrm{ad}\,\Delta > 0. \tag{68}$$

In order to describe the phase portraits, we first determine all possible flows on the boundary of the square.

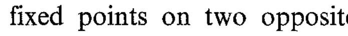
We shall see that apart from degenerate cases such as $a = b = 0$, where the x-axis consists only of fixed points, there are 20 such stable flows on the boundary (up to flow reversal and symmetry operations like rotations and reflexions of the square).

Then we shall try to continue the given flow on the boundary into the interior of the square. We shall see that in some cases this is possible in a unique way but in general there are more possibilities. For shortness we shall not do this for all 20 boundary flows in full detail, but treat all relevant aspects. We conjecture that (63) gives rise to altogether 36 stable flows on the square.

A first discussion of all 20 classes together with a lot of numerical examples can be found in Gottlieb (1980).

4. The Flow on the Boundary

It is easy to determine the possible flows on the boundary. On each side of the square we have at most one fixed point (in the stable case), i.e. up to flow reversal there are two possibilities for each side of $\mathbf{Q}_2$:



From the special form of (63) we obtain only the following restriction: If there are fixed points on two opposite sides of $\mathbf{Q}_2$ then thay have the same type: Either both are attractors (restricted to the boundary) or both are repellors.

This is clear, since the sign of $\dot{x}$ (resp. $\dot{y}$) is constant on each halfplane determined by Φ_1 (resp. Φ_2) and the fixed points on two opposite sides are just the intersection of Φ_1 (or Φ_2) with these two sides.

Therefore we arrive at the 20 flows on the boundary as shown in Fig. 2. In the 7 cases 0a, 0b, 1a, 1b, 2a, 2c, and 2f the intersection point F of the lines Φ_1 and Φ_2 always lies outside of $\mathbf{Q}_2$, in the four cases 0c, 0d, 4a, 4b F lies inside, and in the remaining 9 cases the position of F is not determined by the flow on the boundary.

5. *F* is a Saddle or Outside of the Square

Theorem. If $F \notin \operatorname{int}\mathbf{Q}_2$ or if F is a saddle then the ω-limit of every orbit in $\mathbf{Q}_2$ is a fixed point.

Proof. First Poincaré-Bendixson theory implies that there is no closed orbit in the interior of $\mathbf{Q}_2$ (there must be a fixed point within the closed orbit, which cannot be a saddle). Since there is no closed orbit, the ω-limit

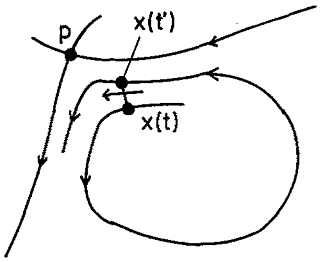


Fig. 3. The flow near a saddle which is contained in the ω-limit of some orbit

of any orbit contains a fixed point, say P. Of course, P cannot be a source. If P is a sink then it *is* the ω-limit of this orbit. There remains the case: P is a saddle. If the considered orbit is not an inset of P, we have the situation described in Fig. 3. One can find $t<t'$ such that the segment connecting $\mathbf{x}(t)$ and $\mathbf{x}(t')$ together with $\{\mathbf{x}(s): t \leqq s \leqq t'\}$ is a Jordan curve and its interior is negatively invariant. Hence it contains a fixed point which cannot be a saddle. That is a contradiction. Hence every orbit is either an inset of a saddle or converges to a sink on the boundary.

1. F is Outside

Let us call a saddle on the boundary which is not a corner, a "proper" saddle.

Then we have the following three situations (up to flow reversal): among the (at least 4, at most 8) fixed points on the boundary there are

a) One source, one sink, no proper saddle.
Then every orbit in the interior goes from the source to the sink.

b) Two sources, one sink, one proper saddle.
Every orbit in int $\mathbf{Q}_2$ converges to the sink. The outset of the saddle separates the basins of repulsion of the two sources.

c) Three sources, one sink, two proper saddles.
Every orbit in int $\mathbf{Q}_2$ converges to the sink, the two outsets of the two saddles divide the square into three regions which are the three basins of repulsion of the three sources (see Fig. 4).

2. F is a Saddle

If F lies inside the square and is a saddle then there are always two sinks and two sources on the boundary. The insets and outsets of F separate $\mathbf{Q}_2$ into four regions where the orbits go from one of the sources to one of the sinks. It is easy to see that in the cases 0d, 1d, 2g, 3b, and 4b the flow on the boundary (and eventually the existence of F in the interior of $\mathbf{Q}_2$) determines the position of the lines Φ_1 and Φ_2 in such a way that by means of (68) Δ is negative and hence, using (67), F is a saddle (see Fig. 5).

In some other cases the position of Φ_1 and Φ_2 may be such that F is a saddle, e.g. in the case 2e, if F lies inside the triangle $F_1F_5F_6$ (see Fig. 5). For further discussion of 2e see Sect. 6, and Sect. 7 for 2b and 2h.

6. A Ljapunov-Function

Theorem. Assume that the fixed point $F=(p,q)$ lies inside the square. Further let $\Delta>0$ (i.e. F is either a sink or a source), and $bf>0$. Then the function

$$V(x,y)=x^p(1-x)^{1-p}[y^q(1-y)^{1-q}]^r$$

is a Ljapunov-function (for some convenient $r>0$) for Eq. (63).

Corollary. Let $\Delta>0$ and $F=(p,q)$ inside the square. If $b,f<0$, then F is a global attractor (each orbit converges to F). If $b,f>0$, then F is a global repellor (each orbit comes from F).

Proof. First it is easy to see that $F=(p,q)$ is the unique global maximum of V.

$$\begin{aligned}\frac{\dot V}{V}&=(\log V)^{\cdot}=p\frac{\dot x}{x}-(1-p)\frac{\dot x}{1-x}+r\left[q\frac{\dot y}{y}-(1-q)\frac{\dot y}{1-y}\right]\\&=\frac{\dot x}{x(1-x)}[p(1-x)-(1-p)x]\\&\quad+r\frac{\dot y}{y(1-y)}[q(1-y)-(1-q)y]\\&=(p-x)(a+bx+cy)+r(q-y)(d+ex+fy).\end{aligned}\tag{69}$$

We now introduce new coordinates

$\xi=x-p$ and $\eta=y-q$ and obtain

$$\begin{aligned}\dot V/V&=-\xi(b\xi+c\eta)-r\eta(e\xi+f\eta)\\&=-b\xi^2-(c+re)\xi\eta-rf\eta^2.\end{aligned}$$

This quadratic form is definite if

$$(c+re)^2 \leqq 4rbf.$$

Now a short calculation shows that whenever $bf>0$ and $\Delta=bf-ec>0$ there exists an $r>0$, such that this condition is satisfied.

This theorem is very useful for our classification, since the nature of the fixed points on the boundary lines determines the sign of the coefficients b and f:

Lemma. If one of the fixed points F_5, F_7 lies on the square and is an attractor (repellor) when restricted to the boundary, then $f<0$ ($f>0$) and similar for F_6, F_8, and b.

Proof. Suppose $F_5=\left(0,-\frac{d}{f}\right)$ is an attractor. Then $\dot y>0$ near F_1, which means $d>0$. Since F_5 lies in $\mathbf{Q}_2$, $f<0$.

The other cases run in a similar way.

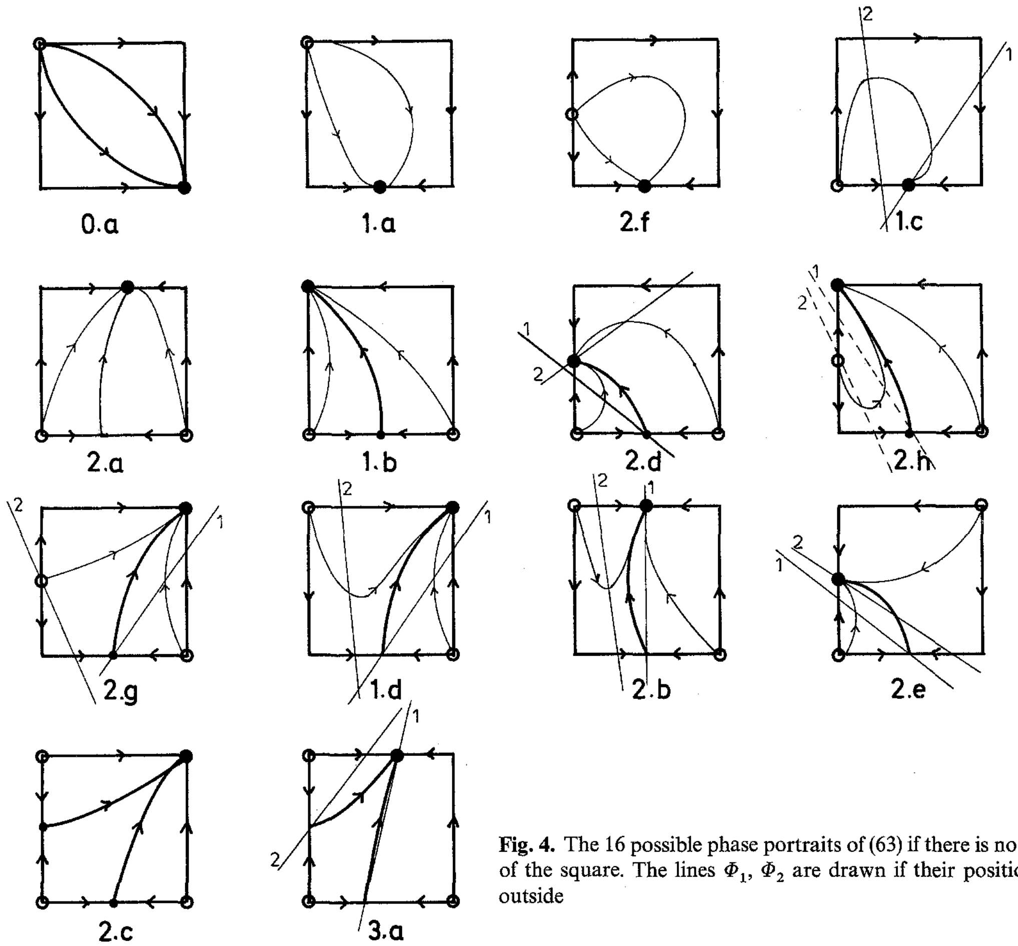


Fig. 4. The 16 possible phase portraits of (63) if there is no fixed point in the interior of the square. The lines Φ_1, Φ_2 are drawn if their position is relevant for F lying outside

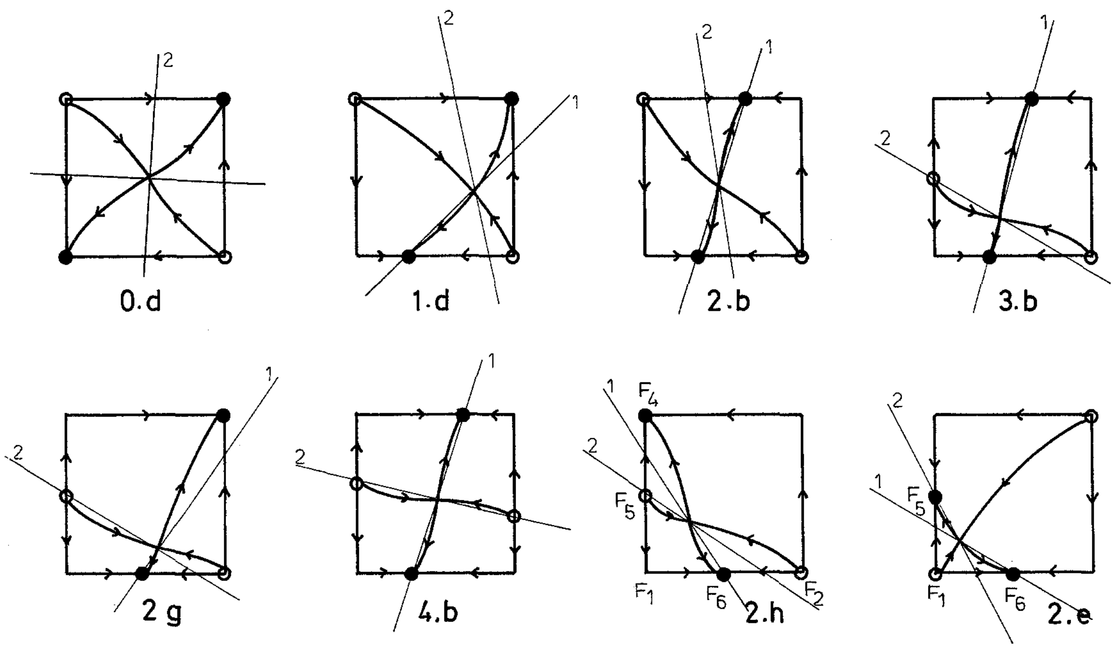


Fig. 5. The 8 phase portraits of (63) if the fixed point F is a saddle

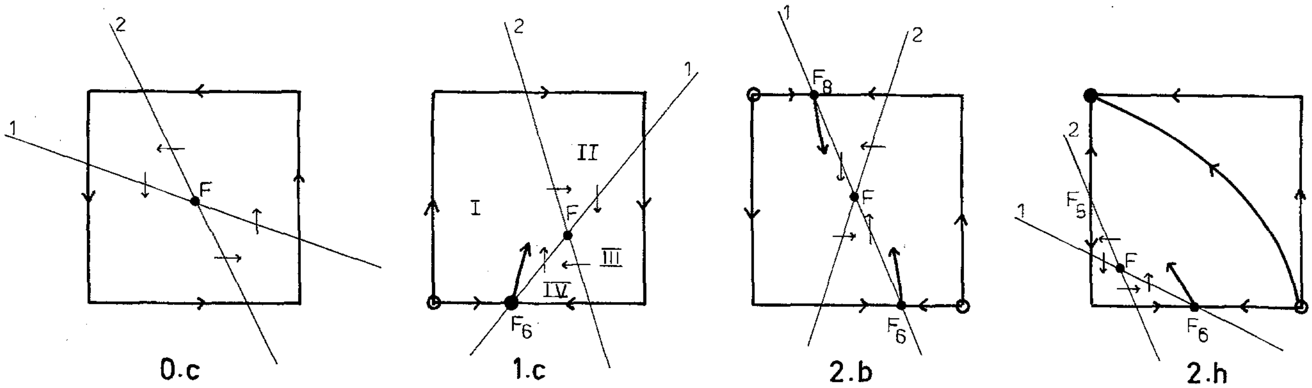


Fig. 6. In these four cases limit cycles can occur. For the flows 1c and 2b a limit cycle exists whenever F is a source. The cyclic flow 0c is discussed in Sect. 8

Corollary. If there is an attractor inside a horizontal and one inside a vertical boundary line and if F is not a saddle ($\Delta > 0$), then F is a global attractor.

This corollary determines the qualitative behaviour of four classes, namely 2e (if F is not a saddle, i.e. if F lies outside the triangle $F_1F_5F_6$, see Fig. 5), 2d, 3a, and 4a.

So 16 of all 20 boundary classes are completely classified. One should pay attention to the fact that in all these 16 classes the flow on the boundary together with the position of the lines Φ_1, Φ_2 (if necessary at all) determines the flow in the interior of the square and that the ω-limit of any orbit is a fixed point. The flow is "gradient-like", there are no limit cycles.

This is in contrast to the remaining four classes 0c, 1c, 2b, and 2h: Note that the position of all 9 fixed points and the flow on the boundary is not changed if we multiply the vectors (a, b, c) and (d, e, f) by arbitrary positive constants.

Now if b and f have different sign (which is fulfilled in 2h and may be the case for 0c, 1c, and 2b) and Δ is positive, then F can change from a sink to a source by such a manipulation, since $\mathrm{tr}J = bp(1-p) + fq(1-q)$ can change sign. So we see that these four cases (with F inside the square and $\Delta > 0$) allow several continuations of the flow into the interior.

Moreover numerical investigations show that in these cases limit cycles can occur. We will prove this in the first three cases; for the boundary flow 2h, however, we are not able to prove occurrence of limit cycles.

7. Limit Cycles

7.1. The Boundary Flow 1c

First the given boundary flow implies (see Fig. 6) that $\sphericalangle(\Phi_1, \Phi_2) > 180°$.

Together with $a > 0$, $d < 0$ and (68) we have $\Delta > 0$. That means by (67): F is either a sink or a source. The lemma in Sect. 6 implies $b > 0$. If Φ_2 is decreasing, $f > 0$, and the theorem in Sect. 6 applies: F is a global sink. If Φ_2 is increasing, $f < 0$, and following the above remark, F may also be a source.

The lines Φ_1, Φ_2 divide the square into four regions, where the signs of $\dot{x}$ and $\dot{y}$ are constant. If F is a source then every orbit in the interior of $\mathbf{Q}_2$ enters in turn the regions I, II, III, IV, I,... (see Fig. 6). If F is a sink, the orbits could also converge to F staying in one region forever. Hence the outset of the saddle F_6 spirals inwards. But if F is a source, Poincaré-Bendixson theory implies that the ω-limit of the outset is a periodic orbit. This situation is similar to that in Kolmogoroff's paper (1936). Numerical investigations suggest that there is only one closed orbit, if F is a source, and that there is no closed orbit, if F is a sink (F is then a global sink).

7.2. The Boundary Flow 2b

The same argument implies the existence of limit cycles if F is a source. Again we conjecture that there is exactly one periodic orbit, if F is a source and that there is no periodic orbit, if F is a sink (see Fig. 6).

However it is also possible in this case, that F is a saddle, namely if Φ_2 crosses the x-axis to the right of F_6 and the line $y = 1$ to the left of F_8. Then F_6 and F_8 are sinks. This corresponds to the situation in Sect. 5, see also Fig. 5.

7.3. The Boundary Flow 2h

If F lies outside of the triangle $F_1F_5F_6$ then F is a saddle. Its outsets go to the sinks F_4, F_6 and its insets come from the sources F_2, F_5 (see Fig. 5).

If F lies inside the triangle $F_1F_5F_6$, F is either a sink or a source, F_5 and F_6 are saddles, $b > 0$, $f < 0$ (see Fig. 6). If we consider the outset of F_6, then it may tend towards F either converging to F or to a limit cycle, it may converge to F_5 (that means it is also the inset of F_5) or it may converge to the sink F_4.

In this case we have no exact results, we even cannot prove the existence of a limit cycle. The outset of F_6 may converge to F_4, it may converge (as inset) to the saddle F_5, it may converge to F or to a limit cycle in the interior of $\mathbf{Q}_2$.

8. The Boundary as Limit-Set

In this case (see Fig. 6) the line Φ_1 has to cross the two vertical boundary lines and Φ_2 the two horizontal boundary lines. Hence the intersection point F of Φ_1 and Φ_2 lies in the interior of $\mathbf{Q}_2$. Since the angle $\sphericalangle(\Phi_1, \Phi_2) > 180°$ and ad <0 we have (68) $\Delta = bf - ec > 0$ and F cannot be a saddle.

The flow around $F=(p,q)$ is determined by the sign of $\operatorname{tr} J = bp(1-p) + fq(1-q)$. If $\operatorname{tr} J > 0$, F is a source, for $\operatorname{tr} J < 0$, F is a sink. If furthermore $b, f < 0$ (that means Φ_1 is increasing and Φ_2 is decreasing) then the Theorem in Sect. 6 applies and F is a global sink.

Now let us determine the flow near the boundary. Using a method which was applied in Hofbauer (1981) to prove cooperation of certain higher dimensional dynamical systems we derive a condition for the boundary *bd* $\mathbf{Q}_2$ to be an attractor or a repellor respectively.

The ω-limit of the orbits on *bd* $\mathbf{Q}_2$ consists just of the four corners of the square. If we now can find a function V with the following properties

$$V \geqq 0 \text{ on } \mathbf{Q}_2 \text{ and } V(x)=0 \text{ iff } x \in bd\mathbf{Q}_2 \tag{70}$$

$$\frac{\dot{V}}{V} > 0 \text{ near the corners} \tag{71}$$

then the boundary is a repellor. If (71) is replaced by

$$\frac{\dot{V}}{V} < 0 \text{ near the corners} \tag{72}$$

then the boundary is an attractor.

We shall use V as in Sect. 6, leaving open the choice of $\bar{p}, \bar{q}$ in (0, 1) and $r>0$ ($\bar{p}, \bar{q}$ need not correspond to the coordinates of F).

Using (69) condition (71) is equivalent to

$$\begin{aligned} &\bar{p}\lambda_1 + r\bar{q}\mu_1 > 0 \\ &(1-\bar{p})\lambda_2 + r\bar{q}\mu_2 > 0 \\ &(1-\bar{p})\lambda_3 + r(1-\bar{q})\mu_3 > 0 \\ &\bar{p}\lambda_4 + r(1-\bar{q})\mu_4 > 0, \end{aligned} \tag{73}$$

where

$$\begin{aligned} \lambda_1 &= a & \mu_1 &= d \\ \lambda_2 &= -a-b & \mu_2 &= d+e \\ \lambda_3 &= -a-b-c & \mu_3 &= -d-e-f \\ \lambda_4 &= a+c & \mu_4 &= -d-f \end{aligned}$$

are the eigenvalues of the corners [which can be obtained from (66)]. According to the cyclic flow on the boundary λ_1, μ_2, λ_3, μ_4 are positive and μ_1, λ_2, μ_3, λ_4 are negative. So (73) becomes

$$\begin{aligned} &\frac{\bar{p}}{\bar{q}} \frac{\lambda_1}{\mu_1} < -r < \frac{1-\bar{p}}{\bar{q}} \frac{\lambda_2}{\mu_2} \\ &\frac{1-\bar{p}}{1-\bar{q}} \frac{\lambda_3}{\mu_3} < -r < \frac{\bar{p}}{1-\bar{q}} \frac{\lambda_4}{\mu_4}. \end{aligned} \tag{74}$$

We can find a positive r satisfying (74) if each term on the left side is smaller than each term on the right side. Setting $\lambda_i/\mu_i = v_i$ we get

$$\begin{aligned} &\bar{p}v_1 < (1-\bar{p})v_2 \\ &(1-\bar{q})v_1 < \bar{q}v_4 \\ &\bar{q}v_3 < (1-\bar{q})v_2 \\ &(1-\bar{p})v_3 < \bar{p}v_4 \end{aligned}$$

or

$$\frac{v_2}{v_1} < \frac{\bar{p}}{1-\bar{p}} < \frac{v_3}{v_4} \quad \text{and} \quad \frac{v_2}{v_3} < \frac{\bar{q}}{1-\bar{q}} < \frac{v_1}{v_4}.$$

Both inequalities are satisfied for some $p, q \in (0, 1)$ iff

$$v := \frac{v_1 v_3}{v_2 v_4} > 1. \tag{75}$$

So we have proved.

Lemma. (i) *bd* $\mathbf{Q}_2$ is a repellor, if $v>1$ ($\lambda_1\mu_2\lambda_3\mu_4 > \mu_1\lambda_2\mu_3\lambda_4$).
(ii) *bd* $\mathbf{Q}_2$ is an attractor, if $v<1$ ($\lambda_1\mu_2\lambda_3\mu_4 < \mu_1\lambda_2\mu_3\lambda_4$).

Hence we may consider v as the eigenvalue of the boundary given by a kind of Poincaré-section.

The condition $v>1$ may also be written as

$$\frac{bc}{(a+b)(a+c)} < \frac{ef}{(d+e)(d+f)} \quad \text{or} \quad bep(1-p) < cfq(1-q). \tag{76}$$

This condition is independent from the conditions $\operatorname{tr} J \gtreqless 0$ which determine the local behaviour around the fixed point F: Multiplying the vectors (a,b,c) and (d,e,f) with positive constants (see also the end of Sect. 6) changes the sign of $\operatorname{tr} J$ (if $bf<0$) and so the flow near F. However condition (76) and hence the flow near the boundary remain the same. We conjecture that this manipulation induces a Hopf-bifurcation (which is generic, if $v \neq 1$ and degenerate, if $v=1$, see Fig. 7). Now if F and *bd* $\mathbf{Q}_2$ are both repellors or both attractors, that is, if $\operatorname{tr} J$ and $v-1$ have the same sign, the existence of a (stable or unstable) limit cycle is guaranteed by Poincaré-Bendixson. What we cannot prove is that there is *only one* periodic orbit in this case and that there are no limit cycles in the other cases.

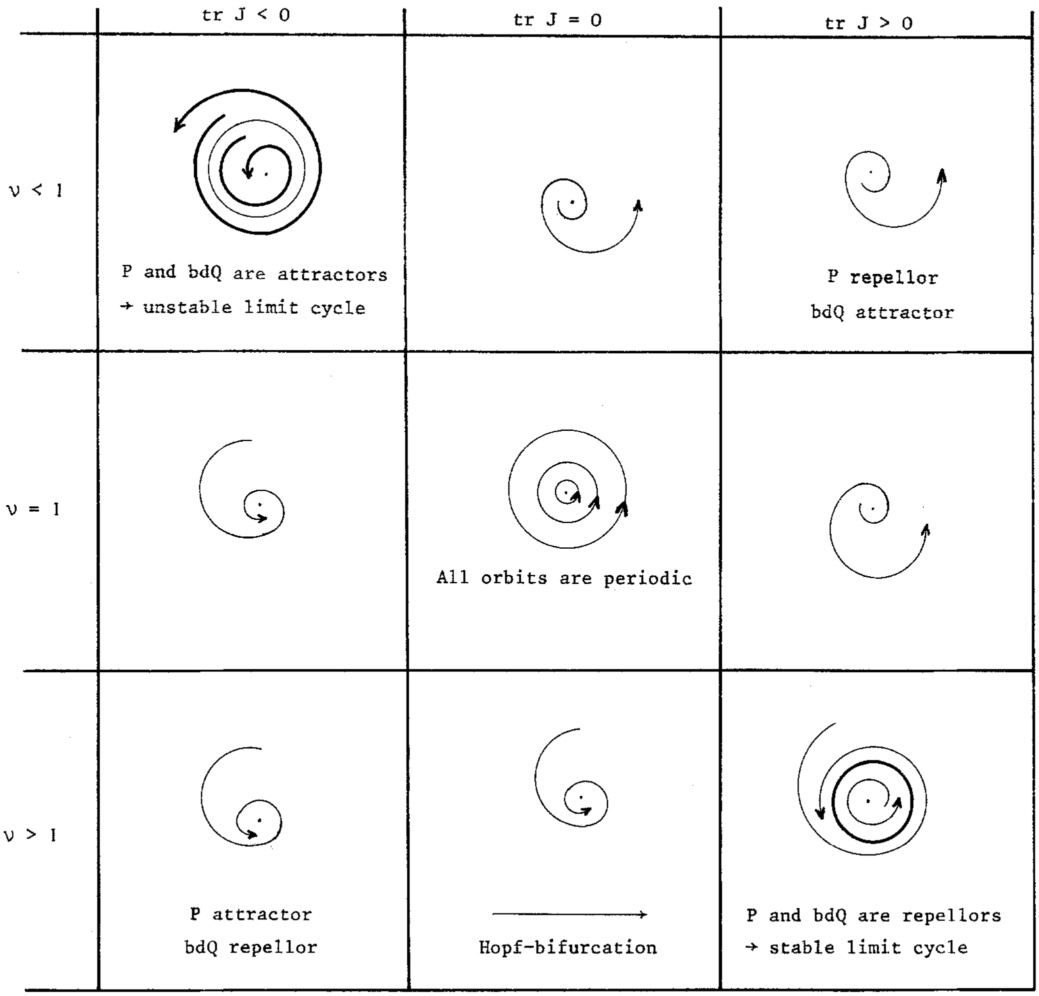


Fig. 7. Qualitative behaviour of (63) for the cyclic boundary flow 0c (under the hypothesis, that there is at most one limit cycle)

If we now make the following
Hypothesis. System (63) admits at most one limit cycle (which is supported by numerical investigations), then we arrive at the qualitative behaviour shown in Fig. 7.

9. An Invariant

The aim of this section is to integrate our differential equation and find a constant of motion in the special case, where both $\operatorname{tr} J = bp\,(1-p) + fq(1-q) = 0$ and $\nu = 1$.

It is easy to check that these two conditions are equivalent with the following situation: Either $b = f = 0$ [this is just the case treated in Schuster and Sigmund (1980)] or

$$e + c = 0 \quad \text{and} \quad (f+d)(bd-ae) = (a+b)(cd-af). \tag{77}$$

In this case a short calculation shows that

$G(x,y)dx + H(x,y)dy = 0$ where

$G(x,y) = x^{-1-\alpha}(1-x)^{\alpha-2}y^{-\beta}(1-y)^{\beta-1}(d+ex+fy)$ and

$H(x,y) = x^{-\alpha}(1-x)^{\alpha-1}y^{-1-\beta}(1-y)^{\beta-2}(a+bx+cy)$

is an exact differential form equivalent to our differential equation (63), if we choose

$$\alpha = \frac{(a+b)d}{bd-ae} = \frac{(f+d)d}{cd-af}$$

$$\text{and} \quad \beta = -\frac{a(a+b)}{bd-ae} = -\frac{a(f+d)}{cd-af}. \tag{78}$$

Its integral $\varphi(x,y)$ cannot be written in a closed form. But we can conclude everything we want to known on the shape of the integral curves $\varphi(x,y) = \text{const}$ from the equations

$\varphi_x = G$ and $\varphi_y = H$.

Theorem. If $\Delta = bf - ec > 0$, the fixed point F lies inside $\mathbf{Q}_2$ and the conditions $\operatorname{tr} J = 0$ and $\nu = 1$ are satisfied (that is, if the eigenvalues at F are purely imaginary and the eigenvalue of $bd\ \mathbf{Q}_2$ is 1), then in some neighbourhood of F all orbits are periodic. If the flow is circulant (flow 0c) then *all* orbits in the interior are closed.

Proof. Obviously $F=(p,q)$ is the only critical point of φ inside $\mathbf{Q}_2$ and the Hessian at F is given by

$$\varphi_{xx}\varphi_{yy}-\varphi_{xy}^2 = (bf-ec)p^{-1-2\alpha}(1-p)^{2\alpha-3}q^{-1-2\beta}(1-q)^{2\beta-3}>0.$$

Hence F is an extremum of φ and orbits near F are periodic. In the case of a circulant flow on the boundary α and β lie in $(0,1)$ and therefore $F_x=G \sim x^{-1-\alpha}(1-x)^{\alpha-2}$ in $x=0$ and $x=1$ and hence is not integrable. That means $F(x,y)\to\infty$, if (x,y) tends to the boundary.

One can easy convince oneself that this situation occurs only in the two boundary classes 0c and 2h.

One could also try to use the invariant $\varphi(x,y)$ as a Ljapunov-function for other parameter values of $a, b, \ldots$ as it was done in Sect. 6 with the invariant V for the case $b=f=0$.

One obtains that this is possible whenever

$$(\operatorname{tr} J)^2 \geqq p(1-p)q(1-q)(e+c)^2. \tag{79}$$

Hence if (79) is fulfilled, there can be no limit cycles. However condition (79) is too weak to prove the existence of a Hopf-bifurcation, as it does not apply to the case $\operatorname{tr} J=0$, $v\neq 1$.

10. Conclusion

In the three parts presented we have shown that a class of ordinary differential equations is applicable to a wide variety of phenomena associated with self-replication. In particular, they offer a very general frame for an understanding of the evolution of animal behaviour. Additionally, they apply to many other questions of biological relevance like self-organization of macromolecules (Eigen and Schuster, 1979), nervous systems (Cowan, 1970) and population genetics. Finally, we mention that Hofbauer has recently shown that equation (5, Part I) is equivalent to the Lotka-Volterra equations (Hofbauer, 1980)

$$\dot{x}_i = x_i\left(\varepsilon_i + \sum_{j=1}^{n} a_{ij}x_j\right), \quad i=1,\ldots,n, \quad x_i \geqq 0$$

used frequently in mathematical ecology. Thereby, he was able to prove that limit cycles cannot occur in two-dimensional Lotka-Volterra systems, but do occur for any dimension $n>2$.

Equation (63), then is interesting for two more reasons. On one hand, it is instructive to see how a two-dimensional Volterra-Lotka equation gets modified by multiplication with terms like $1-x$ and $1-y$. There are remarkable changes in the phase portrait, such as the possibility for limit cycles. On the other hand, (63) occurs as restriction of the three-dimensional Volterra-Lotka equation, and hence is a step towards its investigation. It seems that the non-linearities encountered in self-replication are quite ubiquitous and may all be described essentially by the same very flexible equation.

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