Biol. Cybern. 40, 1–8 (1981)

Biological Cybernetics

Selfregulation of Behaviour in Animal Societies*

I. Symmetric Contests

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Abstract. The ordinary differential equation which transformes the game theoretical model of Maynard-Smith into a dynamical system is discussed and some important theorems and applications to symmetric contests in animal societies are presented.

1. Introduction

This series of three papers deals with different related classes of ordinary differential equations, which arise from a dynamical view of game theoretical models for selfreplication in a wide sense.

The concept of evolutionary stability introduced by Maynard-Smith (1974) and used by himself and by a number of other biologists to explain some features of social behaviour of animals was successful for two reasons: primarily it provides an explanation for "altruism" based on the benefit of the individual's genes. Within this model the widely used concepts of group selection or benefit of the species become dispensible. A second feature consists in the creation of a semi-quantitative scale which may be used to invert observed behaviour into relative genetic values. In general, non trivial quantitative features are rare in the "biology of entire organisms" and hence it appears to be worth-while to analyse this aspect of the theory in more detail.

The contribution presented consists of three parts. In the first paper we discuss models of symmetric contests. Equation (5) derived here covers a wide variety of applications. One of them ($a_{ij}=a_{ji}$) corresponds to the Fisher-Wright-Haldane model for selection in population genetics (see e.g. Hadeler, 1974 or Crow and Kimura, 1970). Another special case is the elementary hypercycle ($a_{ij}=a_j\delta_{i,j+1}$) introduced by Eigen and Schuster (1979). The mathematical features of the general equation were discussed extensively by Hofbauer et al. (1980). Here we mention briefly the relevant results and use them to analyse two concrete models for animal behaviour: 1) The hawk – mouse – bully – retaliator – prober-retaliator game (Maynard-Smith and Price, 1973) and 2) a discrete version of the war of attrition (Maynard-Smith, 1974).

In the second part we derive equations for asymmetric contests without self-interaction. We show that the notion of evolutionary stability is no longer as useful as in the symmetric case. We treat some examples and also show that our equations lead to a simple computation of the minimax strategies for zero-sum games.

Part three introduces self-interaction into asymmetric contests. Special cases of the equations obtained here play an important role in Cowan's theory of nervous networks (Cowan, 1970). We discuss explicitly the two dimensional phase portraits and give a quantitative description and classification.

In order to present a guide line through the concepts involved we sketched a flow chart which will be discussed in the next three sections (Fig. 1).

2. Scores, Payoff, Games, and Differential Equations

In order to start with a semi-quantitative model for animal contests we have to fix certain parameter values for gains, risks and losses. We use the word "investment" as a general expression for these three notions and denote the corresponding input parameters as "scores" $\sigma_1, \sigma_2, \ldots, \sigma_m$. The second class of input consists in the "characters". A character is a type of behaviour. There are several, let us say n different characters in the population under consideration. For the purpose of our analysis a character is completely

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

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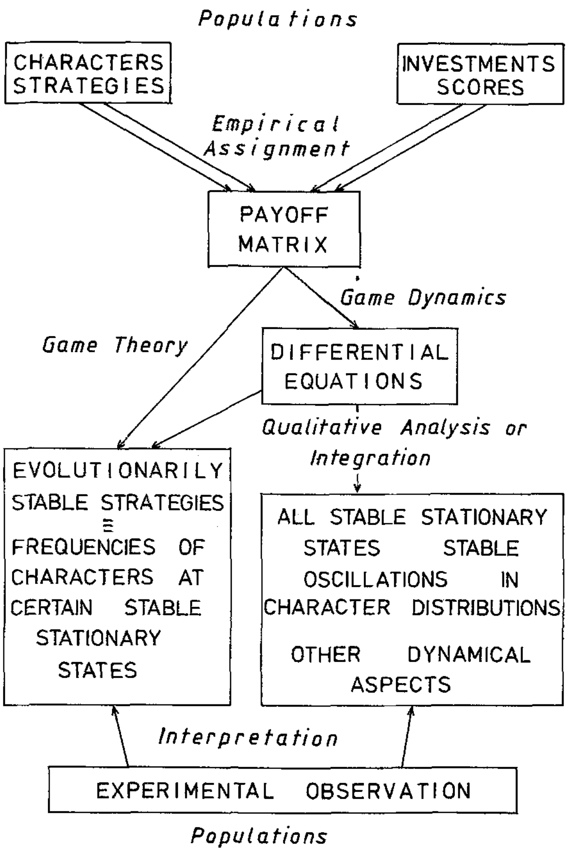

Fig. 1. The flow chart for the analysis of a model for the social behaviour of animals

defined by a listing of outcomes of the contests with all characters present in the population. In general a given character may adopt different strategies with certain frequencies. In this paper we shall assume, however, that all characters use pure strategies only. The strategies are denoted by $X_1, X_2, \ldots, X_n$. Then the entire list of all possible outcomes is given by the payoff-matrix A of the game theoretical approach. The element a_{ij} is the payoff for the player adopting strategy X_i when the opponent uses X_j. The elements of A are assumed to be linear combinations of the score values:

$$a_{ij} = \sum_{k=1}^{m} \gamma_k^{(i,j)} \sigma_k . \tag{1}$$

At a certain instant t the population is characterized by a state vector $\mathbf{x}(t) = (x_1(t), x_2(t), \ldots, x_n(t))$. The components are the probabilities with which the strategies $X_1, X_2, \ldots, X_n$ are played in the population. Hence, the state vector lies on the simplex of strategies:

$$\mathbf{S}_n = \left\{ \mathbf{x} \in \mathbf{R}^n ; 0 \leqq x_i \leqq 1 \forall i = 1, 2, \ldots, n, \sum_{i=1}^{n} x_i = 1 \right\} . \tag{2}$$

The average payoff for strategy X_i in the population is given by

$$E_i = \sum_{j=1}^{n} a_{ij} x_j = \mathbf{e}_i \cdot A\mathbf{x} , \tag{3}$$

where $\mathbf{e}_i$ is the vector pointing to the i-th corner of $\mathbf{S}_n$. The mean values of the average payoffs in the entire population, the "mean average payoff" is simply obtained as

$$\bar{E} = \sum_{i=1}^{n} x_i E_i = \sum_i \sum_j x_i a_{ij} x_j = \mathbf{x} \cdot A\mathbf{x} . \tag{4}$$

According to the basic assumption of the theory the behaviour of an individual is influenced genetically. The strength of this influence ranges from almost complete genetic determination like in insect societies to partial determination like in flocks of mammals where learning through education plays a non negligible role. In any case more payoff will increase the number of offspring and genes causing the underlying behaviour will spread. In "game dynamics" we identify the difference between the average payoff of a certain strategy X_i and the mean average payoff $(E_i - \bar{E})$ with its relative increase in frequency (Taylor and Jonker, 1978):

$$\frac{\dot{x}_i}{x_i} = E_i - \bar{E} = \mathbf{e}_i \cdot A\mathbf{x} - \mathbf{x} \cdot A\mathbf{x} ; \quad i = 1, \ldots, n$$

or

$$\dot{x}_i = x_i(\mathbf{e}_i \cdot A\mathbf{x} - \mathbf{x} \cdot A\mathbf{x}) = x_i \Big(\sum_j a_{ij} x_j - \sum_k \sum_l a_{kl} x_k x_l \Big) . \tag{5}$$

The simplex $\mathbf{S}_n$ is globally invariant under (5). It is likewise easy to see that all faces of $\mathbf{S}_n$ are invariant as well.

The choice of numerical score values σ_k is somewhat arbitrary since they are not accessible to direct experimental determination. On the other hand certain ordering relations, like $\sigma_1 > \sigma_2 > \ldots > \sigma_n$, will always exist. Thus we may suggest to fix the score values up to an affine transformation only:

$$\sigma_k' = \beta \sigma_k + \alpha ; \quad \beta > 0 , \quad \alpha \in \mathbf{R} . \tag{6}$$

Equation (5) at the other end of the mathematical analysis is not uniquely defined in terms of payoff either: a set of payoff matrices yields the same differential equation (Hofbauer et al., 1980). Indeed, let us perform an affine transformation T of the payoff-matrix A:

$$A \xrightarrow{T} B : b_{ij} = \beta'(\alpha' + a_{ij}) . \tag{7}$$

The transformed differential equation is identical (on $\mathbf{S}_n$) with the former, except for a linear change of scale in the time axis.

$$\dot{x}_i = \frac{dx_i}{dt} = x_i(\mathbf{e}_i \cdot B\mathbf{x} - \mathbf{x} \cdot B\mathbf{x}) = \beta' x_i(\mathbf{e}_i \cdot A\mathbf{x} - \mathbf{x} \cdot A\mathbf{x})$$

or

$$\frac{dx_i}{d\tau} = x_i(\mathbf{e}_i \cdot A\mathbf{x} - \mathbf{x} \cdot A\mathbf{x}) \quad \text{with} \quad \tau = \beta' t \quad \text{and} \quad i = 1, \ldots, n. \tag{8}$$

Both dynamical systems thus have identical trajectories.

Let us see now how the affine transformation of score values is related to the invariance properties of the differential equations. Accordingly, we identify $\{\sigma'_k\}$ with the set of scores leading to the payoff matrix B:

$$b_{ij} = \beta'(\alpha' + a_{ij}) = \sum_k \gamma_k^{(ij)} \sigma'_k. \tag{9}$$

Making use of Eqs. (6) and (9) we verify the following relations between both affine transformations:

$$\beta = \beta' \quad \text{and} \quad \alpha = \frac{\alpha'}{\sum_k \gamma_k^{(ij)}}. \tag{10}$$

In general, there exists a common affine transformation of score values and payoff provided the sum of weighting factors $\gamma^{(ij)}$ is independent of the particular pair of indices (i,j)[1]:

$$\sum_k \gamma_k^{(ij)} = C \quad \forall (i,j). \tag{11}$$

Equation (11) does not imply a loss in generality. Although (11) will not be fulfilled automatically by every game of interest we may define a number of dummy scores which are chosen such that the sums of weighting factors are now constant. We shall discuss one concrete example in Sect. 6. There and in most other cases the use of dummy scores simply corresponds to the choice of a proper zero on the seale of scores.

3. Evolutionarily Stable Strategies (ESS)

Maynard-Smith (1974) introduced the notion of an evolutionarily stable strategy (ESS) in order to study stationary distributions of characters by the game theoretical approach. An ESS denoted by the vector $\mathbf{p}$ may be defined by two conditions:

1) It is a best reply when played against itself:

$$\mathbf{p} \cdot A\mathbf{p} \geqq \mathbf{x} \cdot A\mathbf{p} \quad \forall \mathbf{x} \in \mathbf{S}_n. \tag{12}$$

2) In case $\mathbf{x}$ is another best reply against $\mathbf{p}$, $\mathbf{p}$ fares better against $\mathbf{x}$ then $\mathbf{x}$ does against itself:

$$\mathbf{p} \cdot A\mathbf{p} = \mathbf{x} \cdot A\mathbf{p} \rightarrow \mathbf{p} \cdot A\mathbf{x} > \mathbf{x} \cdot A\mathbf{x}. \tag{13}$$

Recently, it has been proven that every ESS corresponds to an asymptotically stable fixed point of (5) (Taylor and Jonker, 1978; Hofbauer et al., 1979; Zeeman, 1979). Indeed, it is easy to check that $\mathbf{p}$ is an ESS iff

$$\mathbf{p} \cdot A\mathbf{x} > \mathbf{x} \cdot A\mathbf{x} \tag{14}$$

for all $\mathbf{x} \neq \mathbf{p}$ in a neighbourhood of $\mathbf{p}$. Now $\mathbf{p}$ is the unique maximum of the function

$$P(\mathbf{x}) = \prod_{i=1}^{n} x_i^{p_i} \tag{15}$$

and the time derivative of $t \rightarrow P(\mathbf{x}(t))$ is

$$\dot{P} = \sum_i \frac{\partial P}{\partial x_i} \dot{x}_i = P(\mathbf{p} \cdot A\mathbf{x} - \mathbf{x} \cdot A\mathbf{x}) \tag{16}$$

which is strictly positive for all $\mathbf{x}$ as above. Hence P has to increase along all orbits in this neighbourhood which therefore must converge to $\mathbf{p}$. The converse, however, is not true: there are asymptotically stable equilibria which are not ESS.

Many useful notions developed in game theory have little relevance in biological situations where the players do not obey any axiom of rationality. For example, the concept of Pareto equilibrium makes little sense here. The dynamical approach allows a better understanding of the effect of fluctuations.

Another advantage of game dynamics consists in the accessibility of time dependent phenomena, like approach to equilibrium, limit cycles, time averages etc. ... In the next sections we shall show this by means of a few examples.

4. Hopf Bifurcations and Limit Cycles

Let us consider

$$A = \begin{bmatrix} 0 & 1 & -\mu & 0 \\ 0 & 0 & 1 & -\mu \\ -\mu & 0 & 0 & 1 \\ 1 & -\mu & 0 & 0 \end{bmatrix}$$

1 Strictly speaking, we would require only $\sum_k \gamma_k^{(ij)} = C_j \forall i$ since the invariance properties of (5) are stronger than just an affine transformation (Hofbauer et al., 1980). The whole procedure becomes somewhat involved and little is gained. We restrict ourselves to the weaker case therefore

with $|\mu|<1$. Cyclic symmetry implies immediately that there exists a unique fixed point in the interior of $\mathbf{S}_4$, namely

$$\mathbf{p}=(\tfrac{1}{4},\tfrac{1}{4},\tfrac{1}{4},\tfrac{1}{4}). \tag{17}$$

The Jacobian $\left(\frac{\partial \dot{x}_i}{\partial x_j}\right)$ of (5) at $\mathbf{p}$ is obviously also circulant. Its first row is given by

$$\left(\frac{\mu-1}{8},\frac{\mu+1}{8},\frac{-\mu-1}{8},\frac{\mu-1}{8}\right) \tag{18}$$

and the eigenvalues of (5), restricted to $\mathbf{S}_4$ at the point $\mathbf{p}$, are easily seen to be

$$\begin{aligned}\omega_{1,3}&=\tfrac{1}{4}(\mu\pm i)\\ \omega_2&=\tfrac{1}{4}(-1-\mu).\end{aligned} \tag{19}$$

The function (15) is now

$$P=(x_1x_2x_3x_4)^{1/4} \tag{20}$$

and

$$\begin{aligned}\dot{P}=P\{&(1+\mu)(x_1+x_3-\tfrac{1}{2})^2\\ &-\tfrac{1}{8}\mu[(x_1-x_3)^2+(x_2-x_4)^2]\}.\end{aligned} \tag{21}$$

For $\mu<0$, $\dot{P}>0$ in the interior of $\mathbf{S}_4$. By (16) it follows that $\mathbf{p}\cdot A\mathbf{x}\geqq\mathbf{x}\cdot A\mathbf{x}$, i.e. that $\mathbf{p}$ is evolutionarily stable.

For $\mu=0$, we have the case of the hypercycle (Schuster et al., 1978). $\mathbf{p}$ is still asymptotically stable, but no longer an ESS, since $\dot{P}$ vanishes on the plane $x_1+x_3=\frac{1}{2}$ through p. It is easy to check that the fixed points in the boundary of $\mathbf{S}_4$ are not stable either, so we have an example of a game without ESS.

For $\mu>0$, $\mathbf{p}$ is no longer stable. A Hopf bifurcation has occurred. Indeed, we see that for small μ, the eigenvalue ω_2 is always negative. The pair $\omega_{1,3}$ of complex conjugate eigenvalues, however, crosses the imaginary axis from left to right, as μ increases from negative to positive values. At $\mu=0$, the real parts of $\omega_{1,3}$ have strictly positive derivatives as functions of μ. The imaginary part is nonvanishing; and $\mathbf{p}$ is asymptotically stable. All the ingredients of the classical Hopf bifurcation theorem are satisfied (Marsden and McCracken, 1976) and we conclude that, for small $\mu>0$, there exists a stable limit cycle, i.e. a periodic orbit which attracts all orbits in some neighbourhood. Hence:

Theorem 1. For $n=4$, there exist equations of type (5) with stable limit cycles.

In Hofbauer et al. (1980) it is shown that stable limit cycles exist for all $n\geqq4$. Zeeman (1979) proved that there are no Hopf bifurcations for $n=3$. Hofbauer (1980) extended this to show that for $n=3$, there are no stable limit cycles.

5. Mean Values and Fixed Points

A fixed point of (5) in the interior of $\mathbf{S}_n$ has to satisfy

$$\mathbf{e}_1\cdot A\mathbf{x}=\mathbf{e}_2\cdot A\mathbf{x}=\ldots=\mathbf{e}_n\cdot A\mathbf{x} \tag{22}$$

as well as

$$\textstyle\sum x_i=1, x_i>0 \quad \text{for} \quad i=1,\ldots,n. \tag{23}$$

Suppose now that an orbit $\mathbf{x}(t)$ in the interior of $\mathbf{S}_n$ remains bounded away from the boundary of $\mathbf{S}_n$. This means that for some $\delta>0$ we have $x_i(t)>\delta$ for $i=1,\ldots,n$ and all t sufficiently large.

Now

$$(\log x_i)^{\cdot}=\frac{\dot{x}_i}{x_i}=\mathbf{e}_i\cdot A\mathbf{x}-\mathbf{x}\cdot A\mathbf{x}$$

which gives, if one integrates from 0 to T

$$\begin{aligned}\log x_i(T)-\log x_i(0)=&\sum_{j=1}^{n}a_{ij}\int_0^T x_j(t)dt\\ &-\int_0^T(\mathbf{x}\cdot A\mathbf{x})dt\end{aligned} \tag{24}$$

The left hand side is bounded. Dividing by T, and letting $T\to+\infty$, it converges to zero, and hence, if

$$y_j=\lim_{T_m\to+\infty}\frac{1}{T_m}\int_0^{T_m}x_j(t)dt$$

($j=1,\ldots,n$) is some accumulation point of time-averages of $x_j(t)$, then $\mathbf{y}$ is a solution of (22) and (23).

It follows:

A) If there is no fixed point in the interior of $\mathbf{S}_n$, then every orbit of (5) comes arbitrarily close to the boundary, for $t\to+\infty$, i.e. some coordinates become arbitrarily small.

B) If there exists a unique fixed point $\mathbf{p}$ in the interior of $\mathbf{S}_n$, then

$$p_i=\lim_{T\to+\infty}\frac{1}{T}\int_0^T x_i(t)dt \qquad i=1,\ldots,n \tag{25}$$

for every orbit bounded away from the boundary (a periodic orbit, for example).

Note that except for degenerate cases one of these two alternatives holds. B) shows that even if the fixed point $\mathbf{p}$ is unstable, it can be of physical relevance, as a time-average. The case of the hypercycle [$a_{ij}\geqq0$, with equality if $i\neq j-1$ (mod n)] is an interesting example for this. It is shown in Schuster et al. (1979) that every orbit is bounded away from the boundary, although for $n\geqq5$ $\mathbf{p}$ is unstable.

Conjecture. If there is no fixed point in the interior of $\mathbf{S}_n$, then every orbit converges to a face of the boundary.

6. Generalized Maynard-Smith Games

As a concrete example we shall analyse the well-known "five character game" introduced by Maynard-Smith and Price (1973).

1) The "hawk"-character (H) represents the most aggressive strategy. A hawk always escalates fighting no matter what strategy is applied by the opponent.

2) The "mouse"-character (M) is the other extreme. The answer of a mouse to an escalation of fighting by the other contestant is always retreat.

3) The behaviour of the "bully"-character (B) is more sophisticated. The bully escalates in case the opponent does not and retreats if it is confronted with an escalation.

4) The "retaliator"-character (R) behaves in a way complementary to the bully. A retaliator escalates only and always after the other contestant escalated.

5) The "prober-retaliator"-character (P) exhibits the most complex behaviour of all five. It escalates eventually, when the opponent avoids escalation but it retreats in case the other contestant starts to escalate by himself.

Following Maynard-Smith and Price (1973) we attribute score values for the various investments:

Gain of object $=\alpha$,

Waste of time $=\gamma$, and

Injury $=\delta$.

At the same time we assume the contestants to be of equal strength in accordance with the prerequisites of a symmetric game. In case two equal characters come upon each other they share the total of all investments 50:50. The payoff matrix as one easily verifies, is of the following form:

A.

$$\begin{array}{c|ccccc} & H & M & B & R & P \\ H & \frac{\alpha+\delta}{2} & \alpha & \alpha & \frac{\alpha+\delta}{2} & \alpha \\ M & 0 & \frac{\alpha+2\gamma}{2} & 0 & \frac{\alpha+2\gamma}{2} & 0 \\ B & 0 & \alpha & \frac{\alpha}{2} & 0 & \alpha \\ R & \frac{\alpha+\delta}{2} & \frac{\alpha+2\gamma}{2} & \alpha & \frac{\alpha+2\gamma}{2} & \frac{\alpha+\delta}{2} \\ P & 0 & \alpha & 0 & \frac{\alpha+\delta}{2} & \frac{\alpha+\delta}{2} \end{array} \qquad (26)$$

Thus, matrix A does not fulfil (11). In order to correct for this deficiency we define a dummy score b for the "loss of object" and redefine $c=2\gamma$. The other two scores remain unchanged $a=\alpha$ and $d=\delta$. For the new list of scores

Gain of object a

Loss of object b

Waste of time c (for both contestants) and

Injury d

we find the payoff matrix:

A.

$$\begin{array}{c|ccccc} & H & M & B & R & P \\ H & \frac{a+d}{2} & a & a & \frac{a+d}{2} & a \\ M & b & \frac{a+c}{2} & b & \frac{a+c}{2} & b \\ B & b & a & \frac{a+b}{2} & b & a \\ R & \frac{a+d}{2} & \frac{a+c}{2} & a & \frac{a+c}{2} & \frac{a+d}{2} \\ P & b & a & b & \frac{a+d}{2} & \frac{a+d}{2} \end{array} \qquad (27)$$

Instead of assigning concrete numerical values to the individual investments we assume the easily conceivable ordering relation $a \geqq b \geqq c \geqq d$. Thereby we state only that the object has a certain value and injury is more serious for the contestants than waste of time. Now we recall that b was a dummy score: by putting $b=0$ we may re-establish the previous case (26).

The five dimensional dynamical system determined by (5) and (27) has no fixed points in the interior of the population simplex, int $\mathbf{S}_5$. According to the results of the previous section this implies already that there is no attractor in int $\mathbf{S}_5$ as well. Moreover, the five simplices $\mathbf{S}_4$, which correspond to the restrictions of the five dimensional faces of $\mathbf{S}_5$ (which are obtained by setting $x_i=0$; $i=1,\ldots,5$) are free of fixed points in their interior as well. The long term behaviour of the system, thus, can be understood completely by an inspection of the ten simplices $\mathbf{S}_3$ determined by $x_i=0$ and $x_j=0$, $i=1,\ldots,4$; $i<j\leqq 5$. The structure of (5), of course, implies that every corner of S_5 is a fixed point. Another general result concerns the edge $\overline{MR}$: from (27) we can easily derive that every point on this edge is a fixed point and we may call such an edge a "fixed point edge" as in our previous paper (Schuster et al., 1978).

In the forthcoming analyis we distinguish properly three different cases which correspond to topologically

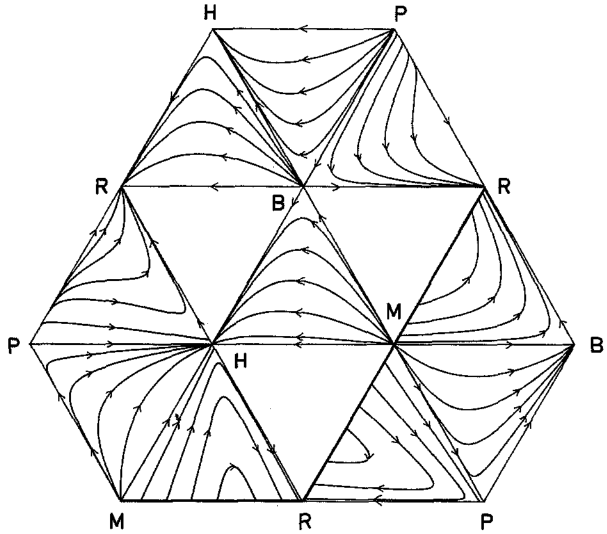

Fig. 2. The phase portrait of the *HMBRP* game defined by (5) and (27). Case 1: $a>2b-d$. (Concrete numerical values: $a=12$, $b=0$, $c=-2$, $d=-10$)

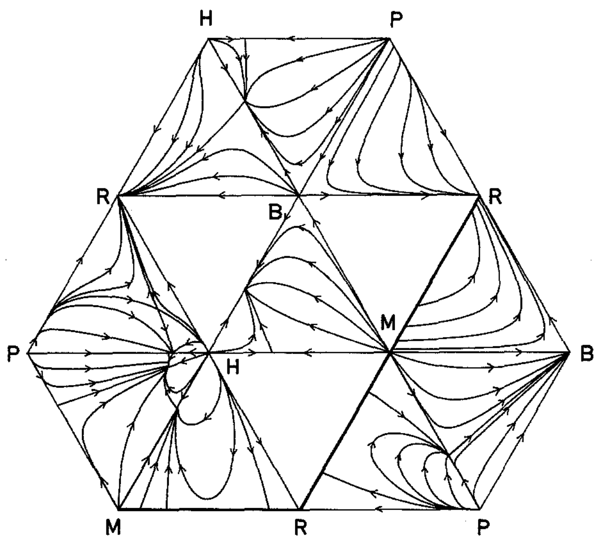

Fig. 3. The phase portrait of the *HMBRP* game defined by (5) and (27). *Case 2*: $2b-d>a>2b-c$ (Concrete numerical values: $a=6$, $b=0$, $c=-2$, $d=-10$)

different phase portraits. In Figs. 2–4 we show the ten phase portraits of the simplices $\mathbf{S}_3$ for each of the three cases.

Case 1

$$a>2b-d. \tag{28}$$

This is the simplest case and represents a situation where the value of the object exceeds the risk of an injury. The phase portrait is shown in Fig. 2. There are no additional fixed points on the edges or inside the faces $\mathbf{S}_3$. The remaining nine edges flow in the directions $M\to H$, $B\to H$, $H\to R$, $P\to H$, $M\to B$, $M\to P$, $B\to R$, $P\to B$, and $P\to R$. Complete qualitative analysis of the phase portrait is straight forward. We make use of the relation

$$\left(\frac{x_i}{x_j}\right)^{\cdot}=\left(\frac{x_i}{x_j}\right)(\mathbf{e}_i\cdot A\mathbf{x}_i-\mathbf{e}_j\cdot A\mathbf{x}_j)$$

and find:

$$\left(\frac{x_2}{x_4}\right)^{\cdot}=\left(\frac{x_2}{x_4}\right)[\tfrac{1}{2}(2b-a-d)(x_1+x_5)+(b-a)x_3]<0.$$

Consequently x_2 will vanish. Furthermore we have

$$\left(\frac{x_4}{x_5}\right)^{\cdot}=\left(\frac{x_4}{x_5}\right)$$
$$\cdot[\tfrac{1}{2}(a+d-2b)x_1+\tfrac{1}{2}(c-a)x_2+(a-b)x_3+\tfrac{1}{2}(c-d)x_4],$$

which is strictly positive if x_2 is sufficiently small. Hence x_2 approaches zero and we come close to the triangle *HBR*, where

$$\left(\frac{x_1}{x_4}\right)^{\cdot}=\left(\frac{x_1}{x_4}\right)\tfrac{1}{2}(d-c)x_4<0.$$

Hence, x_1 vanishes and ultimately we have

$$\left(\frac{x_3}{x_4}\right)^{\cdot}=\left(\frac{x_3}{x_4}\right)[\tfrac{1}{2}(b-a)x_3+\tfrac{1}{2}(2b-a-c)x_4]<0.$$

Thus, the system finally approaches $x_4=1$, which is the only stable fixed point in the system. The retaliator thus represents the strategy which is selected in the HMBRP game.

If we allow for random fluctuations superimposed on the dynamics, a pure retaliator population may be invaded by mice because R is not asymptotically stable along the axis $\overline{RM}$. In the neighbourhood of R the points on this edge are stable against invasions by small numbers of H, B or P. Eventually, the density of mice may exceed the critical point of stability against H, B or P and the state vector can move into the interior of $\mathbf{S}_5$. A whole cycle returning to R may start again. The lack of stability of R against fluctuations along the $\overline{MR}$ axis is essentially the same as in Case 2 where it has been analysed and discussed extensively by Zeeman (1979).

Case 2

$$2b-d>a>2b-c. \tag{29}$$

This is the case of intermediate value of the object. It is worth less than the risk of injury, but more than waste of time. All the concrete numerical examples treated so far (Maynard-Smith, 1972, 1974; Dawkins, 1976; Zeemann, 1979) fall into this case. The phase portraits are given in Fig. 3. In addition to the five corners and the fixed point edge $\overline{MR}$ we find six new fixed points, one on each of the edges $\overline{HM}$, $\overline{HB}$, $\overline{HP}$, and $\overline{MP}$ as well as one on each of the two faces HMP and HRP.

Qualitative analysis is straightforward. We proceed similarly as above and find:

$$\left(\frac{x_3}{x_5}\right)^{\cdot} = \left(\frac{x_3}{x_5}\right) \cdot [\tfrac{1}{2}(a-b)x_3 + \tfrac{1}{2}(2b-a-d)x_4 + \tfrac{1}{2}(a-d)x_5] > 0.$$

Thus, $x_5 \to 0$ and we approach the four dimensional system $HMBR$ on $\mathbf{S}_4$. Zeeman (1979) presented a detailed analysis of this case. We need not repeat his argumentation here. The final result is just as in Case 1 that R is a stable strategy, but not asymptotically stable since it may be invaded by mice. The major difference between Case 1 and Case 2 is found in the restriction to the two dimensional subsystems. To give one example we consider the edge $\overline{HM}$: due to the high values of the object in Case 1 – it exceeds the risk of injury – the trajectory flows $M \to H$ and the hawk is *the* stable strategy. In Case 2 we find a mixture of $\alpha H + (1-\alpha)M$ to be internally stable. The value of

$$\alpha = \frac{a-c}{2b-(c+d)}$$

increases linearly with the value of the object. On the edges $\overline{HB}$, $\overline{HP}$, and $\overline{MP}$ we find a situation completely analogous to that reported for $\overline{HM}$. The only difference consists in the expression for α. Thus, we can conclude: the higher the value of the object the better fares the aggressive character.

Case 3

$$a < 2b - c. \tag{30}$$

In this last example the value of the object is even smaller than the waste of time. The phase portraits are shown in Fig. 4. The whole situation closely resembles Case 2 with only one but nevertheless important difference. There is one additional fixed point on the edge $\overline{BR}$. It is globally asymptotically stable and represents the only asymptotically stable character of the game. In contrast to Case 1 and Case 2 we have no problem with fluctuations. Qualitative analysis is straight forward. One may start with $\left(\frac{x_3}{x_5}\right)^{\cdot} < 0$ as before. Further analysis is reduced to the $HMBR$ game and one may proceed in the same way as Zeeman (1979) did.

Finally, it seems important to stress the fact that the three cases (28)–(30) allow complete qualitative discussion of the $HMBRP$ game as given by the payoff matrix (27). We applied only one restrictive condition, namely $a \geq b \geq c \geq d$.

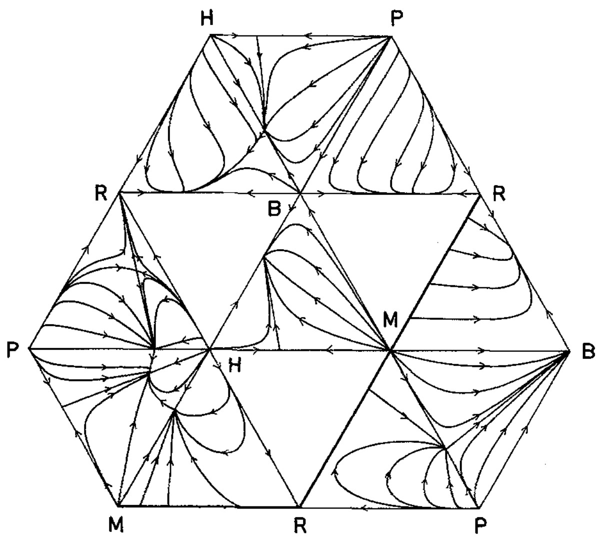

Fig. 4. The phase portrait of the *HMBRP* game defined by (5) and (27). *Case 3*: $a < 2b - c$. (Concrete numerical values: $a = 4$, $b = 0$, $c = -6$, $d = -10$)

7. Games of Partnership

Consider a game of partnership, where the two players always fairly share the outcome. In this case $a_{ij} = a_{ji}$ for all i and j.

Equation (5) with such a symmetric matrix A is well known as the Wright-Fisher-Haldane model in population genetics. The variables $x_1, \ldots, x_n$ are the frequencies of the n possible alleles for a given chromosomal locus, and a_{ij} is the fitness of genotype ij. This corresponds indeed to a game of closest possible partnership, where the two players unite to produce offspring.

Here, we shall only sketch the main features (cf. Hadeler, 1974). Consider the mean average fitness

$$\phi(x) = \mathbf{x} \cdot A\mathbf{x} \tag{31}$$

Using the symmetry of A, one gets

$$\frac{\partial \phi}{\partial x_i} = 2\mathbf{e}_i \cdot A\mathbf{x} = 2(A\mathbf{x})_i \tag{32}$$

and

$$\dot{\phi} = \sum \frac{\partial \phi}{\partial x_i} \dot{x}_i = 2\sum (A\mathbf{x})_i x_i [(A\mathbf{x})_i - \mathbf{x} \cdot A\mathbf{x}]$$
$$= 2[\sum (A\mathbf{x})_i^2 - (\sum (A\mathbf{x})_i x_i)^2] \geq 0. \tag{33}$$

The last inequality is the Cauchy-Schwarz-inequality (recall $\sum x_i = 1$). Equality holds if there exists a c such that

$$(A\mathbf{x})_i x_i^{1/2} = c x_i^{1/2} \quad \forall i.$$

or, equivalently, $(A\mathbf{x})_i = c$ for all i with $x_i > 0$. Thus $\dot{\phi}$ vanishes exactly for the fixed points of (5).

We obtain that Φ is a Lyapunov function; thus if A is symmetric, every orbit converges to the set of fixed points.

9. The War of Attrition

Another situation which has received interest is that of strategies $X_1, \ldots, X_n$ corresponding to increasing levels of escalation and thus of investment $\alpha_1, \ldots, \alpha_n$. If the value of the object is v, and if player A chooses strategy i, player B strategy j, then for $i>j$ player A wins and his payoff is $v-\alpha_j$ (he had only to escalate as far as his opponent did) while the payoff for player B is $-\alpha_j$. If $i=j$, we assume both players have equal chances to win: the payoff for both of them is $\frac{v}{2}-\alpha_j$.

The payoff matrix, then, satisfies condition (*):

(*) in each column, all entries below the diagonal are equal.

Such a game has been analyzed by Bishop and Cannings (1978) with the help of difference equations. The situation for differential equations is completely analogous. Therefore we shall only outline the description of the latter case.

Note first that we may assume that the entries below the diagonal are all zero: it suffices, indeed, to add appropriate constants to each column.

Since for $x_n>0$

$$\left(\frac{x_i}{x_n}\right)^{\cdot}=\left(\frac{x_i}{x_n}\right)((Ax)_i-(Ax)_n)$$

we get

$$\left(\frac{x_i}{x_n}\right)^{\cdot}=\left(\frac{x_i}{x_n}\right)\left(\sum_{j\geq i} a_{ij}x_j-a_{nn}x_n\right). \tag{34}$$

In particular

$$\left(\frac{x_{n-1}}{x_n}\right)^{\cdot}=x_{n-1}\left(a_{n-1,n-1}\left(\frac{x_{n-1}}{x_n}\right)-(a_{nn}-a_{n,n-1})\right)$$

which shows that $\frac{x_{n-1}}{x_n}$ converges to some constant c_n.

Next, we have

$$\left(\frac{x_{n-2}}{x_n}\right)^{\cdot}=\left(\frac{x_{n-2}}{x_n}\right)\cdot(a_{n-2,n-2}x_{n-2}+a_{n-2,n-1}x_{n-1}+a_{n-2,n}x_n-a_{n,n}x_n).$$

Since, for t large enough, x_{n-1} is almost equal to c_nx_n, we obtain that $\left(\frac{x_{n-2}}{x_n}\right)^{\cdot}$ is almost equal to

$$x_{n-2}\left(a_{n-2,n-2}\frac{x_{n-2}}{x_n}-b_n\right) \tag{35}$$

for some constant b_n. Hence $\frac{x_{n-2}}{x_n}$ converges. Proceeding inductively, one sees that all ratios x_i/x_n converge and hence that every orbit converges to a fixed point.

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Received: July 29, 1980

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