

Game Dynamics in Mendelian Populations*

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Abstract. A game theoretical model for the evolution of strategies in animal conflicts is considered, using methods from dynamical systems and population genetics. It is shown that the Hardy-Weinberg-equilibrium is readily approached. The differential equation for the gene frequencies is more complicated than that which has been studied previously in the corresponding asexual case.

1. Introduction

The notion of evolutionarily stable strategy, as developed by Maynard-Smith (1974), has shed much light on the problem of altruism in nature and the role of ritual fighting in animal conflicts. The game theoretical approach has been supplemented by a dynamical model for the evolution of strategies (see Taylor and Jonker, 1978; Zeeman, 1980; Hofbauer et al., 1979; Schuster et al., 1981).

Both the static and the dynamic approach have neglected the genetic mechanism, however, and proceeded as if the species considered would multiply asexually. No doubt it was rightly felt that the insights offered by the idea of evolutionary stability could be best displayed by using the simplest possible models. The widespread recognition of the theory of Maynard Smith makes it seem appropriate now to apply it to more realistic genetic models. The present note is a step in this direction. We first resume, in Sect. 2, some well established results in game dynamics for asexual populations. In Sect. 3 we set up a model for Mendelian populations and obtain a differential equation for the evolution of genotypes. In Sect. 4 we show that a Hardy-Weinberg-law holds and that the gene frequencies obey an equation which has certain similar-

ities to the “replicator equation” of the asexual model. In Sect. 5 we derive a few properties for this equation and in Sect. 6 we consider some examples.

2. Game Dynamics for the Asexual Model

Let E_1, \dots, E_n be the n possible pure strategies for a given type of conflict within an animal species. If x_i denotes the frequency of E_i , then the state of the population is given by the vector $\mathbf{x} = (x_1, \dots, x_n)$ belonging to the simplex

$$S_n = \{\mathbf{x} = (x_1, \dots, x_n) : \sum x_i = 1, x_i \geq 0, i = 1, \dots, n\}. \quad (1)$$

Let a_{ij} be the payoff for an animal using strategy E_i against an opponent using E_j . This payoff, the success in the game of evolution, is just the reproduction rate of the animal. The matrix $A = (a_{ij})$ is the payoff-matrix corresponding to the game. Since x_j is the probability that the opponent uses E_j , the mean payoff for strategy E_i is given by

$$\sum_j a_{ij} x_j = (A\mathbf{x})_i. \quad (2)$$

The mean payoff for a population in state $\mathbf{y} \in S_n$ confronting a population in state \mathbf{x} is given by

$$\sum_{i,j} y_i a_{ij} x_j = \mathbf{y} \cdot A\mathbf{x} \quad (3)$$

and in particular

$$\sum_{i,j} a_{ij} x_i x_j = \mathbf{x} \cdot A\mathbf{x} \quad (4)$$

is the average payoff for conflicts within the population \mathbf{x} . According to Maynard-Smith (1974), a state $\mathbf{p} \in S_n$ is called evolutionarily stable if it satisfies the following conditions:

a) equilibrium condition: for all $\mathbf{x} \in S_n$

$$\mathbf{p} \cdot A\mathbf{p} \geq \mathbf{x} \cdot A\mathbf{p}; \quad (5)$$

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b) stability condition: whenever equality holds in (5) for $\mathbf{x} \neq \mathbf{p}$, then

$$\mathbf{p} \cdot A\mathbf{x} > \mathbf{x} \cdot A\mathbf{x}. \quad (6)$$

These conditions mean, in biological context, that if a random mutation introduces a small population deviating from state \mathbf{p} , then this population will fare less well than average in the total population, and will therefore be wiped out.

Let us now assume that the species is haploid, multiplies asexually, and that each strategy corresponds to a different allele.

The x_i are just the gene frequencies now. The number of offspring of an E_i -individual is given by its payoff, i.e. by $(A\mathbf{x})_i$. Hence the frequency of strategy E_i , one generation later, is given by

$$\Phi x'_i = x_i (A\mathbf{x})_i \quad i = 1, \dots, n, \quad (7)$$

where

$$\Phi = \sum_i x_i (A\mathbf{x})_i.$$

The usual method of deriving a differential equation from the difference equation (7) yields

$$\dot{x}_i = x_i \left(\sum_j a_{ij} x_j - \Phi \right) \quad i = 1, \dots, n \quad (8)$$

on the (invariant) simplex S_n . This ‘‘replicator equation’’ can also be obtained by arguing that the rate of increase \dot{x}_i/x_i of strategy E_i corresponds to the difference between payoff $(A\mathbf{x})_i$ for strategy E_i and the average payoff $\mathbf{x} \cdot A\mathbf{x}$ within the population. The replicator equation has been studied in some details [see the papers quoted in the introduction, and also Zeeman (1981), Hofbauer (1981), and Schuster et al. (1980)]. It is equivalent to the Volterra-Lotka-equation in $n-1$ variables. The special case $a_{ij} = a_{ji}$ corresponds to the selection equation of Fisher, Haldane, and Wright in population genetics. If $\mathbf{p} \in S_n$ is evolutionarily stable, then \mathbf{p} is an asymptotically stable equilibrium of (8). The converse is not valid. For $n \leq 3$, the replicator equation has no limit cycles. For $n \geq 4$, it has limit cycles for certain payoff matrices. If there is no fixed point in the interior of S_n , then every orbit converges to the boundary of S_n . If, on the other hand, the boundary is repelling, then there exists a unique fixed point in the interior, which corresponds to the time average of every orbit in the interior of S_n .

3. Game Dynamics for Mendelian Populations

3.1. The Assumptions

There is, of course, a great variety of possible models for the inheritance of strategies in sexual populations.

We shall make the following assumptions: the strategies are determined by one autosomal locus. Each genotype determines a strategy: but several genotypes may lead to the same strategy. These strategies are used for fighting between males. Hence, the genes influence only male behaviour, although they are carried by females too. Furthermore, we assume random mating. The payoff (for a male) is proportional to the number of its descendants, or (what amounts to the same) to the number of its encounters with females. For the sake of clarity, we shall consider first two, then n alleles.

3.2. The Case of Two Alleles

Let A_1 and A_2 be the two alleles. The three genotypes A_1A_1 , A_1A_2 , and A_2A_2 have frequencies x , $2y$, and z ($x + 2y + z = 1$) and correspond to the strategies E_1 , E_2 , and E_3 , respectively. If $A = (a_{ij})$ is the 3×3 payoff matrix, then the average payoffs for E_1 , E_2 , and E_3 are given by a , b , and c , where

$$a = a_{11}x + 2a_{12}y + a_{13}z$$

$$b = a_{21}x + 2a_{22}y + a_{23}z$$

$$c = a_{31}x + 2a_{32}y + a_{33}z.$$

The following Table 1 yields the frequencies of genotypes in the progeny:

Table 1

Father	Mother	Frequency of progeny (unnormalized)	Probability genotypes in the progeny		
A_1A_1	$\times A_1A_1$	$a x^2$	1	0	0
	$\times A_1A_2$	$2a xy$	1/2	1/2	0
	$\times A_2A_2$	$a xz$	0	1	0
A_1A_2	$\times A_1A_1$	$2b xy$	1/2	1/2	0
	$\times A_1A_2$	$4b y^2$	1/4	1/2	1/4
	$\times A_2A_2$	$2b zy$	0	1/2	1/2
A_2A_2	$\times A_1A_1$	$c xz$	0	1	0
	$\times A_1A_2$	$2c yz$	0	1/2	1/2
	$\times A_2A_2$	$c z^2$	0	0	1

The genotype frequencies x' , $2y'$, and z' among the progeny are given by

$$\Phi x' = (x + y)(ax + by)$$

$$\Phi 2y' = (x + y)(by + cz) + (y + z)(ax + by) \quad (9)$$

$$\Phi z' = (y + z)(by + cz),$$

where Φ is the total progeny, i.e. the sum of the right hand sides:

$$\Phi = ax + 2by + cz. \quad (10)$$

The corresponding differential equation is

$$\begin{aligned}\dot{x} &= (x+y)(ax+by) - x\Phi \\ 2\dot{y} &= (x+y)(by+cz) + (y+z)(ax+by) - 2y\Phi \\ \dot{z} &= (y+z)(by+cz) - z\Phi\end{aligned}\quad (11)$$

on the set defined by $x+2y+z=1$, $x \geq 0$, $y \geq 0$, $z \geq 0$.

3.3. The Case of n Alleles

Let us now consider the case of n alleles A_1, \dots, A_n . We denote by x_{ii} the frequency of homozygotes $A_i A_i$, and by $2x_{ij}$ the frequency of heterozygotes $A_i A_j$ ($i \neq j$). Hence

$$\sum_{i,k} x_{ki} = 1. \quad (12)$$

With $a_{ij,kl}$ we denote the payoff for a male of genotype $A_i A_j$ against another male of type $A_k A_l$. The mean payoff for an $A_i A_j$ -male is then

$$b_{ij} = \sum_{k,l} a_{ij,kl} x_{kl} \quad (13)$$

and the mean total payoff in the male population is

$$\sum_{i,j} b_{ij} x_{ij}.$$

The frequency of $A_i A_j$ -progeny can be computed by using Table 1 as in Sect. 3.2. A shorter approach is the following: the amount of gene A_i in the female gene pool is given by

$$x_i = \sum_l x_{il}. \quad (14)$$

Since the reproductive success for an $A_i A_j$ -male is weighted by his payoff b_{ij} , we may operate as if there were $2b_{ij}x_{ij}$ males of genotype $A_i A_j$ ($i \neq j$) and $b_{ii}x_{ii}$ of type $A_i A_i$. Hence the effective amount of gene A_i in the male gene pool is given by

$$B_i = \sum_k b_{ik} x_{ik} \quad (15)$$

which can be viewed as mean payoff for allele A_i .

Since an $A_i A_j$ -offspring is obtained by drawing at random one gene from the female and one gene from the effective male gene pool, we get for the frequencies x'_{ij} :

$$\Phi x'_{ij} = \frac{1}{2}(x_i B_j + x_j B_i) \quad 1 \leq i, j \leq n,$$

where Φ is the sum of all right hand sides. Clearly

$$\Phi = \sum_i B_i. \quad (16)$$

The corresponding differential equation is

$$\dot{x}_{ij} = \frac{1}{2}(x_i B_j + B_i x_j) - x_{ij} \Phi \quad (17)$$

on the simplex of genotype frequencies.

4. The Hardy-Weinberg-Law and the Selection Equation

On the simplex of genotype frequencies, the orbits approach an equilibrium of Hardy-Weinberg type.

Let us again consider first the case $n=2$. From (11) we get

$$\begin{aligned}(y^2 - xz)' &= 2y\dot{y} - \dot{x}z - z\dot{x} \\ &= y(x+y)(by+cz) + y(y+z)(ax+by) - 2y^2\Phi \\ &\quad - z(x+y)(ax+by) - xz\Phi \\ &\quad - x(y+z)(by+cz) - zx\Phi \\ &= -(y^2 - xz)(ax + 2by + cz).\end{aligned}$$

This implies that the set where $y^2 = xz$ holds is invariant. If $\Phi = ax + 2by + cz$ is positive (as is the case if all elements in the payoff matrix are positive) then every orbit of (11) converges to the subset of $x + 2y + z = 1$ where $y^2 = xz$ (see Fig. 1).

Let us next consider the general case. We obtain from (17)

$$\dot{x}_i = \sum_j \dot{x}_{ij} = \frac{B_i + x_i \Phi}{2} - x_i \Phi = \frac{1}{2}(B_i - x_i \Phi). \quad (18)$$

Hence

$$\begin{aligned}(x_{ij} - x_i x_j)' &= \dot{x}_{ij} - \dot{x}_i x_j - x_i \dot{x}_j \\ &= \frac{1}{2}(B_i x_j + B_j x_i) - x_{ij} \Phi \\ &\quad - \frac{1}{2}(B_i x_j - x_i x_j \Phi) - \frac{1}{2}(B_j x_i - x_i x_j \Phi) \\ &= -(x_{ij} - x_i x_j) \Phi.\end{aligned}$$

Again, the submanifold where

$$x_{ij} = x_i x_j \quad \text{for } 1 \leq i, j \leq n \quad (19)$$

is invariant, and if $\Phi > 0$, then every orbit in the x_{ij} -space converges to this submanifold. In particular

$$x_{ij}^2 - x_{ii} x_{jj} \rightarrow 0 \quad 1 \leq i, j \leq n. \quad (20)$$

We are therefore justified to assume that (19) is valid. Under this condition, Eq. (18) for gene frequencies becomes

$$\begin{aligned}\dot{x}_i &= \frac{1}{2}(B_i - x_i \Phi) = \frac{1}{2} \left(\sum_j b_{ij} x_{ij} - x_i \Phi \right) \\ \text{or} \\ \dot{x}_i &= \frac{x_i}{2} \left(\sum_j b_{ij} x_j - \Phi \right).\end{aligned}\quad (21)$$

Since by (13) and (19)

$$b_{ij} = \sum_{k,l} a_{ij,kl} x_k x_l$$

we obtain the selection equation for gene frequencies

$$\dot{x}_i = \frac{x_i}{2} \left(\sum_{j,k,l} a_{ij,kl} x_j x_k x_l - \Phi \right) \quad (22)$$

on the (invariant) simplex S_n . This is the counterpart of the replicator equation (8) in the Mendelian case.

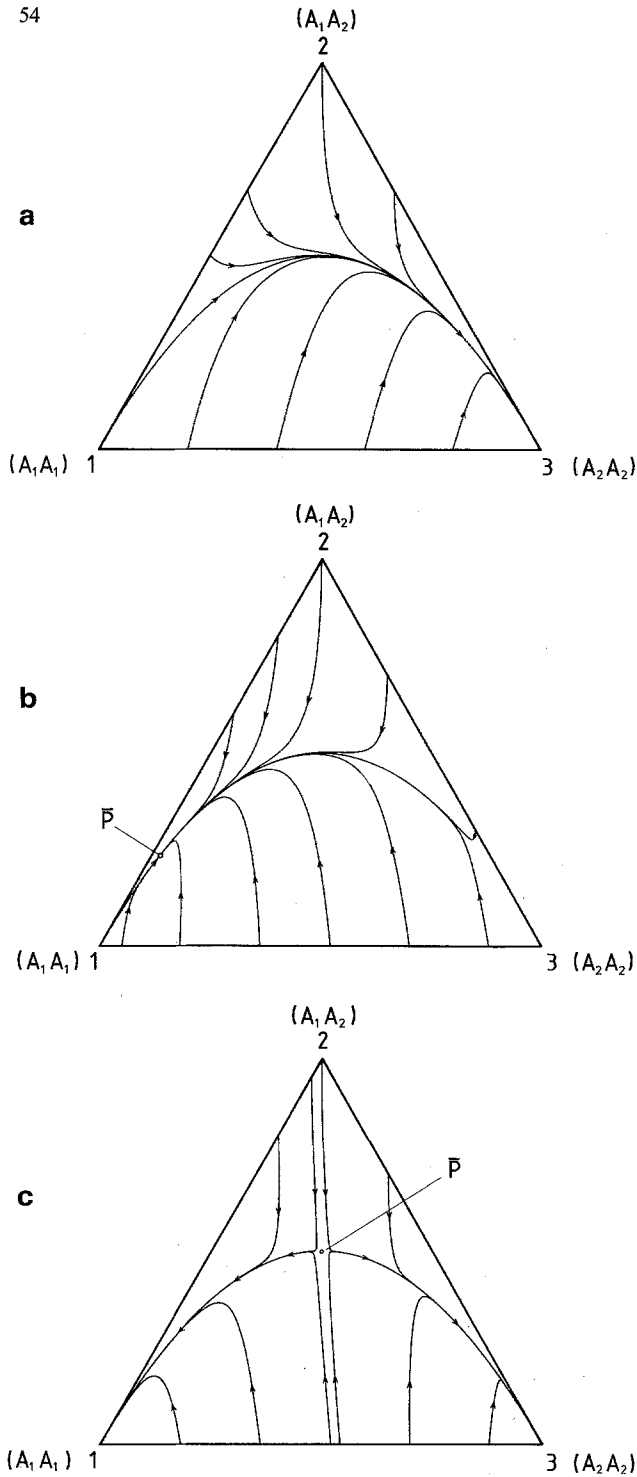


Fig. 1a-c. Phase portraits of Eq. (11) in the special case of two alleles ($n=2$) and dominance of gene A_2 . We distinguish three qualitatively different situations. The numerical values chosen are **a** $w=7, v=-1$, **b** $w=1, v=3$, and **c** $w=-3, v=-1$

5. Some Properties of the Selection Equation for Gene Frequencies

Since $x_i=0$ is a solution of (22), it follows that every subspace of S_n is invariant. The restriction of (22) on a subspace defined by $x_i=0$ for $i \in I$, where I is a proper

subset of the index set $\{1, \dots, n\}$, is of the same type as (22), again.

The equilibria of (22) in the interior of S_n are the positive solutions of the $n-1$ cubic equations

$$\sum_{j,k,l} a_{1j,kl} x_j x_k x_l = \dots = \sum_{j,k,l} a_{nj,kl} x_j x_k x_l \quad (23)$$

together with

$$x_1 + \dots + x_n = 1. \quad (24)$$

For given j, k , and l , we may add a constant c_{jkl} to all coefficients $a_{ij,kl}$ ($i=1, \dots, n$) without affecting (22) on S_n . [Note that Eq. (17) for the genotypes, however, is affected. In particular, the Hardy-Weinberg submanifold which is always invariant as we showed above, can change from an attractor to a repeller. In biologically reasonable cases all elements of the original payoff matrix are positive and this will never happen.] Indeed, if $a_{ij,kl}$ is replaced by $a_{ij,kl} + c_{jkl}$, then

$$\sum_{j,k,l} a_{ij,kl} x_j x_k x_l$$

is replaced by

$$\sum_{j,k,l} a_{ij,kl} x_j x_k x_l + \sum_{j,k,l} c_{jkl} x_j x_k x_l$$

and

$$\Phi = \sum_{i,j,k,l} a_{ij,kl} x_i x_j x_k x_l$$

by

$$\Phi + \sum_{j,k,l} c_{jkl} x_j x_k x_l$$

since (24) holds. Hence (22) remains unchanged.

We also have the relation

$$\left(\frac{x_t}{x_s}\right)' = \left(\frac{x_t}{x_s}\right) \left(\sum_{j,k,l} a_{tj,kl} x_j x_k x_l - \sum_{j,k,l} a_{sj,kl} x_j x_k x_l \right) \quad (25)$$

for $x_s > 0$ ($1 \leq t, s \leq n$).

We show next that just as the replicator equation (8) can be transformed into a Volterra-Lotka equation, so (22) can be transformed into a biquadratic equation on R_n^+ .

Indeed, let us consider an equation of type (22), but in $n+1$ variables $(x_0, x_1, \dots, x_n) \in S_{n+1}$. By adding appropriate constants, we obtain, without loss of generality, that $a_{0j,kl} = 0$ for all j, k, l . For $x_0 > 0$ we set

$$y_i = \frac{x_i}{x_0} \quad i=0, 1, \dots, n. \quad (26)$$

Obviously $y_0 = 1$ and $y_i > 0$ for $i=1, 2, \dots, n$. Our change of coordinates is a diffeomorphism from

$$\{(x_0, x_1, \dots, x_n) \in S_{n+1} : x_0 > 0\}$$

onto $R_n^+ = \{(y_1, \dots, y_n) : y_i \geq 0\}$, its inverse is given by

$$x_i = \frac{y_i}{\sum_{j=0}^n y_j}; \quad i=0, 1, \dots, n. \quad (27)$$

Using (25) and the fact that

$$\sum_{j,k,l=0}^n a_{0,j,kl} x_j x_k x_l = 0$$

one obtains

$$\begin{aligned} \dot{y}_i &= \left(\frac{x_i}{x_0} \right) \cdot \frac{1}{2} \left(\frac{x_i}{x_0} \right) \left(\sum_{j,k,l=0}^n a_{ij,kl} x_j x_k x_l \right) \\ &= \left(\frac{x_0^3}{2} \right) y_i \left(\sum_{j,k,l=0}^n a_{ij,kl} y_j y_k y_l \right). \end{aligned}$$

Since $x_0^3 > 0$ is independent of i , we may simply omit it (up to a change in velocity), and obtain

$$\dot{y}_i = y_i \left(\sum_{j,k,l=0}^n a_{ij,kl} y_j y_k y_l \right); \quad i=1, \dots, n$$

with $y_0 = 1$. This is just the general equation of the form

$$\dot{y}_i = y_i Q_i(y_1, \dots, y_n) \quad i=1, \dots, n, \quad (28)$$

where $Q_i(y_1, \dots, y_n)$ is a polynomial of degree ≤ 3 in y_1, \dots, y_n . Conversely, any equation of this type can be transformed into an equation of type (22).

Note that if the polynomials Q_i are all of degree ≤ 1 , (28) is just an equation of Volterra-Lotka type. It follows that the class of equations of type (22) contains the replicator equation.

This can also be seen in the case that the genotypes act as the sum of the corresponding alleles, without dominance effects, i.e. if

$$a_{ij,kl} = a_{ik} + a_{il} + a_{jk} + a_{jl}.$$

This is the case if the heterozygote $A_i A_j$ plays with probability $1/2$ the strategy of $A_i A_i$ and with probability $1/2$ the strategy of $A_j A_j$.

Inserting the above relation into (22) gives

$$\dot{x}_i = x_k \left(\sum_k a_{ik} x_k - \sum_{j,k} a_{ik} x_j x_k \right),$$

which is just the replicator equation.

An equation of type (22) in three variables may admit a limit cycle. Indeed, it is easy to see that a modified predator-prey equation, namely

$$\dot{y}_1 = y_1(c(a+y_1)(b-y_1) - dy_2)$$

$$\dot{y}_2 = y_2(e y_1 - f)$$

has a limit cycle if

$$\frac{f}{e} < \frac{b-a}{2}.$$

Hence, (28) may admit a limit cycle for $n=2$. Thus, in contrast to the asexual case, the equation for gene frequencies may admit limit cycles already in the case of three alleles.

6. Several Examples

6.1. The Case $n=2$

In order to simplify the selection equation we add constants to the payoff matrix in such a way that $a_{11} = a_{22} = a_{33} = 0$. If we set $x_1 = x$ and $x_2 = 1-x$ we obtain from (22)

$$\dot{x} = \frac{1}{2} x(1-x)g(x)$$

with

$$\begin{aligned} g(x) &= -a_{21}x^3 + (2a_{12} + a_{21} - a_{31})x^2(1-x) \\ &\quad + (a_{13} - a_{23} - 2a_{32})x(1-x)^2 + a_{23}(1-x)^3. \end{aligned}$$

In the case gene A_2 dominates A_1 the payoff matrix becomes

$$\begin{array}{cc} a & b & b \\ c & d & d \\ c & d & d \end{array}$$

or after adding appropriate constants

$$\begin{array}{cc} 0 & v & v \\ w & 0 & 0 \\ w & 0 & 0. \end{array}$$

Then

$$g(x) = x(v - (v+w)x^2).$$

Just as in the asexual case (Schuster et al., 1981) we may distinguish essentially three subcases:

a) if $vw < 0$ there is no inner equilibrium and one of the genes will be wiped out (see Fig. 1a);

b) if $vw > 0$ and $v > 0$ there is a unique inner equilibrium \bar{P} which is stable. A mixture of strategies is established (see Fig. 1b);

c) if $vw > 0$ and $v < 0$ the unique inner equilibrium \bar{P} is unstable. One or the other of the homozygotes will survive depending on the initial values (see Fig. 1c).

Note incidentally that in equilibrium \bar{P} the frequency of strategy E_1 played in the population is just the same as in the asexual case, namely $v/v+w$.

In case there is no dominance we have three different strategies. The dynamics obviously depends on the correspondence between strategies and genotypes. As an illustration let us consider the well known hawk-mouse-retaliator game of Maynard-

Smith (1974). In modified form the payoff matrix reads

	<i>H</i>	<i>R</i>	<i>M</i>
<i>H</i>	0	-4	4
<i>R</i>	0	0	0
<i>M</i>	2	0	0

If we assume now that the heterozygote plays retaliator strategy we obtain

$$g(x) = x(1-x)(4-14x).$$

In this case there is a unique stable equilibrium. If, however, the mouse strategy is assigned to the heterozygote (which admittedly is less plausible) then

$$g(x) = -x(16x^2 - 18x + 4).$$

Depending on the initial value, either the pure retaliator strategy or a stable mixture of all three strategies evolves.

In the most general case we may obtain up to two stable inner equilibria. Obviously, sexual replication introduces a much richer dynamics into the game.

6.2. One Example for $n=3$

Suppose, males play rock-scissors-paper in fighting for females, i.e. there are three strategies E_1, E_2, E_3 where E_2 beats E_1 , E_3 beats E_2 and E_1 beats E_3 . The modified payoff matrix is assumed to be

	E_1	E_2	E_3	wherein $\varepsilon < 1$ (usually $\varepsilon \sim 0$)
E_1	0	-1	$1-\varepsilon$	
E_2	$1-\varepsilon$	0	-1	
E_3	-1	$1-\varepsilon$	0	

Then it is easy to see in the asexual case that the mixed population $M = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ is an attractor, even an ESS if $\varepsilon < 0$, a repeller if $\varepsilon > 0$ and a center (all orbits periodic) if $\varepsilon = 0$.

In the sexual model let us assume, that the homozygotes $A_i A_i (i=1, 2, 3)$ play E_i and the heterozygotes $A_i A_{i+1}$ plays E_i with probability p , E_{i+1} with probability q and, for the sake of generality, may also play the third strategy E_{i+2} (not represented by its two alleles A_i, A_{i+1}) with probability r . (We count indices modulo 3.) Then $p+q+r=1$.

Since the Eq. (22) becomes rather complicated we will only state the results: Of course $M = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ is a fixed point. The linearized equation (for $r < 1$) is essentially the same as in the asexual case. Hence M is an attractor for $\varepsilon < 0$ and a repeller for $\varepsilon > 0$. But in the critical case $\varepsilon = 0$, the behaviour is different: Analysis

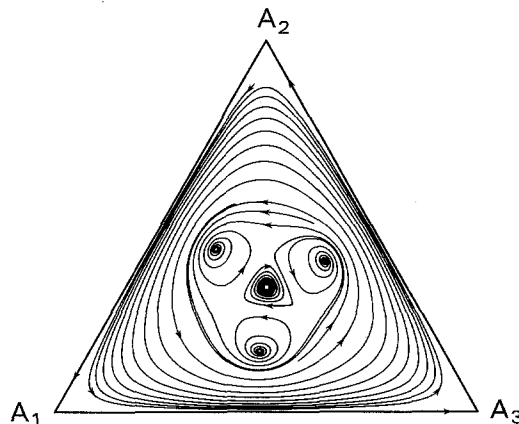


Fig. 2. A phase portrait of Eq. (22) in the special case of three alleles ($n=3$) and a cyclic superiority relation as discussed in Sect. 6.2. The numerical values chosen are $\varepsilon=0.11$, $p=0.05$, $q=0.15$, and $r=0.8$

of the higher order terms, using e.g. formula (4.2) of Marsden and McCracken (1976) shows that M is an attractor also in this case if $q > p$ (i.e. if the heterozygotes prefer the "better" of the two strategies corresponding to their alleles) and a repeller if $q < p$. By the Hopf bifurcation theorem, see Marsden and McCracken (1976), limit cycles occur near M . If $q > p$, the bifurcation is supercritical, the periodic orbits are stable and occur for (small) $\varepsilon > 0$.

If $q < p$, the bifurcation is subcritical, the periodic orbits are unstable and occur for (small) $\varepsilon < 0$.

A local analysis of the flow near the boundary determines the range of ε for which the limit cycle persists: The limit value for which the limit cycle disappears is given by

$$\varepsilon_0 = \frac{q-p}{1-p}$$

(at least when the flow on the boundary is cyclic).

A rather interesting, curious effect occurs in the (admittedly unrealistic) case that r is only a bit smaller than one, i.e. if the heterozygotes play usually the third strategy ($r > 2/3$ will be sufficient): The flow on the boundary edges now is reversed: Although E_2 beats E_1 , the gene A_1 will win (if there is no A_3 -allele) since it fares better against the heterozygote. Near the fixed point $M = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ the flow remains the same, as noted above. Therefore some orbits will change the orientation of their cycling (Fig. 2).

Furthermore there are 6 additional fixed points besides M in the interior: 3 spiral points (see Fig. 2) and 3 saddle points (not to be seen in Fig. 2) which are necessary to separate the basins of the 4 spiral points.

Choosing $0 < \varepsilon < \varepsilon_0$ gives 4 stable limit cycles, one around each of the four foci. If $\varepsilon > \varepsilon_0$, the limit cycles disappear and (almost) all orbits come from the 4

unstable foci and go with reversed direction of cycling to the boundary.

In higher dimensions ($n > 4$) the existence of strange attractors can be expected.

7. Conclusions

In this paper we extended game dynamics for social behaviour of animals to Mendelian populations. This more realistic model for the evolution of behaviour leads to a differential equation which can be interpreted as the fourth order analogue of the replicator equation discussed extensively before. In general the higher order of the non-linearity introduces a very rich dynamics into the system.

The case of two alleles (for one locus) is relatively easy to study. We are able to show that in case of dominance – the heterozygote and one of the two homozygotes behave identically – the dynamics of Mendelian system is closely related to that of asexually multiplying populations. Then the original concept of evolutionarily stable strategies (ESS) retains its meaning and describes properly the steady state of the population. If the heterozygote shows its own characteristic behaviour, however, the dynamics becomes enormously rich and the purely game theoretical approach is no longer sufficient.

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References

- Hofbauer, J., Schuster, P., Sigmund, K.: A Note on evolutionary stable strategies and game dynamics. *J. Theor. Biol.* **81**, 609–612 (1979)
- Hofbauer, J.: On the occurrence of limit cycles in the Volterra-Lotka differential equation. *J. Nonlinear Anal.* **5**, (1981) (to appear)
- Marsden, J., McCracken, M.: The Hopf bifurcation and its applications. In: Applied mathematical sciences, Vol. 19. Berlin, Heidelberg, New York: Springer 1976
- Maynard-Smith, J.: The theory of games and the evolution of animal conflicts. *J. Theor. Biol.* **47**, 209–221 (1974)
- Schuster, P., Sigmund, K., Hofbauer, J., Wolff, R.: Selfregulation of behaviour in animal societies. *Biol. Cybern.* **40**, 1–8 (1981)
- Schuster, P., Sigmund, K., Wolff, R.: Mass action kinetics of selfreplication in flow reactors. *J. Math. Analysis & Applications* **78**, 88–112 (1980)
- Taylor, P., Jonker, L.: Evolutionarily stable strategies and game dynamics. *Math. Biosci.* **40**, 145–156 (1978)
- Zeeman, E.C.: Population dynamics from game theory. In: global theory of dynamical system, Nitecki (ed.). In: Lecture Notes, Vol. 819. Berlin, Heidelberg, New York: Springer 1980
- Zeeman, E.C.: Dynamics of the evolution of animal conflicts. *J. Theor. Biol.* **89**, 249–270 (1981)

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