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IIASA Working Paper

WP-87-021

February 1987

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February 1987
WP-87-21

PREFACE

Game dynamics, as a branch of frequency dependent population
genetics, leads to replicator equations. If phenotypes corre-
spond to mixed strategies, evolution will affect the frequencies
of the phenotypes and of the strategies and thus lead to two
dynamical models. Some examples of this, including the sex
ratio, will be discussed with the help of a non-Euclidean metric
leading to a gradient system. Some other examples from popula-
tion genetics and chemical kinetics confirm the usefulness of
such gradients in describing evolutionary optimization.

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GAME DYNAMICS, MIXED STRATEGIES AND GRADIENT SYSTEMS

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1. Introduction

The theory of frequency dependent selection received a strong boost, and in fact a new meaning, from game theory. The introduction of the notion of evolutionary stability by Maynard-Smith and Price (1973) and the subsequent flourishing of evolutionary game theory must be viewed as a major advance in theoretical biology. But like every new field, it has met with its share of misunderstandings.

In particular, it has probably been unavoidable that the use of the term "strategy" evoked hostile reactions. "Strategy" is closely associated with plotting and scheming: we don't expect much forethought from nonhuman brains. "Mixed strategies", in particular, seem totally misplaced in the animal kingdom. Konrad Lorenz claims not to have met with a single one in all his life. Animals, as others have pointed out, do not have roulette wheels in their heads: so how can they obtain probability distributions for different types of behavior?

But this is a superficial view based on a semantic confusion. Indeed, in evolutionary games, a strategy is a phenotype. The sex ratio is an example of a mixed strategy, and it is common enough. Many species manage to mix male and female offspring with nearly equal probability without playing roulette. Other cases of mixed strategies are to be found in foraging, dispersal, parental care etc. We refer to Maynard-Smith (1982) for a thorough presentation of the biological aspects of this question. On the following pages, we shall be more interested in the mathematical aspects, but stick to the sex ratio for illustration.

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2. The sex ratio

Already Darwin (1859) was puzzled by the prevalence of the sex ratio $\frac{1}{2}$. It is not, as we may first think, an immediate result of the sex determination through X- and Y-chromosomes. In fact, at conception the ratio may be quite different, and subsequently shift to yield the value $\frac{1}{2}$ at birth. What is the evolutionary reason for this? After all, as animal breeders know, a female biased sex ratio leads to a higher overall growth rate. Why are there so many males around?

The ingenious explanation of Fisher (1930) anticipates, as Maynard-Smith notes, thinking in terms of game theory. We shall assume that the number of children is not affected by the sex ratio, and conclude that the number of grandchildren is. Roughly speaking, if there were more males than females, girls would have good prospects. Since the same holds vice versa, this should lead to a sex ratio of $\frac{1}{2}$.

To check this, let us denote by p the sex ratio of a given individual, and by m the average sex ratio in the population. Let N_1 be the population number in the daughter generation F_1 (of which $m\,N_1$ will be male and $(1-m)N_1$ female) and N_2 the number in the following generation F_2. Each member of F_2 has one mother and one father: the probability that a given male in the F_1 generation is its father is $\frac{1}{mN_1}$, and the expected number of children produced by a male in the F_1 generation is therefore $\frac{N_2}{mN_1}$ (assuming random mating). Similarly, a female in the F_2-generation contributes an average of $\frac{N_2}{(1-m)N_1}$ children. Since a p-phenotype produces male and female children in the ratio p to $1-p$, its expected number of grandchildren will be proportional to

$$p\;\frac{N_2}{mN_1} + (1-p)\;\frac{N_2}{(1-m)N_1}$$

i.e., its fitness is proportional to

$$w(p,m) = \frac{p}{m} + \frac{1-p}{1-m} \tag{1}$$

(we may clearly exclude the cases $m = 0$ and $m = 1$ which lead to immediate extinction). For given $m \in (0,1)$, the function $p \to w(p,m)$ is affine linear, increasing for $m < \frac{1}{2}$, decreasing for $m > \frac{1}{2}$ and constant for $m = \frac{1}{2}$.

Let us now consider a phenotype with sex ratio q, and ask whether it is evolutionarily stable in the sense that no other phenotype with sex ratio p can invade. If such a deviant phenotype is introduced in a small proportion ε, the average sex ratio of the population is $r = \varepsilon p + (1-\varepsilon)q$. The q-phenotype fares better than the p-phenotype if and only if

$$w(p,r) < w(q,r) . \qquad (2)$$

This is obviously the case for every p when $q = \frac{1}{2}$ (it is enough to note that p and r are either both smaller, or both larger than $\frac{1}{2}$). For $q < \frac{1}{2}$, a sex ratio $p > q$ will do better, however, and consequently, spread; similarly, any $q > \frac{1}{2}$ can be invaded by a smaller p. Thus $\frac{1}{2}$ is the unique "uninvadable" sex ratio.

A similar game theoretical analysis makes sense whenever the "payoff" for a given "strategy" (or trait) corresponds to its rate of increase in the population. In many examples from biology, this will mean that the trait is inherited, and its payoff Darwinian fitness - a fitness which, in general, will depend on what the others are doing, and hence will be frequency dependent. But examples where the trait spreads through learning, or other means, have also been discussed. We refer in particular to Axelrod (1984) and his computer tournaments between programs for the Repeated Prisoner's Dilemma, a striking approach to the evolution of cooperation.

3. Game dynamics

Following Taylor and Jonker (1978), the evolution of the frequencies of the different phenotypes in the population will be modeled by a game dynamics whose Ansatz consists in setting the growth rate of the frequency of a phenotype equal to the difference between its payoff and the average payoff in the population.

For the sake of simplicity, we shall assume that there are only finitely many phenotypes $E_1, \ldots, E_n$ with frequencies $x_1, \ldots, x_n$. The state of the population is given by the point x in the unit simplex S_n. By $f_i(x)$, we shall denote the payoff for the phenotype E_i in a population in state x. The average payoff in the population, then, is

$$\bar{f}(x) := \sum x_i f_i(x) = x \cdot f(x) . \qquad (3)$$

The rate of increase of the frequency of E_i is $\dfrac{\dot{x}_i}{x_i}$. The dynamics, then, is given by

the

equation

$$\dot{x}_i = x_i (f_i(\underline{x}) - \bar{f}(\underline{x})) \tag{4}$$

on the state space S_n. (It is easy to see that the simplex S_n as well as its boundary consisting of faces $x_i = 0$ is invariant).

This "replicator equation" has been derived and analyzed in many different fields of evolutionary biology, as e.g. in population genetics, chemical kinetics and mathematical ecology (see, e.g., Schuster and Sigmund (1983) and Sigmund (1985)). Of particular interest is the case where the $f_i(\underline{x})$ are linear: as shown by Hofbauer (1981), the replicator equation then is equivalent to the Lotka-Volterra equation $\dot{y}_i = y_i (r_i + \sum a_{ij} y_j)$.

In many situations, the restriction to finitely many phenotypes is unnatural. For the sex ratio, in particular, all values between 0 and 1 should be allowed. It is easy to derive the corresponding differential equation modeling the evolution of the frequency distributions. However, for our purposes this will be only of secondary interest: we shall stick to discrete approximations and assume that only finitely many sex ratios p_i may occur.

The average sex ratio is

$$m = \sum x_i p_i . \tag{5}$$

The fitness $f_i(\underline{x})$ of sex ratio p_i is given by $w(p_i, m)$ (see (1)). It will be useful to write this in a slightly different way. There are two "pure strategies" in the sex ratio model, namely "produce only sons" or "produce only daughters", i.e. $p = 1$ and $p = 0$. The corresponding payoffs are $w(1, m) = \dfrac{1}{m}$ and $w(0, m) = \dfrac{1}{1-m}$. With $F(m) = w(1, m) - w(0, m)$ one obtains

$$f_i(\underline{x}) = w(p_i, m) = p_i F(m) + \frac{1}{1-m} \tag{6}$$

$$\bar{f}(\underline{x}) = \sum x_i f_i(\underline{x}) = m F(m) + \frac{1}{1-m} \tag{7}$$

and

$$\dot{x}_i = x_i (p_i - m) F(m) . \tag{8}$$

Similar equations occur very frequently in game dynamics. The celebrated "Hawk-Dove" game from Maynard-Smith (1974) is a case in point. We may assume that an animal, when faced with a fight, has two basic options: to retreat or to escalate. The success of each move depends on what the opponent is likely to do. To escalate is a good idea if the opponent will retreat: if not, it might be a fatal step. It is conceivable that individuals will display mixed strategies and escalate with a certain probability.

Thus we shall consider games satisfying two assumptions:

(a) There are two strategies R_1 and R_2. Each phenotype E_i will be characterized by its probability p_i of using R_1. Then m as given in (5) will be the frequency of R_1 in the whole population.

(b) The payoffs A_1 and A_2 for R_1 and R_2 depend only on m.

With $F(m) = A_1(m) - A_2(m)$, equations (6) and (7) will become $f_i(\underline{x}) = p_i F(m) + A_2(m)$ and $\bar{f}(\underline{x}) = mF(m) + A_2(m)$. Thus (8) will hold again.

In the sex ratio game,

$$F(m) = \frac{1}{m} - \frac{1}{1-m} . \tag{9}$$

In the Hawk-Dove game, and more generally whenever the payoff depends on (one or repeated) pairwise encounters, $A_1(m)$ and $A_2(m)$ are linear in m. Indeed, if a_{ij} is the payoff for an individual using R_i against an individual using R_j $(i,j = 1,2)$ then $A_1(m) = a_{11}m + a_{12}(1-m)$, $A_2(m) = a_{21}m + a_{22}(1-m)$ and hence

$$F(m) = m(a_{11} - a_{21} + a_{22} - a_{12}) - (a_{22} - a_{12}) . \tag{10}$$

Returning to the general case, we see that for any three phenotypes E_i, E_j and E_k, equation (8) admits a constant of motion, namely

$$Q(\underline{x}) = (p_j - p_k)\log x_i + (p_k - p_i)\log x_j + (p_i - p_j)\log x_k . \tag{11}$$

This induces a foliation of the phase space S_n into one-dimensional invariant manifolds.

The evolution of the average frequency m of R_1 is given by

$$\dot{m} = \sum p_i \dot{x}_i = \sum p_i x_i (p_i - m_i)F(m)$$

i.e.

$$\dot{m} = F(m) \operatorname{Var} P \qquad (12)$$

where P is the random variable taking the value p_i with probability x_i. If we neglect the degenerate situation $\operatorname{Var} P = 0$ (only one phenotype present in the population), we obtain that $\dot{m}$ has the sign of $F(m)$, i.e. that the frequency of R_1 increases if and only if $F(m) > 0$. The set $\{x \in S_n : F(m) = 0\}$, which consists of linear manifolds, is the set of rest points of (8).

We sketch the situation for the sex ratio game and $p_1 = \frac{1}{5}, p_2 = \frac{3}{5}$ and $p_3 = \frac{4}{5}$ in Figure 1. The invariants of motion corresponding to (11) are the curves $x_2^3 = \operatorname{const} x_1 x_3^2$ in S_n. The orbits converge along these curves to the set $m = \frac{1}{2}$ of equilibrium points. This set is evolutionarily stable, in the terminology of Thomas (1985).

In the sex ratio game and many other situations, there holds a "law of diminishing return" in the sense that the payoff for each strategy is a decreasing function of its frequency. In this case (8) is locally adaptive in the sense that $F(m)$ converges monotonically to 0. We shall presently see that (8) is a gradient and hence satisfies a global maximum principle.

4. Shahshahani gradients

As shown by Shahshahani (1979) and Akin (1979), the metric most appropriate for the replicator equation (4) on S_n is not the Euclidean one. It is advantageous to consider another Riemannian metric on the tangent space

$$T_x S_n \sim \{\xi \in \mathbb{R}^n : \sum \xi_i = 0\} .$$

For $\underline{x} \in int\, S_n$ and $\underline{\xi}, \underline{\eta} \in T_{\underline{x}}\, S_n$, it is given by the inner product

$$< \underline{\xi}, \underline{\eta} >_{\underline{x}} = \sum_{i=1}^{n} \frac{1}{x_i}\, \xi_i\, \eta_i$$

(while the Euclidean inner product will be denoted by $\underline{\xi} \cdot \underline{\eta} = \sum_{i=1}^{n} \xi_i \eta_i$).

In particular, the Fisher-Haldane-Wright selection equation

$$\dot{x}_i = x_i\, ((M\underline{x})_i - \underline{x} \cdot M\underline{x})$$

with symmetric matrix M is a gradient with respect to this Shahshahani metric, with $V(\underline{x}) = \frac{1}{2}\underline{x} \cdot M\, \underline{x}$ as potential. This implies Kimura's Maximum Principle: the average fitness $\underline{x} \cdot M\, \underline{x}$ increases at maximal rate under the effect of selection.

In general, let V be a real valued function defined on an open set U in $\mathbb{R}^n$ containing the simplex S_n, and let $D_{\underline{x}}\, V{:}\mathbb{R}^n \to \mathbb{R}$ be its derivative at $\underline{x}$. The vector field $\underline{F}{:}U \to \mathbb{R}^n$ is the Euclidean gradient of V, i.e. $\underline{F}(\underline{x}) = \text{grad}\, V(\underline{x})$ for all $\underline{x} \in U$, if

$$\underline{F}(\underline{x}) \cdot \underline{\eta} = D_{\underline{x}}\, V(\underline{\eta})$$

holds for all $\underline{\eta} \in T_{\underline{x}}\, \mathbb{R}^n \sim \mathbb{R}^n$, while it is the Shahshahani gradient of V, i.e. $\underline{F}(\underline{x}) = \text{Grad}\, V(\underline{x})$ for all $\underline{x} \in int\, S_n$, if

$$<\underline{F}(\underline{p}), \underline{\eta}>_{\underline{x}} = D_{\underline{x}}\, V(\underline{\eta})$$

holds for all $\underline{\eta} \in T_{\underline{x}}\, S_n$.

If $\underline{f} = \text{grad}\, V$ is an Euclidean gradient, then the vector field $\hat{\underline{f}}$ with components

$$\hat{f}_i(\underline{x}) = x_i\, (f_i(\underline{x}) - \bar{f}(\underline{x})) \tag{13}$$

is the corresponding Shahshahani gradient, i.e. $\hat{\underline{f}} = \text{Grad}\, V$ (cf. Sigmund, 1984). For the converse direction, let us define two vector fields $\underline{f}$ and $\underline{g}$ to be equivalent, $\underline{f} \sim \underline{g}$, if $f_i(\underline{x}) - g_i(\underline{x})$ is independent of i for all $\underline{x} \in S_n$. It is easy to see that $\underline{f} \sim \underline{g}$ implies $\hat{\underline{f}} = \hat{\underline{g}}$ on S_n, and vice versa. Now if $\hat{\underline{f}} = \text{Grad}\, V$, then $\underline{f} \sim \text{grad}\, V$. Thus the vector field $\hat{\underline{f}}$ is the Shahshahani gradient of V on $int\, S_n$ if and only if there exists a real valued function Ψ defined in a neighborhood of $int\, S_n$ such that

$$f_i(\underline{x}) = \frac{\partial V}{\partial x_i}(\underline{x}) + \Psi(\underline{x}) \tag{14}$$

holds on int S_n .

Equivalently, the replicator equation (4) is a Shahshahani gradient if and only if

$$f_{i,j} + f_{j,k} + f_{k,i} = f_{i,k} + f_{k,j} + f_{j,i} \tag{15}$$

holds on int S_n for all pairwise different indices $i,j,k \in \{1, \ldots, n\}$. (Here $f_{i,j}$ denotes the partial derivative $\dfrac{\partial f_i}{\partial x_j}$). This "triangular integrability condition", the equivalent of the integrability condition $f_{i,j} = f_{j,i}$ for Euclidean gradients, has been shown by Sigmund (1984) for linear vector fields $\underline{f}(\underline{x}) = A \underline{x}$. It means that there exist constants c_j such that the matrix with elements $a_{ij} - c_j$ is symmetric. The general case was proved by Hofbauer (1985b), and we shall presently see its usefulness. Let us note that for $n = 2$, condition (15) is trivially satisfied and (4) therefore a gradient.

5. Mixed stategist games

Let us consider now a game with N pure strategies R_1 to R_N, and n phenotypes E_1 to E_n playing mixed strategies: E_i plays strategy R_j with probability p_j^i, and hence is characterized by a vector $\underline{p}^i \in S_N$. If we denote the frequency of E_i in the population by x_i, then

$$m_k = \sum_{i=1}^{n} x_i \, p_k^i \tag{17}$$

is the frequency of the strategy R_k in the population. The state of the population is given by $\underline{x} \in S_N$ and the distribution of strategies by $\underline{m} \in S_N$. Let us assume now that the payoff depends on $\underline{x}$ only through the frequency distribution $\underline{m} \in S_N$ of the pure strategies. (Thomas (1984) calls such games degenerating). If we denote the payoff for the pure strategy R_j by $A_j(\underline{m})$, then the payoff for phenotype E_i is given by

$$\underline{p}^i \cdot \underline{A}(\underline{m}) = \sum_{j=1}^{N} p_j^i A_j(\underline{m}) \tag{18}$$

while the average payoff in the population is

$$\sum_{i=1}^{n} x_i \, (\underline{p}^i \cdot \underline{A}(\underline{m})) = \underline{m} \cdot \underline{A}(\underline{m}) . \tag{19}$$

Game dynamics leads to

$$\dot{x_i} = x_i[(\underline{p}^i - \underline{m}) \cdot \underline{A}(\underline{m})] \quad i = 1,\dots,n \tag{20}$$

which for $N = 2$ yields (8).

Whenever there are more phenotypes than strategies ($N < n$), there are non-trivial relations

$$\sum c_i \underline{p}^i = 0 .$$

Since all $\underline{p}^i$ belong to S_N, this implies $\sum c_i = 0$ and hence

$$\sum c_i(\underline{p}^i - \underline{m}) = 0 . \tag{21}$$

Thus one obtains from (20) the constant of motion

$$\sum c_i \log x_i = const \tag{22}$$

which corresponds to (11).

The mean $\underline{m}$ satisfies

$$\dot{\underline{m}} = [\text{Cov } P]\underline{A}(\underline{m}) \tag{23}$$

where Cov P is the covariance matrix of the random variables P_k taking values p_k^i with probability x_i. This corresponds to (12).

Following Thomas (1985) we can also consider the auxiliary game corresponding to the pure strategies. This "pure strategist game" corresponds to (20) with $n = N$ and $\underline{p}^i$ the i-th unit vector of the standard basis in $\mathbb{R}^N$. Denoting by y_i the frequency of R_i, we get $\underline{m} = \underline{y}$ and

$$\dot{y_i} = y_i(A_i(\underline{y}) - \bar{A}(\underline{y})) \quad i = 1,\dots,N \tag{24}$$

on S_N.

Theorem: If the pure strategist dynamics (24) is a Shahshahani gradient, then so is the mixed strategist dynamics (20).

Proof. (20) is a replicator equation of type (4) with

$$f_i(\underline{x}) = \underline{p}^i \cdot \underline{A}(\underline{m}) = \sum_{k=1}^{N} p_k^i A_k(m_1, \dots, m_N) . \tag{25}$$

Hence

$$f_{i,j}(\underline{x}) = \sum_{k=1}^{N} p_k^i \sum_{l=1}^{N} \frac{\partial A_k}{\partial m_l}(\underline{m}) \frac{\partial m_l}{\partial x_j} = \sum_{k,l} p_k^i A_{k,l} \, p_l^j = \underline{p}^i \cdot D_{\underline{m}} A(\underline{p}^j) . \tag{26}$$

If (24) is a gradient, the triangular integrability condition (15) reads

$$A_{i,j} + A_{j,k} + A_{k,i} = A_{i,k} + A_{k,j} + A_{j,i} \ .$$

(27)

This implies that the $N \times N$-matrix $D_{\underline{m}}\underline{A}$ can be written as $S(\underline{m}) + C(\underline{m})$, where $S(\underline{m})$ is symmetric and $C(\underline{m})$ has N equal rows. For some $\underline{c} = \underline{c}(\underline{m}) \in \mathbf{R}^N$ we have

$$C(\underline{m}) = \begin{bmatrix} c_1 & c_2 & \cdots & c_N \\ \vdots & \vdots & & \vdots \\ \vdots & \vdots & & \vdots \\ c_1 & c_2 & \cdots & c_N \end{bmatrix} \ .$$

(28)

Clearly $\underline{p}^i \cdot S(\underline{m}) \underline{p}^j = \underline{p}^j \cdot S(\underline{m}) \underline{p}^i$ and $\underline{p}^i \cdot C(\underline{m}) \underline{p}^j = \underline{c} \cdot \underline{p}^j$. This together with (26) implies that (15) is satisfied and hence that (20) is a Shahshahani gradient.

Equation (20) has actually the same potential as (24). More precisely, if $\underline{y} \mapsto V(\underline{y})$ is a Shashahani gradient for (24), then $\underline{x} \mapsto V(\underline{m})$ is a Shashahani gradient for (20). Indeed, if

$$A_i(\underline{y}) = \frac{\partial V}{\partial y_i}(\underline{y}) + \Psi(\underline{y})$$

(cf. eq. (14)) then

$$f_i(\underline{x}) = \underline{p}^i \cdot A(\underline{m}) = \sum_j p_j^i A_j(\underline{m}) = \sum_j p_j^i (A_j(\underline{m}) - \Psi(\underline{m})) + \Psi(\underline{m})$$

$$= \frac{\partial V}{\partial x_i}(\underline{m}) + \Psi(\underline{m}) \ .$$

As a corollary , we obtain that (8) is always a Shahshahani gradient: indeed, we have only to recall that $N = 2$. Equation (14), in this case, is satisfied with $\Psi(\underline{x}) = A_2(m)$ and V a primitive function of F, since

$$\frac{\partial V}{\partial x_i}(m) = \frac{\partial V}{\partial m}(m)\frac{\partial m}{\partial x_i} = p_i \, F(m) \ .$$

(29)

For the Hawk-Dove game, F is given by (10) and hence we may use

$$V(m) = \tfrac{1}{2}(a_{11} - a_{21} + a_{22} - a_{12}) \left[m - \frac{a_{22} - a_{12}}{a_{11} - a_{21} + a_{22} - a_{12}} \right]^2 \ .$$

(30)

The expression in the square bracket is the difference between the actual frequency of R_1 in the population and its Nash equilibrium value in the Hawk-Dove game, provided it lies in $(0,1)$.

For the sex ratio game, F is given by (9) and hence we may use

$$V(m) = \log m (1-m) . \tag{31}$$

The product $m(1-m)$ of the frequencies of males and females increases to its maximal value, obtained for $m = \frac{1}{2}$. This principle, which was first formulated by Shaw and Mohler (1953), can now be strengthened: the population evolves in such a way that $m(1-m)$ increases at a maximal rate.

It is interesting to consider also the case of $N > 2$ mating types. Every "sex" R_i can mate with any other R_j, $j \neq i$. Since m_i denotes the frequency of R_i and $1-m_i$ the frequency of its possible mates, the frequency of R_i-matings is

$$\frac{m_i(1-m_i)}{\sum m_k(1-m_k)}$$

and the payoff for an R_i-individual, i.e. its share in matings, is

$$A_i(\underline{m}) = \frac{1-m_i}{\sum m_k(1-m_k)} . \tag{32}$$

It is easy to check that

$$A_{i,j} = (1-m_i)(2m_j-1)\left[\sum m_k(1-m_k)\right]^{-2} \tag{33}$$

satisfies the triangular integrability condition (27). This implies that the sex ratio game with N mating types is a gradient system. Now

$$A_i(\underline{m}) = \frac{1-2m_i}{2\sum m_k(1-m_k)} + \frac{1}{2\sum m_k(1-m_k)} \tag{34}$$

is of the form $\frac{\partial V}{\partial m_i}(\underline{m}) + \Psi(\underline{m})$, with

$$V(\underline{m}) = \frac{1}{2}\log \sum_{k=1}^{N} m_k(1-m_k) \tag{35}$$

i.e., since $\sum m_k = 1$, with

$$V(\underline{m}) = \frac{1}{2}\log (1-\frac{1}{N}-\sum_{k=1}^{N}[m_k-\frac{1}{N}]^2) \sum_{k=1}^{N}\left[m_k - \frac{1}{N}\right]^2 . \tag{36}$$

Hence (36) is the potential for the N-type sex ratio game. The state $\underline{x}(t)$ evolves in such a way that $\sum\left[m_k - \frac{1}{N}\right]^2$ converges at a maximal rate towards 0. In equili-

brium, the N sexes will be equally represented in the population. (This is somewhat disappointing. To quote Fisher (1930): "No practical biologist interested in sexual reproduction would be let to work out the detailed consequences experienced by organisms having three or more sexes: yet what else should he do if he wishes to understand why the sexes are, in fact, always two". It would have been nice to find out that the model with N sexes leads to the extinction of all but two of them.)

6. Discussion

(a) Gradient systems with respect to a non-Euclidean metric occur in several fields of theoretical biology. In particular, Hofbauer (1985a) discussed the mutation-selection equation of Hadeler (1981) and related models. Such systems are Shahshahani gradients if and only if the mutation rate from allele A_j to allele A_i does not depend on j. In Hofbauer (1985b) one can find some more gradient systems: for example, fertility equations with two alleles, or with additive fertility contributions of the parents, or with multiplicative but sex-independent contributions.

In Schuster and Sigmund (1985) it is shown that competition of autocatalytic reactions may lead in important cases to gradients and hence to maximum principles.

(b) Our discussion of the sex ratio neglected many biological aspects. For example, we assumed that the "costs" for producing male and female offspring are the same: it frequently happens, however, that they differ. Fisher's argument is still valid: it says now that the total (life time) effort in producing sons and daughters must be equal (see, e.g. Charnov (1982) and Trivers (1985)). We have furthermore failed to consider the case that competition for mates is local rather than global: this case may lead to extraordinary sex ratios (Hamilton (1968)). Another aspect which we neglected is the genetic basis of the sex ratio (this is a common trait of "phenotypic" game dynamics for frequency dependent selection). There is a considerable amount of work on genetic models, which seem independent of Fisher's argument but lead again to the sex ratio $\frac{1}{2}$ (see, e.g., Eshel and Feldman (1982) and Karlin and Lessard (1986)). Sex linked meiotic drive may again lead to extraordinary sex ratios (Hamilton, (1968)).

The outcome of both genetic and game theoretic models is a prediction on the total sex ratio in the population, and not on the sex ratio of individuals. The population may just as well consist of a unique phenotype with sex ratio $\frac{1}{2}$ or of two equally represented phenotypes with sex ratios 0 and 1, say. Why is there in actual populations a prevalence for individual sex ratios close to $\frac{1}{2}$? Numerical simulations by Poethke (1986) suggest that this is due to the finite size of the population.

Finally, we mention that evolutionary dynamics seems well on the way to invade classical game theoretical fields. For example, Samuelson (1985) deals with a sex ratio model as a link between modes of thought in economics and biology.

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