A SURVEY OF REPLICATOR EQUATIONS

Karl Sigmund

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PREFACE

This survey of the "state of the art" of replicator dynamics covers recent developments in the theory of the difference and differential equations which describe the evolution of population frequencies under the influence of selection. Mathematical models of this type play a central role in population genetics, ecology, prebiotic evolution and ethology. They introduce a dynamic element into the theory of normal form games and may also be applied to models of learning and economic evolution. The mathematical aspects considered include fixed-point analysis, the notions of permanence and exclusion, the gradient systems obtained by the introduction of certain Riemann metrics, Hopf bifurcations, and relations with game-theoretical concepts.

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ANDRZEJ WIERZBICKI
Chairman
System and Decision Sciences

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Karl Sigmund

Institute of Mathematics, University of Vienna, Vienna, Austria

1. INTRODUCTION

What are the units of natural selection? This question has aroused considerable debate in theoretical biology. Suggestions range from pieces of polynucleotides, genes or gene complexes to individuals, groups or species. It could turn out, however, that different answers are correct in different contexts, depending on the scale on which selection acts most decisively. This is somewhat analogous to physics, where the dominant force may be gravitational, electromagnetic, or strong or weak inter-particle attractions, depending on the problem.

It is therefore convenient to consider an abstract unit of natural selection in theoretical investigations, which can be replaced by the appropriate real unit (genes, individuals or species) in specific circumstances. This abstract unit is termed a *replicator* in Dawkins' book *The Extended Phenotype* (Dawkins, 1982). The term describes any entity which (a) can give rise to an unlimited (at least in principle) sequence of copies and (b) occurs in variants whose properties may influence the number of copies.

Biomathematical arguments support the usefulness of this concept. Indeed, the remarkable similarity of dynamical systems describing the action of selection in the most diverse fields lends weight to the notion of a common mechanism underlying these different observations. The term *replicator dynamics* has been applied to this mechanism (see Schuster and Sigmund, 1983). In the case of continuous time (generations blending into each other), the dynamics can be described by an ordinary differential equation $\dot{x} = F(x)$ of the type

$$\dot{x}_i = x_i(f_i(x) - \Phi), \quad i = 1,...,n \tag{1.1}$$

while for discrete time (separate generations) the dynamics are given by a difference equation $x \to Tx$ with

$$(T\mathbf{x})_i = x_i \left[\frac{f_i(\mathbf{x})}{\Phi} \right], \quad i = 1,\dots,n \quad. \tag{1.2}$$

In both cases, the term Φ is defined by

$$\Phi(\mathbf{x}) = \sum_{i=1}^{n} x_i f_i(\mathbf{x}) \tag{1.3}$$

and ensures that the state $\mathbf{x}$ of the system remains on the unit simplex

$$S_n = \{\mathbf{x} = (x_1,\dots,x_n) \in \mathbb{R}^n : \sum_{i=1}^{n} x_i = 1, \; x_i \geq 0 \text{ for all } i\} \quad. \tag{1.4}$$

The functions $f_i(\mathbf{x})$ describe the interaction of the different variants of the underlying replicator, and are specified by an appropriate biological model.

In particular, first-order interaction terms, i.e., linear functions $f_i(\mathbf{x}) = (A\mathbf{x})_i$ defined by a matrix $A = (a_{ij})$, where

$$(A\mathbf{x})_i = \sum_{j=1}^{n} a_{ij} x_j \quad, \tag{1.5}$$

lead to dynamics which have been investigated independently in (i) population genetics, (ii) population ecology, (iii) the theory of prebiotic evolution of self-replicating polymers and (iv) sociobiological studies of evolutionarily stable traits of animal behavior. Within these contexts, the dynamics describe the effects of selection upon (i) allele frequencies in a gene pool, (ii) relative frequencies of interacting species, (iii) concentrations of polynucleotides in a dialysis reactor and (iv) distributions of behavioral phenotypes in a given species.

After a brief summary of the biological background in Section 2, we present a survey of the mathematical aspects of continuous- and discrete-time replicator equations. There are many interesting results, in particular for the first-order case, due to the work of Akin, Hofbauer, Zeeman and others. Section 3 is concerned with some general properties of replicator equations, and in Section 4 we discuss the existence and stability of equilibria and present some theorems on time averages and exclusion properties. Results concerning the permanence of the biological components of the system are presented in Section 5. Gradient systems for replicator equations are described in Section 6, and Section 7 gives an overview of the classification of low-dimensional phase portraits. Finally, Section 8 summarizes the relationships between game theory and first-order replicator equations.

2. BIOLOGICAL MOTIVATION

2.1. Population genetics

Genes are the quintessential replicators. It is therefore quite appropriate that the first systematic study of a class of replicator equations was in population genetics: the classical work of Fisher, Haldane and Wright on the effects of natural selection upon the frequencies of alleles at a single locus of a diploid, randomly mating population.

Briefly, if $A_i,...,A_n$ denote the possible alleles and $x_i,...,x_n$ their frequencies within the adult population, then random fusion of gametes yields zygotes of genotype A_iA_j with frequency $2x_ix_j$ for $i \neq j$ and x_i^2 for $i = j$. (This is the Hardy–Weinberg law). Let a_{ij} denote the *fitness* of genotype A_iA_j, which in this context is the probability of its survival from zygote to adulthood. The genotypes A_iA_j and A_jA_i are identical (it does not matter which parent contributes which allele) and hence $a_{ij} = a_{ji}$. Since the heterozygous genotype A_iA_j $(i \neq j)$ carries one gene A_i while the homozygous genotype A_iA_i carries two such genes, the frequency $(Tx)_i$ of allele A_i in the adult stage of the new generation is proportional to

$$\frac{1}{2}\left[\sum_{i \neq j} 2a_{ij}x_ix_j + \sum_i 2a_{ii}x_i^2\right]$$

and hence to $x_i(Ax)_i$. Thus

$$(Tx)_i = x_i\left[\frac{(Ax)_i}{\Phi}\right] \text{ with } a_{ij} = a_{ji} \tag{2.1}$$

under the obvious assumption that Φ (which can be interpreted as the average fitness of the population) is not equal to zero.

The corresponding continuous-time selection equation

$$\dot{x}_i = x_i((Ax)_i - \Phi) \text{ with } a_{ij} = a_{ji} \tag{2.2}$$

has been known since the thirties. It is considerably easier to handle than its discrete counterpart (2.1), but its derivation is less clear. It is usually obtained under the assumption that the population is always in Hardy–Weinberg equilibrium, an assumption which is not strictly valid in general (see Ewens, 1979).

Thus first-order replicator equations with symmetric matrices occur in population genetics.

In the model considered here, selection acts through the different viabilities of the genotypes. Differential fecundities (where the number of offspring depends on the mating pair) lead to equations for the genotype frequencies which are not of replicator type (see Pollak, 1979). Except in some special cases (e.g., multiplicative fecundity), these equations behave rather differently from (2.1) or (2.2) (see Bomze et al., 1983). The effects of mutations and (for models with several genetic loci) recombination are also not described by replicator equations.

On the other hand, frequency-dependent fitness coefficients fall within the general framework of replicator equations. Models for haploid organisms lead to equations of the type

$$(T\mathbf{x})_i = x_i \left[\frac{a_i}{\phi} \right] \tag{2.3}$$

or

$$\dot{x}_i = x_i(a_i - \Phi) \ , \tag{2.4}$$

where x_i is the frequency of chromosome G_i and a_i denotes its fitness. Equations of this type are almost trivial if the coefficients a_i are constant. If they are frequency dependent, however, (e.g., if they are linear functions of x_i) then interesting replicator dynamics occur.

2.2. Prebiotic evolution

Equations of type (2.3) were first studied (initially within the framework of chemical kinetics) in an important series of papers by Eigen (1971) and Eigen and Schuster (1979) on prebiotic evolution. In this context the x_i are the concentrations of self-replicating polynucleotides (RNA or DNA) in a well-stirred dialysis reactor with a dilution flow Φ regulated in such a way that the total concentration $x_1 + \cdots + x_n$ remains constant (without loss of generality we can set this concentration equal to 1). In the absence of mutations this leads to continuous-time replicator equations (generation effects do not play any part even if the initial population of molecules reproduces in some synchronized way).

Independent replication of the polymers leads to (2.3) with constant reproduction rates α_i. This implies (except in the case of kinetic degeneracy) that all but one of the molecular species will vanish, with the loss of the corresponding encoded information. In their search for ways of preserving the initial amount of molecular information, Eigen and Schuster were led to study networks of catalytically interacting polynucleotides. Such interactions (and the corresponding replication rates) are usually quite complicated, but nevertheless some rather general results have been obtained. In addition, certain special cases of linear catalytic (or inhibiting) interactions, yielding first-order replicator equations

$$\dot{x}_i = x_i(\textstyle\sum a_{ij}x_j - \Phi), \quad i = 1,...,n \tag{2.5}$$

have been studied as approximations of more realistic chemical kinetics.

The hypercycle (a closed feedback loop in which each molecular species is catalysed by its predecessor) has attracted particular attention (see Schuster et al., 1979, 1980; Hofbauer et al., 1980). Both the cooperation of the components within a hypercycle and the strict competition between individual hypercycles suggest that such networks may have been involved in some phases of early prebiotic evolution. The hypercycle equation is given by

$$\dot{x}_i = x_i(x_{i-1}H_i(\mathbf{x}) - \Phi), \quad i = 1,...,n \quad, \tag{2.6}$$

where the indices are taken on modulo n and the functions $H_i(\mathbf{x})$ are strictly positive on S_n. If the H_i are constants k_i, the above equation reduces to a special case of the first-order replicator equations:

$$\dot{x}_i = x_i(k_i x_{i-1} - \Phi), \quad k_i > 0 \tag{2.7}$$

obtained if matrix $A = (a_{ij})$ in (2.5) is a permutation matrix:

$$A = \begin{bmatrix} 0 & & & & k_1 \\ k_2 & 0 & & & 0 \\ 0 & k_3 & \cdot & \cdot & 0 \\ \cdot & & & & \cdot \\ \cdot & & & & \cdot \\ \cdot & & & & \cdot \\ 0 & & & & 0 \end{bmatrix} .$$

2.3. Animal behavior

Taylor and Jonker (1978) were the first to introduce first-order replicator equations into models of the evolution of animal behavior. This approach was based on Maynard Smith's use of game theory in the study of animal conflicts within a species, equating "strategies" with behavioral phenotypes and "payoffs" with increments of individual fitness.

These investigations were initially centered on the notion of evolutionary stability (see Maynard Smith, 1974), which may be interpreted as game-theoretic equilibria which are proof against the invasion of behavioral mutants. This static approach assumed certain implicit dynamics which were soon made explicit in the form of equations, once again of replicator type.

Let $E_1,...,E_n$ denote the behavioral phenotypes within a population, $x_1,...,x_n$ the frequencies with which they occur, and a_{ij} $(1 \leq i, j \leq n)$ the expected payoff for an E_i-strategist in a contest against an E_j-strategist. Then, assuming random encounters, we obtain $(Ax)_i$ as the average payoff for an E_i-strategist within a population in state x, and

$$\Phi = x \cdot Ax = \sum x_i (Ax)_i \tag{2.8}$$

as the mean payoff. In the case of asexual reproduction, the rate of increase $\dot{x}_i / x_i$ of phenotype E_i is given by the difference $(Ax)_i - x \cdot Ax$, which once again yields (2.5) (or, in the discrete-time case,

$$(Tx)_i = x_i \left[\frac{(Ax)_i + C}{\Phi + C} \right] , \tag{2.9}$$

where C is a positive constant).

The assumption of asexual reproduction at first seems rather unnatural. It can be shown, however, that in many important examples the essential features of the dynamical model are preserved in the more complicated case of sexual reproduction (see Maynard Smith, 1981; Hofbauer et al., 1982; Hines, 1980; Bomze et al., 1983; Eshel, 1982). Rather than introducing some sort of Mendelian machinery which, given the present state of knowledge of the genetic basis of behavior, is bound to be highly speculative, it seems reasonable to stick to the more robust and manageable asexual model (see Schuster and Sigmund, 1984).

The corresponding replicator equations are examples of frequency-dependent sexual or asexual selection equations. Many specific types of conflicts (e.g., the Hawk–Dove–Bully–Retaliator game, the War of Attrition game and the Rock–Scissors–Paper game) have been examined within this framework (see Zeeman, 1981; Bishop and Cannings,1978; Schuster et al., 1981).

The game-dynamical aspects of the linear replicator equation (2.5) may be expected to lead to applications in fields such as psychology and economics (see Zeeman, 1981). A justification of viewing strategies as replicators is given by Dawkins (1982).

2.4. Population ecology

Equations used to model ecological systems are usually of the form

$$\dot{y}_i = y_i f_i(y_1,...,y_n), \quad i = 1,...,n \quad , \tag{2.10}$$

where the y_i are the densities of different populations interacting through competition, symbiosis, host–parasite or predator–prey relationships. Such equations "live" on $\mathbb{R}_+^n$ and are usually not of replicator type. However, taking *relative* densities yields replicator equations. In particular, Hofbauer (1981a) has shown that the classical $(n-1)$-species Lotka–Volterra equation

$$\dot{y}_i = y_i(b_{in} + \sum b_{ij}y_j), \quad i = 1,...,n-1 \tag{2.11}$$

is equivalent to the first-order replicator equation (2.5) on $S_n \setminus \{\mathbf{x}: x_n = 0\}$ with $a_{ij} = b_{ij} - b_{in}$.

$$x_i = \frac{y_i}{\sum\limits_{j=1}^{n} y_j}, \quad i = 1,...,n \tag{2.12}$$

and $y_n \equiv 1$. The barycentric transformation (2.12), together with a change in velocity, maps the orbits of (2.11) into the orbits of (2.5). Which of these equations is more convenient will depend on the problem considered. Similar results hold for interactions of order higher than linear.

Sexually reproducing organisms are not replicators in the strict sense of the term, but within ecological considerations and disregarding genotypes they may be viewed as such.

3. GENERAL PROPERTIES

The term Φ in (1.3) guarantees that the continuous-time replicator equation (1.1) "lives" on S_n, since $(\sum x_i)^{\bullet} = 0$ on S_n. Thus the simplex and all its faces (which consist of subsimplices characterized by $x_i = 0$ for all i in some non-trivial subset J of $\{1,...,n\}$) are invariant. In particular, the "corners" e_i are equilibria. The solutions of (1.1) in S_n are defined for all $t \in \mathbb{R}$.

For the discrete-time replicator equation (1.2) to have any meaning, the term Φ must be non-vanishing on S_n. It always has the same sign, and we shall assume that the $f_i(x)$ are also of this sign, say positive. In this case the simplex and all of its faces are once again invariant.

If a continuous- or discrete-time replicator equation is restricted to a face of S_n the resulting equation is again of replicator type.

We shall say that two vector fields f and g on S_n are *equivalent* if there exists a function $c : S_n \to \mathbb{R}$ such that $f_i(x) - g_i(x) = c(x)$ holds on S_n for all i. If f and g are equivalent then the restrictions $\dot{x}_i = x_i(f_i(x) - \Phi)$ and $\dot{x}_i = x_i(g_i(x) - \Phi)$ coincide on S_n. In the same way, if there exists a function $c : S_n \to \mathbb{R}^+$ such that $f_i(x) = c(x)g_i(x)$ holds on S_n for all i, then the difference equations $x \to Tx$ with $(Tx)_i = x_i f_i(x)\Phi^{-1}$ and $(Tx)_i = x_i g_i(x)\Phi^{-1}$ coincide on S_n.

In particular, we say that $n \times n$ matrices A and B are equivalent if the vector fields Ax and Bx are equivalent in the sense described above. This is the case iff there exist constants c_j such that $a_{ij} - b_{ij} = c_j$ for all i and j. Equivalent matrices lead to identical first-order replicator equations. Thus, without loss of generality, we may consider only matrices with zeros in the diagonal, for example, or matrices whose first row vanishes.

Another useful property is the quotient rule

$$\left[\frac{x_i}{x_j}\right]^{\bullet} = \left[\frac{x_i}{x_j}\right](f_i(x) - f_j(x)) \tag{3.1}$$

or, in the discrete case,

$$\frac{(Tx)_i}{(Tx)_j} = \left[\frac{x_i}{x_j}\right]\left[\frac{f_i}{f_j}\right] \tag{3.2}$$

for $x_j > 0$.

Losert and Akin (1983) have shown that the discrete-time first-order replicator equation induces a diffeomorphism from S_n into itself. This result is important because it excludes the "chaotic" behavior caused by the non-injectivity of mappings such as $x \rightarrow ax(1-x)$. However, the discrete case is still far less well-understood than the continuous one, and may behave in quite a different way.

4. EQUILIBRIA AND THEIR STABILITY

The fixed points of (1.1) or (1.2) in the interior of S_n are the strictly positive solutions of

$$f_1(\mathbf{x}) = \cdots = f_n(\mathbf{x}) \tag{4.1}$$

and

$$x_1 + \cdots + x_n = 1 \quad . \tag{4.2}$$

If (4.1) holds, the common value is Φ. Similarly, the equilibria in the interior of a face defined by $x_i = 0$ for some $i \in \{1,...,n\}$ are the strictly positive solutions of the analogous equations.

In particular, the inner equilibria of first-order replicator equations are the strictly positive solutions of the linear equations (4.2) and

$$\sum a_{1j} x_j = \sum a_{2j} x_j = \cdots = \sum a_{nj} x_j \quad . \tag{4.3}$$

These solution form a linear manifold. Generically, there is either one or no interior equilibrium. In fact there is an open dense subset of $n \times n$ matrices such that the corresponding replicator equations admit at most one fixed point in the interior of S_n and in the interior of each face (Zeeman, 1980).

In many cases it is easy to perform a local analysis around a fixed point $\mathbf{p}$ by computing the eigenvalues of its Jacobian. One such eigenvalue is $\Phi(\mathbf{p})$; this corresponds to an eigenvector $\mathbf{p}$ which is not in the tangent space. Since we are studying the restriction of (1.1) to S_n, this eigenvalue (or more precisely, one of its multiplicities) is irrelevant. Thus, for example, the relevant eigenvalues of a corner $\mathbf{e}_i$ are the $n-1$ values of $a_{ij} - a_{ii}$ $(j \neq i)$.

For the hypercycle (2.7) there is always a unique fixed point $\mathbf{p}$ in int S_n, which is given by

$$p_i = \frac{k_i^{-1}}{\sum k_j^{-1}}$$

and the eigenvalues of the Jacobian at $\mathbf{p}$ are (up to a positive factor) the n-th roots of unity, except for 1 itself (see Schuster et al., 1980). It follows that $\mathbf{p}$ is asymptotically stable for $n \le 3$, and unstable for $n \ge 5$. In fact, using Πx_i as a Ljapunov function, it can be shown that $\mathbf{p}$ is globally stable for $n \le 4$. For $n \ge 5$, numerical computations show that a periodic attractor exists, although this has not been proved rigorously.

Linearization around the inner equilibrium of (1.1) allows the use of the Hopf bifurcation technique. Zeeman (1980) has shown that for $n = 3$ such bifurcations are degenerate and do not lead to periodic attractors. In fact, the equivalence of (2.5), for $n = 3$, with the two-dimensional Lotka–Volterra equation (2.11) implies that it admits no isolated periodic orbit. For $n \ge 4$, however, there exist nondegenerate Hopf bifurcations, the simplest of which is given by

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

which, for $\mu = 0$, reduces to the hypercycle equation with globally stable interior equilibrium (see Hofbauer et al., 1980). De Carvalho (1984) refined this by showing that for small $\mu > 0$, the periodic orbit is globally attracting in int S_n, except for the stable manifold of the inner equilibrium.

If there is no fixed interior point, then there exists a $\mathbf{c} \in \mathbb{R}^n$ with $\sum c_i = 0$ such that the function $\Pi x_i^{c_i}$ (which is defined on int S_n) increases along the orbits of (2.5) (Hofbauer, 1981b). It follows from Ljapunov's theorem that each orbit $\mathbf{x}(t)$ in the interior of S_n has its ω limit

$$\omega(\mathbf{x}) = \{\mathbf{y} \in S_n : \exists\, t_n \to +\infty \text{ with } \mathbf{x}(t_n) \to \mathbf{y}\}$$

contained in the boundary of S_n. This implies that there are no periodic, or recurrent, or even non-wandering points in int S_n if there is no fixed inner point. However, this does not mean that $\lim_{t \to +\infty} x_i(t) = 0$ for some i. Akin and Hofbauer (1982) give an example, with $n = 4$, where the ω limit of every interior orbit is a "cycle" consisting of the corners $\mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3, \mathbf{e}_4$ and the edges joining them.

Conversely, if the orbit $\mathbf{x}(t)$ is periodic in int S_n or, more generally, has its ω limit in int S_n, then the time averages of this orbit

$$\lim_{T \to +\infty} \frac{1}{T} \int_0^T x_i(t)\,\mathrm{d}t, \quad i = 1,...,n \tag{4.4}$$

exist and correspond to an interior equilibrium of (2.5) (see Schuster et al., 1980). It frequently happens that an interior equilibrium is unstable, and hence physically unattainable, but is nevertheless still empirically relevant as a time average.

5. PERMANENCE

It is often very difficult to derive a full description of the attractors of replicator equations. (Recall that strange attractors have been observed numerically (Arneodo et al., 1980), and that there is still no proof of the existence of a unique limit cycle for the hypercycle (2.7) with $n \geq 5$). More modest results may be obtained in such situations by considering only whether the attractors are in the interior or on the boundary.

In particular, we shall say that the replicator equation (1.1) is *permanent* if there is a compact set in int S_n which contains the ω limits of all orbits starting in int S_n (or, equivalently, if there is a $\delta > 0$ such that $\lim_{t \to +\infty} \inf x_i(t) \geq \delta$ for all i, whenever $x_i(0) > 0$ for all i). Such systems are robust in a sense which is obviously of great practical importance in ecology, genetics or chemical kinetics. On the one hand, the state remains bounded at some distance from the boundary even if it oscillates in some regular or irregular fashion: therefore a population (or component) within this system cannot be wiped out by small fluctuations. On the other hand, if the system starts on the boundary, i.e., with one or more components missing, then mutations introducing these components (even if only in tiny quantities) will spread, with the result that the system will soon be safely cushioned away from the faces of the simplex.

We should make two remarks here. Firstly, permanence is not a structurally stable property (in the same way that the asymptotic stability of a fixed point is not necessarily structurally stable). Secondly, a non-permanent system does not always lead to the exclusion of some components. Zeeman (1980) has shown that there is a specific case of (2.5) which has an attractor on the boundary and one in the interior. It can also happen that each interior orbit

remains bounded away from the faces, but by a threshold which depends on the orbit; for permanence, the threshold must be uniform.

The most useful sufficient condition for permanence is the existence of a function P defined on S_n, with $P(\mathbf{x}) > 0$ for $\mathbf{x} \in$ int S_n and $P(\mathbf{x}) = 0$ for $\mathbf{x} \in$ bd S_n, such that $\dot{P} = P\Psi$, where Ψ is a continuous function with the property that, for all $\mathbf{x} \in$ bd S_n, there is some $T > 0$ such that

$$\frac{1}{T}\int_0^T \Psi(\mathbf{x}(t))\,\mathrm{d}t > 0 \quad . \tag{5.1}$$

We shall describe P as an *average Ljapunov function*. Near the boundary, P increases "on average", so that the orbits move away from the boundary (Hofbauer, 1981b).

It has been shown by Schuster et al. (1981) and by Hofbauer (1981b) that the general hypercycle equation (2.6) has $P(\mathbf{x}) = x_1 x_2 \cdots x_n$ as an average Ljapunov function and is therefore permanent. This is of great importance in the realistic design of catalytic hypercycles, whose dynamics are too complex to be represented by (2.7).

Brouwer's fixed point theorem implies that a necessary condition for permanence is the existence of a fixed point in int S_n (Hutson and Vickers, 1983). For permanent first-order replicator equations (2.5), such an equilibrium is necessarily unique. Another very useful condition for the permanence of (2.5) is that the trace of the Jacobian at this fixed point must be strictly negative (Amann and Hofbauer, 1984).

Amann and Hofbauer obtained a remarkable characterization of permanence for systems (2.5) with matrices A of the form

$$\begin{bmatrix} 0 & - & - & \cdot & \cdot & \cdot & + \\ + & 0 & - & \cdot & \cdot & \cdot & - \\ - & + & 0 & \cdot & \cdot & \cdot & - \\ \cdot & & & & & & \\ \cdot & & & & & & \\ \cdot & & & & & & \\ - & - & \cdot & \cdot & \cdot & + & 0 \end{bmatrix} \quad ,$$

where $+$ means that the corresponding element is strictly positive and $-$ means that it is negative or zero. The following conditions are equivalent for equations of this type:

1. The system is permanent.

2. There is a unique inner equilibrium $\mathbf{p}$ and $\Phi(\mathbf{p})$ is strictly positive.

3. There is a vector $\mathbf{z} \in \mathbb{R}_n$, with $z_i > 0$ for all i, such that all components of $\mathbf{z}A$ are strictly positive.

4. The matrix C obtained from A by setting $c_{ij} = a_{i+1,j}$ (taking indices of modulo n), i.e., by moving the first row to the bottom, is such that its determinant and all its principal minors are strictly positive.

Note that $-\Phi(\mathbf{p})$ is just the trace of the Jacobian at $\mathbf{p}$, and that matrices such as C, which have diagonal terms strictly positive and all other terms non-positive, play an important role in mathematical economics.

As a special case we find that the hypercycle equation (2.7) is always permanent. Another special case has been obtained by Zeeman (1980): the replicator equation (2.5) with $n = 3$ and A of the form

$$\begin{vmatrix} 0 & + & - \\ - & 0 & + \\ + & - & 0 \end{vmatrix}$$

is permanent iff $\det A > 0$ (in this case the inner equilibrium is a global attractor). In addition, Amann and Hofbauer (1984) have used the general theorem to characterize permanence in special types of reaction networks, such as hypercycles of autocatalysts:

$$\dot{x} = x_i(a_i x_i + b_{i-1} x_{i-1} - \Phi) \tag{5.2}$$

or superpositions of counter-rotating hypercycles:

$$\dot{x}_i = x_i(a_{i-1} x_{i-1} + b_{i+1} x_{i+1} - \Phi) \tag{5.3}$$

$(a_i, b_i > 0)$. Hofbauer (1981b) has also proved that inhomogeneous hypercycles

$$\dot{x}_i = x_i(b_i + a_i x_{i-1} - \Phi) \tag{5.4}$$

with $a_i > 0$, are permanent if they have an interior equilibrium. This was done using $\Pi x_i^{a_i^{-1}}$ as an average Ljapunov function. More generally, Hofbauer conjectures that (2.5) is permanent iff for some $\mathbf{p}$ with $p_i > 0$, the function $\Pi x_i^{p_i}$ is an average Ljapunov function or, equivalently, iff for such a $\mathbf{p}$ the inequality $\mathbf{p} \cdot A\mathbf{x} > \mathbf{x} \cdot A\mathbf{x}$ holds for all fixed points $\mathbf{x}$ in bd S_n. This was proved by Amann (1984) for the case $n = 4$.

It can be shown that a necessary condition for the permanence of first-order replicator equations with $a_{ij} \geq 0$ is that an irreducible graph is obtained on drawing an arrow from j to i wherever $a_{ij} > 0$, i.e., that any two vertices can be joined by an oriented graph (see Sigmund and Schuster, 1984). It would be interesting to know if such a graph is necessarily Hamiltonian, i.e., contains a closed oriented path visiting each vertex exactly once. (This has been shown by Amann (1984) for the case $n \leq 4$ and $a_{ii} = 0$.)

An interesting class of examples is provided by models describing the competition between several hypercycles. If these hypercycles are disjoint then the equation is of the form

$$\dot{x}_i = x_i(k_i x_{\pi(i)} - \Phi) \ . \tag{5.5}$$

where π is a permutation of indices containing several cycles. Such systems are not irreducible and hence not permanent. If the cycles are all of length less than 4, then one of them "wins out" and the others vanish (see Schuster et al., 1980). This is probably also true for larger cycles, but has not yet been proven.

Once again, the situation is much less clear in the case of discrete-time replicator equations. A sufficient condition analogous to the existence of an average Ljapunov function has been given by Hutson and Moran (1982). Hofbauer (1984) has shown that the discrete hypercycle

$$(T\mathbf{x})_i = x_i \left[\frac{k_i x_{i-1} + C}{\Phi} \right] \tag{5.6}$$

(with $k_i > 0$) is permanent iff $C > 0$.

6. GRADIENT SYSTEMS OF REPLICATOR TYPE

The evolutionary dynamics defined by the gradients of certain potential functions are of great interest because they correspond to popular notions of adaptive genotypic or phenotypic landscapes and yield biological models with extremum principles of a type familiar in theoretical physics. The action of selection in such situations drives the state uphill along the path of steepest ascent.

Gradients depend on metrics. Shahshahani (1979) provided a geometric framework for population dynamics by using a Riemann metric instead of the more usual Euclidean metric on S_n. Replicator equations which are gradients with respect to this metric are of considerable interest (see Akin, 1979).

Shahshahani defines the inner product of two vectors $\mathbf{x}$ and $\mathbf{y}$ in the tangent space $T_{\mathbf{p}}S_n$ (where $\mathbf{p} \in \text{int } S_n$) in the following way:

$$\langle \mathbf{x},\mathbf{y} \rangle_p = \sum \frac{1}{p_i} x_i y_i \quad .$$

This introduces a notion of orthogonality which depends on $\mathbf{p}$, and a definition of distance which differs from the Euclidean distance by attaching more weight to changes occurring near the boundary of S_n. If V is a differentiable function defined in a neighborhood of $\mathbf{p}$, then the Shahshahani gradient Grad $V(\mathbf{p})$ is defined by

$$\langle \text{Grad } V(\mathbf{p}),\mathbf{y} \rangle_{\mathbf{p}} = DV(\mathbf{p})(\mathbf{y}) \tag{6.1}$$

for all $\mathbf{y} \in T_p S_n$, where $DV(\mathbf{p})$ is the derivative of V at $\mathbf{p}$. The more usual Euclidean gradient grad $V(\mathbf{p})$ is defined by

$$\text{grad } V(\mathbf{p}) \cdot \mathbf{y} = DV(\mathbf{p})(\mathbf{y}) \quad . \tag{6.2}$$

Using the fact that $\mathbf{y} \in T_{\mathbf{p}}S_n$ iff $\mathbf{y} \in \mathbb{R}_n$ satisfies $\sum y_i = 0$, it can be shown that the replicator equation (1.1) is a Shahshahani gradient of V iff $\mathbf{f}$ is equivalent to grad V, in the sense outlined in Section 3.

The case where V is a homogeneous function of degree s is of particular interest, since this implies that $\Phi(\mathbf{x}) = sV(\mathbf{x})$, from Euler's theorem. The average fitness Φ then grows at the largest possible rate and the orbits are "orthogonal" (in the Shahshahani sense) to the constant level sets of Φ.

In particular, if we have

$$V(\mathbf{x}) = \sum a_i x_i \tag{6.3}$$

then the Shahshahani gradient is $x_i(a_i - \Phi)$, i.e., (2.4). If, however, we have

$$V(\mathbf{x}) = \tfrac{1}{2} \sum_{ij} a_{ij} x_i x_j \quad . \tag{6.4}$$

where $a_{ij} = a_{ji}$, then the Shahshahani gradient is the selection equation (2.2). The corresponding extremum principles, which give conditions for the average fitness Φ to increase at the largest possible rate, have been stated by Küppers (1979) and Kimura (1958), respectively. However, they did not specify the appropriate metric. The fact that Φ increases along the orbits of (2.2) is Fisher's Fundamental Theorem of Natural Selection.

An immediate consequence of Fisher's theorem is that the orbits of (2.2) converge to the set of equilibria. In addition, each orbit converges to some equilibrium. This has been proved by Akin and Hofbauer (1982), who once again used a Ljapunov function of type $\Pi x_i^{p_i}$. Analogous results also hold for discrete-time selection equations, but are considerable harder to establish — they have been proven by an der Heiden (1975) for the case $n = 3$ and by Losert and Akin (1983) in the general case. It would be interesting to know whether this convergence holds whenever f is the Euclidean gradient of a homogeneous function.

First-order replicator equations (2.5) are Shahshahani gradients iff

$$a_{ij} + a_{jk} + a_{ki} = a_{ji} + a_{ik} + a_{kj} \tag{6.5}$$

holds for all indices i, j and k (Sigmund, 1984). This is the case iff the matrix A is equivalent (in the sense described in Section 3) to a symmetric matrix, or equivalently, iff there are constants c_i such that $a_{ij} - a_{ji} = c_i - c_j$ holds for all i and j.

Equations of the type

$$\dot{x}_i = x_i(g_i(x_i) - \Phi) \tag{6.6}$$

are obviously Shahshahani gradients. If the functions g_i are monotonically decreasing, they model competition between replicators which inhibit their own growth but are otherwise independent. In this case it can be shown that there exists a unique global attractor. More precisely, we can assume without loss of generality that $g_1(0) \geq g_2(0) \geq \cdots \geq g_n(0) > 0$, in which case there exists a number K and a $p \in S_n$ such that

$$g_1(p_1) = \cdots = g_m(p_m) = K \tag{6.7}$$

$$p_1 > 0, \ldots, p_m > 0, \quad p_{m+1} = 0, \ldots, p_n = 0 \quad . \tag{6.8}$$

where m is the largest integer j with $g_j(0) > K$. The point $\mathbf{p}$ is the limit, as t approaches $+\infty$, of all orbits $\mathbf{x}(t)$ for which $x_i(0) > 0$, $i = 1,...,m$. A variant of this model shows that if the total concentration $\sum x_i$ is kept at a constant value c (not necessarily equal to 1) by replacing Φ by Φ/c, then the number of species that can coexist increases with increasing c (see Hofbauer et al., 1981). The special cases

$$g_i(x_i) = a_i - b_i x_i \quad \text{and} \quad g_i(x_i) = \frac{1}{c_i + d_i x_i} \tag{6.9}$$

have been studied by Epstein (1979).

7. CLASSIFICATION

Except in low-dimensional cases, there is little hope of obtaining a complete classification of first-order replicator equations (2.5) up to topological equivalence. Two such equations are said to be topologically equivalent if there exists a homeomorphism from S_n onto itself which maps the orbits of one equation onto the orbits of the other equation in such a way that orientation is preserved. Two $n \times n$ matrices are described as R-equivalent if the corresponding replicator equations are topologically equivalent.

Zeeman (1980) proposed a method for the classification of stable cases. By analogy to the definition of structural stability, an $n \times n$ matrix A is said to be stable if its R-equivalence class is a neighborhood of A. Thus small perturbations of A do not change the topological structure of the corresponding replicator equation. Zeeman conjectured that the stable matrices form an open dense set in the space of $n \times n$ matrices and are divided into a finite number of R-equivalence classes for each n. He proved this for $n = 2$ and 3, and classified all corresponding stable replicator equations. (For $n = 2$ and 3 there are 2 and 19 stable classes, respectively, up to time reversal.)

A basic requirement for the classification of (2.5) for $n = 3$ is that there are no limit cycles. This is a consequence of the corresponding result for two-dimensional Lotka–Volterra equations (see, e.g., Coppel, 1966) and of the equivalence between such equations and first-order replicator equations (Hofbauer, 1980a). Bomze (1983) extended Zeeman's classification to cover unstable cases, obtaining 102 types of phase portraits up to time reversal.

Little is known about stable matrices for higher dimensions, apart from the fact that stability implies that all fixed points of (2.5) are hyperbolic (the real

parts of the eigenvalues of their Jacobians do not vanish). This was proved by de Carvalho (1984).

Recall that, without loss of generality, the diagonal of a matrix may be assumed to contain only zeros. Let Z_n denote the class of such matrices with non-zero off-diagonal terms. Two matrices A and B in Z_n are said to be *sign equivalent* if the corresponding off-diagonal terms have the same sign, and *combinatorially equivalent* if A can be made sign equivalent to B by permuting the indices. Zeeman (1980) showed that A and B are combinatorially equivalent iff the equations obtained by restricting the corresponding replicator equations to the edges of S_n are topologically equivalent. Within Z_n, R-equivalence classes are refinements of the combinatorial classes. There are 10 such combinatorial classes for $n = 2$ and 114 for $n = 3$ up to sign reversal (Zeeman, 1980). De Carvalho (1984) has studied 19 combinatorial classes without inner equilibria as a first step towards a classification of R-stable matrices for $n = 4$. Another step in this direction was taken by Amann (1984), who characterized all 4×4 matrices which lead to permanent replicator equations.

Another interesting (although highly degenerate) class of examples is provided by circulant matrices ($a_{ij} = a_{i+1,j+1}$ for all i and j, counting indices modulo n). A partial analysis of this class is given in Hofbauer et al. (1980). It is shown that the center of S_n, i.e., the point **m**, where $m_i = 1/n$, is always an equilibrium; it is not hard to compute the eigenvalues of its Jacobian. If **m** is a sink, then **m** is a global attractor; if **m** is a source, then all orbits converge to the boundary. Non-degenerate Hopf bifurcations occur for $n \geq 4$.

8. CONNECTIONS WITH GAME THEORY

It has often been remarked that game theory is essentially static. However, the replicator equations (2.5) and (2.9) offer dynamic models for normal form games which are symmetric in the sense that both players have the same strategies and the same payoff matrix A. In fact, the dynamic extension is already implicit in the notion of an evolutionarily stable state (Maynard Smith, 1974, 1982), which is a refinement of the concept of a Nash equilibrium.

A point $\mathbf{p} \in S_n$ is said to be evolutionarily stable if it satisfies the following two conditions:

1. Equilibrium condition:

$$p \cdot A p \geq x \cdot A p \quad \text{for all} \quad x \in S_n \tag{8.1}$$

2. Stability condition:

$$\text{if} \quad p \cdot A p = x \cdot A p \quad \text{for} \quad x \neq p, \quad \text{then} \quad p \cdot A x > x \cdot A x \quad . \tag{8.2}$$

A game can have zero, one or several evolutionarily stable points. As shown by Selten (1984), the notion is not structurally stable: some matrices which yield evolutionarily stable points can be perturbed into matrices which do not. In this context we also refer the reader to Bomze (1984) for a thorough analysis of the relation of evolutionary stability to the multitude of equilibrium concepts used in game theory.

It can be shown that the following four conditions are equivalent (see Hofbauer et al., 1979; Zeeman, 1980):

(i)   p is evolutionarily stable

(ii) for all $q \in S_n$ with $q \neq p$, we have

$$p \cdot A((1-\varepsilon)p + \varepsilon q) > q \cdot A((1-\varepsilon)p + \varepsilon q) \tag{8.3}$$

      provided that $\varepsilon > 0$ is sufficiently small

(iii) for all $x \neq p$ in some neighborhood of p, we have

$$p \cdot A x > x \cdot A x \tag{8.4}$$

(iv) the function $\Pi x_i^{p_i}$ is a strict local Ljapunov function at p for the replicator equation (2.5), i.e., strictly increasing along all orbits in a neighborhood of p.

Condition (ii) is probably the most intuitively obvious in a biological context: if the state of the population is p, then a fluctuation introducing a small subpopulation in state q eventually gets wiped out, since the p population fares better than the q population against the "mixture" $(1 - \varepsilon)p + \varepsilon q$.

It follows from the equivalence of (i) and (iv) that any evolutionarily stable point p is an asymptotically stable fixed point of (2.5). However, the converse is not true. In particular, (iii) implies that if $p \in \text{int } S_n$ is evolutionarily stable, then it is an attractor for all orbits in int S_n, and hence the unique evolutionarily stable point in S_n; however, Zeeman (1980) has shown that there exist

3×3 games with two asymptotically stable fixed points, one in the interior and the other on the boundary of S_n.

Akin (1980) has shown that (2.5) has no fixed point in int S_n iff there exist two strategies x and y in S_n such that x dominates y in the sense that

$$x \cdot Az > y \cdot Az$$

for all $z \in$ int S_n. This result is supplemented by precise statements concerning the support of strategies x and y and the form of global Ljapunov functions or invariants of motion for (2.5).

The results obtained using the time averages (4.4) described in Section 4 suggest a computational method for finding equilibria (and hence solutions) of normal form games. These results, which can easily be extended to asymmetric games (i.e., games in which the players have different payoff matrices), should be compared with the classical methods (involving differential equations) for finding the solutions of games (see, e.g., Luce and Raiffa, 1957, p. 438).

The discrete analogues of such methods involve iterative procedures. It turns out, however, that discrete-time replicator equations of type (2.9) do not seem to lend themselves very well to game dynamics; in particular, an evolutionarily stable point need not be asymptotically stable for (2.9) (see, e.g., Schuster and Sigmund, 1984).

The behavior of (2.5) and (2.9) for zero-sum games ($a_{ij} = -a_{ji}$) is analyzed in Akin and Losert (1984). If an interior equilibrium exists, then the continuous model (2.5) has an invariant of motion. The equilibrium is stable, but not asymptotically stable, and all non-equilibrium orbits of (2.5) in int S_n have ω limits in int S_n but do not converge to an equilibrium. By contrast, if the discrete time model (2.9) has an interior equilibrium then it is unstable and all non-equilibrium orbits converge to the boundary. If there is no inner equilibrium, then all orbits converge to the boundary in both discrete and continuous cases. In the discrete case all possible attractors may be described using the notion of chain recurrence.

REFERENCES

Akin, E. (1979). The geometry of population genetics. *Lecture Notes in Biomathematics* 31. Springer-Verlag, Berlin, Heidelberg and New York.

Akin, E. (1980). Domination or equilibrium. *Math. Biosciences* 50: 239–250.

Akin, E. and J. Hofbauer (1982). Recurrence of the unfit. *Math. Biosciences* 61: 51–63.

Akin, E. and V. Losert (1984). Evolutionary dynamics of zero-sum games. To appear in *J. Math. Biology*.

Amann, E. (1984). Permanence for catalytic networks. Dissertation, University of Vienna.

Amann, E. and J. Hofbauer (1984). Permanence in Lotka–Volterra and replicator equations. Forthcoming.

Arneodo, A., P. Coullet and C. Tressor (1980). Occurrence of strange attractors in three-dimensional Volterra equations. *Physics Letters* 79A: 259–263.

Bishop, T. and C. Cannings (1978). A generalized war of attrition. *J. Theor. Biology* 70: 85–124.

Bomze, I. (1983). Lotka–Volterra equations and replicator dynamics: a two-dimensional classification. *Biol. Cybernetics* 48: 201–211.

Bomze, I. (1984). Non-cooperative two-person games in biology: symmetric contests. Forthcoming.

Bomze, I., P. Schuster and K. Sigmund (1983). The role of Mendelian genetics in strategic models on animal behavior. *J. Theor. Biology* 101: 19–38.

Coppel, W. (1966). A survey of quadratic systems. *J. Diff. Eqns.* 2: 293–304.

Dawkins, R. (1982). *The Extended Phenotype*. Freeman, Oxford and San Francisco.

De Carvalho, M. (1984). Dynamical systems and game theory. Ph.D. Thesis, University of Warwick.

Eigen, M. (1971). Self-organization of matter and the evolution of biological macromolecules. *Die Naturwissenschaften* 58: 465–523.

Eigen, M. and P. Schuster (1979). *The Hypercycle: A Principle of Natural Self-Organization*. Springer-Verlag, Berlin and Heidelberg.

Epstein, M. (1979). Competitive coexistence of self-reproducing macromolecules. *J. Theor. Biology* 78: 271–298.

Eshel, I. (1982). Evolutionarily stable strategies and natural selection in Mendelian populations. *Theor. Pop. Biol.* 21: 204–217.

Ewens, W.J. (1979). *Mathematical Population Genetics*. Springer-Verlag, Berlin, Heidelberg and New York.

an der Heiden, U. (1975). On manifolds of equilibria in the selection model for multiple alleles. *J. Math. Biol.* 1: 321–330.

Hines, G. (1980). An evolutionarily stable strategy model for randomly mating diploid populations. *J. Theor. Biology* 87: 379–384.

Hofbauer, J. (1981a). On the occurrence of limit cycles in the Volterra–Lotka equation. *Nonlinear Analysis* IMA 5: 1003–1007.

Hofbauer, J. (1981b). A general cooperation theorem for hypercycles. *Monatsh. Math.* 91: 233–240.

Hofbauer, J. (1984). A difference equation model for the hypercycle. *SIAM J. Appl. Math.*, forthcoming.

Hofbauer, J., P. Schuster and K. Sigmund (1979). A note on evolutionarily stable strategies and game dynamics. *J. Theor. Biology* 81: 609–612.

Hofbauer, J., P. Schuster and K. Sigmund (1981). Competition and cooperation in catalytic self-replication. *J. Math. Biol.* 11: 155–168.

Hofbauer, J., P. Schuster and K. Sigmund (1982). Game dynamics for Mendelian populations. *Biol. Cybern.* 43: 51–57.

Hofbauer, J., P. Schuster, K. Sigmund and R. Wolff (1980). Dynamical systems

under constant organization. Part 2: Homogeneous growth functions of degree 2. *SIAM J. Appl. Math.* 38: 282–304.

Hutson, V. and W. Moran (1982). Persistence of species obeying difference equations. *J. Math. Biol.* 15: 203–213.

Hutson, V. and C.T. Vickers (1983). A criterion for permanent coexistence of species, with an application to a two-prey/one-predator system. *Math. Biosci.* 63: 253–269.

Kimura, M. (1958). On the change of population fitness by natural selection. *Heredity* 12: 145–167.

Küppers, B.O. (1979). Some remarks on the dynamics of molecular self-organization. *Bull. Math. Biol.* 41: 803–809.

Losert, V. and E. Akin (1983). Dynamics of games and genes: discrete versus continuous time. *J. Math. Biol.* 17: 241–251.

Luce, R. and H. Raiffa (1957). *Games and Decisions.* John Wiley, New York.

Maynard Smith, J. (1974). The theory of games and the evolution of animal conflicts. *J. Theor. Biology* 47: 209–221.

Maynard Smith, J. (1981). Will a sexual population evolve to an ESS? *Amer. Naturalist* 177: 1015–1018.

Maynard Smith, J. (1982). *Evolutionary Game Theory.* Cambridge University Press, Cambridge.

Pollak, E. (1979). Some models of genetic selection. *Biometrics* 35: 119–137.

Schuster, P. and K. Sigmund (1983). Replicator dynamics. *J. Theor. Biology* 100: 535–538.

Schuster, P. and K. Sigmund (1984). Towards a dynamics of social behavior: strategic and genetic models for the evolution of animal conflicts. *J. Soc. Biol. Structures,* forthcoming.

Schuster, P., K. Sigmund, J. Hofbauer and R. Wolff (1981). Self-regulation of behavior in animal societies. Part 1: Symmetric contests. *Biol. Cybern.* 40: 1–8.

Schuster, P., K. Sigmund and R. Wolff (1979). Dynamical systems under constant organization. Part 3: Cooperative and competitive behavior of hypercycles. *J. Diff. Eqns.* 32: 357–368.

Schuster, P., K. Sigmund and R. Wolff (1980). Mass action kinetics of self-replication in flow reactors. *J. Math. Anal. Appl.* 78: 88–112.

Shahshahani, S. (1979). A new mathematical framework for the study of linkage and selection. *Memoirs* AMS 211.

Selten, R. (1984). Evolutionary stability in extensive two-person games. *Math. Soc. Sciences,* forthcoming.

Sigmund, K. (1984). The maximum principle for replicator equations. Working Paper WP-84-56, International Institute for Applied Systems Analysis, Laxenburg, Austria.

Sigmund, K. and P. Schuster (1984). Permanence and uninvadability for deterministic population models. In P. Schuster (Ed.), *Stochastic Phenomena and Chaotic Behavior in Complex Systems.* Springer-Verlag, Berlin, Heidelberg and New York.

Taylor, P. and L. Jonker (1978). Evolutionarily stable strategies and game dynamics. *Math. Biosciences* 40: 145–156.

Zeeman, E.C. (1980). Population dynamics from game theory. In *Global Theory of Dynamical Systems,* Lecture Notes in Mathematics 819. Springer-Verlag, Berlin, Heidelberg and New York.

Zeeman, E.C. (1981). Dynamics of the evolution of animal conflicts. *J. Theor. Biology* 89: 249–270.