The Probability of Permanence

By

Peter F. Stadler[a,b,*] and Robert Happel[a]

[a]Institut für Theoretische Chemie der Universität Wien

Währingerstraße 17, A-1090 Wien, Austria

[b]Max Planck Institut für Biopysikalische Chemie

080 Biochemische Kinetik

Am Faßberg, D-3400 Göttingen, Germany

[*]Correspondence to: Peter F. Stadler

Institut für Theoretische Chemie, Universität Wien

Währingerstraße 17, A-1090 Wien, Austria

Phone: ** 43 1 - 43 61 41 / 78

Fax: ** 43 1 - 40 28 525

Email: A8443GAD@AWIUNI11.bitnet or studla@tiger.itc.univie.ac.at

Abstract

Numerical experiments suggest that cooperation is a very rare phenomenon in autocatalytic networks with more than some 5 interacting species. There is strong evidence that the probability for a cooperative behaviour in random networks decreases at least exponentially and at most as a^{n^2} with the number n of interacting species.

The evolution of larger persistent networks by subsequent incorporation of additional species into a cooperative network is shown to be even less probable. This leads to the conclusion that hypercycle-type interactions alone are not sufficient to maintain the genetic information of more than a few interacting species in a pure RNA world.

1. Introduction

The replicator equation has become the standard continuous time model for natural selection in the past ten years [22,35]. It turned out however, that the dynamics of this simple-looking nonlinear ODE are much too complicated to allow for a complete classification of the dynamical behaviour except for the lowest dimensional cases $n = 2$ and 3 [4,7,39]. For instance, chaos can be found in a four species community [32].

On the other hand a very detailed analysis is not essential from the biological point of view; one is much more interested whether all species in a given network of interacting species will persist or not. Hofbauer, Schuster and Sigmund [19] introduced the notion of *permanence* in order to cope with this problem. Permanence means coexistence irrespective of the initial conditions. The most prominent example for such a behaviour is the Hypercycle [6,7]. Only in very special cases one can find globally asymptotically stable rest points [13].

It will be shown in this contribution that coexistence is a very rare event in complex networks governed by a second order replicator equation

$$\dot{x}_k = x_k[(Ax)_k - (xAx)] \quad k = 1, \ldots, n$$

with more than $n = 5$ species. Permanence in such a model may be regarded as hypercycle-type behaviour. In three species and particular types of four species models cooperative behaviour is quite common [8,9,10,28,29]. We expect the results of this contribution to carry over also to some models of selection which are closely related to second order replicator equations [18,20,37,38]. We remark, that continuous time models including mutation are permanent by construction [40].

2. Characterization of Permanence

Let S be a closed subset of $\mathbb{R}^n$ and let $f : S \to \mathbb{R}^n$ be such that the solutions $x(t) \in S$ of the initial value problem

$$\dot{x} = f(x), \quad x(0) = x_0 \tag{1}$$

is unique and defined for all $t \geq 0$.

Definition. The dynamical system (1) is called *permanent*, if all orbits are uniformly bounded and there is a compact set C entirely contained in the interior of S, such that for all $x \in \operatorname{int} S$ holds

$$\omega(x) \in C \tag{2}$$

An equivalent formulation for both bounded and unbounded state spaces is the following

Theorem 1. (Hofbauer and Sigmund [33]) The dynamical system (1) is permanent iff there is a $\delta > 0$ and a $M > 0$ such that for all initial conditions $x \in \operatorname{int} S$ holds

$$\begin{aligned} \lim_{t\to\infty} \inf \operatorname{dist}(x(t), \partial S) > \delta \\ \lim_{t\to\infty} \sup |x(t)| < M \end{aligned} \tag{3}$$

If the statespace S is compact, the second condition – uniform boundedness of the orbits – is always satisfied.

We remark that one obtains the definition of *(strong) persistence* for $\delta \to 0$ in equ.(3). [9,41].

Thus far there is only one necessary and sufficient condition for permanence.

Definition. Let $P : S \to \mathbb{R}$ be a nonnegative function, strictly positive in $\operatorname{int} S$ and vanishing on ∂S. Furthermore, suppose that there is a lower semicontinuous function $\Psi : S \to \mathbb{R}$ such that the following conditions hold

(i) For all $x \in \operatorname{int} S$ we have

$$\dot{P}(x) = P(x)\Psi(x) \tag{4}$$

(ii) For all $x \in \partial S$ we have for some $T > 1$

$$\frac{1}{T}\int_0^T \Psi(x(t))dt > 0 \tag{5}$$

Then P is an *Average Ljapunov Function* for the differential equation (1).

Theorem 2. Suppose all orbits are uniformely bounded. Then the dynamical system (1) is permanent iff it admits an Average Ljapunov Function. That existence of an Average Ljapunov Function implies permanence has been shown by Hofbauer [15], the converse is due to Hutson [24]. It has been shown [23] that it is sufficient to require condition (4) for all points in ω-limits on ∂S only.

As a consequence of Brower's fixed point theorem it has been shown that if the dynamical system (1) in permanent then there is a rest point in the interior of S [25].

3. Permanence for Second Order Replicator Equations

In this paper we restrict attention to the following two types of ordinary differential equations:

$$\dot{x}_k = x_k\big[f_k(x) - \sum_{j=1}^{n} x_j f_j(x)\big] \tag{R}$$

$$\dot{y}_k = y_k\varphi_k(x) \tag{E}$$

The *replicator equation* (R) [35] is defined on the *simplex*

$$S_n = \{x \in \mathbb{R}^n_+ | \sum_{j=1}^{n} x_j = 1\}$$

whereas the *ecological equation* (E) — also known as Kolmogorov system — is defined on the *positive orthant* $\mathbb{R}^n_+$. Note that the simplex S_n is $n-1$-dimensional. The ecological and the replicator equation are closely related to each other. Let $\bar{F}_{\{n\}}$ be the face of S_n defined by $x_n = 0$. Let us now investigate the following transfomation:

$$\begin{aligned}
\mathcal{H}: &\quad S_n \setminus \bar{F}_{\{n\}} \to \mathbb{R}^{n-1}_+ : \quad & y_k &= \frac{x_k}{x_n} \qquad k < n \\
\mathcal{H}^{-1}: &\quad \mathbb{R}^n_+ \to S_{n+1} \setminus \bar{F}_{\{n+1\}} : \quad & x_k &= \frac{y_k}{1+\sum_{j=1}^n y_j}, \\
& & x_{n+1} &= \frac{1}{1+\sum_{j=1}^n y_j}
\end{aligned} \tag{6}$$

This diffeomorphism has originally been used by J. Hofbauer [16] to show flow equivalence between the second order replicator equation

$$\dot{x}_k = x_k\big[(Ax)_k - (xAx)\big], \quad k = 1, \dots, n \tag{SR}$$

and the Lotka-Volterra-Equation

$$\dot{y}_k = y_k\big[r_k + (By)_k\big], \qquad k = 1, \dots, n-1. \tag{LV}$$

The transformation allows us more generally to obtain an ODE of the form (E) from any ODE of the form (R) via

$$\varphi_k(y) := f_k\big(\frac{1}{1+\sum_j y_j}(y,1)\big) - f_n\big(\frac{1}{1+\sum_j y_j}(y,1)\big) \tag{7}$$

and *vice versa*.

We will use the notation F_K for the interior of the faces of S_n or $\mathbb{R}^n_+$ defined by $x_k = 0$ for $x \in S_n$ (or $y_k = 0$ for $y \in \mathbb{R}^n_+$, resp.) if and only if $k \in K$.

Jansen [26] proved a sufficient condition for permanence of second order replicator equations (SR) and Lotka-Volterra Equations (LV) based on the Average Ljapunov Function

$$\mathcal{P}(x) = \prod_{j=1}^{n} x_j^{p_j} \qquad \text{with} \quad p = (p_1, \dots, p_n) \in \operatorname{int} S_n \tag{8}$$

and the following theorem on time averages [42]:

Theorem 3. Let $x(t)$ be a trajectory in $\operatorname{int}\mathbb{R}^n_+$ satisfying condition (3). Then there is a unique restpoint $\hat{y}$ in $\operatorname{int}\mathbb{R}^n_+$ satisfying

$$\hat{y} = \lim_{T\to\infty} \frac{1}{T}\int_0^T y(t)dt \tag{9}$$

An analogous results holds for second order replicator equations [34].

Definition. [17] A rest point of (SR) $\hat{x}^K \in F_K$ is called *saturated* if for all transversal eigenvalues

$$\lambda_k(\hat{x}^K) = [A\hat{x}^K]_k - (\hat{x}^K A\hat{x}^K) \qquad k \in K \tag{10}$$

holds $\lambda_k(\hat{x}^K) \le 0$. Analogously we obtain for Lotka-Volterra systems

$$\lambda_k(\hat{y}^K) = r_k - [A\hat{y}^K] \tag{11}$$

for the transversal eigenvalues of a rest point $\hat{y}^K \in F_K$.

Theorem 4. (Jansen [26]) Let $\hat{x}^K$ denote the isolated rest point of (SR) or (LV) in the interior of the boundary face F_K. In case of (LV) assume additionally that all orbits are uniformly bounded. Then (SR) or (LV) is permanent if there is a vector $p \in \operatorname{int} S_n$ such that for all $\hat{x}^K$ holds

$$\sum_{j \in K} p_j \cdot \lambda_j(\hat{x}^K) > 0. \tag{12}$$

Theorem 3 does not apply to the more general systems (R) or (E). Therefore, there seems to be no way to obtain a pure algebraic condition for permanence for more complicated systems than (SR) and (LV).

The following linear programming algorithm to solve the set of linear inequalities (11) is also due to Jansen [26]:

Theorem 5. Let $\hat{x}^K$ as in theorem 4. The solution of the LP-problem

$$\begin{aligned} &z \to min. \\ &\sum_{j \in K}^{n} p_j \lambda_j(\hat{x}^K) + z > 0 \qquad \forall \hat{x}^K \\ &\sum_{j=1}^{n} p_j = 1 \end{aligned} \tag{13}$$

fulfils one of the following three alternatives

(i) $z_{min} < 0$ and all $p_j > 0$. Then (SR) is permanent.

(ii) $z_{min} < 0$ and some $p_i < 0$. Then (SR) is not permanent.

(iii) $z_{min} \ge 0$. Then the permanence-problem remains undecided.

A matrix A for which (SR) fulfils Jansen's permanence criterion (i) will be referred to as *type-j matrix.*

An analogous result holds for Lotka Volterra systems (LV) with uniformly bounded orbits.

Since the second order replicator equation (SR) is invariant under the transformation

$$a_{ij} \to a_{ij} + b_i \tag{14}$$

with arbitrary constants b_i we may assume the *normal form* $a_{ii} = 0$ without loss of generality.

Except for the existence of an interior equilibrium there are three additional necessary conditions for permanence in second order replicator equations

Theorem 6. (Hofbauer and Sigmund [17,21]) If the dynamical system (SR) is permanent and A is in normal form then the follwing conditions are fulfilled:

(i) There is a unique interior equilibrium $\hat{x} \in \operatorname{int} S_n$

(ii) $\Phi(\hat{x}) = \sum_{j=1}^{n} a_{ij}\hat{x}_i\hat{x}_j > 0$

(iii) $(-1)^{n-1}\det A > 0$.

(iv) There is no regular saturated rest point in ∂S_n.

We will say that a matrix A fulfilling (i) and (ii) is *type-a*, if (iii) also holds we call it *type-b* and if finally all four necessary conditions are fulfilled we call A a *type-c matrix.*

Remark. If A is a type-j matrix, it leads to permanence; thus it is also a type-c matrix. The converse is not true: neither type-j nor type-c is equivalent to permanence.

4. The Probability for Permanence

The above conditions provide an algorithm which does not characterize permanence, not even in the generic cases, but which allows to calculate bounds on the probability for an arbitrary second order replicator network to be permanent.

We assume that the entries in interaction matrices A (in normal form) are random variables with a given probability distribution. The assumption of normal form only implies that there is nothing special with the replication of an entity X with itself as catalyst compared to its replication with the aid of other catalysts. Since the flow of the replicator equation does not change when the r.h.s. of equ.(SR) is multiplied by a positive constant we may assume that the measure for the width of the distribution is unity provided the mean is zero.

Table 1: Probability Densitity functions used in this paper. All calculations have been performed for the replicator model (SR) (column A). The results carry over to Lotka Volterra (LV) models with somewhat different distribution functions of the coefficients (column B).

	A	$B\dagger$
Normal	$\frac{1}{\sqrt{\pi}} \exp -x^2/2$	$\frac{1}{\sqrt{2\pi}} \exp -x^2/4$
Uniform	$\frac{1}{2}$ for $x \in [-1,1]$ 0 otherwise	$1+x/2$ for $x \in [-2,0]$ $1-x/2$ for $x \in [0,2]$ 0 otherwise
Cauchy	$\frac{1}{\pi} \frac{1}{1+x^2}$	$\frac{1}{\pi} \frac{2}{4+x^2}$
Laplace	$\frac{1}{2} \exp -\lvert x\rvert$	

†) off-diagonal elements only. r and the diagonal elements of B have the same distribution as A.

For our numerical survey we use

(i) the Gaussian normal distribution $\mathrm{N}(0;1)$ with mean 0 and variance 1;

(ii) the uniform distribution $\mathrm{U}(-1;1)$ on the interval $[-1,1]$;

(iii) the Cauchy distribution $\mathrm{C}(0;1)$ with zero mean and parameter 1.

(iv) the Laplace distribution $\mathrm{L}(0;1)$ with zero mean and unit parameter.

For each of these distributions we expect the probability to find an interior equilibrium in $\operatorname{int} S_n$ to be

$$\mathrm{prob}\{\hat{x} \in \operatorname{int} S_n\} = 1/2^{n-1} \tag{15}$$

since the replicator equation (SR) is topologically equivalent to a a Lotka Volterra equation in $n-1$ dimensions. To find the interior equilibrium of this differential equation we have to find a solution $By = r$ where the entries in B and r are independent random variables with zero mean. Thus the solution y lies in each orthant with equal probability, i.e. with probability $1/2^{n-1}$.

Table 2: Numerical survey for permanence using 1,000,000 random matrices with zero diagonal. Column (1) and (2) indicate dimension of the matrices and density function. Columns (3) through (7) contain the number of matrices fulfilling criterion (n) and all previous ones. Columns (8) and (9) give the number of undecidable cases and of permanent matrices, resp. (see also fig.1)

(1) n	*(2)* p	*(3)* int. equil.	*(4)* *type a*	*(5)* *type b*	*(6)* *type c*	*(8)* undec.	*(9)* **type j**
2	*th.*	500,000	250,000	250,000	250,000	0	250,000
3	N^1	249,730	125,214	69,926	66,954	0	66,954
	U^2	249,860	124,190	66,520	64,330	0	64,330
	C^2	250,550	126,340	74,670	70.780	0	70,780
	L^2	250,370	123,710	71,220	67,630	0	67,630
4	N^1	124,316	62,408	31,274	16,864	5,334	11,530
	U^1	124,758	62,358	31,458	16,028	5,948	10,080
	C^1	124,984	62,296	31,846	19,022	4,330	14,692
	L	124,642	62,455	31,696	18,098	5,077	13,021
5	N^3	62,192	31,256	15,880	4,492	3,024	1,468
	U^1	62,112	31,222	15,652	4,134	3,030	1,104
	C	62,456	31,327	15,748	5,404	2,685	2,719
	L	62,426	31,381	15,676	4,704	2,921	1,783
6	N	31,159	15,451	7,707	1,075	965	110
	U	31,487	15,735	8,004	1,001	938	63
	C	31,307	15,649	7,819	1,412	1,022	390
	L	31,127	15,647	7,794	1,101	999	156
7	N	15,682	7,826	3,969	280	276	4
	U	15,522	7,731	3,917	234	232	2
	C	15,579	7,826	3,936	396	236	50
	L	15,403	7,721	3,839	290	275	15
8	N	7,832	3,884	1,927	48	48	0
	U	7,785	3,940	1,960	65	65	0
	C	7,770	3,962	2,075	116	109	7
	L	7,636	3,823	1,894	67	67	0
9	N	3,889	1,920	964	11	11	0
	U	4,034	2,046	1,026	8	8	0
	C	3,962	1,966	1,003	18	18	0
	L	3,883	1,931	955	4	4	0
10	N	1,989	993	506	6	6	0
	U	1,942	943	464	4	4	0
	C	1,945	975	487	9	9	0
	L	1,953	987	501	4	4	0

$^{1,2,3)}$ Calculated from smaller sample sizes and multiplied by a factor of $2^{1)}$,$10^{2)}$,$4^{3)}$ in order to facilitate comparison.

Figure 1: Probability for Permanence. The probabilities for an internal equilibrium (dashed line) and the appropriate signs of TrJ (dotted line) and det$A$ (dash-dotted line) are equal for all density functions. The dashed line with narrow spaces gives the average of the probabilities for type-c matrices and the solid line shows the probabilities for type-j matrices for different densitiy functions: Gaussian ($\triangle$), uniform ($\diamondsuit$), Cauchy (+) and Laplace ($\bigcirc$).

Note that because of the flow equivalence pointed out in section 3 our estimates for the probability of permanence also apply to Lotka-Volterra (LV) equations with one dimension less and

$$r_k = a_{kn}, \qquad b_{ij} = a_{ij} - a_{nj} \tag{16}$$

However, the probability distributions are not the same for the elements of A in the replicator equation and for the off-diagonal elements of B in the Lotka-Volterra model. Table 1 lists the density functions used in this contribution.

The probability for the quadratic form xAx and det$A$ to have a certain sign is clearly 1/2. Note that these probabilities need not be independent of the existence of an interior equilibrium. In fact, if there is an interior rest point for $n = 2$, then $xAx > 0$ and $detA < 0$ are equivalent. For larger n, however, these two conditions become more and more independent (*cf.* table 2 and figure 1). The conditions (i), (ii) and (iii) in Theorem 6 are readily checked within polynomial time.

All numerial calculations in this contribution have been performed on IBM 3090 mainframes in Vienna and Göttingen. As programming language FORTRAN has been used and various subroutines (random number generators, solving of linear equations, determinant of a matrix and the simplex algorithm) have been taken from the library package NAGLIB. Our numerical results (table 2) show that

$$\text{Prob}\{\text{A is “type-b”}\} \approx 2^{-(n+1)} \tag{17}$$

for large n.

The probability that there is no saturated rest point on the boundary cannot be estimated easily since the events "rest point $x(K) \in S_n$ " and "x(K) is saturated" are not independent. In fact there is always at least one saturated rest point [22] for the replicator equation (R). Numerical results (tab.2) suggest

$$\text{Prob}\{\text{A is "type-c"}\} \approx 4^{-n} \tag{18}$$

5. Special Types of Interaction Matrices

In this section we investigate two special sign patterns of the interaction matrix. The first class consists of *catalytic networks*[1,2,3,22]: $a_{ij} \geq 0$ for $i \neq j$ and $a_{jj} = 0$. Table 3 lists results for them. We remark that the probability for an arbitrary interaction matrix to be a catalytic network is $2^{-n(n-1)}$.

For small catalytic networks there is an algebraic characterization of permanence. Note that whenever there is an interior equilibrium $\hat{x}$ of (SR) with $A \geq 0$ then $(\hat{x}A\hat{x})$ is strictly positive.

n=2 The network is permanent iff the non-diagonal elements of A are strictly positive.

n=3 The network is permanent iff there is an interior rest point.

n=4 The network is permanent iff A is of "type c".

Catalytic networks have been investigated for two distinct probability distributions, a uniform distribution on the unit interval and an exponential distribution with parameter 1. We find that permanence is a relatively probable property compared to permanence in a sample of random matrices.

The second class consists of *essentially hypercyclic networks*, i.e. matrices which, after a suitable permutation of indices, have the following sign pattern

$$A = \begin{pmatrix} 0 & - & - & \dots & - & + \\ + & 0 & - & \dots & - & - \\ - & + & 0 & \dots & - & - \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ - & - & - & \dots & 0 & - \\ - & - & - & \dots & + & 0 \end{pmatrix} \tag{19}$$

For such matrices permanence can be characterized in terms of M-matrices.

Table 3: Numerical survey for permanence in 100,000 random matrices with zero diagonal and positive non-diagonal entries (catalytic networks). A uniform distribution on the unit-interval, U_+, and an exponential distribution with parameter 1, E, was used. As for table 2, columns (3) through (7) display the numbers of matrices passing subsequent "filters" requiring interior equilibria (3), the correct sign of $\det A$ (4) and the absence (5) of saturated rest points on the boundary of S_n. Columns (6) and (7) show the numbers of permanent and undecidable *type-c* matrices.

(1) n	*(2)* p	*(3)* int. equil.	*(4)* $\det A$	*(5)* sat.bd.	*(6)* undec.	*(7)* **perm.**
2	*th.*	100,000	100,000	100,000	0	100,000
3	U_+	62,615	62,615	62,615	0	62,615
	E	46,070	46,070	46,070	0	46,070
4	U_+	34,403	33,457	33,457	0	33,457
	E	20,785	20,785	18,238	0	18,238
5	U_+	17,577	16,080	16,014	0	16,014
	E	9,781	7,171	6,952	16	6,936
6	U_+	8,746	7,385	7,260	40	7,220
	E	4,612	2,861	2,502	110	2,392
7	U_+	4,391	3,318	3,134	73	3,061
	E	2,257	1,263	921	116	805
8	U_+	2,163	1,429	1,280	87	1,193
	E	1,112	599	332	102	230
9	U_+	1,080	667	499	90	419
	E[1]	560_5	299_5	125	74	51
10	U_+	529	286	175	55	120
	E[1]	285_5	142_5	39	29_5	9_5
11	U_+	279	165	91	40	51
	E[1]	127	65_5	12_5	11_5	1
12	U_+[1]	116_5	57	29	20	9
	E[1]	61_5	31	4	4	0

[1]) calculated from 200,000 matrices

Figure 2: Permanence for Catalytic Networks. The dashed line refers to the probability for an interior rest point, the dash-dotted line accounts for the approriate sign of $\det A$, the dotted line corresponds to the probability of type-c matrices and the solid line refers to the probability of type-j matrices. Data are shown for the uniform distribution $\diamondsuit$ and the exponential distribution $\bigcirc$.

Table 4: Numerical survey for permanence in 100,000 random *essentially hypercyclic* matrices for three different probability distributions of $|a_{ij}|$, $i \neq j$.

(1)	(2)	(3)	(4)	(5)	(6)	(7)
	uniform		*Gaussian*		*exponential*	
n	equil.	perm.	equil.	perm.	equil.	perm.
3	100,000	49,927	100,000	50,219	100,000	49,852
4	70,717	2,706	62,691	4,233	55,622	5,836
5^1	56,715	8_3	43,649	57_7	33,506	229_2
6^1	38,036	0	25,323	0_2	17,097	2_6
7^2	25,430	0	17,097	0	14,423	0

$^{1)}$ calculated from 10^6 matrices.

$^{2)}$ calculated from $3{\cdot}10^5$ matrices.

Figure 3: Permanence for essentially hypercyclic networks. The probability for an interior rest point (dashed line) and for permanence (solid line) shown for Gaussian distribution ($\triangle$), uniform distribution ($\diamondsuit$) and exponential distribution ($\bigcirc$).

Theorem 7. (Amann and Hofbauer [3]) Let A be as in equ.(19). Then the following statements are equivalent:

(i) The second order replicator equation with interaction matrix A is permanent.

(ii) The matrix C obtained by moving the top row of A to the bottom is an M-matrix.

(iii) The second order replicator equation has an interior equilibrium $\hat{x}$ and $(\hat{x}A\hat{x}) > 0$.

For $n = 2$ all essentially hypercyclic systems are permanent. For $n = 3$ there is always an interior equilibrium $\hat{x}$. It is stable iff $\det A$ is positive. With $p_i, n_i > 0$ and thus

$$A = \begin{pmatrix} 0 & -n_1 & p_3 \\ p_1 & 0 & -n_2 \\ -n_3 & p_2 & 0 \end{pmatrix} \tag{20}$$

we find $\det A = p_1p_2p_3 - n_1n_2n_3$. Therefore the replicator equation is permanent with probability 1/2.

Numerical results are shown in table 4. Note that although these matrices are closely related to the paradigm of permanence – the hypercycle – it is extremely unlikely to find cooperative behaviour for $n > 5$ for this type of interaction. The reason for this is the large number of negative entries in A likely to violate condition (ii) of theorem 6.

Note that if A is a *nonpositive* matrix the corresponding network may not be permanent since in this case the quadratic form (xAx) is nonpositive on S_n contradicting condition (ii) of theorem 6.

6. Permanence and Graphs

Definition. Let $A \in \mathbb{R}^{n\times n}$ with zero diagonal. By $A^\ddagger$ we denote the positive part of A, i.e. $a^\ddagger_{ij} = a_{ij}$ if $a_{ij} \geq 0$ and $a^\ddagger_{ij} = 0$ if $a_{ij} < 0$. Let $G(A)$ be the directed graph associated with the nonnegative matrix $A^\ddagger$.

Conjecture. (Jansen) If the second order replicator equation with interaction matrix A in normal form is permanent, then $G(A)$ is strongly connected, i.e. $A^\ddagger$ is irreducible.

This conjecture has been proven for catalytic networks ($A = A^\ddagger$) by Sigmund and Schuster [36]. We tested all permanent and undecidable matrices produced by our simulations for irreducibility. The results are tabulated in tab.5. Indeed, there are no reducible matrices among all the thousands of permanent matrices we produced.

Table 5: Permanence and graphs. Columns (3) through (10) give the probability for finding permanent p (or undecideable u) matrices which contain no Hamiltonian circle (n.h.) or which are reducible (red). Probabilities are given in promille.

(1) n	(2) t	(3) Gaussian n.h.	(4) Gaussian red.	(5) Uniform n.h.	(6) Uniform red.	(7) Cauchy n.h.	(8) Cauchy red.	(9) Laplace n.h.	(10) Laplace red.
2	p	0	0	0	0	0	0	0	0
3	p	0	0	0	0	0	0	0	0
4	p	3.8	0	1.2	0	7.8	0	5.4	0
4	u	16	0	9	0	40	0	25	0
5	p	5	0	2	0	9	0	3	0
5	u	13	0	12	0	37	0	23	0
6	p	–	0	–	0	–	0	6	0
6	u	5	0	2	0	2	0	14	0

A directed graph is said to be *Hamiltonian* if it contains a closed circuit visiting every vertex exactly once. For $G(A)$ this means that the Hypercycle would be a subgraph.

Theorem 8. If a catalytic network with $n \leq 5$ is permanent, then its graph is Hamiltonian.

The above theorem due to Amann [22] motivated us to look for Hamiltonian circles in the graphs $G(A)$ of permanent and undecidable matrices although we did not expect that an analogue to theorem 8 holds for general networks, since for $n \geq 6$ counterexamples are known [1,22].

We find that there are indeed permanent matrices with $n \geq 4$ for which $G(A)$ is not Hamiltonian corresponding to many different graphs even for small n. The overwhelming majority of permanent networks however is Hamiltonian. (*cf.* tab.5).

For $n = 3$ there are only non-robust permanent networks with non-hamiltonian graph. This follows from the classification for $n = 3$ [39]. We thus expect probability 0 for finding such a network.

7. Permanence and Connectivity

Definition. Let $A \in \mathbb{R}^n$ with zero diagonal entries and m be the number of positive entries in A; equivalently m is the number of edges in $G(A)$. We define the *connectivity* of A by

$$\mathcal{C}(A) = \frac{m}{n(n-1)} \tag{21}$$

Note that this definition of connectivity is very different form the notion used for the investigation of local stability of equilibria e.g. in [11,12,14,27,30,31].

The probability for finding a matrix A with connectivity $\mathcal{C}(A) = \frac{k}{n(n-1)}$ is clearly

$$\pi_k = \frac{1}{2^{n(n-1)}} \binom{n(n-1)}{k} \tag{22}$$

Let p_k be the probability that a matrix with connectivity $k/n(n-1)$ is permanent and let N_k be the number of permanent matrices with connectivity this among a sample of M random matrices. We may then estimate p_k by

$$p_k = \frac{N_k}{M\pi_k} \tag{23}$$

Table 6: Permanence and connectivity for $n = 3, 4$ and 5. Column (1) gives the dimension of the network and column (2) displays the connectivity. A graphical representation of these data is given in fig.4.

(1) n	(2) $\mathcal{C}(A)$	(3) Gaussian	(4) Uniform	(5) Cauchy	(6) Laplace
3	0.50*	$5 \cdot 10^{-2}$	$5 \cdot 10^{-2}$	$5 \cdot 10^{-2}$	$5 \cdot 10^{-2}$
	0.66	$1.12 \cdot 10^{-1}$	$1.02 \cdot 10^{-1}$	$1.31 \cdot 10^{-1}$	$1.23 \cdot 10^{-1}$
	0.83	$1.76 \cdot 10^{-1}$	$1.62 \cdot 10^{-1}$	$1.89 \cdot 10^{-1}$	$1.78 \cdot 10^{-1}$
	1.00	$5.36 \cdot 10^{-1}$	$5.83 \cdot 10^{-1}$	$3.90 \cdot 10^{-1}$	$4.61 \cdot 10^{-1}$
4	0.33*	$4.23 \cdot 10^{-4}$	$3.28 \cdot 10^{-4}$	–	$7.1 \cdot 10^{-4}$
	0.42	$1.9 \cdot 10^{-3}$	$1.3 \cdot 10^{-3}$	$3.6 \cdot 10^{-3}$	$4.3 \cdot 10^{-3}$
	0.50	$5.3 \cdot 10^{-3}$	$3.7 \cdot 10^{-3}$	$8.7 \cdot 10^{-3}$	$1.26 \cdot 10^{-2}$
	0.58	$1.32 \cdot 10^{-2}$	$9.8 \cdot 10^{-3}$	$1.86 \cdot 10^{-2}$	$2.51 \cdot 10^{-2}$
	0.67	$2.1 \cdot 10^{-2}$	$2.41 \cdot 10^{-2}$	$3.34 \cdot 10^{-2}$	$4.03 \cdot 10^{-2}$
	0.75	$5.0 \cdot 10^{-2}$	$4.5 \cdot 10^{-2}$	$5.3 \cdot 10^{-2}$	$5.6 \cdot 10^{-2}$
	0.83	$7.2 \cdot 10^{-2}$	$7.8 \cdot 10^{-2}$	$7.2 \cdot 10^{-2}$	$7.6 \cdot 10^{-2}$
	0.92	$1.2 \cdot 10^{-2}$	$1.3 \cdot 10^{-1}$	$1.1 \cdot 10^{-1}$	$1.04 \cdot 10^{-1}$
	1.00†	$2.6 \cdot 10^{-1}$	$3.36 \cdot 10^{-1}$	$1.5 \cdot 10^{-1}$	$1.82 \cdot 10^{-1}$
5	0.25*	$9.0 \cdot 10^{-7}$	$1.3 \cdot 10^{-7}$	–	$3.55 \cdot 10^{-6}$
	0.30	–	–	$8 \cdot 10^{-5}$	–
	0.35	–	–	$2 \cdot 10^{-4}$	$5 \cdot 10^{-5}$
	0.40	–	–	$3.3 \cdot 10^{-4}$	$1.9 \cdot 10^{-4}$
	0.45	$1.5 \cdot 10^{-4}$	$5 \cdot 10^{-5}$	$9.0 \cdot 10^{-4}$	$3.5 \cdot 10^{-4}$
	0.50	$4 \cdot 10^{-4}$	$2.3 \cdot 10^{-4}$	$1.5 \cdot 10^{-3}$	$7.7 \cdot 10^{-4}$
	0.55	$9 \cdot 10^{-4}$	$6.6 \cdot 10^{-4}$	$2.8 \cdot 10^{-3}$	$1.9 \cdot 10^{-3}$
	0.60	$2.6 \cdot 10^{-3}$	$1.5 \cdot 10^{-3}$	$4.5 \cdot 10^{-3}$	$2.7 \cdot 10^{-3}$
	0.65	$4.0 \cdot 10^{-3}$	$3.1 \cdot 10^{-3}$	$6.8 \cdot 10^{-3}$	$4.7 \cdot 10^{-3}$
	0.70	$8 \cdot 10^{-3}$	$5.8 \cdot 10^{-3}$	$1.07 \cdot 10^{-2}$	$7.4 \cdot 10^{-3}$
	0.75	$1.4 \cdot 10^{-2}$	$6.6 \cdot 10^{-3}$	$1.6 \cdot 10^{-2}$	$1.4 \cdot 10^{-2}$
	0.80	$1.6 \cdot 10^{-2}$	$9 \cdot 10^{-3}$	$1.9 \cdot 10^{-2}$	$1.8 \cdot 10^{-2}$
	0.85	$2 \cdot 10^{-2}$	$1.9 \cdot 10^{-2}$	$2.5 \cdot 10^{-2}$	$1.8 \cdot 10^{-2}$
	0.90	–	–	$3 \cdot 10^{-2}$	$2 \cdot 10^{-2}$
	0.95	–	–	–	–
	1.00†	–	$1.61 \cdot 10^{-1}$	–	$6.94 \cdot 10^{-2}$

*) calculated from essentially hypercyclic matrices for columns (3),(4) and (6) .

†) calculated from catalytic networks for columns (4) and (6).

Figure 4: The probabilities for type-c (dashed line) and type-j (solid line) are shown for different density functions (symbols as in fig 1.) depending on the connectivity of the matrices for 3, 4 and 5 species networks. The lines refer to the averages for a given connectivity and dimension.

Figure 5: Ratio of type-j matrices and type-c matrices q depending on **a)** the dimension n and **b)** the connectivity of networks for $n=4$ (dashed line) and $n=5$ (solid line). Symbols as in fig.1.

Since most matrices have a connectivity around 1/2 we can expect sufficiently large values of N_k only in this region. Our simulations however provide data for catalytic networks and for essentially hypercyclic networks. It is clear that

$$p_{n(n-1)} = p_{\mathrm{CN}}$$

the probability for finding a permanent catalytic network.

If we assume that Jansen's Conjecture is true at least in the generic cases we may estimate p_n from p_{EH}, the probability for finding a permanent essentially hypercyclic network. There are exactly $(n-1)!$ permutations for the signature equ.(19); on the other hand all other graphs with connectivity $\mathcal{C}(A) = \frac{n}{n(n-1)} = 1/(n-1)$ are reducible and the networks are therefore not permanent. Thus we have

$$p_n = \frac{(n-1)!}{\binom{n(n-1)}{n}} \cdot p_{\mathrm{EH}} \tag{24}$$

Note that for $\mathcal{C}(A) \leq 1/n$ the graph $G(A)$ is reducible and we do not expect permanent networks in this case. Table 6. lists the probability for permanence for $n = 3, 4$ and 5 depending on the connectivity $\mathcal{C}(A)$ for different density functions. These data are shown together with the data for undecidable matrices in figure 4. The probability for finding permanent behaviour depends strongly on the connectivity of the matrix A; it decreases by several orders of magnitude with $\mathcal{C}(A)$.

The frequency $1-q$ for a type-c matrix to be undecidable also depends on the connectivity $\mathcal{C}(A)$. Figure 5 shows how the probability q that a type-c matrix can be shown to be permanent by Jansen's critrion varies with n and $\mathcal{C}(A)$. For $n=3$ we find $q=1$ indepedent of the connectivity. q then decreases by at least 2 orders of magnitude between $n=4$ and $n=7$. For larger networks q cannot be estimated with sufficient accuracy since the number of type-c matrices which can be produced with reasonable amount of computer time is too small.

A plot of q versus connectivity $\mathcal{C}(A)$ shows a minimum for $\mathcal{C}(A)\approx 0.5$ and reaches 1.0 for $\mathcal{C}(A)=\frac{1}{n-1}$, which corresponds to essentially hypercyclic systems for all $n\geq 4$. Unfortunately, thus, the only known sufficient condition for permanence — Jansen's criteririon, theorem 5 — works worst for the most probable type of matrices.

8. Growth of Cooperative Networks

Cooperative behaviour and especially permanence have been shown to be rather rare events in random networks. In this section we will investigate the fate of a cooperative network when an additional species enters, for example a mutant of one of its elements.

For second order replicator equations the minimum requirement for any type of cooperative behavior is the existence of an interior restpoint – otherwise all trajectories converge to the boundary of the simplex.

Suppose $A\in\mathbb{R}^{n\times n}$ leads to an interior equilibrium of (SR) in S_n. An additional species is introduced by extending A to $A'\in\mathbb{R}^{(n+1)\times(n+1)}$ by a random column and a random row. We define

$$\wp_{EE}(n+1)=\mathrm{Prob}\{A' \quad \text{yields an interior equilibrium}\}. \tag{30}$$

In complete analogy we may ask for the probability of permanent network to incorporate an additional species such that the resulting network is again permanent. Since we have no unambigous algebraic characterization of permanence we have to be content with an rather crude estimates, namely the probability $\wp_{jj}$ that a matrix which fulfils Jansen's criterion is extended such that the resulting network again passes this test and the probability $\wp_{cc}$

Table 7: Growth of Cooperative Networks. $\wp_{yx}(n)$ denotes the probability for a network of type-x (E refers to networks with interior equilibrium, c and j to type-c and type-j networks resp.) to form a type-y network by incorporation of an external species. Column (1) gives the dimension of initial network and column (2) specifies the densitity function: Gaussian (N) or Laplace (L).

(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*
n	t	$\wp_{EE}(n)$	$\wp_{cc}(n)$	$\wp_{jc}$	$\wp_{cj}(n)$	$\wp_{jj}(n)$
2	th	$5 \cdot 10^{-1}$	$2.5 \cdot 10^{-1}$	$2.5 \cdot 10^{-1}$	$2.5 \cdot 10^{-1}$	$2.5 \cdot 10^{-1}$
3	N	$2.84 \cdot 10^{-1}$	$1.14 \cdot 10^{-1}$	$1.14 \cdot 10^{-1}$	$1.14 \cdot 10^{-1}$	$1.14 \cdot 10^{-1}$
	L	$2.77 \cdot 10^{-1}$	$1.17 \cdot 10^{-1}$	$1.17 \cdot 10^{-1}$	$1.17 \cdot 10^{-1}$	$1.17 \cdot 10^{-1}$
4	N	$2.17 \cdot 10^{-1}$	$6.68 \cdot 10^{-2}$	$6.30 \cdot 10^{-2}$	$6.68 \cdot 10^{-2}$	$6.30 \cdot 10^{-2}$
	L	$2.12 \cdot 10^{-1}$	$7.01 \cdot 10^{-1}$	$6.66 \cdot 10^{-1}$	$7.01 \cdot 10^{-2}$	$6.66 \cdot 10^{-2}$
5	N	$1.73 \cdot 10^{-1}$	$4.39 \cdot 10^{-2}$	$3.33 \cdot 10^{-2}$	$4.55 \cdot 10^{-2}$	$3.70 \cdot 10^{-2}$
	L	$1.71 \cdot 10^{-1}$	$4.82 \cdot 10^{-2}$	$3.83 \cdot 10^{-2}$	$4.78 \cdot 10^{-2}$	$3.98 \cdot 10^{-2}$
6	N	$1.46 \cdot 10^{-1}$	$3.31 \cdot 10^{-2}$	$1.59 \cdot 10^{-2}$	$3.02 \cdot 10^{-2}$	$1.92 \cdot 10^{-2}$
	L	$1.43 \cdot 10^{-1}$	$3.56 \cdot 10^{-2}$	$1.86 \cdot 10^{-2}$	$3.51 \cdot 10^{-2}$	$2.29 \cdot 10^{-2}$
7	N	$1.27 \cdot 10^{-1}$	$2.50 \cdot 10^{-2}$	$4.71 \cdot 10^{-3}$	$2.30 \cdot 10^{-2}$	$1.03 \cdot 10^{-2}$
	L	$1.23 \cdot 10^{-1}$	$2.77 \cdot 10^{-2}$	$6.50 \cdot 10^{-3}$	$2.67 \cdot 10^{-2}$	$1.28 \cdot 10^{-2}$
8	N	$1.13 \cdot 10^{-1}$	$1.92 \cdot 10^{-2}$	$1.2 \cdot 10^{-3}$	$1.66 \cdot 10^{-2}$	$4.4 \cdot 10^{-3}$
	L	$1.11 \cdot 10^{-2}$	$2.04 \cdot 10^{-2}$	$1.5 \cdot 10^{-3}$	$1.92 \cdot 10^{-2}$	$5.8 \cdot 10^{-3}$
9	N	$1.01 \cdot 10^{-2}$	$1.48 \cdot 10^{-2}$	$2.1 \cdot 10^{-4}$	$1.1 \cdot 10^{-2}$	$2.1 \cdot 10^{-3}$
	L	$9.73 \cdot 10^{-2}$	$1.74 \cdot 10^{-2}$	$3.2 \cdot 10^{-4}$	$1.5 \cdot 10^{-2}$	$3.2 \cdot 10^{-3}$
10	N	$8.99 \cdot 10^{-2}$	$1.09 \cdot 10^{-2}$	$8 \cdot 10^{-5}$	$7 \cdot 10^{-3}$	$\approx 10^{-3}$
	L	$8.88 \cdot 10^{-2}$	$1.33 \cdot 10^{-2}$	$\leq 10^{-4}$	$8 \cdot 10^{-3}$	$\leq 10^{-3}$

Figure 6: Probabilities for incorporation of external species into networks of dimension n. Dashed line $\wp_{EE}$, dash-dotted line $\wp_{cc}$, dotted line $\wp_{jc}$, dashed line with narrow spaces $\wp_{cj}$ and solid line $\wp_{jj}$. $\triangle$ and $\bigcirc$ refer to Gaussian and Laplace distribution resp. See text for further explanation.

for type-c matrices to form type-c matrices again. Other possible estimate are $\wp_{cj}$, the probability for obtaining a type-c matrix from one which passed Jansen's test and $\wp_{jc}$ that a type-c matrix is extended to matrix passing Jansen's test.

Computational results are compiled in table 7. As all four of these estimates seem to decrease (at least) exponentially we conjecure that the probability to extend a permanent system to a system which is permanent again will decrease exponentially with the number n of coexisting species.

Figure 7: Cummulative probabilities for cooperative behaviour by subsequent incorporation of external species into cooperative networks (equ.(31)). For simplicitiy only averages over the different density functions are plotted. + refers to the existence of an interior equilibrium, $\diamondsuit$ refers to type-c networks and $\triangle$ refers to type-j networks. Solid lines give the probabilities for accidentally finding a network of the above types, dashed lines give the probabilities for obtaining a network of given type from a network of the same type by subsequent incorporation of additional species ($\wp_{EE}$,$\wp_{cc}$,$\wp_{jj}$). The dotted lines show $\wp_{jc}$ and $\wp_{cj}$ for comparison.

We may roughly estimate the chance to get a cooperative n-species network by successive incorporation of other species by

$$\hat{\wp}(n) = \prod_{k=2}^{n} \wp(k). \tag{31}$$

Fig.7 compares these values with the probability for finding a cooperative $n \times n$ network by chance. The chance to get permanent networks stepwise by incorporation of random "invaders" is orders of magnitudes smaller than the chance to find a large permanent network at random.

What happens if an invading species is not incorporated therby enlarging the permanent network? If the transversal eigenvalue in the direction of the invader is negativ, than it cannot be successful and the previous network persists. We estimate a probability of 0.5 for this process. If, on the other hand, the network is not stable against invasion, at least one of its members dies out in most cases because – as we have seen above – it is very improbable that the whole system is still cooperative. It may be replaced by the invading species, but we expect that in most cases more than one species disappers. The contact of a cooperative network and an external species might well be lethal for almost all species in the system. Unfortunately there are no algebraic tools known to calculate the outcome of such an event.

9. Conclusions

Numerical calculations for small and moderate size replicator networks show that permanence – and cooperativity in general – is a very rare phenomenon except for very small with networks $n = 2, 3$ or 4 members. The probability for finding cooperative behaviour in random autocatalytic networks of replicator or Lotka-Volterra type decreases at least as 4^{-n} with the number of species involved; maybe even faster than exponential. Permanence is likely in catalytic networks, i.e. in autocatalytic reaction networks in which cross-catalysis is dominant and decreases dramatically with the number of negative interactions. Most permanent networks exhibit a positive feedback loop involving all species in the system, or with other words, they contain a hypercyle. However, this is not necessary. Finally, larger networks are not accessible via successive incorporation of species into cooperative networks with reasonable probability.

The assumption of random couplings between the species might be applicable models of prebiotic evolution [6,7]. Present day ecosystems, however, are the outcome of a very long evolution, thus there is no reason to assume that the relations among species are even close to random. The large number of coexistent species which can be found in a whole lot of natural systems clearly shows that their interactions are indeed far from being random.

Our numerical experiments suggest that permanence of an ecosystem is a very fragile property: even comparably small changes in the coupling constants between the species, which depend on the environment, are likely to destroy permanence.

Acknowledgements

The auther wish to thank Dr. Wolfgang Schnabl (Rechenzentrum der Universität Wien) for invaluable assistence with the mainframe computers and Doz. J. Hofbauer and Prof. P. Schuster for stimulating discussions. Generous supply of computer time by the Vienna University Computer Center – in collaboration with the IBM - EASI project – and the Gesellschaft für wissenschaftliche Datenverarbeitung Göttingen (GWDG) is gratefully acknowledged. This research was, in part, supported by the Jubiläumsfond der Österreichischen Nationalbank, grant No. 3819.

References

[1] Amann E. Permanence of Catalytic Networks. Dissertation. Universitaet Wien. (1989)

[2] Amann E., J. Hofbauer. Permanence in Lotka-Volterra Equations. In: *Lotka-Volterra Approach in Dynamic Systems*, Proceedings Conference Wartburg, DDR, 1984.

[3] Amann E., J. Hofbauer. Permanence in Lotka-Volterra and replicator equations. In *Lotka-Volterra approach to cooperation and competition in dynamical systems.* W. Ebeling and M. Peschl eds. Berlin, Akademie-Verlag, 1985.

[4] Bomze I. Lotka-Volterra equation and replicator dynamics: a two-dimensional classification. *Biol. Cybern.* 48: 201-211 (1983).

[5] Butler G., H.I. Freedman, P. Waltman. Uniformly persistent systems. *Proc. Am. Math. Soc.* 96: 425-430 (1986)

[6] Eigen M. Selforganization of matter and the evolution of biological macromolecules. *Naturwissenschaften* 58: 465-523 (1971).

[7] Eigen M. and P. Schuster. *The Hypercycle.* New York, Berlin: Springer, 1979 and *Naturwissenschaften* 64: 541-565 (1977), 65: 7-41 and 341-369 (1978).

[8] Freedman H.I., P. Waltman. Mathematical analysis of some three species food chain models. *Math. Biosc.* 33: 257-276 (1977).

[9] Freedman H.I., P. Waltman. Persistence in models of some three interacting predator-prey populations. *Math. Biosc.* 68: 309-316 (1984).

[10] Freedman H.I., P. Waltman. Persistence in a model of three competitive populations. *Math. Biosc.* 73: 73-101 (1985).

[11] Gardner M.R. and W.R. Ashby. Connectance of large dynamic (cybernetic) systems: critical value for stability. *Nature* 228: 778 (1970).

[12] Goh B.S. and L.S. Jennings. Feasibility and stability in randomly assembled Lotka-Volterra models. *Ecol. Modelling* 3: 63-71 (1977).

[13] Gopalsamy K. Global asymptotic stability in Volterra's populations systems. *J. Math. Biol.* 19: 157-168 (1984).

[14] Hastings H.M. The May-Wigner stability theorem. *J. Theor. Biol.* 97: 155-166 (1982).

[15] Hofbauer J. A general cooperation theorem for Hypercycles. *Mh. Math.* 91: 233-240 (1981).

[16] Hofbauer J. On the occurrence of limit cycles in Volterra-Lotka equations. *Nonlinear Anal., Theory Methods Appl.* 5: 1003-1007 (1981).

[17] Hofbauer J. Saturated equilibria, permanence, and stability for ecological systems. In: Proceedings on the Second Autumn Course on Mathematical Ecology, Trieste, 1986.

[18] Hofbauer J., V. Hutson and W. Jansen. Coexistence for systems governed by difference equations of Lotka-Volterra type. *J. Math. Biol.* 25: 553-570 (1987).

[19] Hofbauer J., P. Schuster, K. Sigmund. Competition and cooperation in catalytic selfreplication. *J. Math. Biol.* 11: 153-168 (1981).

[20] Hofbauer J., P. Schuster, K. Sigmund. Game dynamics in Mendelian populations. *Biol. Cybern.* 43:, 51-57 (1982).

[21] Hofbauer J., K. Sigmund. Permanence for replicator equations. In: Lect. Notes Econ. Math., vol. 287; Berlin, Heidelberg, New York: Springer, 1987.

[22] Hofbauer J., K. Sigmund. *Dynamical Systems and the Theory of Evolution.* Cambridge Univ. Press, 1988.

[23] Hutson V. A theorem on average Ljapunov functions. *Monatsh. Math.* 98: 267-275 (1984).

[24] Hutson V. The stability under perturbations of repulsive sets. *J. Diff. Eqns.* 76: 77-90 (1988).

[25] Hutson V., G.T. Vickers. A criterion for permanent coexistence of species, with an application to a two-prey, one-predator system. *Math. Biosc.* 63: 253-269 (1983).

[26] Jansen W. A permanence theorem for replicator and Lotka-Volterra systems. *J. Math. Biol.* 25: 411-422 (1987).

[27] Kindlmann P., M. Rejmánek. Number of species at stable equilibrium of complex model ecosystems. *Ecol. Modelling* 16: 85-90 (1982).

[28] Kirlinger G. (1986) Permanence in Lotka-Volterra equations. linked predator prey systems *Math. Biosc.* **82**, 165-191.

[29] Kirlinger G. (1988) Permanence of some ecological systems with several predator and one prey species. *J. Math. Biol.* 82: 217-232.

[30] May R.M. Will a large complex system be stable ? *Nature* 238: 413-414 (1972).

[31] Roberts A. The stability of a feasible ecosystem. *Nature* 251: 607-608 (1974).

[32] Schnabl W., P. Stadler, Ch. Forst, P. Schuster. Full characterization of a strange attractor. *Physica* 48D: 65-90 (1991).

[33] Schuster P., K. Sigmund, R. Wolff. Dynamical systems under constant organization III: cooperative and competitive behaviour of hypercycles. *J. Diff. Eqns.* 32: 357-368 (1979).

[34] Schuster P., K. Sigmund, R. Wolff. Mass Action Kinetics of Selfreplication in Flow Reactors. *J. Math. Anal. Appl.* 78: 88-112 (1980).

[35] Schuster P., K. Sigmund. Replicator Dynamics. *J. Theor. Biol.* 100: 533-538 (1983).

[36] Sigmund K., P. Schuster. Permanence and uninvadability for for deterministic population models. In *Stochastic Phenomena and Chaotic Behaviour in Complex Systems*, P. Schuster ed., Synergetics 21, New York, Springer, 1984.

[37] Stadler B.M.R., P.F. Stadler. Dynamics of Small autocatalytic reaction networks III: monotonous growth functions. *Bull. Math. Biol.* 53: 469-485 (1991).

[38] Stadler P.F. Complementary Replication. *Math. Biosc.* 107: 83-109 (1991)

[39] Stadler P.F., P. Schuster. Dynamics of autocatalytic reaction networks I: Bifurcations, permanence and exlusion. *Bull. Math. Biol.* 52: 485-508 (1990).

[40] Stadler P., P. Schuster . Selection Mutation Equations – An Approach Based on Perturbation Theory. *J. Math. Biol.* in press (1992)

[41] Tang Z.-D. and K.-C. Duan. Persistence in Dynamical Systems. *Quart. Appl. Math.* 48: 463-472 (1990).

[42] Volterra V. *Lecons sur la theorie mathematique de la lutte pour la vie.* Paris: Gauthier-Villars, 1931.

[43] Zeeman E.C. Population dynamics from game theory. In *Global theory of dynamical systems*; Berlin, Heidelberg, New York: Springer, 1980.

Table 1: Probability Densitity functions used in this paper. All calculations have been performed for the replicator model (SR) (column A). The results carry over to Lotka Volterra (LV) models with somewhat different distribution functions of the coefficients (column B).

	A	$B\dagger$
Normal	$\frac{1}{\sqrt{\pi}} \exp -x^2/2$	$\frac{1}{\sqrt{2\pi}} \exp -x^2/4$
Uniform	$\frac{1}{2}$ for $x \in [-1,1]$ 0 otherwise	$1 + x/2$ for $x \in [-2,0]$ $1 - x/2$ for $x \in [0,2]$ 0 otherwise
Cauchy	$\frac{1}{\pi}\frac{1}{1+x^2}$	$\frac{1}{\pi}\frac{2}{4+x^2}$
Laplace	$\frac{1}{2} \exp -\lvert x\rvert$	

$^{\dagger)}$ off-diagonal elements only. r and the diagonal elements of B have the same distribution as A.

Table 2: Numerical survey for permanence using 1,000,000 random matrices with zero diagonal. Column (1) and (2) indicate dimension of the matrices and density function. Columns (3) through (7) contain the number of matrices fulfilling criterion (n) and all previous ones. Columns (8) and (9) give the number of undecidable cases and of permanent matrices, resp. (see also fig.1)

(1) n	*(2)* p	*(3)* int. equil.	*(4)* *type a*	*(5)* *type b*	*(6)* *type c*	*(8)* undec.	*(9)* **type j**
2	$th.$	500,000	250,000	250,000	250,000	0	250,000
3	N^1	249,730	125,214	69,926	66,954	0	66,954
	U^2	249,860	124,190	66,520	64,330	0	64,330
	C^2	250,550	126,340	74,670	70.780	0	70,780
	L^2	250,370	123,710	71,220	67,630	0	67,630
4	N^1	124,316	62,408	31,274	16,864	5,334	11,530
	U^1	124,758	62,358	31,458	16,028	5,948	10,080
	C^1	124,984	62,296	31,846	19,022	4,330	14,692
	L	124,642	62,455	31,696	18,098	5,077	13,021
5	N^3	62,192	31,256	15,880	4,492	3,024	1,468
	U^1	62,112	31,222	15,652	4,134	3,030	1,104
	C	62,456	31,327	15,748	5,404	2,685	2,719
	L	62,426	31,381	15,676	4,704	2,921	1,783
6	N	31,159	15,451	7,707	1,075	965	110
	U	31,487	15,735	8,004	1,001	938	63
	C	31,307	15,649	7,819	1,412	1,022	390
	L	31,127	15,647	7,794	1,101	999	156
7	N	15,682	7,826	3,969	280	276	4
	U	15,522	7,731	3,917	234	232	2
	C	15,579	7,826	3,936	396	236	50
	L	15,403	7,721	3,839	290	275	15
8	N	7,832	3,884	1,927	48	48	0
	U	7,785	3,940	1,960	65	65	0
	C	7,770	3,962	2,075	116	109	7
	L	7,636	3,823	1,894	67	67	0
9	N	3,889	1,920	964	11	11	0
	U	4,034	2,046	1,026	8	8	0
	C	3,962	1,966	1,003	18	18	0
	L	3,883	1,931	955	4	4	0
10	N	1,989	993	506	6	6	0
	U	1,942	943	464	4	4	0
	C	1,945	975	487	9	9	0
	L	1,953	987	501	4	4	0

[1,2,3] Calculated from smaller sample sizes and multiplied by a factor of 2[1)],10[2)],4[3)] in order to facilitate comparison.

Table 3: Numerical survey for permanence in 100,000 random matrices with zero diagonal and positive non-diagonal entries (catalytic networks). A uniform distribution on the unit-interval, U_+, and an exponential distribution with parameter 1, E, was used. As for table 2, columns (3) through (7) display the numbers of matrices passing subsequent "filters" requiring interior equilibria (3), the correct sign of det$A$ (4) and the absence (5) of saturated rest points on the boundary of S_n. Columns (6) and (7) show the numbers of permanent and undecidable *type-c* matrices.

(1) n	*(2)* p	*(3)* int. equil.	*(4)* $\det A$	*(5)* sat.bd.	*(6)* undec.	*(7)* **perm.**
2	*th.*	$100,000$	$100,000$	$100,000$	0	$100,000$
3	U_+	$62,615$	$62,615$	$62,615$	0	$62,615$
	E	$46,070$	$46,070$	$46,070$	0	$46,070$
4	U_+	$34,403$	$33,457$	$33,457$	0	$33,457$
	E	$20,785$	$20,785$	$18,238$	0	$18,238$
5	U_+	$17,577$	$16,080$	$16,014$	0	$16,014$
	E	$9,781$	$7,171$	$6,952$	16	$6,936$
6	U_+	$8,746$	$7,385$	$7,260$	40	$7,220$
	E	$4,612$	$2,861$	$2,502$	110	$2,392$
7	U_+	$4,391$	$3,318$	$3,134$	73	$3,061$
	E	$2,257$	$1,263$	921	116	805
8	U_+	$2,163$	$1,429$	$1,280$	87	$1,193$
	E	$1,112$	599	332	102	230
9	U_+	$1,080$	667	499	90	419
	E^1	560_5	299_5	125	74	51
10	U_+	529	286	175	55	120
	E^1	285_5	142_5	39	29_5	9_5
11	U_+	279	165	91	40	51
	E^1	127	65_5	12_5	11_5	1
12	U_+^1	116_5	57	29	20	9
	E^1	61_5	31	4	4	0

$^{1)}$ calculated from 200,000 matrices

Table 4: Numerical survey for permanence in 100,000 random *essentially hypercyclic* matrices for three different probability distributions of $|a_{ij}|$, $i \neq j$.

(1)	*(2)*	*(3)*	*(4)*	*(5)*	*(6)*	*(7)*
	uniform		*Gaussian*		*exponential*	
n	equil.	perm.	equil.	perm.	equil.	perm.
3	$100,000$	$49,927$	$100,000$	$50,219$	$100,000$	$49,852$
4	$70,717$	$2,706$	$62,691$	$4,233$	$55,622$	$5,836$
5[1]	$56,715$	8_3	$43,649$	57_7	$33,506$	229_2
6[1]	$38,036$	0	$25,323$	0_2	$17,097$	2_6
7[2]	$25,430$	0	$17,097$	0	$14,423$	0

1) calculated from 10^6 matrices.

2) calculated from $3 \cdot 10^5$ matrices.

Table 5: Permanence and graphs. Columns (3) through (10) give the probability for finding permanent p (or undecideable u) matrices which contain no Hamiltonian circle (n.h.) or which are reducible (red). Probabilities are given in promille.

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
n	t	Gaussian		Uniform		Cauchy		Laplace	
		n.h.	red.	n.h.	red.	n.h.	red.	n.h.	red.
2	p	0	0	0	0	0	0	0	0
3	p	0	0	0	0	0	0	0	0
4	p	3.8	0	1.2	0	7.8	0	5.4	0
4	u	16	0	9	0	40	0	25	0
5	p	5	0	2	0	9	0	3	0
5	u	13	0	12	0	37	0	23	0
6	p	–	0	–	0	–	0	6	0
6	u	5	0	2	0	2	0	14	0

Table 6: Permanence and connectivity for $n = 3, 4$ and 5. Column (1) gives the dimension of the network and column (2) displays the connectivity. A graphical representation of these data is given in fig.4.

(1) n	(2) $\mathcal{C}(A)$	(3) Gaussian	(4) Uniform	(5) Cauchy	(6) Laplace
3	0.50*	$5 \cdot 10^{-2}$	$5 \cdot 10^{-2}$	$5 \cdot 10^{-2}$	$5 \cdot 10^{-2}$
	0.66	$1.12 \cdot 10^{-1}$	$1.02 \cdot 10^{-1}$	$1.31 \cdot 10^{-1}$	$1.23 \cdot 10^{-1}$
	0.83	$1.76 \cdot 10^{-1}$	$1.62 \cdot 10^{-1}$	$1.89 \cdot 10^{-1}$	$1.78 \cdot 10^{-1}$
	1.00	$5.36 \cdot 10^{-1}$	$5.83 \cdot 10^{-1}$	$3.90 \cdot 10^{-1}$	$4.61 \cdot 10^{-1}$
4	0.33*	$4.23 \cdot 10^{-4}$	$3.28 \cdot 10^{-4}$	–	$7.1 \cdot 10^{-4}$
	0.42	$1.9 \cdot 10^{-3}$	$1.3 \cdot 10^{-3}$	$3.6 \cdot 10^{-3}$	$4.3 \cdot 10^{-3}$
	0.50	$5.3 \cdot 10^{-3}$	$3.7 \cdot 10^{-3}$	$8.7 \cdot 10^{-3}$	$1.26 \cdot 10^{-2}$
	0.58	$1.32 \cdot 10^{-2}$	$9.8 \cdot 10^{-3}$	$1.86 \cdot 10^{-2}$	$2.51 \cdot 10^{-2}$
	0.67	$2.1 \cdot 10^{-2}$	$2.41 \cdot 10^{-2}$	$3.34 \cdot 10^{-2}$	$4.03 \cdot 10^{-2}$
	0.75	$5.0 \cdot 10^{-2}$	$4.5 \cdot 10^{-2}$	$5.3 \cdot 10^{-2}$	$5.6 \cdot 10^{-2}$
	0.83	$7.2 \cdot 10^{-2}$	$7.8 \cdot 10^{-2}$	$7.2 \cdot 10^{-2}$	$7.6 \cdot 10^{-2}$
	0.92	$1.2 \cdot 10^{-2}$	$1.3 \cdot 10^{-1}$	$1.1 \cdot 10^{-1}$	$1.04 \cdot 10^{-1}$
	1.00†	$2.6 \cdot 10^{-1}$	$3.36 \cdot 10^{-1}$	$1.5 \cdot 10^{-1}$	$1.82 \cdot 10^{-1}$
5	0.25*	$9.0 \cdot 10^{-7}$	$1.3 \cdot 10^{-7}$	–	$3.55 \cdot 10^{-6}$
	0.30	–	–	$8 \cdot 10^{-5}$	–
	0.35	–	–	$2 \cdot 10^{-4}$	$5 \cdot 10^{-5}$
	0.40	–	–	$3.3 \cdot 10^{-4}$	$1.9 \cdot 10^{-4}$
	0.45	$1.5 \cdot 10^{-4}$	$5 \cdot 10^{-5}$	$9.0 \cdot 10^{-4}$	$3.5 \cdot 10^{-4}$
	0.50	$4 \cdot 10^{-4}$	$2.3 \cdot 10^{-4}$	$1.5 \cdot 10^{-3}$	$7.7 \cdot 10^{-4}$
	0.55	$9 \cdot 10^{-4}$	$6.6 \cdot 10^{-4}$	$2.8 \cdot 10^{-3}$	$1.9 \cdot 10^{-3}$
	0.60	$2.6 \cdot 10^{-3}$	$1.5 \cdot 10^{-3}$	$4.5 \cdot 10^{-3}$	$2.7 \cdot 10^{-3}$
	0.65	$4.0 \cdot 10^{-3}$	$3.1 \cdot 10^{-3}$	$6.8 \cdot 10^{-3}$	$4.7 \cdot 10^{-3}$
	0.70	$8 \cdot 10^{-3}$	$5.8 \cdot 10^{-3}$	$1.07 \cdot 10^{-2}$	$7.4 \cdot 10^{-3}$
	0.75	$1.4 \cdot 10^{-2}$	$6.6 \cdot 10^{-3}$	$1.6 \cdot 10^{-2}$	$1.4 \cdot 10^{-2}$
	0.80	$1.6 \cdot 10^{-2}$	$9 \cdot 10^{-3}$	$1.9 \cdot 10^{-2}$	$1.8 \cdot 10^{-2}$
	0.85	$2 \cdot 10^{-2}$	$1.9 \cdot 10^{-2}$	$2.5 \cdot 10^{-2}$	$1.8 \cdot 10^{-2}$
	0.90	–	–	$3 \cdot 10^{-2}$	$2 \cdot 10^{-2}$
	0.95	–	–	–	–
	1.00†	–	$1.61 \cdot 10^{-1}$	–	$6.94 \cdot 10^{-2}$

*) calculated from essentially hypercyclic matrices for columns (3),(4) and (6) .

†) calculated from catalytic networks for columns (4) and (6).

Table 7: Growth of Cooperative Networks. $\wp_{yx}(n)$ denotes the probability for a network of type-x (E refers to networks with interior equilibrium, c and j to type-c and type-j networks resp.) to form a type-y network by incorporation of an external species. Column (1) gives the dimension of initial network and column (2) specifies the densitity function: Gaussian (N) or Laplace (L).

(1) n	(2) t	(3) $\wp_{EE}(n)$	(4) $\wp_{cc}(n)$	(5) $\wp_{jc}$	(6) $\wp_{cj}(n)$	(7) $\wp_{jj}(n)$
2	th	$5 \cdot 10^{-1}$	$2.5 \cdot 10^{-1}$	$2.5 \cdot 10^{-1}$	$2.5 \cdot 10^{-1}$	$2.5 \cdot 10^{-1}$
3	N	$2.84 \cdot 10^{-1}$	$1.14 \cdot 10^{-1}$	$1.14 \cdot 10^{-1}$	$1.14 \cdot 10^{-1}$	$1.14 \cdot 10^{-1}$
	L	$2.77 \cdot 10^{-1}$	$1.17 \cdot 10^{-1}$	$1.17 \cdot 10^{-1}$	$1.17 \cdot 10^{-1}$	$1.17 \cdot 10^{-1}$
4	N	$2.17 \cdot 10^{-1}$	$6.68 \cdot 10^{-2}$	$6.30 \cdot 10^{-2}$	$6.68 \cdot 10^{-2}$	$6.30 \cdot 10^{-2}$
	L	$2.12 \cdot 10^{-1}$	$7.01 \cdot 10^{-1}$	$6.66 \cdot 10^{-1}$	$7.01 \cdot 10^{-2}$	$6.66 \cdot 10^{-2}$
5	N	$1.73 \cdot 10^{-1}$	$4.39 \cdot 10^{-2}$	$3.33 \cdot 10^{-2}$	$4.55 \cdot 10^{-2}$	$3.70 \cdot 10^{-2}$
	L	$1.71 \cdot 10^{-1}$	$4.82 \cdot 10^{-2}$	$3.83 \cdot 10^{-2}$	$4.78 \cdot 10^{-2}$	$3.98 \cdot 10^{-2}$
6	N	$1.46 \cdot 10^{-1}$	$3.31 \cdot 10^{-2}$	$1.59 \cdot 10^{-2}$	$3.02 \cdot 10^{-2}$	$1.92 \cdot 10^{-2}$
	L	$1.43 \cdot 10^{-1}$	$3.56 \cdot 10^{-2}$	$1.86 \cdot 10^{-2}$	$3.51 \cdot 10^{-2}$	$2.29 \cdot 10^{-2}$
7	N	$1.27 \cdot 10^{-1}$	$2.50 \cdot 10^{-2}$	$4.71 \cdot 10^{-3}$	$2.30 \cdot 10^{-2}$	$1.03 \cdot 10^{-2}$
	L	$1.23 \cdot 10^{-1}$	$2.77 \cdot 10^{-2}$	$6.50 \cdot 10^{-3}$	$2.67 \cdot 10^{-2}$	$1.28 \cdot 10^{-2}$
8	N	$1.13 \cdot 10^{-1}$	$1.92 \cdot 10^{-2}$	$1.2 \cdot 10^{-3}$	$1.66 \cdot 10^{-2}$	$4.4 \cdot 10^{-3}$
	L	$1.11 \cdot 10^{-2}$	$2.04 \cdot 10^{-2}$	$1.5 \cdot 10^{-3}$	$1.92 \cdot 10^{-2}$	$5.8 \cdot 10^{-3}$
9	N	$1.01 \cdot 10^{-2}$	$1.48 \cdot 10^{-2}$	$2.1 \cdot 10^{-4}$	$1.1 \cdot 10^{-2}$	$2.1 \cdot 10^{-3}$
	L	$9.73 \cdot 10^{-2}$	$1.74 \cdot 10^{-2}$	$3.2 \cdot 10^{-4}$	$1.5 \cdot 10^{-2}$	$3.2 \cdot 10^{-3}$
10	N	$8.99 \cdot 10^{-2}$	$1.09 \cdot 10^{-2}$	$8 \cdot 10^{-5}$	$7 \cdot 10^{-3}$	$\approx 10^{-3}$
	L	$8.88 \cdot 10^{-2}$	$1.33 \cdot 10^{-2}$	$\leq 10^{-4}$	$8 \cdot 10^{-3}$	$\leq 10^{-3}$

Figure Captions

Figure 1. Probability for Permanence. The probabilities for an internal equilibrium (dashed line) and the appropriate signs of TrJ (dotted line) and det$A$ (dash-dotted line) are equal for all density functions. The dashed line with narrow spaces gives the average of the probabilities for type-c matrices and the solid line shows the probabilities for type-j matrices for different densitiy functions: Gaussian ($\triangle$), uniform ($\diamondsuit$), Cauchy ($+$) and Laplace ($\bigcirc$).

Figure 2. Permanence for Catalytic Networks. The dashed line refers to the probability for an interior rest point, the dash-dotted line accounts for the approriate sign of det$A$, the dotted line corresponds to the probability of type-c matrices and the solid line refers to the probability of type-j matrices. Data are shown for the uniform distribution $\diamondsuit$ and the exponential distribution $\bigcirc$.

Figure 3. Permanence for essentially hypercyclic networks. The probability for an interior rest point (dashed line) and for permanence (solid line) shown for Gaussian distribution ($\triangle$), uniform distribution ($\diamondsuit$) and exponential distribution ($\bigcirc$).

Figure 4. The probabilities for type-c (dashed line) and type-j (solid line) are shown for different density functions (symbols as in fig 1.) depending on the connectivity of the matrices for 3, 4 and 5 species networks. The lines refer to the averages for a given connectivity and dimension.

Figure 5. Ratio of type-j matrices and type-c matrices q depending on **a)** the dimension n and **b)** the connectivity of networks for $n = 4$ (dashed line) and $n = 5$ (solid line). Symbols as in fig.1.

Figure 6. Probabilities for incorporation of external species into networks of dimension n. Dashed line $\wp_{EE}$, dash-dotted line $\wp_{cc}$, dotted line $\wp_{jc}$, dashed line with narrow spaces $\wp_{cj}$ and solid line $\wp_{jj}$. $\triangle$ and $\bigcirc$ refer to Gaussian and Laplace distribution resp. See text for further explanation.

Figure 7. Cummulative probabilities for cooperative behaviour by subsequent incorporation of external species into cooperative networks (equ.(31)). For simplicitiy only averages over the different density functions are plotted. + refers to the existence of an interior equilibrium, $\Diamond$ refers to type-c networks and $\triangle$ refers to type-j networks. Solid lines give the probabilities for accidentally finding a network of the above types, dashed lines give the probabilities for obtaining a network of given type from a network of the same type by subsequent incorporation of additional species ($\wp_{EE}, \wp_{cc}, \wp_{jj}$). The dotted lines show $\wp_{jc}$ and $\wp_{cj}$ for comparison.