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007

A DIFFERENCE EQUATION MODEL FOR THE HYPERCYCLE*

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Abstract. The paper presents a qualitative analysis of a system of n cyclically coupled difference equations $x_i' = x_i(C + k_i x_{i-1})(C+\Phi)^{-1}$ with $\Phi = \sum k_i x_i x_{i-1}$, which may be viewed as a discrete analogue of the "hypercycle" differential equation $\dot{x}_i = x_i(k_i x_{i-1} - \Phi)$. These equations are of particular interest in the theory of self-organization and biological evolution and have applications to the study of the social behaviour of animals.

1. Introduction. A hypercycle, as introduced by Eigen and Schuster [4], is a system of n self-replicating macromolecules, which are coupled together by a closed loop of catalytic reactions, such that each species catalyses the self-reproduction of the next one. The existence of such hypercycles was suggested by Eigen and Schuster as one of the missing links in the prebiotic evolution [17] from simple self-replicating elements with enzyme-free copying mechanism, as observed in the "primordial soup", to the highly organized early RNA. Since self-replicating elements are strongly competing, such a coupling between them is necessary in order to overcome the information crisis and build up larger units with better replication mechanisms. Obviously a cyclic coupling is the simplest one which will guarantee coexistence or "cooperation".

A simplified mathematical model for such a system is given by the following ordinary differential equation

$$(1.1) \qquad \dot{x}_i = x_i(k_i x_{i-1} - \Phi), \qquad i = 1, \cdots, n, \qquad \Phi = \sum_{i=1}^{n} k_i x_i x_{i-1}.$$

Here x_i denotes the concentration of the ith species, whose growth rate $\dot{x}_i / x_i$ is proportional to the concentration of the preceding species x_{i-1}. (Indices are counted modulo n throughout this paper, i.e., $x_0 = x_n$, $x_1 = x_{n+1}, \cdots$.) Φ denotes the general flux which is introduced in order to keep the total number of elements constant: $\sum_{i=1}^n x_i = 1$.

Now the problem arises of giving a mathematical proof of the above "obvious" assertion, that this system indeed guarantees cooperation, i.e., no species dies out. To be more precise, we give the definition:

A dynamical system defined on the probability n-simplex

$$S_n = \left\{ x \in R^n \colon x_i \geqq 0 \text{ and } \sum_{i=1}^{n} x_i = 1 \right\}$$

is called *cooperative*, if the boundary of S_n, ∂S_n, is a repellor, i.e., if there exists a $\delta > 0$, such that $\liminf_{t \to +\infty} x_i(t) \geqq \delta$ for $i = 1, \cdots, n$ for every orbit $x(t)$ starting at $x(0) = x$ with $x_i > 0$.

The contrary behaviour, when almost all orbits go to boundary, and so at least one species dies out, is called *exclusion.* (See [20] for the "right" definition which is somewhat technical and will not be needed in detail in the following.)

Now the hypercycle differential equation (1.1) has been studied in some detail [19], [20] and in particular it was shown in [19, Part III] that it is cooperative. This result was extended further to more general systems in [6], [10]. The concept of

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cooperation and the technique provided for proving it has since then turned out to be very useful in other parts of biomathematics. We mention only the interesting applications to persistence of species in ecological communities [11], [12] and refer the reader to the recent survey on this topic by Schuster and Sigmund [18].

Now most biological systems are characterized by discrete time intervals for reproduction which give rise to sequences of generations described by difference equations. From that point of view it seems to be of interest to consider a discrete analogue of equation (1.1): x_i', the value of x_i in the next generation shall be proportional to x_i and x_{i-1}, i.e. $x_i' \sim x_i(C+k_i x_{i-1})$. To keep the total number of elements constant, we have to set

$$x_i' = \frac{C+k_i x_{i-1}}{C+\Phi} \quad \text{with } \Phi = \sum_{i=1}^{n} k_i x_i x_{i-1}, \quad C>0. \tag{1.2}$$

For a better motivation of this equation, especially of the new constant C, we write (1.2) in the form

$$\frac{x_i'-x_i}{C^{-1}} = x_i(k_i x_{i-1}-\Phi)\frac{C}{C+\Phi}.$$

If we now interpret C^{-1} as the time interval between two generations, i.e., $x_i'(t) = x_i(t+C^{-1})$, then (1.2) approximates the hypercycle differential equation (1.1) as $C\to\infty$ $((C/(C+\Phi))\to 1$ since Φ is bounded).

This observation suggests that (1.2) is an appropriate discrete analogue of (1.1) and one can expect that for large values of C the difference equation has properties similar to those of the differential equation.

Indeed we will see in § 3 that for arbitrary $C>0$ the system (1.2) is cooperative whereas in the degenerate case $C=0$ it leads to exclusion (§ 4). In order to yield more information on the form of the attractor we consider the unique fixed point in the interior of S_n which turns out (§ 5) to be a sink for $n\leqq 3$. In this case we prove that it has the whole interior as its basin of attraction (§ 6). For $n\geqq 4$ the fixed point is a saddle and numerical investigations suggest a stable "limit cycle" as global attractor. Section 7 contains further results on similar types of difference equations.

2. The connection with animal conflicts and game theory. Maynard Smith [14] and Maynard Smith and Price [16] introduced game theory into the study of animal behaviour: Each individual of a population can play one of n strategies, x_i denotes the proportion of the population playing the ith strategy. (A famous example of Maynard Smith treats the strategies dove, hawk, bully, retaliator, etc. [14], [16], [23].) The expected gain which arises after a contest of two individuals is expressed by a $n\times n$-pay-off-matrix (a_{ij}). If an individual playing strategy i fights against one playing j, then the payoff to i is given by a_{ij}, while the payoff to j is given by a_{ji}. If the population is large, the expected payoff to an individual playing i against an arbitrary competitor is $\sum_j a_{ij}x_j$. This can also be interpreted as change of "fitness" as a result of the contest. Hence the fitness of an individual playing i is $E_i = C+\sum_j a_{ij}x_j$, where C is some positive constant, and the "average fitness of the population" is given by $E=\sum_i x_i E_i = C+\sum_{i,j} x_i a_{ij} x_j = C+\Phi$.

Now Maynard Smith [15] proposed to introduce the following dynamics: If each individual reproduces its own kind in a number proportional to its fitness, then x_i', the value of x_i in the next generation, is given by

$$x_i' = x_i\frac{E_i}{E} = x_i\frac{C+\sum_j a_{ij}x_j}{C+\Phi}. \tag{2.1}$$

This is just a generalization of (1.2). Special cases of (2.1) have been studied, for example, in population genetics [5] and in the theory of the war of attrition [3]. We shall briefly return to it in § 7, but first we turn our attention to the hypercycle equation (1.2) which represents a significant special case.

3. Cooperation for $C>0$. Let us consider the recursion, defined on the simplex S_n

$$x_i' = x_i \frac{C+k_i x_{i-1}}{C+\Phi}, \qquad i=1,\cdots,n \tag{3.1}$$

with $\Phi = \sum_{i=1}^n k_i x_i x_{i-1}$. We denote by $x^{(N)}$ the result of iterating (3.1) N times from a starting value $x^{(0)}=x$. With this we have the following theorem:

THEOREM 1. *Suppose $C>0$ and for $i=1,\cdots,n$, $k_i>0$. Then* (3.1) *is cooperative. That is, for some $\delta>0$, $\liminf_{N\to\infty} x_i^{(N)} \geqq \delta$ for $i=1,\cdots,n$ and every $x \in \operatorname{int} S_n$.*

Proof of Theorem 1. We begin with a discussion of the behaviour of our system on the boundary of S_n:

LEMMA 1. *For every $x \in \partial S_m : \Phi(x^{(N)}) \to 0$ for $N\to\infty$.*

Proof of Lemma 1. Let x be on the boundary. Then x has the form $x_i=0$, $x_{i+1}>0$, $x_{i+2}>0, \cdots, x_{i+k}>0$, $x_{i+k+1}=0$ for some i, k $(1\leqq k<n)$. We will show that $x_{i+1}\to 0$, $x_{i+2}\to 0, \cdots, x_{i+k-1}\to 0$. For convenience, we set $i=0$ (according to the cyclic symmetry) and $k_j=1$ $(j=1,\cdots,n)$. (The proof also works for arbitrary rate constants k_j, one has only to replace x_j by $k_{j+1}x_j$, sometimes.)

We prove by induction: *$x_j\to 0$ and x_j/x_{j+1} converges (finally) monotonically to some limit $v_j (1\leqq j<k)$, which may be infinite.*

This statement is trivial for $j=0$. Assuming it for j we consider the quotient

$$\left(\frac{x_{j+1}}{x_{j+2}}\right)' = \frac{x_{j+1}}{x_{j+2}} \frac{C+x_j}{C+x_{j+1}}.$$

Now if $v_j>1$ or $v_j=1$ and $x_j/x_{j+1}\downarrow 1$, then $(C+x_j)/(C+x_{j+1})>1$ and hence x_{j+1}/x_{j+2} increases monotonically to some limit $v_{j+1}>0$. Furthermore $x_j/x_{j+1}\to v_j>0$ and $x_j\to 0$ implies $x_{j+1}\to 0$. It remains the case $v_j<1$ (resp. $v_j=1$ and $x_j/x_{j+1}\uparrow 1$). Then $(C+x_j)/(C+x_{j+1})<1$ and x_{j+1}/x_{j+2} decreases monotonically. If x_{j+1} did not converge to 0, one could find an $\varepsilon>0$ such that $(C+x_j)/(C+x_{j+1})\leqq 1-\varepsilon$ holds for an infinite number of generations. Then the quotient

$$\left(\frac{x_{j+1}}{x_{j+2}}\right)^{(N)} = \frac{x_{j+1}}{x_{j+2}} \prod_{k=0}^{N-1} \frac{C+x_j^{(k)}}{C+x_{j+1}^{(k)}}$$

tends to the limit $v_{j+1}=0$. Now $x_{j+1}\leqq x_{j+1}/x_{j+2}$ and so $x_{j+1}\to 0$ too. So every point on ∂S_n converges to a subface of the boundary where, whenever $x_j>0$ then $x_{j+1}=0$. On such a face we have $\Phi(x)=0$. It is easy to see that the set $\{x\colon \Phi(x)=0\}$ is just the set of all fixed points on the boundary. This completes the proof of Lemma 1.

Let us now consider the function $P(x)=x_1x_2\cdots x_n$. We have $P(x)=0$ if and only if $x\in\partial S_n$. Therefore $P(x)$ is a measure for the distance of x from the boundary.

Let $I(p):=\{x\in \operatorname{int} S_n\colon P(x)\leqq p\}$ for $p>0$. Cooperation is then equivalent to the existence of such a layer $I(p)$ which is left for ever after some time by each orbit starting in the interior of S_n. Note that

$$\frac{P'}{P} = \frac{\prod_{i=1}^n (C+k_i x_{i-1})}{(C+\Phi)^n} \geqq \frac{C^n + C^{n-1}\sum k_i x_{i-1}}{(C+\Phi)^n}.$$

On the set of fixed points $\{\Phi=0\}$ this quotient is greater than 1.

Since S_n is a compact set we have the following two propositions:

(3.2) $\frac{P'}{P} \geqq m > 0$ everywhere on S_n.

(3.3) $\frac{P'}{P} \geqq M > 1$ in some neighbourhood A of the set $\{x \in S_n: \Phi(x) = 0\}$.

Now choose $r \in]0, 1[$ such that $M^r m^{1-r} =: K > 1$.

DEFINITION. For $x \in \partial S_n$ let $N(x)$ be the smallest number $\geqq 1$ such that

$$\text{card}\,\{0 \leqq k < N(x): x^{(k)} \in A\} \geqq r \cdot N(x).$$

This means: the probability that $x^{(k)} \in A$ for a $k < N(x)$ is at least r. Obviously $N(x) = 1$ if and only if $x \in A$.

Now we know from Lemma 1 that for $x \in \partial S_n$, the $x^{(k)}$ lie in A for k large enough. This guarantees the existence of such a number $N(x)$ for each $x \in \partial S_n$.

LEMMA 2. *The function $x \to N(x)$ can be extended to some neighbourhood $I(p)$ of the boundary.*

Proof of Lemma 2. If for some $k < N(x) x^{(k)} \in A$, then each y in some neighbourhood U_k of x satisfies $y^{(k)} \in A$. Therefore, if we choose y in the intersection $U(x)$ of all such neighbourhoods U_k for $k < N(x)$ we get $y^{(k)} \in A$ whenever $x^{(k)} \in A$, and thus $N(y) \leqq N(x)$. Since S_n is compact a finite number of those $U(x)$ will cover ∂S_n. Their union contains a layer $I(p)$ for some $p > 0$. Furthermore $N(x)$ is bounded on $I(p)$ by a certain number $\bar{N}$. This completes the proof of Lemma 2.

Now we are able to prove Theorem 1. This will be done in two steps:

(1) *If $x \in I(p)$ then there exists a N with $x^{(N)} \notin I(p)$, i.e., any orbit leaves the layer $I(p)$ after some time.* Suppose, for all N: $x^{(N)} \in I(p)$, i.e., $d := \sup_{N \geqq 0} P(x^{(N)}) \leqq p$. Now choose N_1 such that $y = x^{(N_1)}$ satisfies $P(y) > d \cdot K^{-1/2}$. According to the definition of $N(y)$ and (3.2) and (3.3) we get

$$\frac{P(y^{(N(y))})}{P(y)} = \prod_{k=0}^{N(y)-1} \frac{P^{(k+1)}}{P^{(k)}} \geqq M^{rN(y)} m^{(1-r)N(y)} = K^{N(y)} \geqq K,$$

and

$$P(y^{(N(y))}) \geqq KP(y) > d \cdot K^{1/2} > d. \tag{3.4}$$

However this contradicts the definition of d.

(2) *There exists a $q < p$ such that the layer $I(q)$ is never reached for large times: If $x \notin I(p)$, then for no $N \geqq 0$ is $x^{(N)} \in I(q)$.* We choose $q = p \cdot m^{(1-r)\bar{N}+1}$, where $\bar{N} = \max\{N(x), x \in I(p)\}$. Suppose $x \notin I(p)$ and let N_2 be the first time when $z = x^{(N_2)} \in I(p)$, thus $P(z) > m \cdot p$. Then

$$\text{card}\,\{0 \leqq k < N(z): z^{(k)} \notin A\} \leqq (1-r)N(z) \leqq (1-r)\bar{N},$$

and this with (3.2) implies that

$$\frac{P(z^{(k)})}{P(z)} = \prod_{i=0}^{k-1} \frac{P(z^{(i+1)})}{P(z^{(i)})} \geqq m^{(1-r)\bar{N}}.$$

Therefore $P(z^{(k)}) \geqq m^{(1-r)\bar{N}} P(z) > m^{(1-r)\bar{N}+1} p = q$ holds for all $k \leqq N(z)$, that means $z^{(k)} \notin I(q)$ for $k \leqq N(z)$. For $k = N(z)$ we even have

$$P(z^{(N(z))}) \geqq KP(z),$$

which follows from (3.4). This shows that after $N(z)$ generations, during which the orbit $z^{(k)}$ never entered the layer $I(q)$, the "distance from the boundary" $P(z)$ has increased at least by the factor $K>1$. Repeating our argument, we see that the orbit will leave the thicker layer $I(p)$ again, without entering the thinner layer $I(q)$ during that time. Then the play begins again: choose a new $x \notin I(p)$ on the orbit and apply the whole argument to it. The orbit can never reach $I(q)$. This completes the proof of Theorem 1.

Remark 1. It is possible to generalize this theorem to the system

$$x_i' = x_i \frac{C + x_{i-1}F_i(x)}{C+\Phi} \quad \text{with } C>0, \quad \Phi = \sum_{i=1}^{n} x_i x_{i-1} F_i(x),$$

where for $i=1,\cdots,n$, $F_i(x)$ is a continuous, strictly positive function on S_n. This requires only a slight change in the proof of Lemma 1 (see [10, Lemma 3]).

Remark 2. It would be interesting to extend the theorem to the "inhomogeneous hypercycle" [20], [6]:

$$x_i' = x_i(q_i + k_i x_{i-1})/\Phi \quad \text{with } q_i, k_i > 0,$$

$$\Phi = \sum_{i=1}^{n} q_i x_i + \sum_{i=1}^{n} k_i x_i x_{i-1},$$

Here of course the existence of an interior fixed point has to be added as necessary condition for cooperation. We conjecture that this is a sufficient condition too, as it has been shown to be for the corresponding differential equation in [6].

Numerical investigations suggest that for $n \geqq 4$ the attractor in the interior of S_n is a "limit cycle", an attractive invariant closed curve. Enlarging the constant C leads to a contraction of this cycle. For $C \to 0$ it tends to the boundary following the edges $123 \cdots n1$. The "period" of the rotation increases about proportionally to C for $C \to \infty$, for $C \to 0$ it goes to $2n$.

For $n=4$, the limit cycle contracts to the interior fixed point (which is evaluated in § 5) for $C \to \infty$. This particular case can be understood as a kind of Hopf bifurcation: The hypercycle differential equation (1.1), which represents the limit $C \to \infty$ satisfies just the conditions for the usual Hopf bifurcation if $n=4$, i.e., two purely imaginary eigenvalues at the fixed point, the rest of the spectrum has negative real part and the fixed point is asymptotically stable (see [19, Parts I or II] or § 5). So a small perturbation of this differential equation, which makes the fixed point unstable creates a stable limit cycle near the fixed point. That this also holds for perturbations to discrete time, is not surprising. However a detailed proof of this general phenomenon is rather technical; it is given in [8].

This proves the existence of an attracting invariant closed curve for large C in dimension $n=4$. For small $C>0$ or $n \geqq 5$ this is an open problem, even for the differential equation (1.1).

For $n \leqq 3$ the fixed point in the interior is a global attractor as we shall see in § 6.

4. $C=0$ leads to exclusion. For the sake of completeness we will also discuss the limit case $C=0$, where a complete analysis is possible. In this case the transformation (3.1) becomes

$$x_i' = \frac{k_i x_i x_{i-1}}{\Phi}, \tag{4.1}$$

which is not defined on that part of the boundary ∂S_n, where $\Phi = 0$. Introducing a barycentric change of coordinates

$$y_i = \frac{k_{i+1}x_i}{\sum k_{j+1}x_j}$$

as in [20, § 3], we can assume without lose of generality that all rate constants are equal, say $k_i = 1$.

First we treat the lower dimensional cases $n = 3, 4$ ($n = 2$ is trivial).

$n = 3$. In this case, the system has period six. In fact,

$$x_1' : x_2' : x_3' = x_3x_1 : x_1x_2 : x_2x_3 = x_2^{-1} : x_3^{-1} : x_1^{-1}$$

implies that

$$x_1'' : x_2'' : x_3'' = x_3 : x_1 : x_2$$

and so $x^{(6)} = x$.

$n = 4$. In this case, we have exclusion. We have the relations

$$x_1' : x_2' : x_3' : x_4' = x_4x_1 : x_1x_2 : x_2x_3 : x_3x_4,$$

$$x_1'' : x_2'' : x_3'' : x_4'' = x_3x_4^2x_1 : x_4x_1^2x_2 : x_1x_2^2x_3 : x_2x_3^2x_4 = \frac{x_4}{x_2} : \frac{x_1}{x_3} : \frac{x_2}{x_4} : \frac{x_3}{x_1},$$

$$x_1^{(4)} : x_3^{(4)} = x_3^4 : x_1^4,$$

$$x_1^{(8)} : x_3^{(8)} = x_1^{16} : x_3^{16}.$$

If $x_1 < x_3$ the quotient $(x_1/x_3)^{(8k)}$ tends to 0, if $x_1 > x_3$ it goes to infinity. So either $x_1^{(8k)}$ or $x_3^{(8k)}$ tends to zero. This means exclusion.

The cases $n > 4$ require refined arguments.

THEOREM 2. *The system* (4.1) *is exclusive for* $n \geqq 4$. *Every orbit in a certain open, dense and invariant subset of* S_n *converges to the boundary of* S_n, *following finally the sequence of corners* 1, 1, 2, 2, $\cdots$, n, n, 1, 1, $\cdots$.

Proof. Iterating $x_i' \sim x_ix_{i-1}$ we get

$$x_i^{(N)} \sim x_i x_{i-1}^N x_{i-2}^{\binom{N}{2}} \cdots x_{i-N} = \prod_{k=0}^{N} x_{i-k}^{\binom{N}{k}} = \prod_{k=0}^{n-1} x_{i-k}^{S_n(N,k)} \tag{4.2}$$

with

$$S_n(N, k) = \binom{N}{k} + \binom{N}{k+n} + \binom{N}{k+2n} + \cdots.$$

This sum of binomial coefficients can easily be computed:

$$\begin{aligned} S_n(N, k) &= \frac{1}{n}\sum_{p=0}^{n-1} \xi^{-pk}(1+\xi^p)^N, \quad \text{where } \xi = e^{2\pi i/n} \\ &= \frac{1}{n}\sum_{p=0}^{n-1} \xi^{p((N/2)-k)}\left(2\cos\frac{\pi p}{n}\right)^N. \end{aligned} \tag{4.3}$$

For the quotient $x_i : x_j$, we get from (4.2) and (4.3)

$$\begin{aligned} \log\frac{x_i^{(N)}}{x_j^{(N)}} &= \sum_{k=0}^{n-1} S_n(N, k)[\log x_{i-k} - \log x_{j-k}] \\ &= \frac{1}{n}\sum_{p=0}^{n-1} \xi^{pN/2}\left(2\cos\frac{\pi p}{n}\right)^N f_p(x; i, j) \end{aligned} \tag{4.4}$$

with $f_p(x; i, j) = \sum_{k=0}^{n-1} \xi^{-pk}(\log x_{i-k} - \log x_{j-k})$.

To determine the asymptotic behaviour as $N\to\infty$ of (4.4), only the leading term is important. Since $f_0(x; i, j)=0$, we obtain

$$\log\left(\frac{x_i}{x_j}\right)^{(N)} \approx \frac{2}{n}\operatorname{Re}\left(\xi^{N/2}f_1(x; i, j)\right)\left(2\cos\frac{\pi}{n}\right)^N. \tag{4.5}$$

This asymptotic relation is true whenever the coefficient is nonzero, which is the case in an open dense subset G of S_n. $S_n\backslash G$ is a finite union of manifolds determined by equations of the form $\sum_{i=1}^n c_i \log x_i = 0$. Equation (4.5) implies $|\log (x_i/x_j)^{(N)}|\to\infty$, since $2\cos\pi/n>1$ for $n\geqq 4$. This means exclusion.

To determine the asymptotic behaviour more explicitly, we note from (4.4) and $f_p(x; i+1, j+1)=\xi^{-p}f_p(x; i, j)$

$$\log\left(\frac{x_{i+1}}{x_{j+1}}\right)^{(N)} \approx \left(2\cos\frac{\pi}{n}\right)^2 \log\left(\frac{x_i}{x_j}\right)^{(N-2)}. \tag{4.6}$$

Iteration gives

$$\log\left(\frac{x_i}{x_j}\right)^{(N)} \approx \left(2\cos\frac{\pi}{n}\right)^{2n} \log\left(\frac{x_i}{x_j}\right)^{(N-2n)}. \tag{4.7}$$

Note that this extends the final relations obtained in the cases $n=3, 4$.

Equation (4.7) shows that the sequence $x^{(2nN)}$ tends as $N\to\infty$ to a corner of the simplex. More precisely, if $x_i>x_j$ for all $j\neq i$, then $x_i^{(2nN)}\to 1$ for $N\to\infty$: the ith coordinate dominates.

From (4.6) we now infer that if species i dominates in the Nth generation, then $i+1$ will dominate two generations later. To exclude the possibility that one generation later j will dominate with $j\neq i$, $i+1$, we use the following consequence of (4.5): A relation $x_i>x_j$ persists during exactly n generations, then for the next n generations $x_i<x_j$ holds, and so on.

This implies finally that every orbit in G tends to the $2n$-periodic "limit cycle", consisting of the sequence of corners $1, 1, 2, 2, \cdots, n, n, 1, 1, \cdots$. Of course this strange doubling is only possible since the map (4.1) is not defined at the corners of the simplex.

5. The fixed point. It is easy to see that our system (3.1) has exactly one fixed point p in the interior of S_n, and it is determined by the equations

$$k_2x_1 = k_3x_2 = \cdots = k_nx_{n-1} = k_1x_n \quad\text{and}\quad \sum x_i = 1. \tag{5.1}$$

In order to compute the eigenvalues of the Jacobian, we write (3.1) in the form

$$x_i' - x_i = x_i\frac{k_ix_{i-1}-\Phi}{C+\Phi}. \tag{5.2}$$

The function on the right side of (5.2) differs from the vector field of the hypercycle differential equation

$$\dot{x}_i = x_i(k_ix_{i-1}-\Phi) \tag{5.3}$$

only by the factor $C+\Phi$. So their Jacobians and hence their eigenvalues are also proportional differing by the factor $C+\Phi$.

Now the eigenvalues of (5.3) were evaluated in [20] and found to be

$$\lambda_j = N\exp\left(\frac{2\pi ij}{n}\right), \qquad j=1,\cdots,n-1 \quad\text{with } N^{-1}=\sum k_i^{-1}.$$

Therefore the eigenvalues of (3.1) are given by

$$\omega_j = 1 + \frac{N}{C+N} \exp\left(\frac{2\pi i j}{n}\right), \qquad j = 1, \cdots, n-1.$$

(The nth eigenvalue $\lambda_0 = -N$ (resp. $\omega_0 = C/(C+N)$) corresponds to the relation $\sum x_i = 1$.)

The ω_j form a regular n-gon with center 1 and radius $N/(C+N) \leqq 1$. Now the fixed point is a sink if and only if $|\omega_j| < 1$ for all $j = 1, \cdots, n-1$. For $n \geqq 4$ this is not possible, since at least $|\omega_1| > 1$. Therefore the fixed point is a saddle.

If $n = 3$ and $C = 0$, we have $|\omega_1| = |\omega_2| = 1$ which "explains" our result of § 4 that there are only periodic orbits. If $n = 3$ and $C > 0$ the fixed point is a sink. The same holds for the trivial case $n = 2$.

This leads to the problem of how to determine the basin of attraction which will be solved next with the help of a Lyapunov function.

6. Dimension $n = 3$.

THEOREM 3. *The function*

$$V = \left(\sum_{i=1}^{3} \frac{1}{k_{i+1}x_i}\right)\left(\sum_{i=1}^{3} k_{i+1}x_i\right) = \sum_{i,j=1}^{3} \frac{k_{i+1}x_i}{k_{j+1}x_j}$$

is a global Lyapunov function for the hypercycle (3.1) *in the case $n = 3$. More exactly, V attains its unique minimum at the fixed point p given by* (5.1) *and $V' \leqq V$ holds everywhere on S_3. For $C > 0$, $V' < V$ holds in* int $S_3 \backslash \{p\}$. *Therefore every orbit in* int S_3 *tends to the fixed point. For $C = 0$, V is an invariant: $V' \equiv V$. Recall that every orbit in* int S_3 *has period* 6.

Proof. Let $y_i = k_{i+1}x_i$. Then $y_i' = y_i(C + y_{i-1}/(C+\Phi))$ and $V = \sum_{i,j=1}^{3} (y_i/y_j)$. It is clear that

$$V = 3 + \sum_{i<j} \left(\frac{y_i}{y_j} + \frac{y_j}{y_i}\right) \geqq 9$$

with equality only for $y_1 = y_2 = y_3$, that is for $x = p$.

$$V' = \sum_{i,j} \frac{y_i'}{y_j'} = \sum_{i,j} \frac{y_i}{y_j} \frac{C + y_{i-1}}{C + y_{j-1}},$$

$$V - V' = \sum_{i,j} \frac{y_i}{y_j} \frac{y_{j-1} - y_{i-1}}{C + y_{j-1}} = \left(\sum_i y_i\right) \sum_j \frac{y_{j-1}}{y_j(C + y_{j-1})} - \left(\sum_i y_i y_{i-1}\right) \sum_j \frac{1}{y_j(C + y_{j-1})}. \tag{6.1}$$

In order to prove $V - V' \geqq 0$, we multiply (6.1) by the common denominator $\prod_{j=1}^{3} y_j(C + y_{j-1})$ and introduce the abbreviations

$$S = y_1 + y_2 + y_3, \quad R = y_1y_2 + y_1y_3 + y_2y_3, \quad P = y_1y_2y_3.$$

It then remains to show the positivity of

$$\begin{aligned} &S \cdot \sum_j y_{j-1}^2 y_{j+1}(C + y_j)(C + y_{j+1}) - R \cdot \sum_i y_i y_{i+1}(C + y_{i-1})(C + y_i) \\ &\quad = I_0(y) + I_1(y)C + I_2(y)C^2 \end{aligned} \tag{6.2}$$

with $I_0(y)=0$. This proves that $V'=V$ for $C=0$. Next

$$\begin{aligned}I_1 &= S\sum y_{i-1}^2 y_{i+1}(y_i+y_{i+1}) - R\sum y_i y_{i+1}(y_i+y_{i-1})\\ &= S(PS+\sum y_i^2 y_{i+1}^2) - R(3P+\sum y_i^2 y_{i+1})\\ &= P(S^2-3R)+S\sum y_i^2 y_{i+1}^2 - R\sum y_i^2 y_{i+1}\\ &= P(\sum y_i^2 - R)+\sum y_i^3 y_{i+1}^2+\sum y_i^2 y_{i+1}^3+\sum y_i^2 y_{i+1}^2 y_{i+2}\\ &\quad -\sum y_{i-1} y_{i+1}^3 y_{i+1} - \sum y_i^3 y_{i+1}^2 - \sum y_i^2 y_{i+1}^2 y_{i+2}\\ &= P(\sum y_i^2 - R)+\sum y_i^2 y_{i+1}^3 - P\sum y_i^2\\ &= \sum y_i^2 y_{i+1} - PR\\ &= \sum (y_i - y_{i+1})^2 y_{i-1} y_i \geqq 0.\end{aligned}$$

And finally,

$$I_2(y) = S\sum y_i y_{i+1}^2 - R^2 = (\sum y_i)(\sum y_i y_{i+1}^2) - (\sum y_i y_{i+1})^2 \geqq 0,$$

which is a consequence of the Cauchy–Schwarz inequality.

Hence the sum in (6.2) is $\geqq 0$ with equality only for $y_1=y_2=y_3$ and the proof of Theorem 3 is complete.

7. Some remarks on more general dynamical systems. It would be of interest to study the more general equation

$$x_i' = x_i \frac{\sum_{j=1}^n a_{ij}x_j}{\Phi} \quad \text{with } \Phi = \sum_{i,j=1}^n a_{ij}x_i x_j. \tag{7.1}$$

which may be considered the discrete analogue of the differential equation

$$\dot{x}_i = x_i\left(\sum_{j=1}^n a_{ij}x_j - \Phi\right). \tag{7.2}$$

As we have pointed out in § 2, both systems arise from evolutionary game theory and provide a dynamics for a symmetric two-person game with pay-off matrix $A=(a_{ij})$. In the special case of symmetric matrices $a_{ij}=a_{ji}$ they arise also in population genetics as selection equations. Together with the application to prebiotic evolution, mentioned in the introduction, these equations therefore play a central role in three parts of biomathematics. Moreover it has been shown [7] that the differential equation (7.2) is equivalent, by a simple change of variables, to the Volterra–Lotka equations

$$\dot{x}_i = x_i\left(\varepsilon_i + \sum_{j=1}^n a_{ij}x_j\right). \tag{7.3}$$

The differential equation (7.2) has been studied extensively, see, e.g., [1], [2], [6], [9], [13], [19, Part II], [20], [21], [22], besides the vast literature on (7.3). For the difference equation (7.1) however much less is known.

For the selection equation ($a_{ij}=a_{ji}$), there is Fisher's fundamental theorem of natural selection, which holds for both systems. It says that the mean fitness Φ is a monotonical increasing function and hence optimized for $t\to+\infty$.

Another important special case is for circulant matrices ($a_{ij}=a_{j-i}$) for which the differential equation was studied in [19, Part II]. For the discrete model we can prove the following theorem on the rock-scissors-paper game.

THEOREM 4. *Consider the system*

$$x_i' = x_i(a_0x_i + a_1x_{i+1} + a_2x_{i+2})/\Phi, \qquad i = 1, 2, 3,$$

where $a_i \geqq 0$. *Then* $V = \Phi/x_1x_2x_3$ *is a Lyapunov function. More precisely*:

(i) *If* $a_1a_2 > a_0^2$, *then* $V' \leqq V$ *and* $(\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ *is a global attractor.*

(ii) *If* $a_1a_2 = a_0^2$, *then* $V' \equiv V$. *V is an invariant. The orbits are rotating on invariant closed curves.*

(iii) *If* $a_1a_2 < a_0^2$, *then* $V' \geqq V$. *The fixed point is a repellor, all orbits tend to the boundary.*

This is analogous to a result on the corresponding differential equation $\dot{x}_i = x_i(a_0x_i + a_1x_{i+1} + a_2x_{i+2} - \Phi)$, obtained in [19, Part II]. There the function V is replaced by $P = x_1x_2x_3$ and the conditions $a_1a_2 \gtreqless a_0^2$ by $a_1 + a_2 \gtreqless 2a_0$.

The proof of Theorem 4 is straightforward like that of Theorem 3, but more technical and much too long to be reproduced here.

Besides this there is a recent paper of Losert and Akin [13] treating both (7.1) and (7.2). They close a long overlooked gap by proving in all detail that in the selection equation all orbits converge to a fixed point. Furthermore they show that the map (7.1) defines a diffeomorphism on S_n, if all $a_{ij} > 0$.

Their results and those obtained in this paper, together with numerical calculations suggest the following rough equivalence principle, also formulated in [13]: The class of discrete time models (7.1) behave similarly to the continuous time models (7.2), but the discrete model is harder. It should be possible to prove this vague statement for $n = 3$, by giving a classification analogous Zeeman [22] gave for the differential equation. Theorems 3 and 4 above are some partial results in this direction. The key to the full classification will be the invariant for the system (7.1) with the special matrix

$$\begin{pmatrix} 1 & a & b^{-1} \\ a^{-1} & 1 & c \\ b & c^{-1} & 1 \end{pmatrix}.$$

This is the discrete analogue of an antisymmetric matrix, for which the invariant of (7.2) is of the form $\prod x_i^{p_i}$, with p a fixed point.

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