of $t \to \log P(\mathbf{x}(t))$ is given by

$$(\log P)^{\cdot} = \sum_{i=1}^{n} \frac{\dot{x}_i}{x_i} = 1 - n \sum_{j=1}^{n} x_j x_{j-1} . \tag{12.9}$$

For $n = 2$ and $n = 3$, this function is positive and vanishes only at $\mathbf{m}$.

Exercise 12.1.1 Show that for $n = 4$, the function $\dot{P}/P$ is still nonnegative, and vanishes on the set $\{\mathbf{x} \in S_4 : x_1 + x_3 = x_2 + x_4\}$, which contains only one invariant set, consisting of $\mathbf{m}$ only.

The following theorem is an immediate consequence.

Theorem 12.1.2 *For short hypercycles (i.e. $n = 2, 3, 4$) the inner rest point is globally stable.*

For $n \geq 5$, however, the interior rest point is unstable, and one is left with the question whether a permanent coexistence of the different types of polynucleotides is possible. This question will be addressed in the next section.

Exercise 12.1.3 An alternative way of proving the global stability of $\mathbf{m}$ for $n = 3$ would be to use other Lyapunov functions than (12.8). Try e.g. $x_1^{-p} + x_2^{-p} + x_3^{-p}$.

Exercise 12.1.4 Write down a global Lyapunov function for (12.1) if $n \leq 4$.

Exercise 12.1.5 Consider the hypercycle equation (12.1) with $n = 3$. For which values of k_i is the unique interior rest point evolutionarily stable? Show that for $n = 4$, the interior rest point (which, as we know, is globally stable) is never an ESS.

12.2 Permanence

As we have just seen, hypercycles do not reach a stable rest point for $n \geq 5$. They may nevertheless serve their purpose, which is to allow the coexistence of several types of self-reproducing macromolecules: whether the concentrations converge or oscillate in a regular or irregular way is of secondary importance. The main thing is that they do not vanish: more precisely, that there exists a *threshold value* $\delta > 0$ such that every solution of (12.6) in $\operatorname{int} S_n$ satisfies $x_i(t) > \delta$ for $i = 1, \dots, n$ whenever t is large enough. This implies that if initially all species are present, even if only in very small quantities, then after some time some sizeable amount of each will be present. No perturbation which is smaller than δ could wipe out a molecular species.

This property, which is important in many other contexts, deserves a name. A dynamical system defined on S_n is said to be *permanent* if there exists a $\delta > 0$ such that $x_i(0) > 0$ for $i = 1, \ldots, n$ implies

$$\liminf_{t \to +\infty} x_i(t) > \delta \tag{12.10}$$

for $i = 1, \ldots, n$.

Let us stress that δ does *not* depend on the initial values $x_i(0)$. Permanence means more than just that no component will vanish. If every state is a rest point, for example, the system is not permanent. Even if initially the concentrations were abundant, a sequence of tiny perturbations could lead to the extinction of a species. For a permanent system, on the other hand, perturbations which are sufficiently small and rare cannot lead to extinction. The boundary of the state space S_n acts as a *repellor.*

The proof that the hypercycle is permanent is not obvious. We shall start with a more general theorem giving conditions for permanence which will also be useful in many other situations.

Theorem 12.2.1 *Let us consider a dynamical system on S_n leaving the boundary invariant. Let $P : S_n \to \mathbb{R}$ be a differentiable function vanishing on* $\mathrm{bd}\, S_n$ *and strictly positive in* $\mathrm{int}\, S_n$. *If there exists a continuous function Ψ on S_n such that the following two conditions hold:*

$$\textit{for } \mathbf{x} \in \mathrm{int}\, S_n, \quad \frac{\dot{P}(\mathbf{x})}{P(\mathbf{x})} = \Psi(\mathbf{x}) \tag{12.11}$$

$$\textit{for } \mathbf{x} \in \mathrm{bd}\, S_n, \quad \int_0^T \Psi(\mathbf{x}(t))dt > 0 \textit{ for some } T > 0\,, \tag{12.12}$$

then the dynamical system is permanent.

The value $P(\mathbf{x})$ measures the distance from $\mathbf{x}$ to the boundary. If one had $\Psi > 0$ on $\mathrm{bd}\, S_n$ — a condition implying (12.12) — then $\dot{P}(\mathbf{x}) > 0$ for any $\mathbf{x} \in \mathrm{int}\, S_n$ near the boundary, and so P would increase, i.e. the orbit would be repelled from $\mathrm{bd}\, S_n$. In that case, P would act like a Lyapunov function. Quite often, however, one cannot find a function P of this type. The weaker version defined above is said to be an *average Lyapunov function*: its time average acts like a Lyapunov function.

Proof The $T > 0$ in (12.12) can obviously be chosen as a locally continuous function $T(\mathbf{x})$. Its infimum τ is positive, since $\operatorname{bd} S_n$ is compact. For $h > 0$, we define

$$U_h = \left\{ \mathbf{x} \in S_n : \text{ there is a } T > \tau \text{ such that } \frac{1}{T}\int_0^T \Psi(\mathbf{x}(t))dt > h \right\} .$$

For $\mathbf{x} \in U_h$ we set

$$T_h(\mathbf{x}) = \inf \left\{ T > \tau : \frac{1}{T}\int_0^T \Psi(\mathbf{x}(t))dt > h \right\} .$$

We show first that U_h is open and T_h upper semicontinuous: in other words, if $\mathbf{x} \in U_h$ and $\alpha > 0$ are given, then for $\mathbf{y} \in S_n$ sufficiently close to $\mathbf{x}$, one has

$$\mathbf{y} \in U_h \quad \text{and} \quad T_h(\mathbf{y}) < T_h(\mathbf{x}) + \alpha . \tag{12.13}$$

Indeed, for α and $\mathbf{x}$ there is a $T \in [\tau, T_h(x) + \alpha[$ such that

$$\varepsilon = \frac{1}{T}\int_0^T \Psi(\mathbf{x}(t))dt - h > 0 .$$

Since the solutions of ordinary differential equations depend continuously on the initial values, $\mathbf{x}(t)$ and $\mathbf{y}(t)$ are near each other, for all $t \in [0, T]$, if $\mathbf{x}$ and $\mathbf{y}$ are sufficiently close. The uniform continuity of Ψ implies $|\Psi(\mathbf{x}(t)) - \Psi(\mathbf{y}(t))| < \varepsilon$ for all times $t \in [0, T]$, and hence

$$\frac{1}{T}\int_0^T \Psi(\mathbf{y}(t))dt > \frac{1}{T}\int_0^T \Psi(\mathbf{x}(t))dt - \varepsilon = h$$

from which (12.13) follows.

By (12.12) the family of nested sets U_h (with $h > 0$) is an open covering of the compact set $\operatorname{bd} S_n$. There exists one $h > 0$, then, such that U_h is an open neighbourhood of $\operatorname{bd} S_n$ (in S_n). Since $S_n \backslash U_h$ is also compact, P attains its minimum on this set. If we choose $p > 0$ smaller than this minimum, then the set

$$I(p) = \{\mathbf{x} \in S_n : 0 < P(\mathbf{x}) \leq p\}$$

is contained in U_h. $I(p)$ is a 'boundary layer' which is very thin if p is small. We shall show that if $\mathbf{x} \in I(p)$, then there exists a $t > 0$ such that $\mathbf{x}(t) \notin I(p)$. Indeed, otherwise $\mathbf{x}(t)$ would have to be in U_h for all $t > 0$. In this case, there exists a $T \geq \tau$ such that

$$\frac{1}{T}\int_t^{T+t} \Psi(\mathbf{x}(s))ds > h \, .$$

But since $\Psi = (\log P)^{\cdot}$ holds in $\operatorname{int} S_n$, this implies

$$h < \frac{1}{T}\int_t^{T+t} (\log P)^{\cdot}(\mathbf{x}(s))ds = \frac{1}{T}[\log P(\mathbf{x}(T+t)) - \log P(\mathbf{x}(t))] \, ,$$

that is,

$$P(x(T+t)) > P(\mathbf{x}(t))e^{hT} \geq P(\mathbf{x}(t))e^{h\tau} \, .$$

Hence there would exist a sequence t_n for which $P(\mathbf{x}(t_n))$ tends to $+\infty$, in contradiction to the boundedness of P.

Let us denote by $\bar{I}(p)$ the union of $I(p)$ with $\operatorname{bd} S_n$. All that remains to be shown is that there exists a $q \in]0,p[$ such that $\mathbf{x}(0) \notin \bar{I}(p)$ implies $\mathbf{x}(t) \notin I(q)$ for all $t \geq 0$.

The upper semicontinuous function T_h admits an upper bound $\bar{T}$ on the compact set $\bar{I}(p)$. Let t_0 be the first time when $\mathbf{x}(t)$ reaches $\bar{I}(p)$, i.e.

$$t_0 = \min\{t > 0 : \mathbf{x}(t) \in \bar{I}(p)\},$$

and let $\mathbf{x}(t_0) = \mathbf{y}$. Obviously $P(\mathbf{y}) = p$. Let m be the minimum of Ψ on S_n. For $m \geq 0$, all is clear, since P never decreases. In case $m < 0$ we set $q = pe^{m\bar{T}}$. For $t \in]0, \bar{T}[$,

$$\frac{1}{t}\int_0^{t} \Psi(\mathbf{y}(s))ds \geq m,$$

and hence, just as above

$$P(\mathbf{y}(t)) \geq P(\mathbf{y})e^{mt} > pe^{m\bar{T}} = q \, .$$

Hence the solution does not reach $I(q)$ for $t \in]0, \bar{T}[$. Furthermore, since $\mathbf{y} \in I(p)$, there is a time $T \in [\tau, \bar{T}[$ such that

$$P(\mathbf{y}(T)) \geq pe^{h\tau} \geq p \, .$$

At time $t + T$, thus, the orbit of $\mathbf{x}$ has left $I(p)$ without having reached $I(q)$. Repeating this argument, one sees that the orbit can never reach $I(q)$. □

Theorem 12.2.2 *It is sufficient to verify* (12.12) *for all* $\mathbf{x}$ *in the* ω*-limits of orbits on the boundary of* S_n.

Proof There exists, as before, an $h > 0$ such that U_h is an open neighbourhood of $\omega(\mathbf{x})$ (in S_n) for all $\mathbf{x} \in \operatorname{bd} S_n$. Since $\mathbf{x}(t)$ converges to $\omega(\mathbf{x})$, there is a t_1 such that $\mathbf{x}(t) \in U_h$ for all $t \geq t_1$. There is a $t_2 \geq t_1 + \tau$ such that

$$\frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \Psi(\mathbf{x}(t))dt > h ,$$

similarly a $t_3 \geq t_2 + \tau$ such that

$$\frac{1}{t_3 - t_2} \int_{t_2}^{t_3} \Psi(\mathbf{x}(t))dt > h,$$

etc. We obtain a sequence $t_1, t_2, t_3, \ldots$ satisfying

$$\frac{1}{t_k - t_1} \int_{t_1}^{t_k} \Psi(\mathbf{x}(t))dt > h .$$

If k is sufficiently large, the time average

$$\frac{1}{t_k} \int_{0}^{t_k} \Psi(\mathbf{x}(t))dt$$

is close to the previous expression and hence positive. □

Exercise 12.2.3 Show that theorems 12.2.1 and 12.2.2 are valid if Ψ is only assumed to be lower semicontinuous. This can always be achieved by defining, for $\mathbf{x} \in \operatorname{bd} S_n$,

$$\Psi(\mathbf{x}) = \liminf_{\mathbf{y} \to \mathbf{x}} \frac{\dot{P}}{P}(\mathbf{y})$$

where $\mathbf{y}$ belongs to $\operatorname{int} S_n$.

12.3 The permanence of the hypercycle

Theorem 12.3.1 *The hypercycle* (12.1) *is permanent.*

Proof We shall use theorem 12.2.1. As the average Lyapunov function $P(\mathbf{x})$ we choose the product $x_1 x_2 \ldots x_n$ which has already stood us in good stead in section 12.1. We have $\dot{P} = P\Psi$ with $\Psi = \sum k_i x_{i-1} - n\bar{f}$, where $\bar{f} = \sum k_j x_j x_{j-1}$. In order to show that P is an average Lyapunov function, it remains to verify condition (12.12). Thus we have to show that for every $\mathbf{x} \in \operatorname{bd} S_n$, there exists a $T > 0$ such that

$$\frac{1}{T}\int_0^T \sum_{i=1}^n (k_i x_{i-1} - n\bar{f})dt > 0 \tag{12.14}$$

i.e. such that

$$\frac{1}{T}\int_0^T \bar{f}(\mathbf{x}(t))dt < \frac{1}{nT}\int_0^T \sum k_i x_{i-1} dt \,. \tag{12.15}$$

Since $k := \min k_i > 0$ and $\sum k_i x_{i-1} \geq k$ for all $\mathbf{x} \in S_n$, the right hand side of (12.15) is not smaller than k/n. It is enough, therefore, to show that there is no $\mathbf{x} \in \operatorname{bd} S_n$ such that for all $T > 0$

$$\frac{1}{T}\int_0^T \bar{f}(\mathbf{x}(t))dt \geq \frac{k}{n} \,. \tag{12.16}$$

Let us proceed indirectly and assume that there is such an $\mathbf{x} \in S_n$. We shall show by induction that

$$\lim_{t\to+\infty} x_i(t) = 0 \tag{12.17}$$

for $i = 1, \ldots, n$. Since $\mathbf{x} \in \operatorname{bd} S_n$, there exists an index i_0 such that $x_{i_0}(t) \equiv 0$. Now if $x_i(t)$ converges to 0, then so does x_{i+1}; indeed, if $x_{i+1}(t) > 0$, one obtains from

$$\left(\log x_{i+1}\right)^{\cdot} = \frac{\dot{x}_{i+1}}{x_{i+1}} = k_{i+1}x_i - \bar{f}$$

by integrating from 0 to T and dividing by T

$$\begin{aligned}\frac{\log x_{i+1}(T) - \log x_{i+1}(0)}{T} &= \frac{1}{T}\int_0^T \left(\log x_{i+1}\right)^{\cdot} dt \\ &= \frac{1}{T}\int_0^T k_{i+1}x_i(t)dt - \frac{1}{T}\int_0^T \bar{f}(\mathbf{x}(t))dt \,.\end{aligned}$$

From $x_i(t) \to 0$ it follows that

$$\frac{1}{T}\int_0^T k_{i+1}x_i(t)dt < \frac{k}{2n}$$

for all sufficiently large T. Together with (12.16) this implies

$$\log x_{i+1}(T) - \log x_{i+1}(0) < -\frac{kT}{2n}$$

or

$$x_{i+1}(T) < x_{i+1}(0)\exp\left(-\frac{kT}{2n}\right) . \tag{12.18}$$

Hence $x_{i+1}(t) \to 0$ and (12.17) must hold. This contradicts the relation $\sum x_i = 1$. Hence P is an average Lyapunov function and (12.1) is permanent. □

Let us mention that the same proof shows that the considerably more general equation obtained by replacing the constants $k_i > 0$ in (12.1) by positive functions $F_i(\mathbf{x})$ is also permanent. Such equations describe the reaction kinetics for more realistic hypercycle models.

Exercise 12.3.2 Analyse the discrete time dynamics (7.23) for the hypercycle. Prove permanence for $C > 0$. Analyse the local stability for the interior fixed point $\mathbf{p}$. Prove that $\mathbf{p}$ is globally stable if $n \leq 3$ and $C > 0$. Analyse the asymptotic behaviour for $C = 0$.

12.4 The competition of disjoint hypercycles

Let us assume now that the 'primordial soup' contains n types of RNA molecules organized into *several* disjoint hypercycles. This can be described by a permutation π of the set $\{1, \ldots, n\}$. Every permutation can be decomposed into *elementary cycles* $\Gamma_1, \ldots \Gamma_s$: these correspond to hypercycles. The dynamics is given by

$$\dot{x}_i = x_i \left(k_i x_{\pi(i)} - \sum k_j x_j x_{\pi(j)}\right) \tag{12.19}$$

with $k_i > 0$ for $i = 1, \ldots, n$.

If π consists of a unique cycle, we obtain — up to a reordering of the indices — the familiar hypercycle equation (12.1). If the elementary cycle Γ_j consists of a unique element i (a fixed point of the permutation π), then M_i is an autocatalytic molecular type. As in section 12.1 we may perform a transformation

$$y_i = \frac{k_{\tau(i)} x_i}{\sum_j k_{\tau(j)} x_j} \tag{12.20}$$

(with $\tau = \pi^{-1}$) and get rid of the k_i. Again there is a unique rest point in $\operatorname{int} S_n$, namely the centre $\mathbf{m} = \frac{1}{n}\mathbf{1}$.

with respect to U (or with respect to $\operatorname{int} S_n$), which is $(-1)^{n-1}$. For (13.6) this implies that the interior fixed point exists and is unique and therefore regular. Hence its index is $(-1)^{n-1}$. □

Exercise 13.4.9 Prove a similar result for robustly persistent systems (13.2) with uniformly bounded orbits.

13.5 Necessary conditions for permanence

Theorem 13.5.1 *If* (13.6) *or* (13.7) *is permanent, then there exists a unique interior rest point* $\hat{\mathbf{x}}$ *and, for each* $\mathbf{x}$ *in the interior of the state space,*

$$\lim_{T\to+\infty} \frac{1}{T} \int_0^T \mathbf{x}(t)dt = \hat{\mathbf{x}}.$$

Proof Theorem 13.3.1 implies that there exists at least one interior rest point. If there were two of them, the line l joining them would consist only of rest points, and intersect the boundary of the state space. But since the boundary is a repellor, there cannot be fixed points arbitrarily close by. The convergence of the time averages, finally, follows from theorems 5.2.3 and 7.6.4, and the fact that by permanence, if $\mathbf{x}$ is in the interior of the state space, then so is $\omega(\mathbf{x})$. □

Theorem 13.5.2 *Let* (13.7) *be permanent and denote the Jacobian at the unique interior rest point* $\hat{\mathbf{x}}$ *by* D. *Then*

$$(-1)^n \det D > 0 \ , \tag{13.19}$$

$$\operatorname{tr} D < 0 \ , \tag{13.20}$$

$$(-1)^n \det A > 0 \ . \tag{13.21}$$

Proof The conditions on the signs of the determinants are simple consequences of the index theorem 13.3.1. Indeed, since $\hat{\mathbf{x}}$ is the unique solution of $-\mathbf{r} = A\mathbf{x}$, the matrix A is nonsingular. Also, theorem 13.3.1 implies that $i(\hat{\mathbf{x}}) = (-1)^n$. Now

$$d_{ij} = \hat{x}_i a_{ij} \tag{13.22}$$

and so D is also nonsingular. Thus $i(\hat{\mathbf{x}})$ is just the sign of $\det D$. This establishes (13.19) and via (13.22) also (13.21).
In order to prove the trace condition (13.20), we shall have to use the

such that $\mathbf{c} \cdot \mathbf{y}$ is positive for all $\mathbf{y} \in K$. (Here, $\mathbf{x} \cdot \mathbf{y} = \sum x_i y_i$ is the usual inner product in $\mathbb{R}^n$.) Setting

$$V(\mathbf{x}) = \sum c_i \log x_i \,, \tag{5.3}$$

we see that V is defined on $\operatorname{int} \mathbb{R}^n_+$. If $\mathbf{x}(t)$ is a solution of (5.1) in $\operatorname{int} \mathbb{R}^n_+$, then the time derivative of $t \to V(\mathbf{x}(t))$ satisfies

$$\dot{V} = \sum c_i \frac{\dot{x}_i}{x_i} = \sum c_i y_i = \mathbf{c} \cdot \mathbf{y} > 0 \,. \tag{5.4}$$

Thus V is increasing along each orbit. But then no point $\mathbf{z} \in \operatorname{int} \mathbb{R}^n_+$ may belong to its ω-limit: indeed, by Lyapunov's theorem 2.6.1, the derivative $\dot{V}$ would have to vanish there. This contradiction completes the proof. □

As a consequence, we see that *if* (5.1) *admits no interior rest point, then it is gradient-like in* $\operatorname{int} \mathbb{R}^n_+$.

In general, (5.2) will admit at most one solution in $\operatorname{int} \mathbb{R}^n_+$. It is only in the degenerate case $\det A = 0$ that (5.2) can have more than one solution: these will form a continuum of rest points.

Exercise 5.2.2 Construct an invariant of motion in the case of a continuum of fixed points. (Hint: try (5.3) for suitable $\mathbf{c}$.)

If there exists a unique interior rest point $\mathbf{p}$, and if the solution $\mathbf{x}(t)$ converges neither to the boundary nor to infinity, then its time average converges to $\mathbf{p}$.

Theorem 5.2.3 *If there exist positive constants a and A such that $a < x_i(t) < A$ for all i and all $t > 0$, and* $\mathbf{p}$ *is the unique rest point in* $\operatorname{int} \mathbb{R}^n_+$, *then*

$$\lim_{T \to \infty} \frac{1}{T} \int_0^T x_i(t) dt = p_i \qquad i = 1, \ldots, n \,. \tag{5.5}$$

Proof Let us write (5.1) in the form

$$(\log x_i)^{\cdot} = r_i + \sum_j a_{ij} x_j \tag{5.6}$$

and integrate it from 0 to T. After division by T, we obtain

$$\frac{\log x_i(T) - \log x_i(0)}{T} = r_i + \sum a_{ij} z_j(T) \tag{5.7}$$

where

$$z_j(T) = \frac{1}{T}\int_0^T x_j(t)dt\,. \tag{5.8}$$

Clearly $a < z_j(T) < A$ for all j and all $T > 0$. Now consider any sequence T_k converging to $+\infty$. The bounded sequence $z_j(T_k)$ admits a convergent subsequence. By diagonalization we obtain a subsequence — which we are going to denote by T_k again — such that $z_j(T_k)$ converges for every j towards some limit which we shall denote by $\bar{z}_j$. The sequences $\log x_i(T_k) - \log x_i(0)$ are also bounded. Passage to the limit in (5.7) thus leads to

$$0 = r_i + \sum a_{ij}\bar{z}_j\,.$$

The point $\bar{\mathbf{z}} = (\bar{z}_1, \ldots, \bar{z}_n)$ is therefore a rest point. Since $\bar{z}_j \geq a > 0$, it belongs to $\operatorname{int}\mathbb{R}^n_+$. Hence it coincides with $\mathbf{p}$. This implies (5.5). □

Exercise 5.2.4 Give another proof of theorem 5.2.1, using a similar time-average argument. (This will work at least in the generic case.)

Exercise 5.2.5 Show that a similar averaging principle holds for the difference equation $\mathbf{x} \to \mathbf{x}'$ with

$$x_i' = x_i \exp(r_i + \sum_j a_{ij}x_j).$$

Exercise 5.2.6 What happens with theorem 5.2.3 if the assumption concerning the uniqueness of the rest point is dropped?

5.3 The Lotka–Volterra equations for food chains

Let us investigate food chains with n members (chains with up to six members are found in nature). The first population is the prey for the second, which is the prey for the third, and so on up to the n-th, which is at the top of the food pyramid. Taking competition within each species into account, and assuming constant interaction terms, we obtain

$$\begin{aligned} \dot{x}_1 &= x_1(r_1 - a_{11}x_1 - a_{12}x_2) \\ \dot{x}_j &= x_j(-r_j + a_{j,j-1}x_{j-1} - a_{jj}x_j - a_{j,j+1}x_{j+1}) \quad j = 2, \ldots, n-1 \\ \dot{x}_n &= x_n(-r_n + a_{n,n-1}x_{n-1} - a_{nn}x_n) \end{aligned} \tag{5.9}$$

with all $r_j, a_{ij} > 0$. The case $n = 2$ is just (2.15). We shall presently see that the general case leads to nothing new:

Exercise 7.6.2 Prove this exclusion principle directly: (a) show that there exists a $\mathbf{c} \in \mathbb{R}^n$ such that $\mathbf{c}\cdot\mathbf{z} > \mathbf{c}\cdot\mathbf{y}$ for all $\mathbf{z} \in W$ and all $\mathbf{y} \in D$, where $W = A(\operatorname{int} S_n)$ and $D = \{\mathbf{y} \in \mathbb{R}^n : y_1 = \cdots = y_n\}$ (W and D are convex); (b) show that $\sum c_i = 0$; (c) show that $V(\mathbf{x}) = \sum c_i \log x_i$ is strictly increasing along the orbits in $\operatorname{int} S_n$.

Exercise 7.6.3 Show that the game with payoff matrix A admits a Nash equilibrium in $\operatorname{int} S_n$ if and only if there is no strategy $\mathbf{u}$ dominating a strategy $\mathbf{v}$ in the sense that $\mathbf{u}\cdot A\mathbf{x} > \mathbf{v}\cdot A\mathbf{x}$ for all $\mathbf{x} \in \operatorname{int} S_n$. (Hint: the vector $\mathbf{c}$ from the previous exercise can be written as the difference $\mathbf{u} - \mathbf{v}$ of two strategies.)

Theorem 7.6.4 *If* (7.3) *admits a unique rest point* $\mathbf{p}$ *in* $\operatorname{int} S_n$, *and if the* ω*-limit of the orbit of* $\mathbf{x}(t)$ *is in* $\operatorname{int} S_n$, *then*

$$\lim_{t\to\infty} \frac{1}{T} \int_0^T x_i(t)dt = p_i \qquad i = 1, \ldots, n\,. \tag{7.31}$$

This does not follow immediately from the corresponding theorem 5.2.3 for Lotka–Volterra equations, since a coordinate transformation or a change in velocity could affect the time average. Hence, we have the following:

Exercise 7.6.5 Prove the previous theorem. (Hint: proceed along the same lines as in the Lotka–Volterra case.)

Exercise 7.6.6 Show that the solutions of the discrete time version

$$x_i \to x_i \frac{e^{(A\mathbf{x})_i}}{\sum x_k e^{(A\mathbf{x})_k}} \tag{7.32}$$

also have this averaging property.

7.7 The rock–scissors–paper game

We shall now analyse the general rock–scissors–paper game, which is characterized by having three pure strategies such that R_1 is beaten by R_2, which is beaten by R_3, which is beaten by R_1. Since we can normalize the payoff matrix such that the diagonal terms are 0, we obtain

$$A = \begin{bmatrix} 0 & -a_2 & b_3 \\ b_1 & 0 & -a_3 \\ -a_1 & b_2 & 0 \end{bmatrix} \tag{7.33}$$