PERMANENCE IN POLYMATRIX REPLICATORS

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ABSTRACT. Generally a biological system is said to be permanent if under small perturbations none of the species goes to extinction. In 1979 P. Schuster, K. Sigmund, and R. Wolff [14] introduced the concept of permanence as a stability notion for systems that models the self-organization of biological macromolecules. After, in 1987 W. Jansen [8], and J. Hofbauer and K. Sigmund [5] give sufficient conditions for permanence in the usual replicators. In this paper we extend these results for polymatrix replicators.

1. INTRODUCTION

In the 1970's J. Maynard Smith and G. Price [10] applied the theory of strategic games developed by J. von Neumann and O. Morgenstern [17] in the 1940's to investigate the dynamical processes of biological populations, giving rise to the feld of the Evolutionary Game Theory (EGT).

Some classes of ordinary differential equations (odes) which play a central role in EGT are the Lotka-Volterra (LV) systems, the replicator equation, the bimatrix replicator and the polymatrix replicator.

In 1979 P. Schuster, K. Sigmund, and R. Wolff introduced in [14] the concept of permanence as a stability notion for systems that models the self-organization of biological macromolecules.

Generally, we say that a biological system is permanent if, for small perturbations, none of the species goes to extinction.

The Lotka-Volterra systems, independently introduced in 1920s by A. J. Lotka [9] and V. Volterra [16], are perhaps the most widely known systems used in scientific areas as diverse as physics, chemistry, biology, and economy.

Another classical model widely used is the replicator equation which in some sense J. Hofbauer [4] proved is equivalent to the LV system.

The replicator equation was introduced by P. Taylor and L. Jonker [15]. It models the time evolution of the probability distribution of strategical behaviors within a biological population. Given a *payoff matrix*

2010 *Mathematics Subject Classification.* 34D05, 34D20, 37B25, 37C75, 37N25, 37N40, 91A22, 92D15.

Key words and phrases. Permanence, Polymatrix Replicator, Stability, Replicator equation, Evolutionary game theory, Lotka-Volterra.

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$A \in \mathrm{M}_n(\mathbb{R})$, the replicator equation refers to the following ode

$$x_i' = x_i \left((Ax)_i - x^T A\, x \right), \quad i = 1, \ldots, n,$$

on the simplex $\Delta^{n-1} = \{x \in \mathbb{R}^n_+ : \sum_{j=1}^n x_j = 1\}$.

In the case we want to model the interaction between two populations (or a population divided in two groups, for example, males and females), where each group have a different set of strategies (asymmetric games), and all interactions involve individuals of different groups, the common used model is the bimatrix replicator, that first appeared in [11] and [13]. Given two payoff matrices $A \in \mathrm{M}_{n\times m}(\mathbb{R})$ and $B \in \mathrm{M}_{m\times n}(\mathbb{R})$, for the strategies in each group, the bimatrix replicator refers to the ode

$$\begin{cases} x_i' &= x_i \left((Ay)_i - x^T A\, y \right) \quad i = 1, \ldots, n \\ y_j' &= y_j \left((Bx)_j - y^T B\, x \right) \quad j = 1, \ldots, m \end{cases}$$

on the product of simplices $\Delta^{n-1} \times \Delta^{m-1}$. Each state in this case is a pair of frequency vectors, representing respectively the two groups' strategic behavioral frequencies. It describes the time evolution of the strategy usage frequencies in each group.

Suppose now that we want to study a population divided in a finite number of groups, each of them with finitely many behavioral strategies. Bilateral interactions between individuals of any two groups (including the same) are allowed, but competition takes place inside the groups, i.e., the relative success of each strategy is evaluated within the corresponding group.

H. Alishah and P. Duarte [1] introduced the model that they designated as polymatrix games to study this kind of populations. In [2] H. Alishah, P. Duarte and T. Peixe study particular classes of polymatrix games, namely the conservative and dissipative. The system of odes, designated as the polymatrix replicator, that model this game, will be presented later in section 3. The phase space of these systems are prisms, products of simplexes $\Delta^{n_1-1} \times \ldots \Delta^{n_p-1}$, where p is the number of groups and n_j the number of behavioral strategies inside the j-th group, for $j = 1, \ldots, p$. This class of evolutionary systems includes both the replicator (the case of only one group of individuals) and bimatrix replicator models (the case of two groups of individuals).

In 1987 J. Hofbauer and K. Sigmund [5] and W. Jansen [8] give sufficient conditions for permanence in the usual replicators. Besides we introduce the concept of permanece in the polymatrix replicators, in this paper we also extend these results for polymatrix replicators.

This paper is organized as follows. In section 2, we recall the replicator equation, its relation with the LV systems, some properties of these systems, and the concept of permanence. In section 3 we introduce and recall the definition of polymatrix replicator. In section 4 we extend the concept of permanence to polymatrix replicators and the results given by J. Hofbauer and K. Sigmund [5] and W. Jansen [8]. Finally, in section 5 we illustrate our main results of permanence in polymatrix replicators with two examples.

2. Replicator equation and Permanence

In this section we present some elementary definitions and properties of the replicator equation. For more details on the subject see [6] for instance.

Consider a population where individuals interact with each other according to a set of n possible strategies. The state of the population concerning this interaction is fully described by a vector $x = (x_1, \ldots, x_n)^T$, where x_i represents the frequency of individuals using strategy i, for $i = 1, \ldots, n$. The set of all population states is the simplex $\Delta^{n-1} = \{x \in \mathbb{R}^n_+ : \sum_{j=1}^n x_j = 1\}$.

If an individual using strategy i interacts with an individual using strategy j, the coefficient a_{ij} represents the average payoff for that interaction. Let $A = (a_{ij}) \in \mathrm{M}_n(\mathbb{R})$ be the matrix consisting of these a_{ij}'s. Assuming random encounters between individuals of that population, the average payoff for strategy i is given by

$$(Ax)_i = \sum_{k=1}^n a_{ik} x_k \,,$$

and the global average payoff of all population strategies is given by

$$x^T A\, x = \sum_{i=1}^n \sum_{k=1}^n a_{ik} x_i x_k \,.$$

The logarithmic growth rate $\frac{dx_i}{dt}/x_i$ of the frequency of strategy i is equal to the payoff difference $(Ax)_i - x^T A\, x$, which yields the *replicator equation*

$$\frac{dx_i}{dt} = x_i \left((Ax)_i - x^T A\, x \right), \quad i = 1, \ldots, n \,, \tag{2.1}$$

defined on the simplex Δ^{n-1}, that is invariant under (2.1) (see for example [6, Section 7.1]).

The replicator equation models the frequency evolution of certain strategical behaviours within a biological population. In fact, the equation says that the logarithmic growth of the usage frequency of each behavioural strategy is directly proportional to how well that strategy fares within the population.

This system of odes was introduced in 1978 by P. Taylor and L. Jonker [15] and was designated as *replicator equation* by P. Schuster and K. Sigmund [12] in 1983.

In 1981 J. Hofbauer [4] stated an important relation between the LV systems and the replicator equation. The replicator equation is a cubic equation on the compact set Δ^{n-1} while the LV equation is quadratic on $\mathbb{R}^n_+$. However, Hofbauer proved that the replicator equation in $n+1$ variables is equivalent to the LV equation in n variables (see also [6]).

In LV systems the existence of an equilibrium point in $\mathbb{R}^n_+$ is related with the orbit's behaviour. Namely, a LV system admits an interior equilibrium point if and only if $\mathrm{int}(\mathbb{R}^n_+)$ contains α or ω-limit points. Moreover, if there exists a unique interior equilibrium point and if the solution does not converge to the boundary neither to infinity, then its time average converges to the equilibrium point, as stated in the following result.

Theorem 2.1. *Suppose that $x(t)$ is a solution of a n-dimensional LV system such that $0 < m \leq x_i(t) \leq L$, for all $t \geq 0$ and $i \in \{1, \ldots, n\}$. Then, there exists a sequence $(T_k)_{k\in\mathbb{N}}$ such that $T_k \to +\infty$ and an equilibrium point $q \in \mathrm{int}(\mathbb{R}^n_+)$ such that*

$$\lim_{k\to+\infty} \frac{1}{T_k} \int_0^{T_k} x(t)\, dt = q.$$

Moreover, if the LV system has only one equilibrium point $q \in \mathrm{int}(\mathbb{R}^n_+)$, then

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

Proof. A proof of this theorem can be seen in [3]. □

By the equivalence between the LV and the replicator equation, together with the observation above about the existence of interior equilibrium points, we have the following known result.

Proposition 2.2. *If the replicator* (2.1) *has no equilibrium point in* $\mathrm{int}(\Delta^{n-1})$*, then every solution converges to the boundary of* Δ^{n-1}.

J. Hofbauer in [7] prove also a natural extension of Theorem 2.1 in LV systems to the replicator equation.

Theorem 2.3. *If the replicator* (2.1) *admits a unique equilibrium point* $q \in \mathrm{int}(\Delta^{n-1})$*, and if the ω-limit of the orbit of $x(t)$ is in* $\mathrm{int}(\Delta^{n-1})$*, then*

$$\lim_{t\to\infty} \frac{1}{T} \int_0^{T} x(t)\, dt = q\,.$$

We recall now the concept of *permanence* in the replicator equation, that is a stability notion introduced by Schuster *et al.* in [14].

Definition 2.4. A replicator equation (2.1) defined on Δ^{n-1} is said to be *permanent* if there exists $\delta > 0$ such that, for all $x \in \mathrm{int}(\Delta^{n-1})$,

$$\liminf_{t\to\infty} d\left(\varphi^t(x), \partial\Delta^{n-1}\right) > \delta\,,$$

where φ^t denotes the flow determined by system (2.1) and $\partial\Delta^{n-1}$ is the boundary of Δ^{n-1}.

In the context of biology, a system to be permanent means that sufficiently small perturbations cannot lead any species to extinction.

The following theorem due to Jansen [8] is also valid for LV systems.

Theorem 2.5. *Let X be the replicator vector field defined by* (2.1). *If there is a point $p \in \operatorname{int}(\Delta^{n-1})$ such that for all boundary equilibria $x \in \partial\Delta^{n-1}$,*

$$p^T A\, x > x^T A\, x\,, \tag{2.2}$$

then the vector field X is permanent.

This Theorem 2.5 is a corollary of the following theorem which gives sufficient conditions for a system to be permanent. This result is stated and proved by Hofbauer and Sigmund in [5, Theorem 1] or [6, Theorem 12.2.1].

Theorem 2.6. *Let $P : \Delta^{n-1} \longrightarrow \mathbb{R}$ be a smooth function such that $P = 0$ on $\partial\Delta^{n-1}$ and $P > 0$ on $\operatorname{int}(\Delta^{n-1})$. Assume there is a continuous function $\Psi : \Delta^{n-1} \longrightarrow \mathbb{R}$ such that*

(1) for any orbit $x(t)$ in $\operatorname{int}(\Delta^{n-1})$, $\frac{d}{dt} \log P(x(t)) = \Psi(x(t))$,

(2) for any orbit $x(t)$ in $\partial\Delta^{n-1}$, $\exists\, T > 0$ s. t. $\int_0^T \Psi(x(t))\, dt > 0$.

Then the vector field X is permanent.

3. Polymatrix Replicator

In this section we present the definition of polymatrix replicator. For more details on the subject, namely some of its properties or special classes, see [1] and [2].

Consider a population divided in p groups, labelled by an integer α ranging from 1 to p. Individuals of each group $\alpha \in \{1, \dots, p\}$ have exactly n_α strategies to interact with other members of the population, including the same group.

Fer each $\alpha, \beta \in \{1, \dots, p\}$, consider a real matrix, say $A^{\alpha,\beta}$, of the type $n_\alpha \times n_\beta$ whose entries $a_{ij}^{\alpha,\beta}$, where $i \in \{1, \dots, n_\alpha\}$ and $j \in \{1, \dots, n_\beta\}$, represents the average payoff of an individual of the group α using the i^{th} strategy (of the group α) when interacting with an individual of the group β using the j^{th} strategy (of the group β). Thus, considering a matrix, say A, consisting of all of these entries $a_{ij}^{\alpha,\beta}$ for all $\alpha, \beta \in \{1, \dots, p\}$ and $i \in \{1, \dots, n_\alpha\}$ and $j \in \{1, \dots, n_\beta\}$, we have that A is a square block matrix of order n, made up of these block matrices $A^{\alpha,\beta}$, where $n = n_1 + \dots + n_p$.

Let $\underline{n} = (n_1, \dots, n_p)$. The *state* of the population in time t is described by a point $x(t) = (x^\alpha(t))_{1 \leq \alpha \leq p}$ in the *prism*

$$\Gamma_{\underline{n}} := \Delta^{n_1 - 1} \times \dots \times \Delta^{n_p - 1} \subset \mathbb{R}^n\,,$$

where $\Delta^{n_\alpha - 1} = \{x \in \mathbb{R}_+^{n_\alpha} : \sum_{i=1}^{n_\alpha} x_i^\alpha = 1\}$, $x^\alpha(t) = (x_1^\alpha(t), \dots, x_{n_\alpha}^\alpha(t))$ and the entry $x_i^\alpha(t)$ represents the usage frequency of the i^{th} strategy within the group α in time t. The prism $\Gamma_{\underline{n}}$ is a $(n-p)$-dimensional simple polytope whose affine support is the $(n-p)$-dimensional subspace of $\mathbb{R}^n$ defined by the p equations

$$\sum_{i=1}^{n_\alpha} x_i^\alpha = 1, \quad \alpha \in \{1, \ldots, p\} .$$

We denote by $\partial\Gamma_{\underline{n}}$ the boundary of $\Gamma_{\underline{n}}$.

Assuming random encounters between individuals of that population, for each group $\alpha \in \{1, \ldots, p\}$, the average payoff for a strategy $i \in \{1, \ldots, n_\alpha\}$, is given by

$$(Ax(t))_{i'} = \sum_{\beta=1}^{p} \left(A^{\alpha,\beta}\right)_i x^\beta(t) = \sum_{\beta=1}^{p} \sum_{k=1}^{n_\beta} a_{ik}^{\alpha,\beta} x_k^\beta(t) ,$$

where $i' := n_1 + \cdots + n_{\alpha-1} + i$, and the average payoff of all strategies in α is given by

$$\sum_{i=1}^{n_\alpha} x_i^\alpha(t) \, (Ax(t))_{i'} ,$$

which can also be written as

$$\sum_{\beta=1}^{p} (x^\alpha(t))^T A^{\alpha,\beta} x^\beta(t) .$$

The growth rate $\frac{dx_i^\alpha(t)}{dt} / x_i^\alpha(t)$ of the frequency of the strategy $i \in \{1, \ldots, n_\alpha\}$, for each $\alpha \in \{1, \ldots, p\}$, is equal to the payoff difference $(Ax(t))_{i'} - \sum_{\beta=1}^{p} (x^\alpha(t))^T A^{\alpha,\beta} x^\beta(t)$, which yields the following ode on the prism $\Gamma_{\underline{n}}$,

$$\frac{dx_i^\alpha}{dt} = x_i^\alpha \left((Ax)_{i'} - \sum_{\beta=1}^{p} (x^\alpha)^T A^{\alpha,\beta} x^\beta \right), \alpha \in \{1, \ldots, p\}, i \in \{1, \ldots, n_\alpha\}, \tag{3.1}$$

called the *polymatrix replicator*. The (t)'s were intentionally omitted in equation (3.1) for notation simplification.

Notice that interactions between individuals of any two groups (including the same) are allowed. Notice also that this equation implies that competition takes place inside the groups, i.e., the relative success of each strategy is evaluated within the corresponding group.

The flow $\phi_{\underline{n},A}^t$ of this equation leaves the prism $\Gamma_{\underline{n}}$ invariant. (The proof of this result follows by the same argument presented in the proof that the Cartesian product $\Delta^{n-1} \times \Delta^{m-1}$ is invariant for the bimatrix replicator, see [6, Section 10.3]). Hence, by compactness of $\Gamma_{\underline{n}}$, the flow $\phi_{\underline{n},A}^t$ is complete. The underlying vector field on $\Gamma_{\underline{n}}$ will be denoted by $X_{A,\underline{n}}$.

In the case $p = 1$, we have $\Gamma_{\underline{n}} = \Delta^{n-1}$ and (3.1) is the usual replicator equation associated to the payoff matrix A.

When $p = 2$, and $A^{11} = A^{22} = 0$, $\Gamma_{\underline{n}} = \Delta^{n_1-1} \times \Delta^{n_2-1}$ and (3.1) becomes the bimatrix replicator equation associated to the pair of payoff matrices (A^{12}, A^{21}).

More generally, it also includes the replicator equation for n-person games (when $A^{\alpha,\alpha} = 0$ for all $\alpha \in \{1, \dots, p\}$).

4. Permanence in the Polymatrix Replicator

In this section we extend to polymatrix replicators the definition and some properties of *permanence* stated in the context of LV and replicator systems.

If an orbit in the interior of the state space converges to the boundary, this corresponds to extinction. Despite we give a formal definition of permanence in polymatrix replicators (see Definition 4.2), as we saw in the context of the LV systems and the replicator equation, we say that a system is *permanent* if there exists a compact set K in the interior of the state space such that all orbits starting in the interior of the state space end up in K. This means that the boundary of the state space is a repellor.

Consider a polymatrix replicator (3.1) and $X := X_{A,\underline{n}}$ its associated vector field defined on the $(n-p)$-dimensional prism $\Gamma_{\underline{n}}$. For each $\alpha \in \{1, \dots, p\}$, we denote by $\pi_\alpha : \mathbb{R}^n \to \mathbb{R}^n$ the projection $x \mapsto y$ defined by

$$y_i^\beta := \begin{cases} x_i^\alpha & \text{if} \quad \beta = \alpha \\ 0 & \text{if} \quad \beta \neq \alpha \end{cases}, \text{ for all } \beta \in \{1, \dots, p\}, i \in \{1, \dots, n_\beta\}.$$

The following result is an extension of the average principle in LV systems (see Theorem 2.1) and replicator equation (see Theorem 2.3) to the framework of the polymatrix replicator systems.

Proposition 4.1 (Average Principle). *Let $x(t) \in \operatorname{int}(\Gamma_{\underline{n}})$ be an interior orbit of the vector field X such that for some $\varepsilon > 0$ and some time sequence $T_k \to +\infty$, as $k \to +\infty$, one has*

(1) $d\left(x(T_k), \partial\Gamma_{\underline{n}}\right) \geq \varepsilon$ *for all* $k \geq 0$,

(2) $\displaystyle\lim_{k\to+\infty} \frac{1}{T_k} \int_0^{T_k} x(t)\, dt = q$,

(3) $\displaystyle\lim_{k\to+\infty} \frac{1}{T_k} \int_0^{T_k} \pi_\alpha\left(x(t)\right)^T A x(t)\, dt = a_\alpha$, *for all* $\alpha \in \{1, \dots, p\}$.

Then q is an equilibrium of X and $a_\alpha = \pi_\alpha(q)^T A q$, for all $\alpha \in \{1, \dots, p\}$. Moreover,

$$\lim_{k\to+\infty} \frac{1}{T_k} \int_0^{T_k} x(t)^T A x(t)\, dt = q^T A q\,.$$

Proof. Let $\alpha \in \{1,\ldots,p\}$ and $i,j \in \{1,\ldots,n_\alpha\}$. Let $i' := n_1 + \cdots + n_{\alpha-1} + i$ and $j' := n_1 + \cdots + n_{\alpha-1} + j$. Observe that from (2) we obtain

$$\lim_{k\to+\infty} \frac{1}{T_k} \int_0^{T_k} (Ax(t))_{i'}\, dt = (Aq)_{i'} \,.$$

By (1) we have for all k, $\varepsilon < x_i^\alpha(T_k) < 1-\varepsilon$. Hence, considering e_k the k^{th}-vector of the canonical basis of $\mathbb{R}^n$,

$$\begin{aligned}
(Aq)_{i'} - (Aq)_{j'} &= e_{i'}^T Aq - e_{j'}^T Aq \\
&= \lim_{k\to+\infty} \frac{1}{T_k} \int_0^{T_k} \left(e_{i'}^T Ax(t) - e_{j'}^T Ax(t) \right) dt \\
&= \lim_{k\to+\infty} \frac{1}{T_k} \left(\log \frac{x_i^\alpha(T_k)}{x_j^\alpha(T_k)} - \log \frac{x_i^\alpha(0)}{x_j^\alpha(0)} \right) = 0 \,.
\end{aligned}$$

It follows that q is an equilibrium of X, and for all $i,j \in \{1,\ldots,n_\alpha\}$, $(Aq)_i = (Aq)_j = \pi_\alpha(q)^T A\, q$.

Finally, using (1)-(3),

$$\begin{aligned}
0 &= \lim_{k\to+\infty} \frac{1}{T_k} \left(\log x_i^\alpha(T_k) - \log x_i^\alpha(0) \right) \\
&= \lim_{k\to+\infty} \frac{1}{T_k} \int_0^{T_k} \frac{\frac{dx_i^\alpha}{dt}(t)}{x_i^\alpha(t)}\, dt \\
&= \lim_{k\to+\infty} \frac{1}{T_k} \int_0^{T_k} \left((Ax(t))_{i'} - \sum_{\beta=1}^{p} (x^\alpha(t))^T A^{\alpha\beta} x^\beta(t) \right) dt \\
&= \lim_{k\to+\infty} \frac{1}{T_k} \int_0^{T_k} \left((Ax(t))_{i'} - \pi_\alpha(x(t))^T Ax(t) \right) dt \\
&= (Aq)_{i'} - \lim_{k\to+\infty} \frac{1}{T_k} \int_0^{T_k} \pi_\alpha\left(x(t)\right)^T Ax(t)\, dt = (Aq)_{i'} - a_\alpha \,,
\end{aligned}$$

which implies that $a_\alpha = \pi_\alpha(q)^T Aq$, and hence

$$\lim_{k\to+\infty} \frac{1}{T_k} \int_0^{T_k} x(t)^T Ax(t)\, dt = q^T Aq \,.$$

□

The definition of permanence in the replicator equation (see Definition 2.4) can be naturally extended to the polymatrix replicator, as follows.

Definition 4.2. Given a vector field X defined in $\Gamma_{\underline{n}}$, we say that the associated flow φ_X^t is *permanent* if there exists $\delta > 0$ such that $x \in \operatorname{int}(\Gamma_{\underline{n}})$ implies

$$\liminf_{t\to+\infty}\ d\left(\varphi_X^t(x), \partial\Gamma_{\underline{n}} \right) \geq \delta \,.$$

The following theorem extends Theorem 2.6 for polymatrix replicators.

Theorem 4.3. *Let $\Phi : \Gamma_{\underline{n}} \to \mathbb{R}$ be a smooth function such that $\Phi = 0$ on $\partial\Gamma_{\underline{n}}$ and $\Phi > 0$ on $\mathrm{int}\,(\Gamma_{\underline{n}})$. Assume there is a continuous function $\Psi : \Gamma_{\underline{n}} \to \mathbb{R}$ such that*

(1) for any orbit $x(t)$ in $\mathrm{int}\,(\Gamma_{\underline{n}})$, $\frac{d}{dt}\log\Phi(x(t)) = \Psi(x(t))$,
(2) for any orbit $x(t)$ in $\partial\Gamma_{\underline{n}}$, $\exists\, T > 0$ s.t. $\int_0^T \Psi(x(t))\,dt > 0$.

Then the vector field X is permanent.

J. Hofbauer and K. Sigmund in [6, Theorem 12.2.1] state and prove a result that is abstract and applicable to a much wider class of systems, including polymatrix replicator systems. In fact, where they refer S_n we can consider any d-dimensional simple polytope, since the proof is exactly the same replacing S_n by this polytope. Hence, the result stated in Theorem 4.3 as the one stated in the following Remark 4.4 are just an adaptation for polymatrix replicator systems of the result in [6, Theorem 12.2.1] and [6, Theorem 12.2.2], respectively, whose proofs are exactly the same as the ones made by J. Hofbauer and K. Sigmund, just needing to replace S_n by $\Gamma_{\underline{n}}$.

Remark 4.4. If we consider $\Gamma_{\underline{n}}$ instead of S_n in the result stated and proved by J. Hofbauer and K. Sigmund in [6, Theorem 12.2.2], we obtain an analogous result for polymatrix replicator systems saying that for the conclusion in Theorem 4.3 it is enough to check *(2)* for all ω-limit orbits in $\partial\Gamma_{\underline{n}}$. Thus, defining

(2') for any ω-limit orbit $x(t)$ in $\partial\Gamma_{\underline{n}}$, $\int_0^T \Psi(x(t))\,dt > 0$ for some $T > 0$,

we have that condition *(2')* implies *(2)*.

Let $k \in \mathbb{N}_0$ with $0 \le k \le n - p - 1$, where p is the number of groups in some population and $n = \sum_{\alpha=1}^{p} n_\alpha$, with n_α being the the number of strategies in each group $\alpha \in \{1, \ldots, p\}$, as defined in the beginning of section 3. Now let the k-dimensional face skeleton of $\Gamma_{\underline{n}}$, denoted by $\partial_k\Gamma_{\underline{n}}$, to be the union of all j-dimensional faces of $\Gamma_{\underline{n}}$, with $0 \le j \le k$. In particular, the vertex skeleton of $\Gamma_{\underline{n}}$ is the union $\partial_0\Gamma_{\underline{n}}$ of all vertices of $\Gamma_{\underline{n}}$, and the edge skeleton of $\Gamma_{\underline{n}}$ is the union $\partial_1\Gamma_{\underline{n}}$ of all vertices and edges of $\Gamma_{\underline{n}}$. We will use this sets in the proof of the following theorem, which is an extension of Theorem 2.5 to polymatrix replicator systems.

Theorem 4.5. *If there is a point $q \in \mathrm{int}\,(\Gamma_{\underline{n}})$ such that for all boundary equilibria $x \in \partial\Gamma_{\underline{n}}$,*

$$q^T A\, x > x^T A\, x\,, \tag{4.1}$$

then X is permanent.

Proof. The proof we present here is essentially an adaptation of the argument used in the proof of Theorem 13.6.1 in [6].

Take the given point $q \in \mathrm{int}\,(\Gamma_{\underline{n}})$ and consider $\Phi : \Gamma_{\underline{n}} \to \mathbb{R}$,

$$\Phi(x) := \prod_{\alpha=1}^{p} \prod_{i=1}^{n_\alpha} (x_i^\alpha)^{q_i^\alpha} \ .$$

We can easily see that $\Phi = 0$ on $\partial\Gamma_{\underline{n}}$ and $\Phi > 0$ on $\mathrm{int}\,(\Gamma_{\underline{n}})$. Consider now the continuous function $\Psi : \Gamma_{\underline{n}} \to \mathbb{R}$,

$$\Psi(x) := q^T A x - x^T A x \ .$$

We have that

$$\frac{d}{dt} \log \Phi(x(t)) = \Psi(x(t))\,.$$

It remains to show that for any orbit $x(t)$ in $\partial\Gamma_{\underline{n}}$, there exists a $T > 0$ such that

$$\int_0^T \Psi\left(x(t)\right)\, dt > 0\,. \tag{4.2}$$

We will prove by induction in $k \in \mathbb{N}_0$ that if $x(t) \in \partial_k\Gamma_{\underline{n}}$ then (4.2) holds for some $T > 0$.

If $x(t) \in \partial_0\Gamma_{\underline{n}}$ then $x(t) \equiv q'$ for some vertex q' of $\Gamma_{\underline{n}}$. Since by (4.1) $\Psi(q') > 0$, (4.2) follows. Hence the induction step is true for $k = 0$.

Assume now that conclusion (4.2) holds for every orbit $x(t) \in \partial_{m-1}\Gamma_{\underline{n}}$, and consider an orbit $x(t) \in \partial_m\Gamma_{\underline{n}}$. Then there is an m-dimensional face $\sigma \subset \partial_m\Gamma_{\underline{n}}$ that contains $x(t)$. We consider two cases:

(i) If $x(t)$ converges to $\partial\sigma$ (the boundary of σ), i.e., $\lim_{t\to+\infty} d\left(x(t), \partial\sigma\right) = 0$, then the ω-limit of $x(t)$, $\omega(x)$, is contained in $\partial\sigma$. By induction hypothesis, (4.2) holds for all orbits inside $\omega(x)$, and consequently, by Remark 4.4 the same is true about $x(t)$.

(ii) If $x(t)$ does not converge to $\partial\sigma$, there exists $\varepsilon > 0$ and a sequence $T_k \to +\infty$ such that $d\left(x(T_k), \partial\sigma\right) \geq \varepsilon$ for all $k \geq 0$. Let us write

$$\bar{x}(T) = \frac{1}{T}\int_0^T x(t)\, dt \quad \text{ and } \quad a_\alpha(T) = \frac{1}{T}\int_0^T \pi_\alpha(x(t))^T A x(t)\, dt$$

for all $\alpha \in \{1, \ldots, p\}$. Since the sequences $\bar{x}(T_k)$ and $a_\alpha(T_k)$ are bounded, there is a subsequence of T_k, that we will keep denoting by T_k, such that $\bar{x}(T_k)$ and $a_\alpha(T_k)$ converge, say to q' and a_α, respectively, for all $\alpha \in \{1, \ldots, p\}$. Thus, since $x(t)$ is contained in the m-dimensional face σ and we are in the case where $x(t)$ does not converge to $\partial\sigma$, considering the system restricted to σ, we can apply Proposition 4.1 and deduce that q' is an equilibrium point in σ and $a_\alpha = \pi_\alpha(q')^T A q'$. Therefore

$$\frac{1}{T_k}\int_0^{T_k} \Psi\left(x(t)\right)\, dt$$

converges to $q^T A q' - q'^T A q'$, which by (4.1) is positive. This implies (4.2) and hence proves the permanence of X. $\square$

A particular class of interest in the setting of the polymatrix replicators is the *dissipative polymatrix replicator*. For formal definitions and properties on conservative and dissipative polymatrix replicators see [2]. For this class of systems we have that if a dissipative polymatrix replicator only has one globally attractive interior equilibrium, then it is permanent.the following remark.

Given this, and by the definition of permanence, an interesting question is whether dissipativity is a necessary condition for permanence. This is not true, as illustrated by the first example in the next section, since we prove that the system is permanent but not dissipative.

5. Example

We present here two examples of polymatrix replicators that are permanent.

We prove that the first example is permanent because it satisfies condition (4.1) of Theorem 4.5. Moreover, we show that this system is not dissipative, illustrating that dissipativity is not necessary for permanence.

In the second example, we prove that the system is permanent since it is dissipative and have a unique globally attractive interior equilibrium. However, it does not satisfy condition (4.1) (of Theorem 4.5), what illustrates that this condition (4.1) is not necessary for permanence.

There is much more to analyse in the structure/dynamics of these two examples, but this will be done in future work to appear.

All computations and pictures presented in this section were done with *Wolfram Mathematica* and *Geogebra* software.

5.1. Example 1.

5.1. **Example 1.** Consider a population divided in 4 groups where individuals of each group have exactly 2 strategies to interact with other members of the population, whose the associated payoff matrix is

$$A = \begin{pmatrix} 1 & -1 & -1 & 1 & -100 & 100 & -100 & 100 \\ -1 & 1 & 1 & -1 & 100 & -100 & 100 & -100 \\ 101 & -101 & -10 & 10 & -1 & 1 & -100 & 100 \\ -101 & 101 & 10 & -10 & 1 & -1 & 100 & -100 \\ 1 & -1 & 100 & -100 & -190 & 190 & -101 & 101 \\ -1 & 1 & -100 & 100 & 190 & -190 & 101 & -101 \\ 1 & -1 & 5 & -5 & 100 & -100 & -100 & 100 \\ -1 & 1 & -5 & 5 & -100 & 100 & 100 & -100 \end{pmatrix}.$$

The phase space of the associated polymatrix replicator defined by the payoff matrix A is the *prism*

$$\Gamma_{(2,2,2,2)} := \Delta^1 \times \Delta^1 \times \Delta^1 \times \Delta^1 \equiv [0,1]^4 .$$

Besides the 16 vertices of $\Gamma_{(2,2,2,2)}$ (see Table 1), this system has 2 equilibria on $3d$-faces of $\Gamma_{(2,2,2,2)}$ (see Table 2), 6 equilibria on $2d$-faces of $\Gamma_{(2,2,2,2)}$ (see Table 3), and 12 equilibria on $1d$-faces (the edges) of $\Gamma_{(2,2,2,2)}$ (see Table 4).

Vertices of $\Gamma_{(2,2,2,2)}$	$f(v_i)$
$v_1 = (1,0,1,0,1,0,1,0)$	-394
$v_2 = (1,0,1,0,1,0,0,1)$	-4
$v_3 = (1,0,1,0,0,1,1,0)$	-392
$v_4 = (1,0,1,0,0,1,0,1)$	-6
$v_5 = (1,0,0,1,1,0,1,0)$	-602
$v_6 = (1,0,0,1,1,0,0,1)$	-592
$v_7 = (1,0,0,1,0,1,1,0)$	-204
$v_8 = (1,0,0,1,0,1,0,1)$	-198
$v_9 = (0,1,1,0,1,0,1,0)$	-198
$v_{10} = (0,1,1,0,1,0,0,1)$	-204
$v_{11} = (0,1,1,0,0,1,1,0)$	-592
$v_{12} = (0,1,1,0,0,1,0,1)$	-602
$v_{13} = (0,1,0,1,1,0,1,0)$	-6
$v_{14} = (0,1,0,1,1,0,0,1)$	-392
$v_{15} = (0,1,0,1,0,1,1,0)$	-4
$v_{16} = (0,1,0,1,0,1,0,1)$	-394

TABLE 1. The vertices of $\Gamma_{(2,2,2,2)}$ and the value of $f(v_i)$, where $f(x) = (x-q)^T Ax$ and $q = \left(\frac{1}{2},\frac{1}{2},\frac{1}{2},\frac{1}{2},\frac{1}{2},\frac{1}{2},\frac{1}{2},\frac{1}{2}\right) \in \operatorname{int}\left(\Gamma_{(2,2,2,2)}\right)$.

Equilibria on $3d$-faces of $\Gamma_{(2,2,2,2)}$	$f(q_i)$
$q_1 = \left(0.05266, 0.9473, 0.93275, 0.0672483, 0.991199, \frac{9049}{1028189}, 0, 1\right)$	-201.7
$q_2 = \left(0.9473, 0.05266, 0.0672483, 0.93275, \frac{9049}{1028189}, 0.991199, 1, 0\right)$	-201.7

TABLE 2. The equilibria on $3d$-faces of $\Gamma_{(2,2,2,2)}$ and the value of $f(q_i)$, where $f(x) = (x-q)^T Ax$ and $q = \left(\frac{1}{2},\frac{1}{2},\frac{1}{2},\frac{1}{2},\frac{1}{2},\frac{1}{2},\frac{1}{2},\frac{1}{2}\right) \in \operatorname{int}\left(\Gamma_{(2,2,2,2)}\right)$.

All these equilibria belong to $\partial\Gamma_{(2,2,2,2)}$ and satisfy

(1) $(Ax)_1 = (Ax)_2\,, (Ax)_3 = (Ax)_4\,, (Ax)_5 = (Ax)_6\,, (Ax)_7 = (Ax)_8$,

(2) $x_1^\alpha + x_2^\alpha = 1$, for all $\alpha \in \{1,\dots,4\}$,

where $x = (x_1^1, x_2^1, x_1^2, x_2^2, x_1^3, x_2^3, x_1^4, x_2^4) \in \mathbb{R}^8$.

We have that all equilibria on $\partial\Gamma_{(2,2,2,2)}$ satisfy (4.1). In fact, we have that for all equilibria $x \in \partial\Gamma_{(2,2,2,2)}$,

$$(x-q)^T\, A\, x < 0,$$

Equilibria on $2d$-faces of $\Gamma_{(2,2,2,2)}$	$f(q_i)$
$q_3 = \left(0, 1, 0, 1, \frac{9803}{29100}, \frac{19297}{29100}, \frac{893}{2910}, \frac{2017}{2910}\right)$	-19.2
$q_4 = \left(0, 1, 1, 0, \frac{9649}{14550}, \frac{4901}{14550}, \frac{994}{1455}, \frac{461}{1455}\right)$	-76.7
$q_5 = \left(0, 1, \frac{171}{400}, \frac{229}{400}, \frac{29}{40}, \frac{11}{40}, 0, 1\right)$	-197.4
$q_6 = \left(1, 0, 0, 1, \frac{4901}{14550}, \frac{9649}{14550}, \frac{461}{1455}, \frac{994}{1455}\right)$	-76.7
$q_7 = \left(1, 0, 1, 0, \frac{19297}{29100}, \frac{9803}{29100}, \frac{2017}{2910}, \frac{893}{2910}\right)$	-19.2
$q_8 = \left(1, 0, \frac{229}{400}, \frac{171}{400}, \frac{11}{40}, \frac{29}{40}, 1, 0\right)$	-197.4

TABLE 3. The equilibria on $2d$-faces of $\Gamma_{(2,2,2,2)}$ and the value of $f(q_i)$, where $f(x) = (x-q)^T Ax$ and $q = \left(\frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}\right) \in \operatorname{int}\left(\Gamma_{(2,2,2,2)}\right)$.

Equilibria on $1d$-faces of $\Gamma_{(2,2,2,2)}$	$f(q_i)$
$q_9 = \left(0, 1, 0, 1, 1, 0, \frac{97}{100}, \frac{3}{100}\right)$	-5.94
$q_{10} = \left(1, 0, 1, 0, 0, 1, \frac{3}{100}, \frac{97}{100}\right)$	-5.94
$q_{11} = \left(0, 1, 1, 0, 0, 1, \frac{1}{50}, \frac{49}{50}\right)$	-593.96
$q_{12} = \left(1, 0, 0, 1, 1, 0, \frac{49}{50}, \frac{1}{50}\right)$	-593.96
$q_{13} = \left(0, 1, 1, 0, \frac{47}{95}, \frac{48}{95}, 1, 0\right)$	-207.1
$q_{14} = \left(1, 0, 0, 1, \frac{48}{95}, \frac{47}{95}, 0, 1\right)$	-207.1
$q_{15} = \left(0, 1, \frac{2}{5}, \frac{3}{5}, 1, 0, 0, 1\right)$	-307.2
$q_{16} = \left(1, 0, \frac{3}{5}, \frac{2}{5}, 0, 1, 1, 0\right)$	-307.2
$q_{17} = \left(0, 1, 0, 1, \frac{1}{2}, \frac{1}{2}, 0, 1\right)$	-203
$q_{18} = \left(1, 0, 1, 0, \frac{1}{2}, \frac{1}{2}, 1, 0\right)$	-203
$q_{19} = \left(0, 1, \frac{1}{2}, \frac{1}{2}, 0, 1, 0, 1\right)$	-488
$q_{20} = \left(1, 0, \frac{1}{2}, \frac{1}{2}, 1, 0, 1, 0\right)$	-488

TABLE 4. The equilibria on $1d$-faces of $\Gamma_{(2,2,2,2)}$ and the value of $f(q_i)$, where $f(x) = (x-q)^T Ax$ and $q = \left(\frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}\right) \in \operatorname{int}\left(\Gamma_{(2,2,2,2)}\right)$.

with

$$q = \left(\frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}\right) \in \operatorname{int}\left(\Gamma_{(2,2,2,2)}\right),$$

as we can see in Table 1, Table 2, Table 3, and Table 4.

Hence, by Theorem 4.5, we can conclude that the system defined by the payoff matrix A is permanent.

We prove now that this system is not dissipative. By definition [2, Definition 5.1] this system is dissipative if there exists a positive diagonal matrix D of the form

$$D = \begin{bmatrix} \mathrm{d}_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \mathrm{d}_1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \mathrm{d}_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \mathrm{d}_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \mathrm{d}_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \mathrm{d}_3 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \mathrm{d}_4 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathrm{d}_4 \end{bmatrix},$$

such that the quadratic form $Q_{AD} : H_{(2,2,2,2)} \longrightarrow \mathbb{R}$ defined by $Q_{AD}(x) = x^T ADx$ is negative semidefinite, where $H_{(2,2,2,2)}$ is the subspace (as defined in [2])

$$H_{(2,2,2,2)} = \{x \in \mathbb{R}^8 \ : \ x_1^\alpha + x_2^\alpha = 0, \text{ for all}\, \alpha \in \{1, \dots, 4\}\}.$$

By the definition of $H_{(2,2,2,2)}$ we have that the symmetric matrix associated to the quadratic form $Q_{AD}(x)$ is the four dimensional square matrix

$$S = \begin{bmatrix} 2\mathrm{d}_1 & 101\mathrm{d}_1 - \mathrm{d}_2 & \mathrm{d}_1 - 100\mathrm{d}_3 & \mathrm{d}_1 - 100\mathrm{d}_4 \\ 101\mathrm{d}_1 - \mathrm{d}_2 & -20\mathrm{d}_2 & 100\mathrm{d}_2 - \mathrm{d}_3 & 5\mathrm{d}_2 - 100\mathrm{d}_4 \\ \mathrm{d}_1 - 100\mathrm{d}_3 & 100\mathrm{d}_2 - \mathrm{d}_3 & -380\mathrm{d}_3 & 100\mathrm{d}_3 - 101\mathrm{d}_4 \\ \mathrm{d}_1 - 100\mathrm{d}_4 & 5\mathrm{d}_2 - 100\mathrm{d}_4 & 100\mathrm{d}_3 - 101\mathrm{d}_4 & -200\mathrm{d}_4 \end{bmatrix}.$$

We can see, for example by the criterion of the principal minors, that this symmetric matrix S is not negative semidefinite (notice that d_1, d_2, d_3 and d_4 must be positive). Hence, we conclude that the system defined by the payoff matrix A is not dissipative. Since we have already seen that this system is permanent, this example illustrates that dissipativity is not necessary for permanence.

5.2. **Example 2.** Consider a population divided in 3 groups where individuals of each group have exactly 2 strategies to interact with other members of the population, whose the associated payoff matrix is

$$A = \begin{bmatrix} 0 & -102 & 0 & 79 & 0 & 18 \\ 102 & 0 & 0 & -79 & -18 & 9 \\ 0 & 0 & 0 & 0 & 9 & -18 \\ -51 & 51 & 0 & 0 & 0 & 0 \\ 0 & 102 & -79 & 0 & -18 & -9 \\ -102 & -51 & 158 & 0 & 9 & 0 \end{bmatrix}.$$

The phase space of the associated polymatrix replicator defined by the payoff matrix A is the *prism*

$$\Gamma_{(2,2,2)} := \Delta^1 \times \Delta^1 \times \Delta^1 \equiv [0,1]^3.$$

This system only has one interior equilibrium,

$$q = \left(\frac{1}{2}, \frac{1}{2}, \frac{71}{158}, \frac{87}{158}, \frac{2}{3}, \frac{1}{3}\right) \in \operatorname{int}\left(\Gamma_{(2,2,2,2)}\right) .$$

Moreover, besides the 8 vertices of $\Gamma_{(2,2,2)}$,

$$\begin{aligned} v_1 &= (1,0,1,0,1,0) \ , & v_2 &= (1,0,1,0,0,1) \ , \\ v_3 &= (1,0,0,1,1,0) \ , & v_4 &= (1,0,0,1,0,1) \ , \\ v_5 &= (0,1,1,0,1,0) \ , & v_6 &= (0,1,1,0,0,1) \ , \\ v_7 &= (0,1,0,1,1,0) \ , & v_8 &= (0,1,0,1,0,1) \ , \end{aligned}$$

it has 2 equilibria on two opposite $2d$-faces of $\Gamma_{(2,2,2)}$,

$$q_1 = \left(\frac{7}{17}, \frac{10}{17}, \frac{37}{79}, \frac{42}{79}, 1, 0\right), \quad \text{and} \quad q_2 = \left(\frac{23}{34}, \frac{11}{34}, \frac{65}{158}, \frac{93}{158}, 0, 1\right),$$

as represented in Figure 1. In fact, all these equilibria satisfy

(1) $(Ax)_1 = (Ax)_2\,, (Ax)_3 = (Ax)_4\,, (Ax)_5 = (Ax)_6$,
(2) $x_1^\alpha + x_2^\alpha = 1$, for all $\alpha \in \{1, \ldots, 3\}$,

where $x = (x_1^1, x_2^1, x_1^2, x_2^2, x_1^3, x_2^3) \in \mathbb{R}^6$.

Consider the positive diagonal matrix

$$D = \begin{bmatrix} \frac{1}{51} & 0 & 0 & 0 & 0 & 0 \\ 0 & \frac{1}{51} & 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{1}{79} & 0 & 0 & 0 \\ 0 & 0 & 0 & \frac{1}{79} & 0 & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{9} & 0 \\ 0 & 0 & 0 & 0 & 0 & \frac{1}{9} \end{bmatrix},$$

and the affine subspace (as defined in [2])

$$H_{(2,2,2)} = \{x \in \mathbb{R}^6 \ : \ x_1^\alpha + x_2^\alpha = 0, \text{ for all } \alpha \in \{1, \ldots, 3\}\} .$$

The quadratic form $Q_{AD} : H_{(2,2,2)} \longrightarrow \mathbb{R}$ defined by $Q_{AD}(x) = x^T ADx$, is $Q_{AD}(x) = -2\,(x_1^3)^2 \leq 0$. Hence, by [2, Definition 5.1], this system is dissipative.

Computing the eigenvalues of the matrix of the linearized system around the interior equilibrium point, we find that it is a globally attractive equilibrium. Since the interior equilibrium is unique it follows that the system is permanent. However, this second example does not satisfies condition (4.1) of Theorem 4.5. In fact there is no $q \in \operatorname{int}\left(\Gamma_{(2,2,2)}\right)$ such that

$$x^T A\, x - q^T A\, x < 0\,,$$

for all equilibria $x \in \partial\Gamma_{(2,2,2)}$. Hence, this example illustrates that condition (4.1) is not necessary for permanence.

We give now a brief description of the dynamics of this example, as illustrated by the plot of three orbits in Figure 1. This system has a

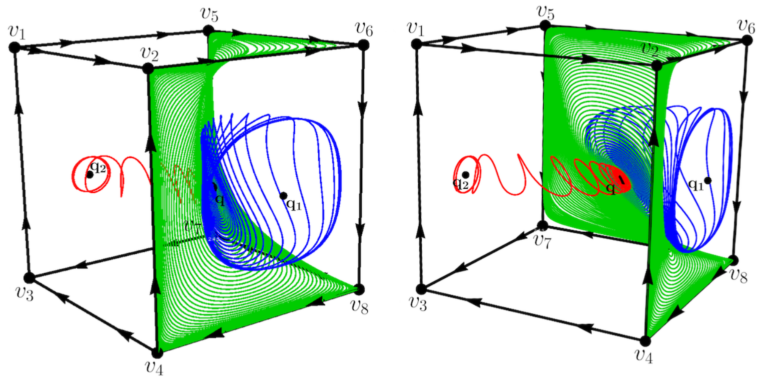

FIGURE 1. Two different perspectives of the polytope $\Gamma_{(2,2,2)}$ where the polymatrix replicator given by the payoff matrix A is defined. Namelly, the plot of its equilibria and three interior orbits.

strict global Lyapunov function $h : \mathrm{int}\left(\Gamma_{(2,2,2,2)}\right) \to \mathbb{R}$ for X_A, defined by

$$h\left(x\right) = -\sum_{\alpha=1}^{3}\sum_{i=1}^{2}\frac{q_i^\alpha}{d_\alpha}\log x_i^\alpha\,,$$

where X_A is the associated vector field, q is the interior equilibrium, and $d_1 = \frac{1}{51}$, $d_2 = \frac{1}{79}$, $d_3 = \frac{1}{9}$ (the elements on the main diagonal of matrix D). In fact this function h has an absolute minimum at q and satisfy $\dot{h} = Dh_x(X_A) < 0$ for all $x \in \mathrm{int}\left(\Gamma_{(2,2,2,2)}\right)$ with $x \neq q$. Hence, by Proposition 13 and Proposition 17 in [2], the ω-limit of any interior point $x \in \mathrm{int}\left(\Gamma_{(2,2,2,2)}\right)$ is the equilibrium q. The equilibria q_1 and q_2 in faces of $\Gamma_{(2,2,2)}$ are centres in each corresponding face, *i.e.*, for any initial condition in one of these faces the corresponding orbit will be periodic around the equilibrium point in that same face.

Acknowledgements

The author would like to thank the referees for their relevant and constructive comments and suggestions that helped to improve the manuscript.

The author was supported by FCT - Fundação para a Ciência e a Tecnologia, under the project CEMAPRE - UID/MULTI/00491/2013 through national funds.

The author also wishes to express his gratitude to Pedro Duarte for stimulating conversations, continuous encouragement and suggestions.

References

[1] H. N. Alishah and P. Duarte, *Hamiltonian evolutionary games*, Journal of Dynamics and Games **2** (2015), no. 1, 33–49.

[2] H. N. Alishah, P. Duarte, and T. Peixe, *Conservative and dissipative polymatrix replicators*, Journal of Dynamics and Games **2** (2015), no. 2, 157–185.

[3] P. Duarte, R. L. Fernandes, and Waldyr M. Oliva, *Dynamics of the attractor in the Lotka-Volterra equations*, J. Differential Equations **149** (1998), no. 1, 143–189. MR1643678 (99h:34075)

[4] J. Hofbauer, *On the occurrence of limit cycles in the Volterra-Lotka equation*, Nonlinear Anal. **5** (1981), no. 9, 1003–1007. MR633014 (83c:92063)

[5] J. Hofbauer and K. Sigmund, *Permanence for replicator equations* (Alexander B. Kurzhanski and Karl Sigmund, eds.), Springer Berlin Heidelberg, Berlin, Heidelberg, 1987.

[6] ———, *Evolutionary games and population dynamics*, Cambridge University Press, Cambridge, 1998.

[7] Josef Hofbauer, *A general cooperation theorem for hypercycles*, Monatsh. Math. **91** (1981), no. 3, 233–240. MR619966

[8] Wolfgang Jansen, *A permanence theorem for replicator and Lotka-Volterra systems*, J. Math. Biol. **25** (1987), no. 4, 411–422. MR908382 (89a:92044)

[9] Alfred J. Lotka, *Elements of mathematical biology. (formerly published under the title Elements of Physical Biology)*, Dover Publications, Inc., New York, N. Y., 1958. MR0094263 (20 #782)

[10] J. Maynard Smith and G. Price, *The logic of animal conflicts.*, Nature **246** (1973), 15–18.

[11] P. Schuster and K. Sigmund, *Coyness, philandering and stable strategies*, Animal Behaviour **29** (1981), no. 1, 186 –192.

[12] ———, *Replicator dynamics*, J. Theoret. Biol. **100** (1983), no. 3, 533–538. MR693413 (85i:92006)

[13] P. Schuster, K. Sigmund, J. Hofbauer, and R. Wolff, *Self-regulation of behaviour in animal societies. II. Games between two populations without self-interaction*, Biol. Cybernet. **40** (1981), no. 1, 9–15. MR609926 (82e:92039b)

[14] P Schuster, K Sigmund, and R Wolff, *Dynamical systems under constant organization. iii. cooperative and competitive behavior of hypercycles*, Journal of Differential Equations **32** (1979), no. 3, 357 –368.

[15] P. D. Taylor and L. B. Jonker, *Evolutionarily stable strategies and game dynamics*, Math. Biosci. **40** (1978), no. 1-2, 145–156. MR0489983 (58 #9351)

[16] Vito Volterra, *Leçons sur la théorie mathématique de la lutte pour la vie*, Les Grands Classiques Gauthier-Villars. [Gauthier-Villars Great Classics], Éditions Jacques Gabay, Sceaux, 1990. Reprint of the 1931 original. MR1189803 (93k:92011)

[17] John von Neumann and Oskar Morgenstern, *Theory of Games and Economic Behavior*, Princeton University Press, Princeton, New Jersey, 1944. MR0011937 (6,235k)

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