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Lotka-Volterra equation and replicator dynamics: new issues in classification

Immanuel M. Bomze

Institut für Statistik, Operations Research und Computerverfahren, Universität Wien, Universitätsstrasse 5, A-1010 Vienna, Austria

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Abstract. Replicator dynamics serves for modelling many biological processes, e.g. evolution of animal behaviour, but also selection in population genetics, and even prebiotic evolution. The Lotka-Volterra system is used in mathematical ecology to describe the interaction of two populations over time. Here, predator/prey situations can be modelled as well as competition for a resource. After a short account on applications and ramifications of planar classification results, a lacuna is closed which appeared in an earlier publication on classification (Biol Cybern 48: 201–211, 1983). The now complete list of possible phase portraits under the replicator dynamics as well as under the Lotka-Volterra system is specified and contains, up to flow reversal, 49 qualitatively different cases for the former, and 110 or 67 for the latter dynamics, depending on whether or not one discriminates between different asymptotic slope behaviour. Furthermore, a systematic investigation of the flow under the replicator dynamics exhibits a variety of non-robust models which illustrate dynamic aspects of some solution concepts in evolutionary game theory, a field that is receiving widespread interest in the recent literature.

1 Introduction: the models and some applications

Two dynamical models frequently employed in theoretical biology are the replicator system and the Lotka-Volterra equation. The planar case of the latter has been investigated extensively by many authors in the past, and several attempts have been made to achieve a complete classification, e.g. Reyn (1987) and the references therein. In an article published more than 10 years ago, Bomze (1983) attacked the problem of completely classifying the possible planar flows of both the replicator dynamics and the Lotka-Volterra system. The aim of this note is to give an account of related subsequent work; of different approaches to classification; of new relationships between these systems and dynamical aspects of evolutionary game theory; to provide an explicit complete classification of the planar Lotka-Volterra flows; and – last but not least — to close a lacuna in the above-mentioned paper.

For the convenience of the reader, I shall now sketch very roughly the main features of the topic. For more details, notation and terminology, see Bomze (1983). Replicator dynamics were introduced by Taylor and Jonker (1978) to model evolution of behaviour in intraspecific conflicts under random pairwise mating in a large, ideally infinite population. It formalizes the idea that the growth rates $\dot{x}_i/x_i$ of relative frequency x_i of the ith behaviour pattern ($i = 1, \ldots, n$) is equal to the (dis)advantage

$$e_i \cdot Ax - x \cdot Ax = \sum_j a_{ij}x_j - \sum_{j,k} x_k a_{kj} x_j$$

measured by incremental fitness relative to the average performance within the population in state $x = [x_1, \ldots, x_n]$. Here a_{ij} denotes incremental individual fitness attributed to an i-individual when encountering a j-individual, and $A = [a_{ij}]$ is the resulting fitness matrix. Throughout the paper, a dot ˙ denotes derivative w.r.t. time t. In the main body of the article, I shall concentrate on the case of $n = 3$ behaviour patterns. These patterns are often called 'pure strategies' in evolutionary game theory, in which context the matrix A is termed the 'payoff matrix'. So interest is focussed on the system of cubic differential equations

$$\dot{x}_i = x_i \sum_j \left[a_{ij} - \sum_k x_k a_{kj} \right] x_j, \quad i = 1, 2, 3 \tag{1}$$

operating on the state space $S = S^3$, where for general n

$$S^n = \{x = [x_1, \ldots, x_n]: x_i \geqslant 0, \text{ all } i, \sum_i x_i = 1\}$$

denotes the standard simplex in n-dimensional Euclidean space.

As and example for application in models of behavioural evolution, we derive the payoff matrix from a 'live-scenario', considering the well-known Hawk-Dove-Retaliator game (Maynard Smith 1982), in which animals are contesting a resource of value $V > 0$:

The first pattern (called 'Hawk') represents an escalating behaviour: escalation will be continued until injury (which costs $C > 0$) or retreat of the opponent;
The second behavioural pattern (called 'Dove') consists of displaying in a ritual way. A Dove retreats if the opponent escalates;
Individuals following the third pattern (called 'Retaliator') behave like a Dove against a Dove and like a Hawk against a Hawk, but never escalate first.

Assume that each of two escalating opponents have a 50% chance of injuring the other one and obtaining the resource, and a 50% chance of being injured. Similarly, two displaying contestants will have a 50% chance of winning the resource. Now it is easy to derive A:

$$A = \begin{bmatrix} \frac{V-C}{2} & V & \frac{V-C}{2} \\ 0 & V/2 & V/2 \\ \frac{V-C}{2} & V/2 & V/2 \end{bmatrix}.$$

If, for example, $V = 2$ and $C = 4$, then

$$A = \begin{bmatrix} -1 & 2 & -1 \\ 0 & 1 & 1 \\ -1 & 1 & 1 \end{bmatrix}$$

which yields under (1) the flow as depicted in Fig. 1 of Bomze (1983). The analysis there shows that any mixed population will evolve according to its initial state: either to one of a set of possible populations where Hawks are extinct and with at most twice as many Doves as Retaliators, or to a 1:1 mixture of Hawks and Doves, where Retaliators are extinct. The latter will happen if there are sufficient Doves at the start, so that Retaliators can survive only if there are just a few Doves from the beginning.

Population genetics is a second important field for the application of replicator dynamics. Indeed, consider a game of partnership in which the two contestants share their outcome equally, which means $a_{ij} = a_{ji}$, for all i and j. If x_i are the frequencies of n possible alleles for a given chromosomal locus, and a_{ij} is the fitness of genotype (ij), then (1) is nothing else than the well-known Wright-Fisher-Haldane equation for continuous time (Hadeler 1974). The average payoff $x \cdot Ax$ here is mean fitness and increases with time, and every population approaches some fixed point (Akin and Hofbauer, 1982). For example, a simple three-allele model where the heterozygote is fitter than the homozygotes yields

$$A = \begin{bmatrix} 1 & 2 & 2 \\ 2 & 1 & 2 \\ 2 & 2 & 1 \end{bmatrix}$$

which generates the flow under (1) depicted in [7] of Fig. 6 in Bomze (1983), where all three gene types will converge in frequency to 1/3. Another example of a selection PP is [20] in Fig. 1 below, where the final state again depends on the initial state. In contrast to [7], here sensitivity to the initial conditions is quite drastic in that not only the (inevitable) extinction of one allele, but also the final balance between the remaining ones depends on their starting value.

In modelling prebiotic evolution, the simplest possible hypercycle consists of three interacting species of macromolecules with concentrations x_1, x_2, x_3, respectively. Assume that by a catalytic mechanism species 2 favours the growth of species 1, which in turn favours species 3, which again favours species 2. Schuster and Sigmund (1983) show that (1) then describes the time evolution of this model if

$$A = \begin{bmatrix} 0 & k_1 & 0 \\ 0 & 0 & k_2 \\ k_3 & 0 & 0 \end{bmatrix} \quad \text{with } k_i > 0, \quad \text{for all } i$$

The corresponding PP is [17] in Fig. 6 of Bomze (1983). As in PP [7], every state evolves to an interior equilibrium with positive concentrations of all three species, so that here also cooperation results. The difference between [7] and [17] is the spiralling motion in the latter corresponding to damped oscillations of frequencies, which increase or decrease monotonically in [7].

The planar Lotka-Volterra system describes evolution of two interacting populations with densities $x \geqslant 0$ and $y \geqslant 0$:

$$\left.\begin{aligned} \dot{x} &= x[a + bx + cy] \\ \dot{y} &= y[d + ex + fy] \end{aligned}\right\} \tag{2}$$

This is the simplest formal description of interaction since the growth rates $\dot{x}/x$ and $\dot{y}/y$ depend linearly on the densities x and y, the signs of b, c, e, f representing growth enhancing (if positive), indifference (if zero), or inhibiting effect (if negative) of one species upon itself or the other one. Choosing an appropriate sign structure one obtains, e.g. predator/prey models or competition models for resources that decrease linearly with the densities, cf. Sect. 2.4 in Bomze (1983). For instance, the model investigated originally by Lotka and Volterra exhibits an interior fixed point, the predator-prey equilibrium, which is surrounded by closed orbits corresponding to endless periodic oscillations in the densities.

To show equivalence of the replicator dynamics (1) and the Lotka-Volterra system (2), Hofbauer (1981) used the transformation

$$x_1 = \frac{1}{1 + x + y}, \quad x_2 = \frac{x}{1 + x + y}, \quad x_3 = \frac{y}{1 + x + y} \tag{3}$$

which maps trajectories under (2) onto those under (1) with

$$A = \begin{bmatrix} 0 & 0 & 0 \\ a & b & c \\ d & e & f \end{bmatrix} \tag{4}$$

respecting the direction of flow. For instance, the classical Lotka-Volterra model described above would via (3) be transformed into PP [16] in Fig. 1 below.

Since (1) has the advantage of operating on the compact set S while (2) is of a simpler analytic form, the projective transformation (3) enabled exploitation of the advantageous features of either system in Bomze (1983) with the aim to obtain a complete classification of both dynamics by distinquishing cases according to the fixed point structure (i.e. a number, position and stability properties of fixed points). A similar but different compactification approach is followed by Reyn (1987), who uses a variant of polar coordinates instead of the transformation (3). A more detailed account on this work is deferred to Sect. 4.

The results of Bomze (1983) have been used in several publications since then, mostly in connection with questions concerning bifurcation, perturbation and characterization of chaotic attractors in low dimensions (which of course cannot occur in the planar systems investigated here), or application to (human non-cooperative) game theory. Section 2 will shortly comment on these, and also on recent ramifications in flow classification. Last but not least, a lacuna in the paper of Bomze (1983) will be closed here, adding two more (non-robust) cases to the list specified there. Section 3 is concerned with dynamical properties of certain sets of fixed points which typically can occur in non-robust situations, and which are closely related to a set-valued solution concept in evolutionary game theory that is receiving increasing interest in recent literature. Here, a complete account is given to the different cases related with the specified payoff matrices A, which may be helpful in constructing counter-examples for more general assertions. In Section 4 an explicit systematic classification of planar Lotka-Volterra flows is specified, which takes into account also some differences in asymptotic slopes. As a consequence, in some cases two phase portraits (PPs) are distinguished from each other, although they are isomorphic in a topological sense. Section 5 forms the conclusion while the Appendix contains results which are used in Sect. 3, but which are valid also for the general case of n behaviour patterns.

2 Classification: applications, ramifications and a correction

Stadler and Schuster (1990) investigated small autocatalytic reaction networks and used the classifications in Hofbauer et al. (1980) and Bomze (1983) in a systematic search for all egeneric bifurcations, but also for major classes of degeneracies. Fortunately (see below), from the latter paper they do not use assertions on pointwise fixed straight lines in the relative interior of S.

Schnabl et al. (1991) established the simplest strange attractors possible in Lotka-Volterra systems with three species, and replicator systems with $n = 4$, respectively, investigating a two-dimensional subspace of the twelve-dimensional parameter space. In order to systematically establish robust saddle-point connections on the planar boundary of S^4, these authors also use results from Bomze (1983).

In their paper on mutation in autocatalytic reaction networks dealing with perturbation analysis of the replicator equation, Stadler and Schuster (1992) use facts from their article (1990) referred to above, and correctly report that the number of PPs under (1) specified in Bomze (1983) is 47. However, the complete list of possible PPs under (1) contains 49 different cases (see below).

Relating classical non-cooperative game theory to the approach of evolutionary stability, Bomze (1986) asserted that non-regular ESSs are degenerate also from a dynamics point of view (cf. the paragraph preceding Example n). As Fig. 1 shows, the argument used there remains valid also under the corrected classification (see below).

In a recent paper on quality patterns in public contracting, Antoci and Sacco (1995) used the classification from Bomze (1983) for qualitative analysis of dynamics of a game where a firm has three choices of quality levels in, e.g., building bridges. Also here, no case of interior straight line of fixed points occurs, so that their results are not afflicted by the lacuna.

Recently, Christopher and Devlin (1993) proposed an alternative, efficient and attractive way of classifying all matrices generating robust flows of (1), which were already classified by Zeeman (1980). They argue that there and in Bomze (1983), only one example per PP was presented. While this might be true for Zeeman's classification, this assertion ignores in some sense the appendix in Bomze (1983). Apart from the fact that the efficiency of Christopher and Devlin's (1993) method appears to be confined to the 19 robust cases, it seems to be a matter of taste whether to use their approach or to proceed as follows, applying the classification results in Bomze (1983).

If a replicator system (1) is given by the matrix A, first standardize it by subtracting a_{1j} from each column $j = 1, 2, 3$. This transformation does not alter the behaviour of (1) and results in a matrix with zeroes in its first row, as in (4). For a Lotka-Volterra system (2), this is the initial situation. Next determine the sign structure of the four coefficients a, b, d, f (recall that positive coefficients signify growth enhancing, while negative ones represent inhibiting effects), together with those of the differences $e - b$, $c - f$, and of the product differences $bd - ae$, $af - cd$, $bf - ce$. Due to Propositions 1, 2, 5 and 6 in Bomze (1983), this information already suffices to determine all the eigenvalues of vertices and to establish the existence and eigenvalues of all other isolated fixed points in S. Finally, use the systematic approach there, distinguishing cases according to the number of pointwise fixed lines or fixed points in the relative interior of S, to obtain a PP compatible with the stability structure of fixed points established previously.

However, due to a wrong argument in Bomze (1983), a subcase of case I.b (exactly one pointwise fixed straight line $\bar{g}$ which is not an edge) was excluded erroneously. As a consequence, the classification there has a lacuna corresponding to two further PPs, which can be viewed as limiting cases of [5] and [6]: indeed, if $\bar{g}$ intersects the

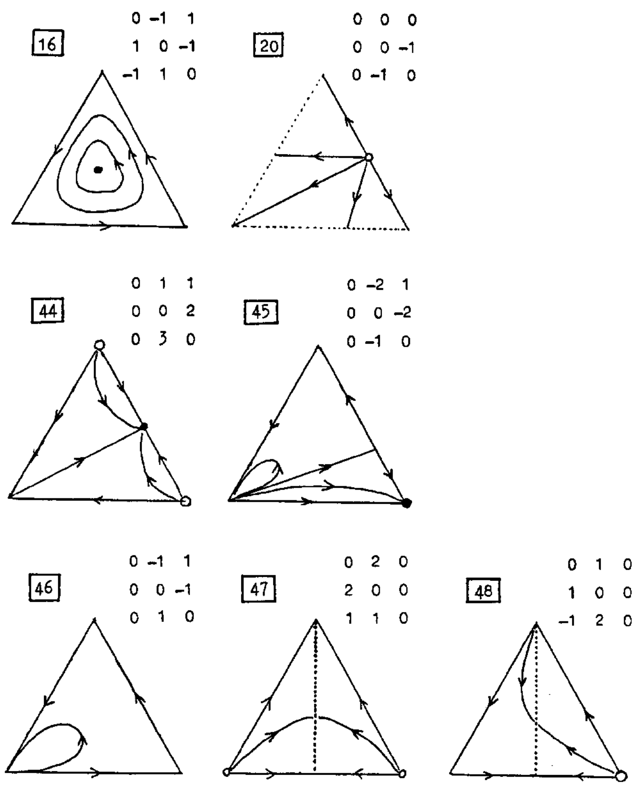

Fig. 1. Phase portraits of the replicator equation (1): correction of Fig. 6 in Bomze (1983)

relative boundary of S in a vertex, say e_3, and also the edge joining e_1 and e_2, then necessarily by Propositions 2, 5 and 6 of Bomze (1983): $ab < 0$; $bd = ae$; $c = f = 0$; but neither $d = 0$ nor $d = a$ (otherwise an edge would be pointwise fixed). The general solution of (2) is therefore in this case

$$y(x) = Cx^{d/a}$$

and all points $[-a/b, y]$, $y \geqslant 0$, are fixed. Depending on the sign of d, one so obtains, up to geometric equivalence, for $0 < d/a < 1$ the PPs $\boxed{47}$ and $-\boxed{47}$ (related to PP $\boxed{5}$, appropriately rotated), and for $d/a < 0$ or $d/a > 1$ the PPs $\boxed{48}$ and $-\boxed{48}$ (related to $\boxed{6}$), which are depicted in Fig. 1. As in Bomze (1983), representative matrices are specified. Unfortunately, the lacuna was accompanied by a series of misprints in the entries of the matrices adjacent to the PPs $\boxed{16}$, $\boxed{20}$, $\boxed{44}$, $\boxed{45}$ and $\boxed{46}$ in Bomze (1983). Therefore, in Fig. 1 also specify these PPs again, together with the corrected matrices.

Let us close this section by a further observation concerning different approaches of proving completeness of the classification: in Bomze (1983) it was argued that in cases II.b, II.c, II.d and III.c, non-robust flows can only occur if both eigenvalues of one vertex, say $[1, 0, 0]$ or $[0, 0]$ for (2), vanish. This can be seen directly by noting that in any other case, the sign of $\dot{x}$ and/or $\dot{y}$ remains constant in a neighbourhood of $[0, 0]$, thus ruling out the possibility of elliptic sectors around that fixed point. However, this argument also follows from far more general principles on central manifolds, see e.g. Carr (1981) or Wiggins (1990, Chapter 2): indeed, since only robust flows on the edges can occur, Theorem 2 of Carr (1981) yields the result if the boundary flow is compatible with a source or a sink, while relation (4) on p. 29 of Carr (1981) settles – together with a short reasoning concerning trajectory slopes – the case of a flow compatible with a saddle point, so that indeed the vertex must be of the type indicated. Finally, the case of vertices with two vanishing eigenvalues is treated completely in Bomze (1983).

3 Evolutionarily stable sets and neutrally stable states

In the recent literature on evolutionary game theory, a solution concept called 'evolutionarily stable (ES) set' is receiving increasing interest. See for example the excellent recent monograph by Cressman (1992), where the following formal definition is given [the notion was introduced by Thomas (1985) who used an equivalent yet different definition originally]: a set of states $\mathscr{P}$ is said to be an ES set if for every $p \in \mathscr{P}$ we have

$$x \cdot Ap \leqslant p \cdot Ap \quad \text{for all } x \in S^n,$$

and

$$x \cdot Ax < p \cdot Ax, \quad \text{if } x \notin \mathscr{P} \text{ with } x \cdot Ap = p \cdot Ap$$

ES sets are the set-valued counterpart to ES states p in the sense that p is an ES state in the sense of Maynard Smith (1974) if and only if the singleton $\{p\}$ is an ES set. Thus, p is an ES state (cf. Hofbauer and Sigmund 1988)

$$x \cdot Ap \leqslant p \cdot Ap \quad \text{for all } x \in S^n,$$

and

$$x \cdot Ax < p \cdot Ax, \quad \text{if } x \neq p \text{ with } x \cdot Ap = p \cdot Ap$$

If one relaxes the strict inequality above, one arrives at the weaker concept of neutrally stable states.

Many games of interest in economics do not possess any ES state. This problem is particularly pertinent in (undiscounted) repeated games and 'cheap talk' games alike. In such games, players can 'signal intentions' to each other without cost by either deviating in a finite number of periods or sending pre-play messages, respectively. Due to these possibilities, no strategies meet the strict inequality in the criterion of evolutionary stability. Therefore, researchers have turned to weaker stability concepts such as neutral stability or ES sets. See e.g. Farrell and Ware (1988), Fudenberg and Maskin (1990), Binmore and Samuelson (1991), Wärneryd (1991, 1993), Blume et al. (1993). For a discussion of the relevance of neutral stability for extensive-form analysis, see Van Damme (1987).

From the viewpoint of qualitative dynamic properties, ES sets are asymptotically stable sets consisting entirely of fixed points under the replicator dynamics (1), see Cressman (1992). Hence, an ES state is always an asymptotically stable fixed point under (1), as was noted already by Taylor and Jonker (1978). However, if a connected component of an ES set has more than one point, none of them can be an ES state, since it can be approximated by other fixed points. In this case, the states in such an ES set are still neutrally stable (see Theorem 2 of the Appendix), and as such Lyapunov stable, according to Thomas (1985), who uses the term 'weakly ES state' instead of 'neutrally stable state'.

A systematic investigation of the flows under (1) shows that not every subset consisting of neutrally stable states is an ES set. Furthermore, there are attracting sets of fixed points which are not ES sets. For singletons, i.e. ES states, this was already observed by Zeeman (1981). Similarly, a set of Lyapunov stable states must not contain neutrally stable states. However, since any attracting fixed point on an edge or a vertex of S occurring in Fig. 6 of Bomze (1983), and Fig. 1 above, is hyperbolic, Proposition 1 (see the Appendix) guarantees that any such fixed point is an ES state. For the sake of completeness, we now list (a) the PPs where, under the matrix A specified, there are ES sets with connected non-singleton components; (b) the PPs with attracting sets (also the singletons) that are not ES; (c) the PPs where neutrally stable states occur which do not belong to ES sets, showing that the converse of Theorem 2 is not true in general; (d) the PPs where Lyapunov stable states occur which are not neutrally stable. The notation $(-)\boxed{k}$ means that PP $\boxed{k}$ and also the PP $-\boxed{k}$ obtained by flow reversal from $\boxed{k}$ belong to this class.

(a) $\boxed{21}$; $-\boxed{24}$; $-\boxed{29}$; and $\boxed{47}$.

(b) $\boxed{5}$: $\mathscr{P} = \{p{:}p_1 = \frac{1}{2}\}$ is attractive, but no ES set, since no $p \in \mathscr{P}$ is neutrally stable; $\boxed{9}$, $\boxed{15}$: $p = [\frac{1}{3}, \frac{1}{3}, \frac{1}{3}]$ is no ES state, but globally attracting; $\boxed{12}$: this is Zeeman's (1981) counterexample; $\boxed{26}$: $\mathscr{P} = \{p{:}p_3 = 0\}$ is attractive, consists of neutrally stable states, but is no ES set; $-\boxed{30}$: $\mathscr{P} = \{p{:}p_3 = 0\}$ is attractive, but is no ES set, since it contains no neutrally stable states except $[1, 0, 0]$.

(c) $\boxed{18}$, $\boxed{19}$, $-\boxed{20}$: every p with $p_2 = 0$ is neutrally stable, but there is no ES set, since there is no asymptotically stable set; $-\boxed{18}$, $-\boxed{19}$, $\boxed{20}$, $\boxed{27}$: as $\boxed{18}$, but with p_1 instead of p_2; $\boxed{22}$, $-\boxed{23}$, $\boxed{28}$, $\boxed{33}$: every p with $p_3 = 0$ and $p_1 > \frac{1}{2}$ is neutrally stable, but there is no ES set, since there is no asymptotically stable set; $-\boxed{22}$, $\boxed{23}$, $-\boxed{28}$, $-\boxed{33}$: as $\boxed{22}$, but with p_2 instead of p_1; $-\boxed{30}$: see (b);

(d) $\boxed{3}$, $(-)\boxed{28}$, $(-)\boxed{33}$: $p = [\frac{1}{2}, \frac{1}{2}, 0]$ is Lyapunov stable, but not neutrally stable; $\boxed{13}$: as $\boxed{3}$, but with $p = [\frac{3}{5}, \frac{1}{5}, \frac{1}{5}]$; $\boxed{5}$, $\boxed{9}$, $\boxed{12}$, $\boxed{15}$: see (b); $\boxed{6}$: all p with $p_1 = \frac{1}{2}$ and $p_2 > \frac{1}{4}$ are Lyapunov stable, but neither of these states is neutrally stable; $\boxed{48}$: all p with $p_1 = p_2 > 0$ are Lyapunov stable, but only those with $\frac{1}{3} \leqslant p_1 \leqslant \frac{1}{2}$ are also neutrally stable.

4 Explicit classification of the planar Lotka-Volterra flows

Apparently being unaware of Bomze (1983), Reyn (1987) provided a long list of possible PPs under (2) on the whole plane, i.e. for arbitrary signs of x and y. Note that this can be accomplished using the results presented here by considering the following four parameters constellations, cycling clockwise through the four quadrants:

(a, b, c, d, e, f); $(a, b, -c, d, e, -f)$;

$(a, -b, -c, d, -e, -f)$; $(a, -b, c, d, -e, f)$

However, Reyn's (1987) list does not contain, e.g. the cases I.a or III.a below, since interest was focussed on a finite number of fixed points there. Here we specify in a systematic way a representative list of PPs under (2) which emerge from the PPs under (1) in Fig. 6 from Bomze (1983), and completed by Fig. 1 above. To this end, we project a PP $\boxed{k}$ from the left, upper or right vertex, respectively, and denote the corresponding PPs by $\boxed{k}_E$, $\boxed{k}_N$ and $\boxed{k}_W$, respectively. Up to coordinate permutation, the projections are given by inversion of formula (3), i.e. $x = x_2/x_1$, $y = x_3/x_1$, which applies to $\boxed{k}_E$.

Since in most applications, not only the limiting behaviour of $x(t)$, $y(t)$ as $t \to +\infty$ or $t \to -\infty$ is important but also the asymptotic slope in case of unbounded trajectories, i.e. the limit of $y(t)/x(t)$ as $t \to \pm\infty$, it seems reasonable to proceed as in Reyn (1987), namely to distinguish PPs from each other if they are topologically equivalent, given that they exhibit different asymptotic slope behaviour. However, we also indicate which PPs should be identified from a purely topological point of view.

Any PP under (2) which does not occur below can be obtained by one PP of the following list by exchanging x with y (denoted by $x \leftrightarrow y$) and/or by flow reversal, replacing t with $-t$.

To proceed in a systematic way, we follow the approach in Bomze (1983) using the case distinctions there. In parentheses we specify the numbers of different cases and the robust PPs among them, if applicable (note that these can only occur in cases II and III.c below):

Case 0: anything fixed. $\boxed{0}_E$ (1)
Case I: straight line of fixed points in the positive quadrant
Case I.a.1: one fixed edge, single fixed point on the other edge. $\boxed{1}_E$, $\boxed{3}_E$ (2)
Case I.a.2: one fixed edge, no fixed point on the other edge. $\boxed{2}_W$, $\boxed{3}_W$, $\boxed{4}_E$ (3)
Case I.b.1: two single fixed points on edges. $\boxed{1}_N$, $\boxed{5}_E$, $\boxed{6}_E$ (3)
Case I.b.2: one single fixed point on an edge, none on the other edge. $\boxed{2}_N$, $\boxed{5}_N$, $\boxed{5}_W$, $\boxed{6}_N$ (4)
Case I.b.3: no fixed points on edges. $\boxed{4}_N$, $\boxed{47}_N$, $\boxed{48}_N$ (3)
Case II: a single fixed point in the positive quadrant
Case II.a: two single fixed points on edges. $\boxed{7}_E$, $\boxed{8}_E$, $\boxed{8}_N$, $\boxed{9}_N$, $\boxed{10}_N$, $\boxed{11}_N$, $\boxed{12}_N$, $\boxed{13}_E$ (8/7 robust)
Case II.b: one single fixed point on an edge, none on the other edge. $\boxed{9}_E$, $\boxed{9}_W$, $\boxed{10}_E$, $\boxed{10}_W$, $\boxed{11}_E$, $\boxed{12}_E$, $\boxed{12}_W$, $\boxed{13}_N$, $\boxed{14}_E$, $\boxed{15}_E$, $\boxed{15}_W$ (11/10 robust)
Case II.c: no fixed points on edges. $\boxed{14}_N$, $\boxed{15}_N$, $\boxed{16}_E$, $\boxed{17}_E$ (4/3 robust)
Case III: no fixed point in the positive quadrant
Case III.a: two fixed edges. $\boxed{18}_E$, $\boxed{19}_E$, $\boxed{20}_E$ (3)

Case III.b.1: one fixed edge, a single fixed point on the other edge. $\boxed{20}_N$, $\boxed{21}_E$, $\boxed{21}_W$, $\boxed{22}_E$, $\boxed{23}_E$, $\boxed{24}_E$, $\boxed{25}_E$, $\boxed{26}_E$, $\boxed{27}_E$, $\boxed{28}_E$ (10)

Case III.b.2: one fixed edge, no fixed point on the other edge. $\boxed{18}_N$, $\boxed{19}_N$, $\boxed{19}_W$, $\boxed{23}_W$, $\boxed{24}_W$, $\boxed{25}_W$, $\boxed{26}_W$, $\boxed{27}_W$, $\boxed{28}_W$, $\boxed{30}_E$, $\boxed{30}_W$, $\boxed{31}_E$, $\boxed{32}_E$, $\boxed{32}_W$, $\boxed{33}_E$ (15)

Case III.c.1: two single fixed points on edges. $\boxed{21}_N$, $\boxed{22}_N$, $\boxed{34}_E$, $\boxed{34}_N$, $\boxed{34}_W$, $\boxed{35}_E$, $\boxed{35}_N$, $\boxed{36}_N$, $\boxed{37}_N$, $\boxed{38}_N$, $\boxed{39}_N$ (11/9 robust)

Case III.c.2: one single fixed point on an edge, no fixed point on the other edge. $\boxed{23}_N$, $\boxed{24}_N$, $\boxed{25}_N$, $\boxed{26}_N$, $\boxed{27}_N$, $\boxed{28}_N$, $\boxed{36}_E$, $\boxed{36}_W$, $\boxed{37}_E$, $\boxed{37}_W$, $\boxed{38}_E$, $\boxed{38}_W$, $\boxed{39}_E$, $\boxed{40}_E$, $\boxed{41}_E$, $\boxed{41}_W$, $\boxed{42}_E$, $\boxed{44}_N$, $\boxed{45}_N$, $\boxed{45}_W$ (20/11 robust).

Case III.c.3: only [0,0] is fixed. $\boxed{29}_N$, $\boxed{30}_N$, $\boxed{31}_N$, $\boxed{32}_N$, $\boxed{33}_N$, $\boxed{40}_N$, $\boxed{41}_N$, $\boxed{42}_N$, $\boxed{44}_E$, $\boxed{45}_E$, $\boxed{46}_E$, $\boxed{46}_N$ (12/5 robust)

From a topological point of view, the following PPs are indistinguishable from each other: $\boxed{1}_N$ and $\boxed{5}_E$; $\boxed{2}_N$ and $\boxed{5}_N (x \leftrightarrow y)$; $\boxed{7}_E$ and $\boxed{9}_N$; $\boxed{8}_E$ and $-\boxed{11}_N$; $\boxed{8}_N$ and $\boxed{10}_N$; $\boxed{9}_E$, and $\boxed{15}_W$; $\boxed{10}_W$, $-\boxed{11}_E (x \leftrightarrow y)$, and $\boxed{14}_E$; $\boxed{15}_N$ and $\boxed{17}_E (x \leftrightarrow y)$; $-\boxed{18}_N$, $-\boxed{19}_N$, $\boxed{24}_W (x \leftrightarrow y)$, and $\boxed{32}_W (x \leftrightarrow y)$; $\boxed{19}_W$, $\boxed{30}_E (x \leftrightarrow y)$, and $\boxed{31}_E (x \leftrightarrow y)$; $\boxed{20}_N (x \leftrightarrow y)$, $\boxed{21}_E$, $\boxed{25}_E$, and $\boxed{26}_E$; $-\boxed{21}_N$, $\boxed{34}_N$, $\boxed{35}_E (x \leftrightarrow y)$, $\boxed{37}_N$, and $\boxed{38}_N (x \leftrightarrow y)$; $\boxed{21}_W$ and $\boxed{27}_E$; $\boxed{22}_E$ and $\boxed{23}_E$; $-\boxed{24}_N$, $\boxed{26}_N$, $\boxed{39}_E (x \leftrightarrow y)$, $-\boxed{41}_W$, and $-\boxed{42}_E$; $-\boxed{25}_N$, $\boxed{38}_W (x \leftrightarrow y)$, and $\boxed{44}_N$; $\boxed{27}_N$, $\boxed{28}_N$, $\boxed{36}_E$, $-\boxed{37}_W$, $-\boxed{40}_E (x \leftrightarrow y)$, and $\boxed{45}_W$; $\boxed{29}_N$, $\boxed{30}_N$, $\boxed{40}_N$, and $-\boxed{42}_N$; $\boxed{31}_N$, $\boxed{32}_N$, $\boxed{33}_N$, $\boxed{41}_N$, and $-\boxed{46}_N$; $-\boxed{34}_W$ and $\boxed{36}_N (x \leftrightarrow y)$; $\boxed{38}_E$ and $-\boxed{45}_N$.

As a consequence we obtain 67 topologically different PPs of (2).

5 Conclusion

The replicator dynamics (1) arises if one equips a certain game theoretical model for the evolution of behaviour in animal conflicts with dynamics. It serves to model many biological processes not only in animal behaviour, but also in population genetics, and even in prebiotic evolution. On the other hand, the Lotka-Volterra system (2) is used in mathematical ecology to describe the interaction of two populations over time. Here, predator/prey situations can be modelled as well as competition for a resource. Since both dynamics are equivalent from a qualitative point of view which focuses on the analysis of long-term behaviour, classification of all possible planar flows has a wide range of applications.

After a short account on applications and ramifications of planar classification, a lacuna in the classification from Bomze (1983) is closed, so that the complete list of possible PPs under (1) now counts 49 qualitatively (up to flow reversal) different cases: 19 robust ones and 30 non-robust. Through a systematic investigation of these flows, we obtained a class of models which illustrate the asymptotic behaviour under the replicator dynamics of certain solution concepts in evolutionary game theory. Finally, a complete explicit classification of the flows under (2) is presented: there are 42 robust PPs and 68 non-robust PPs, summing up to a total of 110 PPs. If one ignores different asymptotic slope behaviour, then one arrives at 67 topologically different PPs under (2), up to flow reversal.

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Appendix

Proposition 1:

Let p be a hyperbolic fixed point on an edge of S^n. Then the following assertions are equivalent:

(a) p is asymptotically stable;
(b) p is an ES state.

Proof: see, e.g. Bomze (1986), Theorem 30. □

Theorem 2:

If p belongs to an evolutionarily stable set $\mathscr{P}$, i.e. if

$$x \cdot Ap \leqslant p \cdot Ap \quad \text{for all } x \in S^n,$$

and

$$x \cdot Ax < p \cdot Ax, \quad \text{if } x \notin \mathscr{P} \text{ with } x \cdot Ap = p \cdot Ap,$$

then p is neutrally stable, i.e.

$$x \cdot Ap \leqslant p \cdot Ap \quad \text{for all } x \in S^n$$

and

$$x \cdot Ax \leqslant p \cdot Ax, \quad \text{if } x \cdot Ap = p \cdot Ap$$

Proof: All we have to show is $x \cdot Ax \leqslant p \cdot Ax$ whenever $x \in \mathscr{P}$ and $x \cdot Ap = p \cdot Ap$. But since $\mathscr{P}$ is an ES set, $p \cdot Ax \leqslant x \cdot Ax$. So assume that this inequality is strict and put $y = (1-\varepsilon)x + \varepsilon p \in S^n$ for some small $\varepsilon > 0$. Then $y \cdot Ap = (1-\varepsilon)x \cdot Ap + \varepsilon p \cdot Ap = p \cdot Ap = x \cdot Ap$ and therefore

$$\begin{aligned} x \cdot Ay - y \cdot Ay &= \varepsilon[x \cdot Ap - y \cdot Ap] + (1-\varepsilon)[x \cdot Ax - y \cdot Ax] \\ &= (1-\varepsilon)\varepsilon[x \cdot Ax - p \cdot Ax] > 0 \end{aligned}$$

so that $y \notin \mathscr{P}$ results. Thus, evolutionary stability of $\mathscr{P}$ and the relation $p \in \mathscr{P}$ yields the contradiction

$$\begin{aligned} 0 < p \cdot Ay - y \cdot Ay &= (1-\varepsilon)[p \cdot Ay - x \cdot Ay] \\ &= (1-\varepsilon)^2[p \cdot Ax - x \cdot Ax] < 0 \end{aligned}$$

Hence, we have even shown the following property: if both x and p belong to an ES set, then either both quantities $x \cdot Ap - p \cdot Ap$ and $p \cdot Ax - x \cdot Ax$ are strictly negative or both vanish. □

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