

USING CHEMICAL REACTION NETWORK THEORY TO SHOW STABILITY OF DISTRIBUTIONAL DYNAMICS IN GAME THEORY

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ABSTRACT. This article shows how to apply results of chemical reaction network theory (CRNT) to prove uniqueness and stability of a positive equilibrium for pairs/groups distributional dynamics that arise in game theoretic models. Evolutionary game theory assumes that individuals accrue their fitness through interactions with other individuals. When there are two or more different strategies in the population, this theory assumes that pairs (groups) are formed instantaneously and randomly so that the corresponding pairs (groups) distribution is described by the Hardy–Weinberg (binomial) distribution. If interactions times are phenotype dependent the Hardy-Weinberg distribution does not apply. Even if it becomes impossible to calculate the pairs/groups distribution analytically we show that CRNT is a general tool that is very useful to prove not only existence of the equilibrium, but also its stability. In this article, we apply CRNT to pair formation model that arises in two player games (e.g., Hawk-Dove, Prisoner’s Dilemma game), to group formation that arises, e.g., in Public Goods Game, and to distribution of a single population in patchy environments. We also show by generalizing the Battle of the Sexes game that the methodology does not always apply.

1. Introduction. Classic two-player evolutionary game theory [13, 22] assumes that individuals interact in pairs and, depending on the strategies they use, they gain or lose payoffs. For example, in two-strategy games, there are three possible types of pairs: two homogeneous and one heterogeneous pair types. To calculate individual payoffs at given frequencies of the two strategies in the population, the theory assumes that pairs are formed at random. This leads to the Hardy-Weinberg proportions of the three pair types. The situation changes when pairing is not random. One reason this can happen is when interaction times are strategy dependent

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[19, 20, 6, 1, 18]. For these models, pair formation dynamics as described by differential equations are needed for the calculation of individual fitness (i.e., payoff). It is then important to know that the pair formation dynamics converge to a unique equilibrium. This can be shown analytically only for the most simple models [e.g., 19]. For more complex models, [11] gave conditions under which a single positive equilibrium exists, without showing its stability.

As many of these distributional models are in the form of mass action kinetics, it is appealing to use powerful results of chemical reaction network theory [10]. This theory originated in the work of F. J. M. Horn [15, 16, 17] and led to the Deficiency Zero and One Theorems that provide conditions on the structure of the reaction network that guarantee a unique and locally stable positive equilibrium. The question of global stability led to the Global Attractor Conjecture that was proved recently [4]. The chemical reaction network theory is based on constructing an appropriate Lyapunov function as illustrated by the two examples in Section 2. In principle, the theory applies to very complex networks and so is not limited to the small networks considered in these examples.

Křivan et al. [20] consider a two strategy game where individuals are either paired or single. The time individuals want to stay in the pair depends on their strategies. The equilibrium distribution at given strategy frequencies and population size requires to solve a system of quadratic equations and the resulting solution can be obtained using computer algebra software, but it is far too complex for further stability analysis. Instead, numerical simulations showed that distributional dynamics were converging to a single interior equilibrium. In this article, we apply chemical reaction network theory to show that this is really true and we also extend the result to any number of strategies (Section 2.1).

Our second example (Section 2.2) investigates the group formation process for multi-player games. Křivan and Cressman [18] showed that in the public goods game where individuals are free to leave their current group and search for a new group hoping to receive a higher payoff, there are some counter-intuitive opt-out rules. In particular, opting out against cooperators is as good as opting out against defectors. The opting out rules were based on the number of defectors/cooperators in the current group, and they were fixed at the beginning of the game. Once again, to calculate fitnesses it was crucial to calculate the distribution of groups with respect to the number of cooperators they contain. As it was not possible to calculate analytically the equilibrium distribution, numerical simulations were performed instead that suggested that there was a unique and stable equilibrium distribution. Again, we show this result can be proven using chemical reaction network theory.

Section 3 considers pair formation for two asymmetric games. The first example (Section 3.1) is the Battle of the Sexes (BoS) game [9] where pair interaction times and times to care for offspring or for courtship are strategy dependent. Cressman and Křivan [7] assumed that the resulting distributional equilibrium is unique and stable and they analysed the Nash equilibria of the game as a function of interaction times. Again, using chemical reaction theory (CRNT) we prove that the distributional equilibrium is stable. The BoS game is somewhat particular in that it assumes that some interaction times are equal to zero (e.g., Philanderer males do not interact with Coy females or Philanderer males do not spend any time caring for offspring) which simplifies the distributional dynamics. As a second example, we consider a generalised BoS game of [7] where we assume all pair interaction

times as well as times to recover for disbanded individuals before pairing again can be positive. Then we show that this additional “mixing” prevents us to apply the Deficiency Zero Theorem for the resulting distributional dynamics.

Finally, Section 3.3 briefly considers individual movement in a patchy environment. The results here illustrate that the methods of chemical reaction network theory apply to biological systems that are not based on pair/group formation.

2. Models for symmetric games. Here we consider two models of pairs/groups formation in systems with different phenotypes. Both of these models assume that pairs/groups are formed at random but the time they stay together depends on the phenotypes involved. Differential equations describing these processes assume mass action kinetics which is the usual assumption in models of population dynamics. In both these cases, we prove existence and stability of a single positive equilibrium using results of chemical reaction network theory [CRNT; 10]. This theory provides a procedure that leads to differential equations describing an arbitrary chemical reaction network. It also provides conditions under which these differential equations have a single positive equilibrium which is globally asymptotically stable [10, 4]. We also show that this theory is useful to prove stability in distribution of a population dispersing between several patches. We start with uniqueness and stability of the pair distribution equilibrium.

2.1. Stability of pair distribution dynamics. Suppose the population has m possible phenotypes (also called [pure] strategies) $i = 1, \dots, m$. Individuals are either single or in pairs. Singles meet each other at random with rate $\lambda > 0$ and form pairs. Each ij pair stays together for an expected time $\tau_{ij} > 0$, $i, j = 1, \dots, m$ (i.e., ij pairs disband at rate τ_{ij}). Let n_i be the number of singles with phenotype i and n_{ij} be the number of (ordered) ij pairs. The distributional dynamics are

$$\begin{aligned} \frac{dn_i}{dt} &= -\lambda n_i \sum_{j=1}^m n_j + \sum_{j=1}^m \frac{n_{ij}}{\tau_{ij}} + \sum_{j=1}^m \frac{n_{ji}}{\tau_{ji}} \\ \frac{dn_{ij}}{dt} &= \frac{\lambda}{2} n_i n_j - \frac{n_{ij}}{\tau_{ij}}. \end{aligned} \tag{1}$$

where n_i and n_{ij} are functions of time t . In particular, n_{ij} pairs are formed at rate $\frac{\lambda}{2} n_i n_j$ since these pairs consist of two individuals.¹ For two phenotypes, distributional dynamics (1) were used, e.g., in [20] to model distribution of single Hawks, single Doves and their pairs. In fact, we will analyze the following more general distributional dynamics where singles of phenotypes i and j meet at random at rate $\lambda_{ij} = \lambda_{ji}$ (i.e., the rate n_{ij} pairs are formed, $\frac{\lambda_{ij}}{2} n_i n_j$, depends on the phenotypic pair)

$$\begin{aligned} \frac{dn_i}{dt} &= -n_i \sum_{j=1}^m \lambda_{ij} n_j + \sum_{j=1}^m \frac{n_{ij}}{\tau_{ij}} + \sum_{j=1}^m \frac{n_{ji}}{\tau_{ji}} \\ \frac{dn_{ij}}{dt} &= \frac{\lambda_{ij}}{2} n_i n_j - \frac{n_{ij}}{\tau_{ij}}. \end{aligned} \tag{2}$$

¹Here and throughout the article, distributional dynamics such as (1) ignore finite population effects by assuming that population sizes are sufficiently large that they evolve according to expected rates of change.

Under the condition assumed for the remainder of this section that ij and ji pairs stay together for the same expected amount of time (i.e., $\tau_{ij} = \tau_{ji}$ for $i, j = 1, \dots, m$),

$$\frac{d(n_{ij} - n_{ji})}{dt} = -\frac{n_{ij} - n_{ji}}{\tau_{ij}}.$$

Thus, all trajectories of the $(m + m^2)$ -dimensional dynamics (2) converge to the invariant $\frac{m(m+3)}{2}$ -dimensional subspace where $n_{ij} = n_{ji}$ for $i, j = 1, \dots, m$. The distributional dynamics on this subspace can be rewritten as

$$\begin{aligned} \frac{dn_i}{dt} &= -n_i \sum_{j=1}^m \lambda_{ij} n_j + 2 \sum_{j=1}^m \frac{n_{ij}}{\tau_{ij}} \\ \frac{dn_{ij}}{dt} &= \frac{\lambda_{ij}}{2} n_i n_j - \frac{n_{ij}}{\tau_{ij}}. \end{aligned} \quad (3)$$

We are interested in the equilibria and their stability for this system of differential equations. The equilibria cannot be calculated analytically except in some special cases. For instance, if all pairs stay together for the same expected amount of time and all singles meet at the same rate, we get

Proposition 1. *Let $\tau_{ij} = \tau > 0$ and $\lambda_{ij} = \lambda > 0$ for all $i, j = 1, \dots, m$. Then for each total number of individuals of phenotype i , $N_i \equiv n_i + 2 \sum_{j=1}^m n_{ij}$, system (3) has a unique, positive equilibrium*

$$n_i = \frac{2N_i}{1 + \sqrt{1 + 4N\lambda\tau}}, \quad n_{ij} = \frac{2N_i N_j \lambda \tau}{(1 + \sqrt{1 + 4N\lambda\tau})^2}, \quad (4)$$

where $N \equiv \sum_{j=1}^m N_j$ is the population size.

Proof. When $\tau_{ij} = \tau$ and $\lambda_{ij} = \lambda$ for all $i, j = 1, \dots, m$, the equilibrium for (3) satisfies

$$N_i = n_i + 2 \sum_{j=1}^m n_{ij} = n_i + \lambda \tau n_i \sum_{j=1}^m n_j = n_i \left(1 + \lambda \tau \sum_{j=1}^m n_j \right) \quad (5)$$

and

$$N = \sum_{i=1}^m N_i = \sum_{i=1}^m n_i + \lambda \tau \left(\sum_{i=1}^m n_i \right)^2.$$

Thus

$$\sum_{i=1}^m n_i = \frac{-1 + \sqrt{1 + 4\lambda\tau N}}{2\lambda\tau}.$$

Substituting this expression into (5) yields

$$N_i = n_i \left(1 + \lambda \tau \frac{\sqrt{1 + 4\lambda\tau N} - 1}{2\lambda\tau} \right) = n_i \left(\frac{1 + \sqrt{1 + 4\lambda\tau N}}{2} \right).$$

Thus

$$\begin{aligned} n_i &= \frac{2N_i}{1 + \sqrt{1 + 4\lambda\tau N}}, \\ n_{ij} &= \frac{\lambda \tau n_i n_j}{2} = \frac{2\lambda \tau N_i N_j}{(1 + \sqrt{1 + 4\lambda\tau N})^2}. \end{aligned}$$

□

Notice that, under the conditions of Proposition 1, the total number of pairs at equilibrium (4) satisfies

$$\sum_{i,j=1}^m n_{ij} = \frac{2\lambda\tau}{(1 + \sqrt{1 + 4\lambda\tau N})^2} \left(\sum_{i=1}^m N_i \right)^2.$$

Thus, the frequency distribution of unordered pairs $p_{ij} = \frac{n_{ij} + n_{ji}}{\sum_{i,j=1}^m n_{ij}}$ at the unique equilibrium are given by

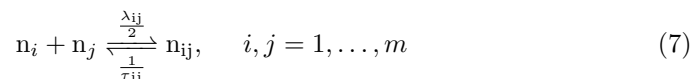
$$p_{ii} = \frac{N_i^2}{(\sum_{i=1}^m N_i)^2},$$

$$p_{ij} = \frac{2N_i N_j}{(\sum_{i=1}^m N_i)^2},$$

and so satisfy the Hardy-Weinberg principle

$$p_{ii}p_{jj} = \frac{1}{4}p_{ij}^2. \tag{6}$$

The purpose of this section is to generalize the existence of this equilibrium to arbitrary choices of positive τ_{ij} and λ_{ij} in (3) and to examine its stability. Unfortunately, an analytic expression for the equilibrium is not feasible in general. One way to investigate its uniqueness and stability is to treat (3) as the dynamical system corresponding to the mass action kinetics (MAK) given by the following “reactions”



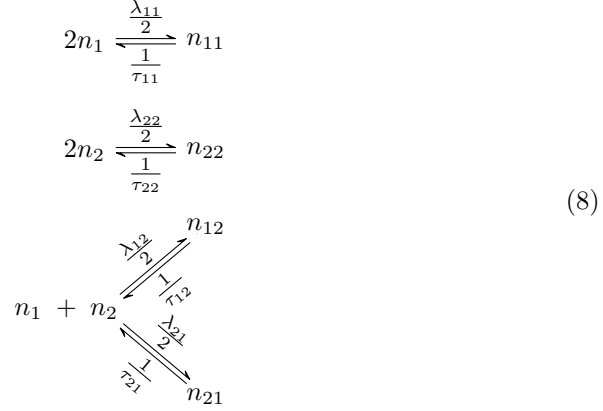
describing (ordered) pair formation with rate $\lambda_{ij}/2$ and pair disbanding with rate $1/\tau_{ij}$.

Following CRNT, there are $m + m^2$ “species” $\mathcal{S} = \{n_i, n_{ij} \mid 1 \leq i, j \leq m\}$ and $n = \frac{m(m+1)}{2} + m^2$ complexes $\mathcal{C} = \{n_i + n_j \mid 1 \leq i \leq j \leq m\} \cup \{n_{ij} \mid 1 \leq i, j \leq m\}$.² The reaction network (7) has $\ell = \frac{m(m+1)}{2}$ linkage classes³ $\{n_i + n_j, n_{ij}, n_{ji}\}$ for $1 \leq i \leq j \leq m$ (i.e., disjoint subsets of \mathcal{C} connected by reaction arrows, see Example 1) [Definition 6.1.1. in 10]. The following example illustrates how (7) generates the distributional dynamics (2) when $m = 2$.

Example 1. For two-strategy games ($m = 2$), the reaction network is

²Note that $n_i + n_j$ is the same complex as $n_j + n_i$ but n_{ij} and n_{ji} are different complexes if $j \neq i$.

³If there is a chain of one or more reactions through which two complexes are connected, these complexes are said to be linked. Being linked induces a partition on the set of complexes into equivalence of linkage classes.



There are 6 species $\mathcal{S} = \{n_1, n_2, n_{11}, n_{12}, n_{21}, n_{22}\}$, $n = 7$ complexes

$$\mathcal{C} = \{2n_1, 2n_2, n_{11}, n_{12}, n_{21}, n_{22}, n_1 + n_2\}$$

and $\ell = 3$ linkage classes $\{\{2n_1, n_{11}\}, \{2n_2, n_{22}\}, \{n_1 + n_2, n_{12}, n_{21}\}\}$.

Reaction network (8) defines a kinetics matrix K which has initial complexes in columns and final complexes in rows and the entries of the matrix are the corresponding reaction rates. With elements of \mathcal{C} and \mathcal{S} listed in the same order as above, the kinetics matrix is

$$K = \begin{array}{c} \begin{array}{c} 2n_1 \\ 2n_2 \\ n_1 + n_2 \\ n_{11} \\ n_{22} \\ n_{12} \\ n_{21} \end{array} \end{array} \begin{array}{c} \begin{array}{ccccccc} 2n_1 & 2n_2 & n_1 + n_2 & n_{11} & n_{22} & n_{12} & n_{21} \end{array} \\ \left[\begin{array}{ccccccc} 0 & 0 & 0 & \frac{1}{\tau_{11}} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{\tau_{22}} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \frac{1}{\tau_{12}} & \frac{1}{\tau_{21}} \\ \frac{\lambda_{11}}{2} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \frac{\lambda_{22}}{2} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{\lambda_{12}}{2} & 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{\lambda_{21}}{2} & 0 & 0 & 0 & 0 \end{array} \right] \end{array} .$$

Together with the stoichiometric matrix Y which has complexes in columns and species in rows with stoichiometric coefficients as entries,

$$Y = \begin{array}{c} \begin{array}{c} n_1 \\ n_2 \\ n_{11} \\ n_{22} \\ n_{12} \\ n_{21} \end{array} \end{array} \begin{array}{c} \begin{array}{ccccccc} 2n_1 & 2n_2 & n_1 + n_2 & n_{11} & n_{22} & n_{12} & n_{21} \end{array} \\ \left[\begin{array}{ccccccc} 2 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 2 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{array} \right] ,
\end{array}$$

CRNT defines differential equations describing the network dynamics for the evolution of species numbers. This is done through the 6-dimensional vector field

$$f = Y(K - \text{DiagonalMatrix}(K^\top \mathbf{1}))\psi. \tag{9}$$

Here $\mathbf{1}$ denotes the vector consisting of 1s, and DiagonalMatrix transforms a vector into a diagonal matrix where elements of the vector form the matrix diagonal. Vector ψ has dimension equal to the number of complexes in the network. For each complex, the corresponding entry in this vector is given as the product of species that compose the complex. That is, $\psi = \{n_1^2, n_2^2, n_1 n_2, n_{11}, n_{22}, n_{12}, n_{21}\}$. By performing the

matrix calculations in (9), we obtain the right-hand side of the following network dynamics corresponding to reaction network (8) which assumes $\lambda_{12} = \lambda_{21}$

$$\begin{aligned}
\frac{dn_1}{dt} &= -n_1(\lambda_{11}n_1 + \lambda_{12}n_2) + \frac{2n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{21}}{\tau_{21}} \\
\frac{dn_2}{dt} &= -n_2(\lambda_{21}n_1 + \lambda_{22}n_2) + \frac{n_{12}}{\tau_{12}} + \frac{n_{21}}{\tau_{21}} + \frac{2n_{22}}{\tau_{22}} \\
\frac{dn_{11}}{dt} &= \frac{\lambda_{11}n_1^2}{2} - \frac{n_{11}}{\tau_{11}} \\
\frac{dn_{22}}{dt} &= \frac{\lambda_{22}n_2^2}{2} - \frac{n_{22}}{\tau_{22}} \\
\frac{dn_{12}}{dt} &= \frac{\lambda_{12}n_1n_2}{2} - \frac{n_{12}}{\tau_{12}} \\
\frac{dn_{21}}{dt} &= \frac{\lambda_{21}n_1n_2}{2} - \frac{n_{21}}{\tau_{21}}.
\end{aligned} \tag{10}$$

This is the distribution dynamics (2) when $m = 2$.

When the kinetics matrix K and stoichiometric matrix Y as well as the vector ψ are extended to games with a general number m of strategies, f in (9) becomes the $(m + m^2)$ -dimensional vector field for the distributional dynamics (2). To apply CRNT to this MAK system, we must consider the set of reactions in (7) given by

$$\mathcal{R} = \{n_{ij} - (n_i + n_j) \mid 1 \leq i, j \leq m\}$$

as well as the reverse of these reactions $(n_i + n_j) - n_{ij}$ (which we do not list). In particular, the network is reversible as the arrows in (7) point both ways. The set of reactions \mathcal{R} can be represented as an $m^2 \times (m^2 + m)$ matrix R where each column corresponds to a species and the m^2 rows provide the species coefficients of the corresponding reaction. If the species columns are arranged to have all singles first and all the pairs n_{ij} last, then the last m^2 columns of R form the identity matrix. Thus, the rank of R is $s = m^2$, an essential fact in the proof of Proposition 2 below.

For Example 1, the set of reactions is $\mathcal{R} = \{n_{11} - 2n_1, n_{22} - 2n_2, n_{12} - (n_1 + n_2), n_{21} - (n_1 + n_2)\}$, where we do not list the reverse reactions for simplicity. The corresponding reaction matrix is

$$R = \begin{array}{c} n_{11}-2n_1 \\ n_{22}-2n_2 \\ n_{12}-n_1-n_2 \\ n_{21}-n_1-n_2 \end{array} \begin{bmatrix} n_1 & n_2 & n_{11} & n_{22} & n_{12} & n_{21} \\ -2 & 0 & 1 & 0 & 0 & 0 \\ 0 & -2 & 0 & 1 & 0 & 0 \\ -1 & -1 & 0 & 0 & 1 & 0 \\ -1 & -1 & 0 & 0 & 0 & 1 \end{bmatrix}$$

which clearly has rank $s = 4$.

In what follows we denote by $\mathbb{R}_{\geq 0}$ the set of non-negative real numbers and by \mathbb{R}_+ the set of positive numbers. It is important to note that for fixed positive N_i ($i = 1, \dots, m$), the affine subspace

$$\{(n_1, \dots, n_m, n_{11}, \dots, n_{1m}, \dots, n_{m1}, \dots, n_{mm}) \mid N_i = n_i + \sum_{j=1}^m n_{ij}, \quad i = 1, \dots, m\}$$

is invariant for dynamics (3). The intersection of this affine subspace with $\mathbb{R}_+^{m+m^2}$ is called a positive stoichiometric compatibility class [Definition 3.4.6 in 10].

Proposition 2. *Let $\tau_{ij} > 0$ and $\lambda_{ij} > 0$ for all $i, j = 1 \dots, m$. Then for each total positive number of individuals of phenotype $i = 1, \dots, m$, $N_i \equiv n_i + 2 \sum_{j=1}^m n_{ij}$, system (3) has a unique, positive equilibrium (i.e., in $\mathbb{R}_+^{m+m^2}$) which is globally asymptotically stable with respect to $\mathbb{R}_{\geq 0}^{m+m^2}$.*

Proof. The existence and uniqueness of the positive equilibrium follows from the Deficiency Zero Theorem [Theorem 7.1.1 in 10].⁴ Indeed, network (7) is reversible and its deficiency, defined as $\delta = n - \ell - s = \frac{m(m+1)}{2} + m^2 - \frac{m(m+1)}{2} - m^2$ is zero.⁵ Thus, for each total positive number of individuals of phenotype $i = 1, \dots, m$, $N_i = n_i + 2 \sum_{j=1}^m n_{ij}$, there exists a positive equilibrium $n^* = (n_i^*, n_{ij}^*) \in \mathbb{R}_+^{m+m^2}$ of system (3) which is unique. In fact, this equilibrium is in the positive stoichiometric class defined by N_1, \dots, N_m . The same theorem also shows that the equilibrium is locally asymptotically stable using the Lyapunov function [10]

$$V = \sum_{i=1}^m \left(n_i \ln \frac{n_i}{n_i^*} - (n_i - n_i^*) \right) + \sum_{i,j=1}^m \left(n_{ij} \ln \frac{n_{ij}}{n_{ij}^*} - (n_{ij} - n_{ij}^*) \right). \quad (11)$$

To see this, rewrite system (3) as

$$\begin{aligned} \frac{dn_i}{dt} &= 2 \sum_{j=1}^m \frac{n_{ij}^*}{\tau_{ij}} \left(\frac{n_{ij}}{n_{ij}^*} - \frac{n_i n_j}{n_i^* n_j^*} \right), \quad i = 1, \dots, m \\ \frac{dn_{ij}}{dt} &= \frac{n_{ij}^*}{\tau_{ij}} \left(\frac{n_i n_j}{n_i^* n_j^*} - \frac{n_{ij}}{n_{ij}^*} \right), \quad 1 \leq i, j \leq m. \end{aligned} \quad (12)$$

since the components of $n^* \in \mathbb{R}_+^{m+m^2}$ satisfy $2 \frac{n_{ij}^*}{\tau_{ij}} = \lambda n_i^* n_j^*$. It is straightforward to show that V is positive at all interior positive points $n = (n_i, n_{jk}) \in \mathbb{R}_+^{m+m^2}$ where $i, j, k = 1, \dots, m$ except at $V(n^*) = 0$. Moreover, the derivative of V along

⁴Here we state for readers convenience a slightly reworded Deficiency Zero Theorem taken from Feinberg [10].

Theorem 1. *Let us consider a reaction network of deficiency zero.*

1. *If the network is not weakly reversible, then, for an arbitrary kinetics, the differential equations for the kinetic system cannot admit a positive equilibrium, nor can they admit a cyclic composition trajectory containing a composition at which all species concentrations are positive.*
2. *If the network is weakly reversible (in particular, if it is reversible) and the kinetics is mass action, then, regardless of rate constant values, the resulting differential equations have the following properties: There exists within each positive stoichiometric compatibility class precisely one equilibrium; that equilibrium is asymptotically stable; and there cannot exist a nontrivial cyclic composition trajectory along which all species concentrations are positive.*

⁵For our purposes, these results imply that our model satisfies the conditions of The Deficiency Zero Theorem (DZT). In particular, since our kinetics are mass action, the resulting differential equation has precisely one equilibrium which is asymptotically stable regardless of the values of the rate constants.

trajectories of (3) is

$$\begin{aligned} \frac{dV}{dt} &= \sum_{i=1}^m \frac{dn_i}{dt} \ln \frac{n_i}{n_i^*} + \sum_{i,j=1}^m \frac{dn_{ij}}{dt} \ln \frac{n_{ij}}{n_{ij}^*} \\ &= \sum_{i,j=1}^m \frac{n_{ij}^*}{\tau_{ij}} \left(\frac{n_{ij}}{n_{ij}^*} - \frac{n_i n_j}{n_i^* n_j^*} \right) \left(2 \ln \frac{n_i}{n_i^*} - \ln \frac{n_{ij}}{n_{ij}^*} \right) \\ &= \sum_{i,j=1}^m \frac{n_{ij}^*}{\tau_{ij}} \left(\frac{n_{ij}}{n_{ij}^*} - \frac{n_i n_j}{n_i^* n_j^*} \right) \left(\ln \frac{n_i}{n_i^*} + \ln \frac{n_j}{n_j^*} - \ln \frac{n_{ij}}{n_{ij}^*} \right) \end{aligned}$$

where the last equality follows from the symmetries $n_{ij} = n_{ji}$, $n_{ij}^* = n_{ji}^*$, and $\tau_{ij} = \tau_{ji}$ (i.e., $\frac{n_{ij}^*}{\tau_{ij}} \left(\frac{n_{ij}}{n_{ij}^*} - \frac{n_i n_j}{n_i^* n_j^*} \right)$ is symmetric in ij). Thus, the derivative of V along trajectories of (12) is

$$\frac{dV}{dt} = \sum_{i=1}^m \sum_{j=i}^m \frac{n_{ij}^*}{\tau_{ij}} \left(\frac{n_{ij}}{n_{ij}^*} - \frac{n_i n_j}{n_i^* n_j^*} \right) \left(\ln \frac{n_i n_j}{n_i^* n_j^*} - \ln \frac{n_{ij}}{n_{ij}^*} \right) < 0$$

except at the equilibrium n^* where $dV/dt = 0$. That is, V is a Lyapunov function and so the equilibrium n^* is l.a.s.

To prove global stability,⁶ we need to show that each trajectory which starts in $\mathbb{R}_{\geq 0}^{m+m^2}$ converges to n^* . If this is not the case, there is such a trajectory that contains an ω -limit point n^ω other than n^* since each stoichiometric compatibility class is compact. Let us first consider points n on the boundary face where $n_i = 0$. From (3), $\frac{dn_i}{dt} = 2 \sum_{j=1}^m \frac{n_{ij}}{\tau_{ij}}$ and $N_i = 2 \sum_{j=1}^m n_{ij}$ at any such point. Thus $\frac{dn_i}{dt} \geq \min_{ij} \{1/\tau_{ij}\} N_i$ on this boundary face, i.e., this face is repelling, which cannot then contain n^ω . Moreover, for some $\epsilon > 0$ and t sufficiently large, $n_i(t) > \epsilon$ for all i . Now consider points n on the boundary face where $n_{ij} = 0$. From (3), $\frac{dn_{ij}}{dt} = \frac{\lambda_{ij}}{2} n_i n_j \geq \frac{1}{2} \min_{ij} \{\lambda_{ij}\} \epsilon^2$ for t sufficiently large and $1 \leq i, j \leq m$. Thus n^ω must be in the interior of the stoichiometric compatibility class corresponding to N_1, \dots, N_m . This is impossible since V is strictly decreasing at n^ω . \square

Distributional dynamics for two phenotypes ($m = 2$) and a choice of model parameters are shown in Figure 1A. The beauty of Proposition 2 is that, qualitatively, this plot is independent of the values of interaction rates, provided they are positive. Specifically, all trajectories will converge to the same unique distribution for a given choice of N_1 and N_2 along with reaction rates in (8).

2.2. Stability of group distribution dynamics for two strategy games. Now suppose the population has 2 phenotypes, Cooperate (C) and Defect (D), and that individuals are either single or in groups of size m .⁷ The prototypical example of interactions within a group is the m -player public goods game (PGG) where each group member contributes a portion of their identical endowment to the public good and receives an equal share of the total contribution multiplied by an enhancement

⁶There has been controversy (see Discussion) in the CRNT community whether the equilibrium arising from a system satisfying the conditions of the Deficiency Zero Theorem is automatically globally asymptotically stable (g.a.s.) as well as l.a.s., i.e., all trajectories in its stoichiometric compatibility class converge to the equilibrium. To avoid this controversy, we provide an independent proof for our MAK system.

⁷That is, in this section, m is the group size and not the number of phenotypes as in Section 2.1 where the group size is 2.

factor r . In the classic set-up for the one-shot PGG, individuals are always in groups that play the game once. Under the usual assumption that $1 < r < m$, it is best from an individual perspective to contribute nothing given the choices of the other members of his/her group (i.e., mutual Defection is the only Nash equilibrium (NE)) [e.g., 8, 23, 18]. PGG then models a social dilemma since it is best for the group if everyone contributes their entire endowment (i.e., Cooperates).

In this section, groups form and disband at rates dependent on the group composition. Specifically, we assume that each individual either always plays C or always D. Let n_C and n_D be the number of singles playing C and D, respectively, and n_i be the number of (unordered) groups with i Cooperators and $m - i$ Defectors. We assume that groups with i Cooperators stay together for an expected time τ_i (i.e., these groups disband at rate τ_i). Furthermore, when i Cooperators and $m - i$ Defectors meet at random, they form a group of size m at rate λ_i . The group distributional dynamics are then

$$\begin{aligned}\frac{dn_C}{dt} &= \sum_{i=1}^m \left(\frac{in_i}{\tau_i} - \lambda_i i n_C^i n_D^{m-i} \right) \\ \frac{dn_D}{dt} &= \sum_{i=0}^{m-1} \left(\frac{(m-i)n_i}{\tau_i} - \lambda_i (m-i) n_C^i n_D^{m-i} \right) \\ \frac{dn_i}{dt} &= \lambda_i n_C^i n_D^{m-i} - \frac{n_i}{\tau_i}, \quad i = 0, \dots, m.\end{aligned}\tag{13}$$

An important special case assumes that all singles meet at random and groups are formed at rate λ . Then $\lambda_i = \frac{\lambda}{m} \binom{m}{i}$ and the distributional dynamics are

$$\begin{aligned}\frac{dn_C}{dt} &= \sum_{i=1}^m \frac{in_i}{\tau_i} - \lambda n_C (n_C + n_D)^{m-1} \\ \frac{dn_D}{dt} &= \sum_{i=0}^{m-1} \frac{(m-i)n_i}{\tau_i} - \lambda n_D (n_C + n_D)^{m-1} \\ \frac{dn_i}{dt} &= \frac{\lambda}{m} \binom{m}{i} n_C^i n_D^{m-i} - \frac{n_i}{\tau_i}, \quad i = 0, \dots, m.\end{aligned}\tag{14}$$

For instance, if $m = 2$ (i.e., groups consist of pairs) and unordered heterogeneous pairs n_1 are replaced by ordered pairs n_{12} and n_{21} where $n_{12} = n_{21}$, then these group dynamics (14) are the same as the pair dynamics (3) with appropriate reaction rates in the case when Section 2.1 has two strategies.

If, in addition, all groups stay together for the same expected amount of time, we get

Proposition 3. *Let $\tau_i = \tau > 0$ and $\lambda_i = \frac{\lambda}{m} \binom{m}{i}$ for all $i = 0, \dots, m$. Then for each total number of Cooperators N_C and of Defectors N_D , system (14) has a unique positive equilibrium $n = (n_C, n_D, n_1, \dots, n_m)$ that is globally asymptotically stable with respect to $R_{\geq 0}^{m+3}$. The distribution of groups at this equilibrium is the binomial distribution⁸*

$$n_i = \frac{\lambda \tau}{m} \binom{m}{i} n_C^i n_D^{m-i}$$

⁸When $m = 2$, this distribution satisfies the Hardy-Weinberg principle (6).

where $\frac{n_C}{N_C} = \frac{n_D}{N_D} = \frac{g(N_C+N_D)}{N_C+N_D}$ and $g(N_C + N_D)$ is the unique positive solution for $n_C + n_D$ of the implicit equation

$$N_C + N_D = n_C + n_D + \lambda\tau(n_C + n_D)^m. \quad (15)$$

Proof. The existence, uniqueness and stability of n follows from Proposition 4 below. From (14),

$$n_i = \frac{\lambda\tau_i}{m} \binom{m}{i} n_C^i n_D^{m-i} = \frac{\lambda\tau}{m} \binom{m}{i} n_C^i n_D^{m-i}$$

since $\tau_i = \tau$ for all $i = 0 \dots, m$. Thus

$$\begin{aligned} N_C + N_D &= n_C + \sum_{i=0}^m i n_i + n_D + \sum_{i=0}^m (m-i) n_i \\ &= n_C + n_D + m \sum_{i=1}^m n_i = n_C + n_D + \lambda\tau(n_C + n_D)^m. \end{aligned} \quad (16)$$

Since $\lambda\tau > 0$, Descartes' rule of signs implies existence of exactly one positive solution $g(N_C + N_D)$ for $n_C + n_D$ of (16) in terms of $N_C + N_D$.

Moreover, from (14), $N_C = n_C + \sum_{i=1}^m i n_i = n_C + \lambda\tau n_C (n_C + n_D)^{m-1} = n_C \frac{N_C + N_D}{n_C + n_D}$. By the analogous result for N_D , we obtain

$$\frac{n_C}{N_C} = \frac{n_D}{N_D} = \frac{n_C + n_D}{N_C + N_D} = \frac{g(N_C + N_D)}{N_C + N_D}. \quad (17)$$

□

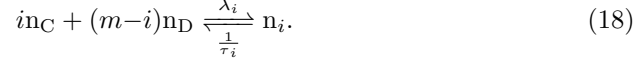
Although Proposition 3 does not provide the explicit solution for the equilibrium of (14),⁹ the implicit solution can be used to determine game outcomes in this special case. Indeed, if payoffs per unit time are given solely through group interactions, then (17) implies the game's payoff functions are the same as those of the one-shot game (or of a game where singles from disbanded groups instantaneously form new groups at random) up to a positive constant. Thus, for example, the NE outcome of PGG under this special random group formation process will remain mutual Defection when all groups disband at the same rate.

Křivan and Cressman [18] considered a corresponding discrete-time group distribution dynamics for the repeated PGG when groups form instantaneously and the expected number of rounds a group plays depends on the number of Cooperators in the group. They showed that the NE outcome of PGG can be mutual coexistence of Cooperators and Defectors, especially if Defectors display intolerance of Cooperators by disbanding after one round any groups they are in that contain Cooperators. They based their results on the observation that the discrete-time dynamics has a unique equilibrium for a given number of Cooperators and Defectors (showing this analytically for $m = 2$ and numerically for larger group sizes) but did not address the question of its stability. Here, we address these questions for system (13).

Again, we follow the chemical reaction network theory to prove stability and uniqueness of a positive equilibrium when the number of Cooperators $N_C \equiv n_C +$

⁹Explicit solutions can be obtained when group size m is small. For instance, if $m = 2$, the equilibrium is given by Proposition 1 when this result is translated to the appropriate notation of Proposition 3.

$\sum_{i=0}^m in_i$ and Defectors $N_D \equiv n_D + \sum_{i=0}^m (m-i)n_i$ is fixed. This network is described by the following $m+1$ reactions together with their rates



There are $m+3$ species $\mathcal{S} = \{n_C, n_D, n_0, \dots, n_m\}$ and $n = 2(m+1)$ complexes $\mathcal{C} = \{n_i, in_C + (m-i)n_D \mid 0 \leq i \leq m\}$. The reaction network (18) has $\ell = m+1$ linkage classes given by $\{in_C + (m-i)n_D, n_i\}$, $0 \leq i \leq m$.

The set of reactions in (18) is described by

$$\mathcal{R} = \{n_i - (in_C + (m-i)n_D) \mid 0 \leq i \leq m\}$$

as well as the reverse of these reactions which we do not list. In particular, the network is reversible. The reaction network can be represented as an $(m+1) \times (m+3)$ matrix where each row lists the species coefficients of the corresponding reaction. If the species are arranged in order $\{n_0, \dots, n_m, n_C, n_D\}$, then the sub-matrix consisting of the first $m+1$ columns of reaction matrix R forms the identity matrix. Thus, the rank of R is $s = m+1$, which is the dimension of the stoichiometric subspace $L = \text{span}R$. The network deficiency is then $\delta = n - \ell - s = 2(m+1) - (m+1) - (m+1) = 0$. Thus, the Deficiency Zero Theorem applies and so there exists a unique, stable equilibrium $\{n_C^*, n_D^*, n_0^*, \dots, n_m^*\}$ for each stoichiometric compatibility class and each choice of (positive) reaction rates in (18). Since the null space of the stoichiometric subspace L is generated by the two vectors corresponding to $n_C + n_1 + \dots + mn_m$ and $n_D + mn_0 + \dots + n_{m-1}$ and these expressions equal N_C and N_D , each stoichiometric compatibility class is specified by a fixed choice of N_C, N_D . The following Proposition summarizes these facts.

Proposition 4. *Let $\tau_i > 0$ and $\lambda_i > 0$ for all $i = 0 \dots, m$. Then for each total positive number of individuals of phenotype C , $N_C \equiv n_C + n_1 + \dots + mn_m$ and of D , $N_D = n_D + mn_0 + \dots + n_{m-1}$, system (13) has a unique, positive equilibrium (i.e., in \mathbb{R}_+^{m+3}) which is globally asymptotically stable with respect to $\mathbb{R}_{\geq 0}^{m+3}$.*

Proof. Once again, the existence and uniqueness of the positive equilibrium follows from The Deficiency Zero Theorem [Theorem 7.1.1 in 7] because network (18) is reversible and its deficiency $\delta = 0$. Thus, for each total number of individuals N_C and N_D there exists a positive equilibrium $n^* = (n_C^*, n_D^*, n_0^*, \dots, n_m^*) \in \mathbb{R}_+^{m+3}$ of system (13) which is unique.

For the positive constant reaction rates in (13), global asymptotic stability of the unique equilibrium follows from Lyapunov methods. Since $n_i^* = \lambda_i \tau_i n_C^{*i} n_D^{*m-i}$, (13) can be rewritten in the following form

$$\begin{aligned} \frac{dn_C}{dt} &= \sum_{i=1}^m \frac{in_i^*}{\tau_i} \left(\frac{n_i}{n_i^*} - \frac{n_C^i n_D^{m-i}}{n_C^{*i} n_D^{*m-i}} \right) \\ \frac{dn_D}{dt} &= \sum_{i=0}^{m-1} \frac{(m-i)n_i^*}{\tau_i} \left(\frac{n_i}{n_i^*} - \frac{n_C^i n_D^{m-i}}{n_C^{*i} n_D^{*m-i}} \right) \\ \frac{dn_i}{dt} &= \frac{n_i^*}{\tau_i} \left(\frac{n_C^i n_D^{m-i}}{n_C^{*i} n_D^{*m-i}} - \frac{n_i}{n_i^*} \right), \quad i = 0, \dots, m. \end{aligned} \quad (19)$$

For interior trajectories, we have the following Lyapunov function

$$V = n_C \log \left(\frac{n_C}{n_C^*} \right) - (n_C - n_C^*) + n_D \log \left(\frac{n_D}{n_D^*} \right) - (n_D - n_D^*) + \sum_{i=0}^m n_i \log \left(\frac{n_i}{n_i^*} \right) - (n_i - n_i^*)$$

the kinetics matrix is

$$K = \begin{array}{c} 4n_D \\ n_C+3n_D \\ 2n_C+2n_D \\ 3n_C+n_D \\ 4n_C \\ n_0 \\ n_1 \\ n_2 \\ n_3 \\ n_4 \end{array} \begin{bmatrix} 4n_D & n_C+3n_D & 2n_C+2n_D & 3n_C+n_D & 4n_C & n_0 & n_1 & n_2 & n_3 & n_4 \\ 0 & 0 & 0 & 0 & 0 & \frac{1}{\tau_0} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{\tau_1} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{\tau_2} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{\tau_3} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{\tau_4} \\ \lambda_0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \lambda_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \lambda_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \lambda_3 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \lambda_4 & 0 & 0 & 0 & 0 & 0 \end{bmatrix},$$

and the vector $\psi = \{n_D^4, n_C n_D^3, n_C^2 n_D^2, n_C^3 n_D, n_C^4, n_0, n_1, n_2, n_3, n_4\}$. From (9), the MAK distributional dynamics corresponding to reaction network (18) when $m = 4$ is

$$\begin{aligned} \frac{dn_C}{dt} &= \frac{n_1}{\tau_1} + \frac{2n_2}{\tau_2} + \frac{3n_3}{\tau_3} + \frac{4n_4}{\tau_4} - \lambda_1 n_C n_D^3 - 2\lambda_2 n_C^2 n_D^2 - 3\lambda_3 n_C^3 n_D - 4\lambda_4 n_C^4 \\ \frac{dn_D}{dt} &= \frac{4n_0}{\tau_0} + \frac{3n_1}{\tau_1} + \frac{2n_2}{\tau_2} + \frac{n_3}{\tau_3} - 4\lambda_0 - 3\lambda_1 n_C n_D^3 - 2\lambda_2 n_C^2 n_D^2 - \lambda_3 n_C^3 n_D \\ \frac{dn_0}{dt} &= \lambda_0 n_D^4 - \frac{n_0}{\tau_0} \\ \frac{dn_1}{dt} &= \lambda_1 n_C n_D^3 - \frac{n_1}{\tau_1} \\ \frac{dn_2}{dt} &= \lambda_2 n_C^2 n_D^2 - \frac{n_2}{\tau_2} \\ \frac{dn_3}{dt} &= \lambda_3 n_C n_D^3 - \frac{n_3}{\tau_3} \\ \frac{dn_4}{dt} &= \lambda_4 n_C^4 - \frac{n_4}{\tau_4}. \end{aligned} \tag{20}$$

Distributional dynamics for (20) in the special case where λ_i is given in terms of binomial coefficients (i.e., $\lambda_i = \frac{\lambda}{4} \binom{4}{i}$) (cf. (14)) are shown in Figure 1B for a particular choice of τ_i . As in Panel A, all trajectories will converge to the same unique distribution for a given choice of N_C and N_D .

3. Pair formation process for asymmetric games. Section 2 applies CRNT to the distributional dynamics of a single population where all individuals are indistinguishable except for their strategy. In this section, there are two types of individuals corresponding to an underlying evolutionary game that is asymmetric. Here we show that CRNT again proves the existence and global stability of the distributional equilibrium in a specific example (the Battle of the Sexes (BoS) game of Section 3.1) but not in general (Section 3.2).

3.1. Pair formation process for battle of the sexes game. Cressman and Křivan [18] considered the Battle of the Sexes game where duration of interactions between males and females depend on their strategies. They assumed that interactions between Philanderer males and Coy females do not take any time, while interactions between Coy females and Faithful males involve time for courtship τ_c

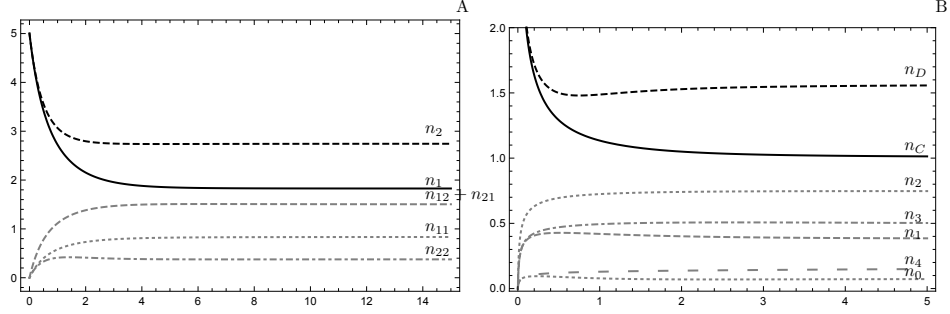


FIGURE 1. Distributional dynamics (10) of pairs (panel A) and groups of size four (panel B) for PGG (20). Both panels assume that initially there are only singles and initial conditions are $n_1(0) = n_2(0) = 5$ ($n_C(0) = n_D(0) = 5$) in panel A (panel B). Parameters used in Panel A: $\lambda_{11} = \lambda_{12} = \lambda_{21} = \lambda_{22} = \lambda = 0.1$, $\tau_{11} = 5$, $\tau_{12} = \tau_{21} = 3$, $\tau_{22} = 1$. Parameters used in Panel B: $\lambda_i = \frac{\lambda}{4} \binom{4}{i}$ with $\lambda = 0.05$, $\tau_0 = 1$, $\tau_1 = 2$, $\tau_2 = 4$, $\tau_3 = 6$, $\tau_4 = 15$.

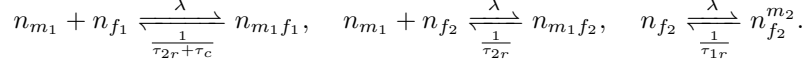
and time for rising offsprings, τ_{2r} . Interactions between Faithful males and Fast females take time τ_{2r} only, as there is no courtship. Duration of interactions between Philanderer male and Fast female also take no time but the time until ready to pair again is now sex dependent since it takes no time for the male while females raise offsprings for time τ_{1r} . Let n_{m_1} be the number of single Faithful males that are ready to pair and n_{m_2} be the number of single Philanderer males that are ready to pair. Similarly, let n_{f_1} be the number of single Coy females that are ready to pair and n_{f_2} be the number of single Fast females that are ready to pair. We call these individuals “searchers”. Also, let $n_{m_1 f_1}$, be the number of Faithful/Coy pairs, and $n_{m_1 f_2}$, be the number of Faithful/Fast pairs. Finally, let $n_{f_2}^{m_2}$ be the number of females who are raising offspring on their own (note that these arise when Fast females encounter Philanderer males).

We also denote the (fixed) population sizes of different strategy users as follows: N_{m_1} is the number of Faithful males, N_{m_2} the number of Philanderer males, N_{f_1} the number of Coy females and N_{f_2} the number of Fast females. Since Philanderer males never form pairs or help raise offspring, $n_{m_2} = N_{m_2}$.

The pair distribution dynamics in [7] is

$$\begin{aligned}
 \frac{dn_{m_1}}{dt} &= -\lambda n_{m_1} (n_{f_1} + n_{f_2}) + \frac{n_{m_1 f_1}}{\tau_{2r} + \tau_c} + \frac{n_{m_1 f_2}}{\tau_{2r}} \\
 \frac{dn_{f_1}}{dt} &= -\lambda n_{m_1} n_{f_1} + \frac{n_{m_1 f_1}}{\tau_{2r} + \tau_c} \\
 \frac{dn_{f_2}}{dt} &= -\lambda (n_{m_1} + n_{m_2}) n_{f_2} + \frac{n_{m_1 f_2}}{\tau_{2r}} + \frac{n_{f_2}^{m_2}}{\tau_{1r}} \\
 \frac{dn_{m_1 f_1}}{dt} &= \lambda n_{m_1} n_{f_1} - \frac{n_{m_1 f_1}}{\tau_{2r} + \tau_c} \\
 \frac{dn_{m_1 f_2}}{dt} &= \lambda n_{m_1} n_{f_2} - \frac{n_{m_1 f_2}}{\tau_{2r}} \\
 \frac{dn_{f_2}^{m_2}}{dt} &= \lambda n_{m_2} n_{f_2} - \frac{n_{f_2}^{m_2}}{\tau_{1r}}.
 \end{aligned} \tag{21}$$

The reaction network corresponding to this pair formation dynamics is



This reaction network has

- 6 species $\{n_{m_1}, n_{f_1}, n_{f_2}, n_{m_1 f_1}, n_{m_1 f_2}, n_{f_2}^{m_2}\}$
- $n = 6$ complexes $\{n_{m_1} + n_{f_1}, n_{m_1} + n_{f_2}, n_{m_1 f_1}, n_{m_1 f_2}, n_{f_2}, n_{f_2}^{m_2}\}$
- $\ell = 3$ linkage classes $\{n_{m_1} + n_{f_1}, n_{m_1 f_1}\}, \{n_{m_1} + n_{f_2}, n_{m_1 f_2}\}, \{n_{f_2}, n_{f_2}^{m_2}\}.$

The reaction matrix (with reverse reactions omitted) is

$$R = \begin{matrix} & & m_1 & m_2 & f_1 & f_2 & m_1 f_1 & m_1 f_2 & f_2^{m_2} \\ \begin{matrix} n_{m_1} + n_{f_1} - n_{m_1 f_1} \\ n_{m_1} + n_{f_2} - n_{m_1 f_2} \\ n_{f_2} - n_{f_2}^{m_2} \end{matrix} & \begin{bmatrix} 1 & 0 & 1 & 0 & -1 & 0 & 0 \\ 1 & 0 & 0 & 1 & 0 & -1 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & -1 \end{bmatrix} \end{matrix}$$

which clearly has rank $s = 3$. Thus, the reaction matrix has deficiency $\delta = n - s - \ell = 6 - 3 - 3 = 0$ and so the Deficiency Zero Theorem applies showing there exists a unique, l.a.s. equilibrium $(n_{m_1}^*, n_{f_1}^*, n_{f_2}^*, n_{m_1 f_1}^*, n_{m_1 f_2}^*, n_{f_2}^{m_2*})$ for each number of Philanderer males, Faithful males, Coy females and Fast females.

Similar to Section 2, Lyapunov methods can be used with respect to

$$\begin{aligned} V = & n_{m_1} \ln \frac{n_{m_1}}{n_{m_1}^*} - (n_{m_1} - n_{m_1}^*) + n_{f_1} \ln \frac{n_{f_1}}{n_{f_1}^*} - (n_{f_1} - n_{f_1}^*) + n_{f_2} \ln \frac{n_{f_2}}{n_{f_2}^*} - (n_{f_2} - n_{f_2}^*) + \\ & n_{m_1 f_1} \ln \frac{n_{m_1 f_1}}{n_{m_1 f_1}^*} - (n_{m_1 f_1} - n_{m_1 f_1}^*) + n_{m_1 f_2} \ln \frac{n_{m_1 f_2}}{n_{m_1 f_2}^*} - (n_{m_1 f_2} - n_{m_1 f_2}^*) + \\ & n_{f_2}^{m_2} \ln \frac{n_{f_2}^{m_2}}{n_{f_2}^{m_2*}} - (n_{f_2}^{m_2} - n_{f_2}^{m_2*}) \end{aligned}$$

to prove that the equilibrium is g.a.s.

The BoS game is somewhat particular as Philanderer males do not spend any time interacting with Coy females, which simplifies the distributional dynamics. In the next section, we consider a generalization of the BoS game that assumes all interactions take some time and we show this precludes application of the DZT.

3.2. A generalized BoS game for which the Deficiency Zero Theorem does not apply.

In this section, we study a generalized Battle of the Sexes game, where we assume interactions between males and females can take any positive time and all disbanded individuals need some recovery time before making new pairs. Let us consider m_i (males) and f_j (females) ($i, j = 1, 2$) strategists. Let $\tau_{ij} > 0$ be the time these two individuals stay together (i.e., the first subindex i in τ_{ij} refers to the male strategy while the second refers to the female strategy) and $\tau_{m_i}^{f_j} > 0$ ($\tau_{f_j}^{m_i} > 0$) be the time these males (females) need to recover before they are ready to pair again.¹⁰

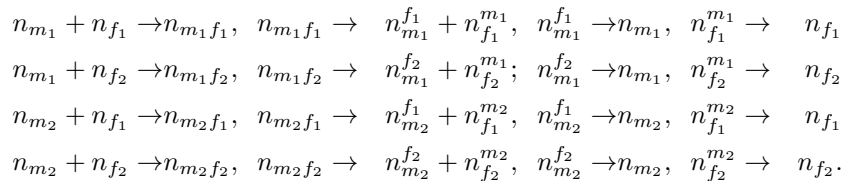
¹⁰This model does not apply to the BoS game of Section 3.1 since many of these times are 0 there. For example, $\tau_{22} = 0$ for the (Philanderer, Fast) pair and all $\tau_{m_i}^{f_j} = \tau_{f_j}^{m_i} = 0$ except $\tau_{f_2}^{m_2} = \tau_{1r}$.

The corresponding distributional dynamics are

$$\begin{aligned}
\frac{dn_{m_1}}{dt} &= -\lambda n_{m_1} n_{f_1} + \frac{n_{m_1}^{f_1}}{\tau_{m_1}^{f_1}} - \lambda n_{m_1} n_{f_2} + \frac{n_{m_1}^{f_2}}{\tau_{m_1}^{f_2}} \\
\frac{dn_{m_2}}{dt} &= -\lambda n_{m_2} n_{f_1} + \frac{n_{m_2}^{f_1}}{\tau_{m_2}^{f_1}} - \lambda n_{m_2} n_{f_2} + \frac{n_{m_2}^{f_2}}{\tau_{m_2}^{f_2}} \\
\frac{dn_{f_1}}{dt} &= -\lambda n_{m_2} n_{f_1} + \frac{n_{f_1}^{m_2}}{\tau_{f_1}^{m_2}} - \lambda n_{m_1} n_{f_1} + \frac{n_{f_1}^{m_1}}{\tau_{f_1}^{m_1}} \\
\frac{dn_{f_2}}{dt} &= -\lambda n_{m_2} n_{f_2} + \frac{n_{f_2}^{m_2}}{\tau_{f_2}^{m_2}} - \lambda n_{m_1} n_{f_2} + \frac{n_{f_2}^{m_1}}{\tau_{f_2}^{m_1}} \\
\frac{dn_{m_1 f_1}}{dt} &= \lambda n_{m_1} n_{f_1} - \frac{n_{m_1 f_1}}{\tau_{11}} \\
\frac{dn_{m_1}^{f_1}}{dt} &= \frac{n_{m_1 f_1}}{\tau_{11}} - \frac{n_{m_1}^{f_1}}{\tau_{m_1}^{f_1}} \\
\frac{dn_{f_1}^{m_1}}{dt} &= \frac{n_{m_1 f_1}}{\tau_{11}} - \frac{n_{f_1}^{m_1}}{\tau_{f_1}^{m_1}} \\
\frac{dn_{m_1 f_2}}{dt} &= \lambda n_{m_1} n_{f_2} - \frac{n_{m_1 f_2}}{\tau_{12}} \\
\frac{dn_{m_1}^{f_2}}{dt} &= \frac{n_{m_1 f_2}}{\tau_{12}} - \frac{n_{m_1}^{f_2}}{\tau_{m_1}^{f_2}} \\
\frac{dn_{f_2}^{m_1}}{dt} &= \frac{n_{m_1 f_2}}{\tau_{12}} - \frac{n_{f_2}^{m_1}}{\tau_{f_2}^{m_1}} \\
\frac{dn_{m_2 f_1}}{dt} &= \lambda n_{m_2} n_{f_1} - \frac{n_{m_2 f_1}}{\tau_{12}} \\
\frac{dn_{m_2}^{f_1}}{dt} &= \frac{n_{m_2 f_1}}{\tau_{21}} - \frac{n_{m_2}^{f_1}}{\tau_{m_2}^{f_1}} \\
\frac{dn_{f_1}^{m_2}}{dt} &= \frac{n_{m_2 f_1}}{\tau_{21}} - \frac{n_{f_1}^{m_2}}{\tau_{f_1}^{m_2}} \\
\frac{dn_{m_2 f_2}}{dt} &= \lambda n_{m_2} n_{f_2} - \frac{n_{m_2 f_2}}{\tau_{22}} \\
\frac{dn_{m_2}^{f_2}}{dt} &= \frac{n_{m_2 f_2}}{\tau_{22}} - \frac{n_{m_2}^{f_2}}{\tau_{m_2}^{f_2}} \\
\frac{dn_{f_2}^{m_2}}{dt} &= \frac{n_{m_2 f_2}}{\tau_{22}} - \frac{n_{f_2}^{m_2}}{\tau_{f_2}^{m_2}}.
\end{aligned} \tag{22}$$

These 16 equations describing distributional dynamics are in the form of mass-action kinetics.

The reaction network corresponding to this pair formation dynamics is



We observe that this network is not reversible, nor weakly reversible¹¹ (for example, there is no chain of reactions in the reaction network that starts with the complex $n_{m_1} + n_{f_1}$ and leads to the same complex) and, consequently, the ZDT does not apply.

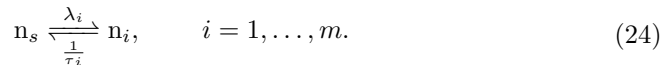
On the other hand, the method of [11] can be generalized to show that there is a unique distributional equilibrium that numerical simulations suggest is g.a.s. under the distributional dynamics [7]. As far as we are aware, an analytic proof of this result is not known.

3.3. Stability of a population distribution in a patchy environment. CRNT can also be applied to biological systems that do not involve pair or group interactions. Here, we consider a population in a patchy environment consisting of m patches. We assume that the expected time τ_i an individual stays in patch i (i.e., the residence (or retention) time of patch i) is patch dependent. Individuals leaving a patch become searchers who move to another patch at random in such a way that their encounter rate with patch i is λ_i . For example, they may encounter patch i at a rate that is proportional to its area A_i , in which case $\lambda_i = A_i/(A_1 + \dots + A_m)$ up to a positive constant.

Let n_s denote the number of individuals who are currently searching and n_i those in patch i . Then the distributional dynamics are

$$\begin{aligned} n'_s &= -(\lambda_1 + \dots + \lambda_m)n_s + \frac{n_1}{\tau_1} + \dots + \frac{n_m}{\tau_m} \\ n'_i &= \lambda_i n_s - \frac{n_i}{\tau_i}, \end{aligned} \quad i = 1, \dots, m, \quad (23)$$

which corresponds to the reaction network



There are $m + 1$ species as well as complexes, i.e., $\mathcal{S} = \mathcal{C} = \{n_s, n_1, \dots, n_m\}$, only one linkage class consisting of all complexes, and m independent reactions $\mathcal{R} = \{n_1 - n_s, \dots, n_m - n_s\}$ (we do not list the reverse reactions). Thus $n = m + 1$, $\ell = 1$, $r = m$, and so the deficiency of the network is $\delta = n - \ell - r = 0$. Furthermore, the network is reversible. Thus, for each positive stoichiometric compatibility class, which is given by the fixed positive number of individuals $N = n_s + n_1 + \dots + n_m$, there exists a unique positive equilibrium $n^* = (n_s^*, n_1^*, \dots, n_m^*)$. CRNT applied to reaction network (24) yields the following result.

Proposition 5. *Let $\tau_i > 0$ and $\lambda_i > 0$ for all $i = 1 \dots, m$. Then, for each positive total population size N , system (23) has a unique, positive equilibrium n^* in \mathbb{R}_+^{m+1} which is globally asymptotically stable with respect to $\mathbb{R}_{\geq 0}^{m+1}$.*

Proof. From (23), the components of n^* satisfy $\lambda_i n_i^* = \frac{n_s^*}{\tau_i}$ and so

$$n_s^* = \frac{N}{1 + \sum_{i=1}^m \lambda_i \tau_i}, \quad n_i^* = \lambda_i \tau_i n_s^*. \quad (25)$$

¹¹Weak reversibility requires that if one complex is connected to another complex through a chain of reactions, then the final complex is also connected to the original complex [10].

Global asymptotic stability of n^* follows from Lyapunov methods. First, (23) can be rewritten in the following form

$$\begin{aligned} \frac{dn_s}{dt} &= \sum_{i=1}^m \frac{n_i^*}{\tau_i} \left(\frac{n_i}{n_i^*} - \frac{n_s}{n_s^*} \right) \\ \frac{dn_i}{dt} &= \frac{n_i^*}{\tau_i} \left(\frac{n_s}{n_s^*} - \frac{n_i}{n_i^*} \right), \quad i = 1, \dots, m. \end{aligned} \quad (26)$$

Then the following is a Lyapunov function

$$V = \left(n_s \ln \frac{n_s}{n_s^*} - (n_s - n_s^*) \right) + \sum_{i=1}^m \left(n_i \ln \frac{n_i}{n_i^*} - (n_i - n_i^*) \right).$$

Indeed, the derivative of V along trajectories of (12) is

$$\frac{dV}{dt} = \sum_{i=1}^m \frac{n_i^*}{\tau_i} \left(\frac{n_i}{n_i^*} - \frac{n_s}{n_s^*} \right) \left(\ln \frac{n_s}{n_s^*} - \ln \frac{n_i}{n_i^*} \right) < 0$$

except at the equilibrium where $dV/dt = 0$. \square

For example, when $\lambda_i = A_i/(A_1 + \dots + A_m)$ and all residence times are equal (i.e., $\tau_i = \tau, i = 1, \dots, m$), the equilibrium distribution is

$$n_s^* = \frac{N}{1 + \tau}, n_i^* = \frac{A_i}{A_1 + \dots + A_m} \frac{N\tau}{1 + \tau}.$$

In particular, the equilibrium distribution satisfies

$$\frac{n_i^*}{n_1^* + \dots + n_m^*} = \frac{A_i}{A_1 + \dots + A_m},$$

which corresponds to balanced dispersal [14] where the distribution of animals corresponds to the distribution of patch areas. The same distribution is obtained when residence times are proportional to the patch area, i.e., $\tau_i \sim A_i$ and all λ_i s are the same. This also corresponds to balanced dispersal [14].

Proposition 5 can also be proved by analyzing (23) as the following linear system of differential equations.

$$\begin{pmatrix} n'_s \\ n'_1 \\ \vdots \\ n'_m \end{pmatrix} = \begin{pmatrix} -(\lambda_1 + \dots + \lambda_m) & \frac{1}{\tau_1} & \frac{1}{\tau_2} & \dots & \frac{1}{\tau_m} \\ \lambda_1 & -\frac{1}{\tau_1} & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \lambda_m & 0 & \dots & 0 & -\frac{1}{\tau_m} \end{pmatrix} \begin{pmatrix} n_s \\ n_1 \\ \vdots \\ n_m \end{pmatrix}. \quad (27)$$

Indeed, fix $N > 0$ and let n^* be given by (25). Then $Ln^* = 0$ and so L has eigenvalue 0 with (right) eigenvector n^* . Since the hyperplane $H \equiv \{n | n_s + \sum_{i=1}^m n_i = N\}$ is invariant under (23), L is invariant on the m -dimensional subspace $X \equiv \{x = (x_s, x_1, \dots, x_m) \in R^{m+1} | x_s + \sum_{i=1}^m x_i = 0\}$. Moreover, L is nonsingular with respect to this subspace since n^* is the unique equilibrium of (23) in H . Thus, all eigenvalues of L with respect to X are non-zero. On the other hand, by Gershgorin's Theorem [25] applied to the columns of L , all eigenvalues of L are either 0 or have negative real part. Thus, all eigenvalues of L restricted to X have negative real part. That is, the origin is g.a.s. under (23) restricted to X and n^* is g.a.s. under (23) restricted to H .

4. Discussion. In this article, we applied results of chemical reaction network theory to show uniqueness and stability of positive equilibrium for pairs/groups distributional dynamics that arise in game theoretic models.

Evolutionary game theory assumes that individuals accrue their fitness through interactions with other individuals. When there are two or more different phenotypes (strategies) in the population, this theory assumes that pairs or groups are formed instantaneously and randomly so that the corresponding pairs (groups) distribution is described by the Hardy–Weinberg (binomial) distribution. If individual fitness is defined as payoff per unit time at this distributional equilibrium (e.g., payoffs may arise solely from pair interactions), we then have an evolutionary (population) game [19, 6, 1, 2].

In some recent models, it has been argued that interactions times may be phenotype dependent [19, 20, 6, 1, 18] and that, in these situations, the Hardy-Weinberg distribution does not apply. In fact, except in the simplest cases, it becomes impossible to calculate the pairs/groups distribution analytically which raises a question about uniqueness of the equilibrium and its stability. It has been shown that, for some particular models, the equilibrium exists and is unique [12, 11]. In this article, we show that CRNT is a general tool that is very useful to prove not only existence of the equilibrium, but also its stability through the Deficiency Zero Theorem (DZT). On the other hand, we also show using the generalized Battle of the Sexes game that DZT does not always apply to pair formation models.

As mentioned in Section 2.1, there has been controversy in the CRNT community whether the equilibrium arising from a system satisfying the conditions of the Deficiency Zero Theorem is automatically globally asymptotically stable. Horn and Jackson [17] stated that the interior positive equilibrium is not only locally asymptotically stable, but also a global attractor. Horn [16] clarified that the global stability was not proved and posed this global convergence property as a conjecture which was later called the Global Attractor Conjecture [5]. The conjecture was proved in [4].

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