Two-strategy games with time constraints on regular graphs

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Abstract

Evolutionary game theory is a powerful method for modelling animal conflicts. The original evolutionary game models were used to explain specific biological features of interest, such as the existence of ritualised contests, and were necessarily simple models that ignored many properties of real populations, including the duration of events and spatial and related structural effects. Both of these areas have subsequently received much attention. Spatial and structural effects have been considered in evolutionary graph theory, and a significant body of literature has been built up to deal with situations where the population is not homogeneous. More recently a theory of time constraints has been developed to take account of the fact that different events can take different times, and that interaction times can explicitly depend upon selected strategies, which can, in turn, influence the distribution of different opponent types within the population. Here, for the first time, we build a model of time constraint games which explicitly considers a spatial population, by considering a population evolving on an underlying graph, using two graph dynamics, birth-death and death-birth. We consider one short time scale along which frequencies of pairs and singles change as individuals interact with their neighbours, and another, evolutionary time scale, along which frequencies of strategies change in the population. We show that for graphs with large degree, both dynamics reproduce recent results from well-mixed time constraint models, including two ESSs being common in Hawk-Dove and Prisoner's Dilemma games, but for low degree there can be marked differences. For birth-death processes the effect of the graph degree is small, whereas for death-birth dynamics there is a large effect. The general prediction for both Hawk-Dove and Prisoner's dilemma games is that as the graph degree decreases, i.e., as the number of neighbours decreases, mixed ESS do appear. In particular, for the Prisoner's dilemma game this means that cooperation is easier to establish in situations where individuals have low number of neighbours. We thus see that solutions depend non-trivially on the combination of graph degree, dynamics and game.

Keywords: birth-death and death-birth updating, evolutionary game theory, games on regular graphs, Hawk-Dove game, Prisoner's dilemma

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1. Introduction

Evolutionary game theory, as conceived by Maynard Smith and Price (1973), is a powerful method for modelling animal conflicts (e.g., Maynard Smith, 1982; Dugatkin and Reeve, 1998; Hofbauer and Sigmund, 1998; Broom and Rychtář, 2013). The original, two-strategy matrix evolutionary game models were used to explain specific biological features of interest, such as the existence of ritualized contests (e.g., the Hawk and Dove model), and were necessarily simple models that ignored many properties of real populations, including the duration of events and spatial and related structural effects. Both of these areas have subsequently received much attention.

Two-strategy matrix models assume that individuals gain/lose fitness during pair-wise interactions only. They also assume that all interactions take the same time which leads to the Hardy-Weinberg equilibrium distribution of pairs. Fitnesses for the two strategies are then calculated at this equilibrium distribution using the payoff matrix. This methodology then leads to the classical predictions such as that when the cost of a fight is lower than the value of the contested resource the Hawk strategy (i.e., aggressive behaviour) is the

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evolutionary outcome in the Hawk-Dove model, or defection is the ESS in the repeated Prisoner's dilemma game. Thus, implicitly, two-strategy matrix models assume time scale separation between pair formation that runs on a fast time scale and payoff accrual that operates on a slow time scale.

These predictions sharply change when interaction times are not the same (Křivan and Cressman, 2017) in that in both cases mixed ESS appear. For example, in the case of the repeated Prisoner's dilemma game, it is reasonable to assume that individuals prefer to interact with a cooperator because such an interaction is more beneficial than interacting with a defector. If individuals are free to stay or leave the pair after each round of the game, pairs that contain a defector will last only a single round, while pairs with two cooperators will last for the maximum number of rounds. Repeated games where individuals are free to break interaction with their current partner were also considered in the literature. E.g., Aktipis (2004) considered the "walk-away" strategy while Zhang et al. (2016) called such a game the opting out game. Křivan and Cressman (2017) showed that opting out promotes the evolution of cooperation, provided that the probability of another round is high enough (i.e. interacting individuals stay together for long enough). Another game that models evolution of aggressivity is the Hawk-Dove game (Maynard Smith and Price, 1973). When interaction times are strategy independent, this game predicts that if the cost of fighting is not too high when compared to benefits the individual can obtain from the fight, all individuals will behave aggressively. Křivan and Cressman (2017) showed that e.g., when the interaction time between two Hawks is long enough, individuals will play a mixed strategy, i.e., they will not always fight. In fact, as the cost, measured in time lost in a fight (or in recovery after the fight) increases, the probability of aggressive behaviour will decrease. However, differences in interaction times lead to pair interaction distributions that are not given by the Hardy-Weinberg equation and are much more difficult to calculate (e.g., Garay et al., 2017; Křivan and Cressman, 2017; Garay et al., 2018; Křivan et al., 2018; Cressman and Křivan, 2019; Broom et al., 2019). Following the classic theory, these models that assume well mixed populations consider time scale separation in that payoffs are calculated at the pair equilibrium distribution. This methodology has been applied also to asymmetric two-strategy games such as the Owner-Intruder game (Cressman and Křivan, 2019).

The classical models also assume that every pair of individuals within a population are equally likely to meet. This is very often not the case, especially if a population covers a wide area, and individuals are far more likely to play games against those that are close to them. Population structure has been included in several ways, and in particular a general and elegant theory, evolutionary graph theory, has been developed following Lieberman et al. (2005). Here a population of N individuals lives on the vertices V of a graph $G = (V, E)$ and individuals can only interact with, and replace, neighbours, i.e., those for which they are connected by an edge from the edge set E. Fixed fitness models (where there are no games and the fitness of an individual depends only upon its type) are much more complicated now (Lieberman et al., 2005; Broom and Rychtář, 2008), and different structures can have a significant effect on the evolution of the population, either enhancing or suppressing selection (increasing/decreasing the advantage of fitter strategies). The order of selection birth before death or death before birth (and when fitness acts) which was not important for well-mixed populations, is now important (Ohtsuki et al., 2006; Antal et al., 2006; Masuda, 2009). Classical evolutionary models including the Hawk Dove game (Hauert and Doebeli, 2004; Broom et al., 2010) and the Prisoner's dilemma (Ohtsuki et al., 2006; Santos et al., 2006) have been considered, and in the latter case a lot of research has gone into finding the conditions for which cooperation can thrive (see e.g., Santos and Pacheco, 2005).

In this paper we incorporate time delays and population structure. In particular we consider two strategy games where each combination of pure strategies yields both a specific payoff and specific interaction time for each player. Games are played between neighbours on a regular graph. Each neighbouring pair meet at a constant rate, providing that they are both free (i.e., not involved in a game with another player). Thus the probability of facing any given opponent depends both upon the structure and the strategies played. We assume that the evolution of the population takes place at a slower timescale than the interaction dynamics, so that a long period of interactions takes place between a fixed population of individuals (and we show that the population converges to a steady state under these circumstances).

In section 2 we outline the modelling methodology of evolutionary games with time constraints and extend it to consider a population evolving on a regular graph. Then in section 3 we consider evolution following a birth-death and death-birth dynamics. In section 4 we consider the evolution of the population to find the ESSs, and consider two classic evolutionary games, the Hawk-Dove game and the Prisoner's Dilemma. Finally, section 5 is a discussion.

2. Two strategy games with interaction times on regular graphs

Let us consider a population playing a game on a large regular graph of degree $k > 2$ (We do not consider the case with $k = 2$ as it is simply a large circle graph and is a very special case that would require some different mathematical treatment). We assume that each vertex is occupied by a single individual and neighbouring individuals play a symmetric two-strategy game described by the payoff matrix

$$\pi = \begin{array}{c c} & \begin{array}{cc} e_1 & e_2 \end{array} \\ \begin{array}{c} e_1 \\ e_2 \end{array} & \left[\begin{array}{cc} \pi_{11} & \pi_{12} \\ \pi_{21} & \pi_{22} \end{array} \right] \end{array} \tag{1}$$

where e_1 and e_2 are the two strategies used.

We consider a population involving two types of individuals; A-type which play e_1 with probability p, and B-type which play e_1 with probability $p + h$, where h is a small (positive or negative) number such that $0 \leq p + h \leq 1$. We denote the proportion of A (B) individuals in the population as a ($0 \leq a \leq 1$, $b = 1 - a$). We particularly consider a resident monomorphic population of A-type, potentially invaded by a small proportion of B-type.

By

$$\Pi = \begin{array}{c c} & \begin{array}{cc} \mathrm{A} & \mathrm{B} \end{array} \\ \begin{array}{c} \mathrm{A} \\ \mathrm{B} \end{array} & \left[\begin{array}{cc} \Pi_{AA} & \Pi_{AB} \\ \Pi_{BA} & \Pi_{BB} \end{array} \right] \end{array} = \left[\begin{array}{cc} \mathbf{p}\pi\mathbf{p}^\top & \mathbf{p}\pi(\mathbf{p}+\mathbf{h})^\top \\ (\mathbf{p}+\mathbf{h})\pi\mathbf{p}^\top & (\mathbf{p}+\mathbf{h})\pi(\mathbf{p}+\mathbf{h})^\top \end{array} \right] \tag{2}$$

with matrix π given in (1), we denote the payoff matrix for the two types where Π_{XY} is the payoff to an X-type individual when it meets a Y-type individual and $\mathbf{p} = (p, 1-p)$, $\mathbf{q} = \mathbf{p} + \mathbf{h} = (p + h, 1 - p - h)$ are strategies of these two individuals.

In our model, allowing h to be small means that our game can use assumptions based upon the limit of weak selection, which then allow for the use of good linear approximations to payoffs. The key assumption for this is that the fitnesses of the different strategies are vanishingly small. In our model, we do not have vanishingly small fitness differences between the pure strategies, but we consider two mixed strategies with probabilities arbitrarily close together, which then also have vanishingly small fitness differences. Thus the assumption of considering close mixed strategies makes it possible for the consequences of the weak selection limit to hold. We note that the time delays in our model make it fundamentally non-linear in mixed strategies. Similar local linearity could be established through pure strategies and weak selection, but then this would lead to linearity over the whole range of possible mixtures (the only conclusions then mirroring standard two-player games). It is important for us to reconstruct the more complex situations that come about through the games with time-constraints, as we discuss in sections 4 and 5.

Classical matrix game models assume that all interactions take the same time (τ) independently of the strategies the interacting individuals use. Then all interactions finish at a rate $1/\tau$ and singles then search among their neighbours for a partner to interact with. Let $r > 0$ be the rate with which a single individual can meet any given single neighbour. This rate depends, for example, on the speed with which individuals move. If each individual has k neighbours, the rate with which it can meet one of its neighbours is rk.

In this article we assume that interactions between different strategies can take different times. In particular, these times are given by the symmetric time interaction matrix

$$T = \begin{array}{c c} & \begin{array}{cc} e_1 & e_2 \end{array} \\ \begin{array}{c} e_1 \\ e_2 \end{array} & \left[\begin{array}{cc} \tau_{11} & \tau_{12} \\ \tau_{12} & \tau_{22} \end{array} \right] \end{array}. \tag{3}$$

To calculate the fitnesses of A and B individuals, we need to know the pair distribution. Two neighbours can start a new interaction only if they are both free, i.e., not involved in some other interactions and we denote the probability that X and Y are free by y_{XY}. The list of symbols used in the article is given in Table 1. Let $x_{X_iY_j}$ be the probability that a neighbouring pair of X-type and Y-type are involved in an interaction where the X-type uses strategy e_i and the Y-type uses strategy e_j ($i, j = 1, 2$). As interactions between these two strategies finish at a constant rate $1/\tau_{ij}$, at the distributional equilibrium, where the rate with which pairs disband equals the rate with which pairs are formed, we have

$$\begin{aligned}
\frac{x_{A_1A_1}}{\tau_{11}} &= y_{AA}rp^2, \\
\frac{x_{A_1A_2}}{\tau_{12}} &= y_{AA}rp(1-p), \\
\frac{x_{A_2A_2}}{\tau_{22}} &= y_{AA}r(1-p)^2, \\
\frac{x_{A_1B_1}}{\tau_{11}} &= y_{AB}rp(p+h), \\
\frac{x_{A_1B_2}}{\tau_{12}} &= y_{AB}rp(1-p-h), \\
\frac{x_{A_2B_1}}{\tau_{12}} &= y_{AB}r(1-p)(p+h), \\
\frac{x_{A_2B_2}}{\tau_{22}} &= y_{AB}r(1-p)(1-p-h), \\
\frac{x_{B_1B_1}}{\tau_{11}} &= y_{BB}r(p+h)^2, \\
\frac{x_{B_1B_2}}{\tau_{12}} &= y_{BB}r(p+h)(1-p-h), \\
\frac{x_{B_2B_2}}{\tau_{22}} &= y_{BB}r(1-p-h)^2,
\end{aligned} \tag{4}$$

where we assume that h is such that $0 \leq p+h \leq 1$. In particular, if $p=1$ ($p=0$) then $h<0$ ($h>0$).

Let us consider a focal individual of X-type and one of its neighbours who is of Y-type (where X, Y are either an A- or B-type individuals throughout this article). These two individuals are then interacting with probability

$$x_{XY} = \begin{cases} x_{X_1Y_1} + x_{X_1Y_2} + x_{X_2Y_1} + x_{X_2Y_2} & \text{when } X \neq Y \\ x_{X_1X_1} + 2x_{X_1X_2} + x_{X_2X_2} & \text{when } X = Y. \end{cases} \tag{5}$$

This leads to

$$\begin{aligned}
x_{AA} =& r y_{AA}\tau_{AA}, \\
x_{AB} =& r y_{AB}\tau_{AB}, \\
x_{BB} =& r y_{BB}\tau_{BB},
\end{aligned} \tag{6}$$

where

$$\tau_{AA} = g(p,p), \;\; \tau_{AB} = g(p,p+h), \;\; \tau_{BB} = g(p+h,p+h) \tag{7}$$

are the mean interaction times and

$$g(p,q) = (p,1-p)T(q,1-q)^\top = pq\tau_{11} + \tau_{12}(p-2pq+q) + (1-p)(1-q)\tau_{22}, \tag{8}$$

with matrix T given in (3). We observe that when all interaction times are strategy independent and equal to τ, $x_{XY} = \tau r y_{XY}$.

To calculate the fitness of both types we denote by $q_{Y|X}$ the conditional probability that a random neighbour of a focal X-type is of type Y. This was shown by Ohtsuki et al. (2006), under assumptions that we discuss below, to be

$$\begin{aligned}
q_{A|A} &= \frac{(k-2+\frac{1}{a})a}{k-1} = \frac{1+(k-2)a}{k-1}, \\
q_{B|A} &= 1 - q_{A|A} = \frac{k-2}{k-1}(1-a), \\
q_{A|B} &= \frac{k-2}{k-1}a, \\
q_{B|B} &= 1 - q_{A|B} = \frac{1+(k-2)(1-a)}{k-1}.
\end{aligned} \tag{9}$$

The above expressions allow us to calculate pair distributions. Let p_{XY} be the proportion of XY pairs among all pairs. This proportion depends on the frequency a (b) of type A (B) individuals in the population, the probability $q_{Y|X}$ that a random neighbour of an X type individual is of Y type, and the probability x_{XY} that the two individuals are interacting, i.e.,

$$\begin{aligned} p_{AA} &\sim x_{AA} q_{A|A} a \\ p_{AB} &\sim x_{AB} (q_{A|B} b + q_{B|A} a) \\ p_{BB} &\sim x_{BB} q_{B|B} b. \end{aligned}$$

In general, these are not in Hardy–Weinberg proportions due to the graph structure. We observe that as the graph degree tends to infinity, i.e., individuals interact at random, $p_{AA} \sim x_{AA}a^2$, $p_{AB} \sim 2x_{AB}ab$, and $p_{BB} \sim x_{BB}b^2$. If all interaction times are the same, i.e., $\tau_{AA} = \tau_{AB} = \tau_{BB}$, then we show in Appendix A that $x_{AA} = x_{AB} = x_{BB}$, and so the pair proportions are at Hardy–Weinberg equilibrium.

In this article we assume that the population size is very large (i.e., much larger than is the graph degree k, Ohtsuki et al., 2006) and we are interested to find out when a finite number of mutants B can invade under (effective) monomorphism where the proportion of A-type individuals in the population is $a = 1$, and so the proportion of B individuals is 0, i.e. in the limit of the population size tending to infinity. For this situation qs in (9) simplify to

$$\begin{aligned} q_{A|A} &= 1, \\ q_{B|A} &= 0, \\ q_{A|B} &= \frac{k-2}{k-1}, \\ q_{B|B} &= \frac{1}{k-1}. \end{aligned} \tag{10}$$

In particular, we observe that the probability that a mutant has a resident as its neighbour is higher than is the probability that a mutant has a mutant as its neighbour once $k > 3$.

If individuals were completely randomly distributed, then $q_{B|B} = q_{B|A} = 1 - a$ and $q_{A|A} = q_{A|B} = a$, so that for a smaller but very close to 1, the probability of a B individual having a B neighbour would seem to be small. Although we assume that individuals start out allocated randomly, evolution happens such that an individual is randomly selected to give birth and copies itself into a random neighbour (the individual there is then replaced). Thus over time individuals will tend to be near others of their own type (at least more likely than pure random allocation). In particular, given an individual is alive, there is a reasonable probability it is connected to its parent or an offspring, although as we see in equation (9), this effect is strongest for the smallest values of k. In particular Ohtsuki et al. (2006) showed that the conditional probabilities in equation (9) hold, given the following assumptions: (i) the population is evolving under weak selection, so that the difference between the fitnesses of the two types of individuals is (vanishingly) small, which holds for our model for (vanishingly) small h, (ii) the population size N is large, and it is much larger than the degree of the graph k, and (iii) the graph has no clustering. The pair approximation was developed for Bethe lattices, regular graphs with no cycles. In particular the approximation will not be accurate for heavily clustered graphs, such as triangular lattices. We note that this means that the usual assumptions about small invading groups, that almost all interactions are with the resident population and so the population can effectively be treated as monomorphic, do not automatically hold. We thus consider our analysis for all possible interactions between individuals of the two types throughout the sections that follow.

To calculate the probability x_{XY} that two neighbours are interacting we define $z_{X|Y}$ to be the conditional probability of an X being free given its neighbour is of type Y. Let us consider a focal individual of X-type and one of its neighbours who is of Y-type. These two individuals can be interacting with probability x_{XY}, or the focal individual can be free with probability $z_{X|Y}$, or it can be interacting with one of the other neighbours, that can be either of A- or B-type, with probability $q_{A|X}x_{XA} + q_{B|X}x_{XB}$. We obtain the following equations for $z_{X|Y}$ and y_{XY}

$$\begin{aligned} (q_{A|A}x_{AA} + q_{B|A}x_{AB})(k-1) + x_{AA} + z_{A|A} &= 1, \\ (q_{A|A}x_{AA} + q_{B|A}x_{AB})(k-1) + x_{AB} + z_{A|B} &= 1, \\ (q_{A|B}x_{AB} + q_{B|B}x_{BB})(k-1) + x_{AB} + z_{B|A} &= 1, \\ (q_{A|B}x_{AB} + q_{B|B}x_{BB})(k-1) + x_{BB} + z_{B|B} &= 1. \end{aligned} \tag{11}$$

We shall assume that neighbours are effectively independent, given not interacting with each other. This is approximately true for large graphs with no clustering, but this will not be accurate for highly clustered graphs, i.e., in the same circumstance as when the approximations in equation (9) are not accurate. This then gives for a pair of neighbours who are of X- and Y-type

$$\begin{aligned} P[\text{both } X \text{ and } Y \text{ free}] =& P[\text{not interacting with each other}] \\ & \times P[X \text{ does not interact with another neighbour}] \\ & \times P[Y \text{ does not interact with another neighbour}], \end{aligned}$$

giving

$$\begin{aligned} y_{AA} &= (1 - x_{AA}) \frac{z_{A|A}}{1 - x_{AA}} \frac{z_{A|A}}{1 - x_{AA}} = \frac{z_{A|A}^2}{1 - x_{AA}}, \\ y_{BB} &= (1 - x_{BB}) \frac{z_{B|B}}{1 - x_{BB}} \frac{z_{B|B}}{1 - x_{BB}} = \frac{z_{B|B}^2}{1 - x_{BB}}, \\ y_{AB} &= (1 - x_{AB}) \frac{z_{A|B}}{1 - x_{AB}} \frac{z_{B|A}}{1 - x_{AB}} = \frac{z_{A|B} z_{B|A}}{1 - x_{AB}}. \end{aligned} \tag{12}$$

Equations (11) and (12) allow us to calculate ys as functions of xs:

$$\begin{aligned} y_{AA} =& \frac{(1 - (k-1)(q_{A|A} x_{AA} + q_{B|A} x_{AB}) - x_{AA})^2}{1 - x_{AA}}, \\ y_{BB} =& \frac{(1 - (k-1)(q_{A|B} x_{AB} + q_{B|B} x_{BB}) - x_{BB})^2}{1 - x_{BB}}, \\ y_{AB} =& (1 - (k-1)(q_{A|A} x_{AA} + q_{B|A} x_{AB}) - x_{AB}) \times \\ & \frac{(1 - (k-1)(q_{A|B} x_{AB} + q_{B|B} x_{BB}) - x_{AB})}{1 - x_{AB}}. \end{aligned}$$

Substituting these formulae in (6) leads to a system of algebraic equations

$$\begin{aligned} x_{AA} =& r\tau_{AA} \frac{(1 - (k-1)(q_{A|A} x_{AA} + q_{B|A} x_{AB}) - x_{AA})^2}{1 - x_{AA}}, \\ x_{BB} =& r\tau_{AB} \frac{(1 - (k-1)(q_{A|B} x_{AB} + q_{B|B} x_{BB}) - x_{BB})^2}{1 - x_{BB}}, \\ x_{AB} =& r\tau_{BB} (1 - (k-1)(q_{A|A} x_{AA} + q_{B|A} x_{AB}) - x_{AB}) \frac{(1 - (k-1)(q_{A|B} x_{AB} + q_{B|B} x_{BB}) - x_{AB})}{1 - x_{AB}} \end{aligned} \tag{13}$$

for equilibrium pair distribution (x_{AA}, x_{AB}, x_{BB}).

Substituting (10) in (13) leads to the following equations for equilibrium distribution of interacting pairs

$$\begin{aligned} x_{AA} =& r\tau_{AA} \frac{(1 - k x_{AA})^2}{1 - x_{AA}}, \\ x_{BB} =& r\tau_{BB} \frac{(1 - (k-2) x_{AB} - 2 x_{BB})^2}{1 - x_{BB}}, \\ x_{AB} =& r\tau_{AB} \frac{(1 - (k-1) x_{AA} - x_{AB})(1 - (k-1) x_{AB} - x_{BB})}{1 - x_{AB}}. \end{aligned} \tag{14}$$

We observe that from (10) and (11) and because all zs are non-negative

$$\begin{aligned} 1 - k x_{AA} >& 0, \\ 1 - (k-1) x_{AA} - x_{AB} >& 0, \\ 1 - (k-1) x_{AB} - x_{BB} >& 0, \\ 1 - (k-2) x_{AB} - 2 x_{BB} >& 0. \end{aligned} \tag{15}$$

We shall be interested in considering evolutionary dynamics models where individuals can only replace or be replaced by neighbours. In the next section we derive fitnesses at the equilibrium pair distribution for two replacement processes.

Table 1: List of used symbols

y_{XY}	probability that two neighbours of type X and Y are both free
x_{XY}	probability that two neighbours of type X and Y are interacting, irrespective of what strategy they use
$x_{X_iY_j}$	probability that two interacting neighbours of type X and Y use strategy e_i and e_j, respectively
$q_{Y\|X}$	probability that a random neighbour of a focal type X is of type Y
$z_{X\|Y}$	probability of X being free given its neighbour is of type Y
$a(b)$	proportion of type A (B) individuals in the population
$E(X,a)$	payoff of type X in a population with proportion of type A being a
r	the rate with which a free individual meets with a free neighbour
p	strategy of type A, i.e., probability with which type A plays strategy e_1

3. Fitnesses for two replacement processes

In this section we derive fitnesses for A and B individual types. These fitnesses depend on the details of the replacement process in which one individual is replaced by another individual. Here we consider two types of replacement models: a birth-death replacement process where an individual is selected for birth proportional to its fitness and then replaces a random neighbour, and a death-birth process where an individual dies at random and is then replaced by a copy of a neighbour, with the neighbour selected with probability proportional to its fitness. In both cases we assume that these population processes operate on a time scale that is much longer than is the time scale at which pairs are formed. This means that we assume that when a new individual replaces another individual, the pairs are at their equilibrium distribution calculated above.

We want to find a strategy p of residents A (i.e., the probability with which type A individuals play strategy e_1), at which any other strategy that slightly differs cannot invade. To do this we will assume that frequencies of pairs change on a short time scale (see Sections 3.1 and 3.2) while frequencies of strategies (Section 4) change on a long, evolutionary time scale. This assumption corresponds to time scale separation, where frequencies of pairs instantaneously track frequencies of strategies. If a mutant strategy achieves a higher payoff than the resident strategy we assume that mutants invade, replace the current residents, and become new residents. This corresponds to the methodology from adaptive dynamics (Dercole and Rinaldi, 2008; Broom and Rychtář, 2013). We note, however, that there are also crucial differences. In unstructured populations any two individuals are neighbours. Thus, if B represents a small invading mutant group, almost all interactions for either A or B are with the resident A type so, e.g., interactions between two B individuals are not considered. However, this is not the case in structured populations, where the number of neighbours stays fixed, as equations (9) and (10) make clear, and we have to consider all interactions between residents and mutants.

3.1. Birth-death updating

In this process one individual is chosen to give birth proportional to its fitness and the newborn then replaces a randomly selected neighbouring individual (Figure 1A). Here we assume that the focal individual can interact with all of its neighbours and obtains payoffs from these interactions even if it is interacting with the neighbour that will be chosen to die. We calculate the payoff to a random focal individual in the population for both types

$$\begin{aligned}
E(A|A,a) =& r\left(\big(q_{A|A}y_{AA}\Pi_{AA} + q_{B|A}y_{AB}\Pi_{AB}\big)(k-1) + y_{AA}\Pi_{AA}\right),\\
E(A|B,a) =& r\left(\big(q_{A|A}y_{AA}\Pi_{AA} + q_{B|A}y_{AB}\Pi_{AB}\big)(k-1) + y_{AB}\Pi_{AB}\right),\\
E(B|A,a) =& r\left(\big(q_{A|B}y_{AB}\Pi_{BA} + q_{B|B}y_{BB}\Pi_{BB}\big)(k-1) + y_{AB}\Pi_{BA}\right),\\
E(B|B,a) =& r\left(\big(q_{A|B}y_{AB}\Pi_{BA} + q_{B|B}y_{BB}\Pi_{BB}\big)(k-1) + y_{BB}\Pi_{BB}\right),
\end{aligned} \tag{16}$$

where $E(X|Y,a)$ is the expected payoff to a type X individual with a given neighbour of type Y. Here, the first part of each formula denotes the fitness the focal individual gets from when it interacts with a neighbour that will not die in that interaction, while the last term describes the interaction with the individual that will die in the interaction. For example, assume that the focal individual is of type A and the individual that

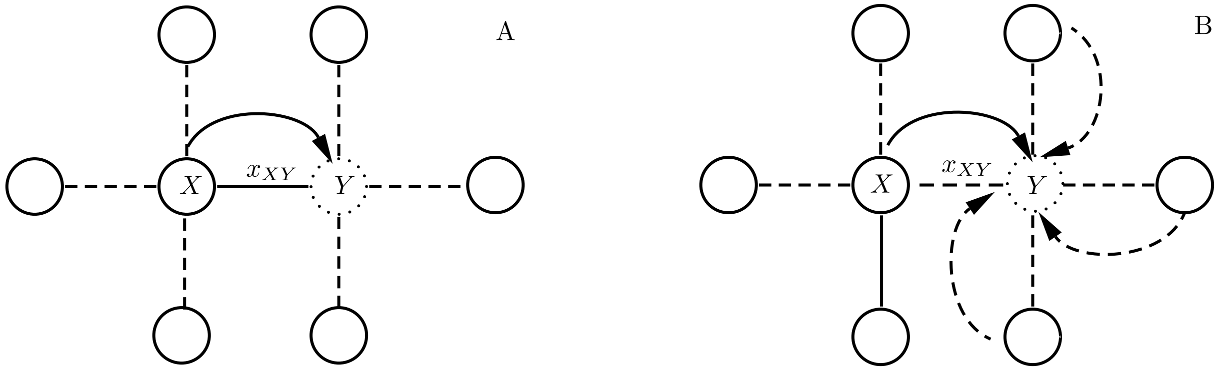

Figure 1: Panel A shows Birth-Death updating while panel B shows Death-Birth updating. For BD updating an individual is selected to give birth, a copy of that individual replacing a randomly chosen neighbour. In DB updating an individual is chosen at random to die, and a neighbour is selected to replace it. Thus, all neighbours are competing for the vacant place as shown in Panel B. In both panels the focal individual X is the one that gives birth and that in the dashed circle is the one that dies. In the case of BD updating X can interact (and it does in panel A) with the individual it replaces, while in DB updating, after a random death, competing individuals do not interact with each other. The solid line shows who interacts with whom.

will be replaced is of type B. The fitness of the focal individual E(A—B,a) is then calculated as the mean payoff the individual obtains from interacting with its neighbours. We consider the start of the contests as a way of finding the payoff per unit time over a long period, as once a contest has started the expected payoff associated with it will subsequently be accrued. The focal individual can interact with a neighbour only if both the focal individual and the neighbour are free. Also, we know that the neighbour that will be replaced is of type B, but we do not know what types the other $k-1$ neigbours are. For that reason we need to take into account the probability that a random neighbour of our focal type A individual is either of type A (with probability $q_{A|A}$) or B (with probability $q_{B|A}$).

We want to find a strategy p of residents A, at which any other strategy that slightly differs cannot invade. In a population consisting of residents only ($a = 1$), the fitness of any other mutant with a slightly different strategy $h \neq 0$ (h small) must satisfy the local ESS condition $E(A, 1) > E(B, 1)$ (Hofbauer and Sigmund, 1998; Broom and Rychtář, 2013). Such a strategy can be either a strict NE, i.e., $p = 1$ or $p = 0$, or it can be an interior strategy with $0 < p < 1$. We assume that payoffs (16) and (19) are calculated at the pair distribution equilibrium. To calculate this equilibrium distribution x_{XY}, y_{XY} we consider the situation where mutants B are infinitesimally different from residents, i.e., effectively we consider the limiting case where all individuals play the same mixed strategy by setting $h = 0$. Letting $h \to 0$ we have that τ_{AB} and τ_{BB} tend to τ_{AA}, see (7), and thus equations (14) simplify to

$$\begin{aligned} x_{AA} =& r\tau_{AA}\frac{(1-kx_{AA})^2}{1-x_{AA}}, \\ x_{BB} =& r\tau_{AA}\frac{(1-(k-2)x_{AB}-2x_{BB})^2}{1-x_{BB}}, \\ x_{AB} =& r\tau_{AA}\frac{(1-(k-1)x_{AA}-x_{AB})(1-(k-1)x_{AB}-x_{BB})}{1-x_{AB}}. \end{aligned} \tag{17}$$

We note that for ease of presentation, we keep the same notation as in (14) even though x_{XY} are calculated from here on at $\tau_{AA} = \tau_{AB} = \tau_{BB}$.

Since interactions times are the same for both types, it is not surprising that the monomorphic resident system (17) where all individuals play strategy p together with constraints (15) has (for $k > 2$, as we assume), a unique solution

$$x_{AA} = x_{AB} = x_{BB} = \frac{1 + 2\tau_{AA}kr - \sqrt{4\tau_{AA}(k-1)r + 1}}{2\tau_{AA}k^2r + 2}, \tag{18}$$

see Appendix A. We show in Appendix B that following a natural distributional dynamics, the population converges to this solution. We observe, that when pairing is instantaneous, i.e., when r tends to infinity,

$$\lim_{r\to\infty} x_{AA} = \lim_{r\to\infty} x_{AB} = \lim_{r\to\infty} x_{BB} = \frac{1}{k}.$$

Thus, if there are no singles, the probability that two neighbours are interacting tends to zero as the graph degree increases.

When $a = 1$ and we substitute (10) in payoffs (16) we obtain

$$\begin{aligned} E(A|A,1) =& rky_{AA}\Pi_{AA}, \\ E(A|B,1) =& r\left(y_{AA}\Pi_{AA}(k-1) + y_{AB}\Pi_{AB}\right), \\ E(B|A,1) =& r\left((k-1)y_{AB}\Pi_{BA} + y_{BB}\Pi_{BB}\right), \\ E(B|B,1) =& r\left((k-2)y_{AB}\Pi_{BA} + 2y_{BB}\Pi_{BB}\right). \end{aligned} \tag{19}$$

3.2. Death-birth updating

In this process one individual is chosen at random to die and it is replaced by a copy of one of its neighbours. Only the neighbours of the dying individual are competing for the vacant space (Figure 1B). Because the dying individual can be either of type A or type B, we need to calculate the payoffs of its neighbours that can also be of both types. Using equation (19), we obtain

$$E(A|A,1) - E(B|A,1) = rky_{AA}\Pi_{AA} - r\left((k-1)y_{AB}\Pi_{BA} + y_{BB}\Pi_{BB}\right) \tag{20}$$

if the dying individual was of type A, and

$$E(A|B,1) - E(B|B,1) = r\left(y_{AA}\Pi_{AA}(k-1) + y_{AB}\Pi_{AB}\right) - r\left((k-2)y_{AB}\Pi_{BA} + 2y_{BB}\Pi_{BB}\right) \tag{21}$$

if the dying individual was of type B. Since

$$y_{AA}\Pi_{AA} - y_{AB}\Pi_{BA} - y_{AB}\Pi_{AB} + y_{BB}\Pi_{BB} \tag{22}$$

is of order h^2 using equation (2), and because $y_{AA} = y_{AB} = y_{BB}$ as all τ's are the same in (6) and (18), we have that equations (20) and (21) are effectively the same, i.e., the payoff difference between type A vs. type B does not depend on the dying individual, and we thus simply write this as

$$E(A,1) - E(B,1) = r\left(ky_{AA}\Pi_{AA} - (k-1)y_{AB}\Pi_{BA} - y_{BB}\Pi_{BB}\right)$$

where

$$\begin{aligned} E(A,1) =& y_{AA}\Pi_{AA}rk, \\ E(B,1) =& \big((k-1)y_{AB}\Pi_{BA} + y_{BB}\Pi_{BB}\big)r, \end{aligned} \tag{23}$$

see (19).

4. Evolutionary dynamics

Evolutionary dynamics for the BD updating can be described by an adjusted replicator dynamics

$$\frac{dp}{dt} = -p(1-p)\operatorname{sgn}(h)(E(A|B,1) - E(B|A,1)) \tag{24}$$

with the evolutionary dynamics for the DB updating similarly given by

$$\frac{dp}{dt} = -p(1-p)\operatorname{sgn}(h)(E(A,1) - E(B,1)). \tag{25}$$

In the former case individuals play games against the neighbour that they might replace, and the key factors are the fitness of a type A given that it is adjacent to a type B, and the corresponding fitness of a type B given that it is adjacent to a type A.

In the latter case all neighbours compete for the vacant place. If the dying individual is an A type and there are j As and $k-j$ Bs as neighbours, the new individual will be an A with probability $jE(A,1)/(jE(A,1) + (k-j)E(B,1))$. This is greater than j/k (so each A reproduces faster than each B) iff $E(A,1) - E(B,1) > 0$, and this ensures that the population of As increases in the long term.

We should note that we do not necessarily need to select the above dynamics, and that any alternative dynamics which had the same sign for all values of p (i.e., where the effect of the payoff differences $(E(A,1) - E(B,1))$ and $(E(A|B,1) - E(B|A,1))$ causes evolution to act in the same direction) would yield the same result.

Equations (24) and (25) that describe changes in the proportion p of strategy e_1 are adjusted replicator equations with the right hand side multiplied by -1 (1) when $h > 0$ ($h < 0$). The reason for this adjustment is the following. Let us assume that $h > 0$, i.e., B-type individuals use strategy e_1 more often than A-type individuals. If $E(A, 1) > E(B, 1)$ this means that the A-type has a higher fitness, and strategy e_1 should be decreasing in proportion. Similarly, if $h < 0$ and $E(A, 1) > E(B, 1)$, the A-type uses strategy e_1 more often than the B-type and strategy e_1 should be increasing in proportion.

We also note that in equations (24) and (25) we show the start of the evolutionary dynamics process when the population only comprises A-type individuals ($a = 1$). As is standard in adaptive dynamics models we assume the mutant strategy is only infinitesimally different from residents so that we have that all ys are the same and equal to y_{AA} for all as. Appendix C then shows that the equilibria of (24) and (25) are independent of the as.

Replicator dynamics (25) and (24), respectively, evaluated at the equilibrium distribution of interacting pairs (14), form a system of algebraic-differential equations that can be solved numerically. A rest point of the dynamics will occur if and only if there is an NE (assuming we start with some non-zero number of each of the As and Bs). In what follows we apply these results to the Hawk-Dove and repeated Prisoner's Dilemma games.

4.1. Hawk-Dove game

The Hawk–Dove game is given by the payoff matrix

$$\pi = \begin{array}{c c} & \begin{array}{cc} H & D \end{array} \\ \begin{array}{c} H \\ D \end{array} & \left[\begin{array}{cc} \frac{V-C}{2} & V \\ 0 & \frac{V}{2} \end{array} \right] \end{array} \tag{26}$$

where $V > 0$ denotes the value of the reward and $C > 0$ is the cost of the fight. Then the payoff matrix for the two types A and B is

$$\Pi = \begin{bmatrix} \frac{V - C p_H^2}{2} & \frac{V(1-h) - C p_H (p_H + h)}{2} \\ \frac{V(1+h) - C p (p_H + h)}{2} & \frac{V - C (p_H + h)^2}{2} \end{bmatrix}$$

where p_H denotes the frequency of Hawk played by the type A.

For the BD updating, the key payoff terms (19) are

$$\begin{aligned} E(A|B,1) =& \frac{1}{2} r \Big(V \big((h-1) y_{AB} - k y_{AA} + y_{AA} \big) - \\ & C p_H \big(h y_{AB} + p_H ((k-1) y_{AA} + y_{AB}) \big) \Big), \\ E(B|A,1) =& \frac{1}{2} r \Big(V \big((1+h)(k-2) y_{AB} + h y_{BA} + y_{BA} + y_{BB} \big) - \\ & C (p_H + h) \big(h y_{BB} + p_H ((k-2) y_{AB} + y_{BA} + y_{BB}) \big) \Big), \end{aligned}$$

while for DB updating payoffs (23) are

$$\begin{aligned} E(A,1) =& \frac{1}{2} k r y_{AA} \left(V - C p_H^2 \right), \\ E(B,1) =& \frac{1}{2} \Big(r V \big((1+h)(k-1) y_{AB} + y_{BB} \big) - \\ & C r (p_H + h) \big(h y_{BB} + p_H ((k-1) y_{AB} + y_{BB}) \big) \Big). \end{aligned} \tag{27}$$

The equilibrium value of p_H as a function of the time an interaction between two Hawks takes (τ_{11}) for various graph degrees ($k = 4, 10, 20, 50$) are shown in Figures 2 and 3. The cases with birth-death updating for small (k=4) and large (k=50) degree are shown in Figure 2 (panels A and B assume $V > C$ while panels C and D assume $V < C$). We see these solutions (as well as other solutions for other graph degree values that are not shown here) are close to those obtained for unstructured and well-mixed populations (cf. Figure 2 vs. Figure 3A,B in Křivan and Cressman, 2017), and so there is little variation with changing graph degree.

Figure 3 (panels A–D assume $V > C$ while panels E and F assume $V < C$) corresponds to death-birth updating. For low values of k, these solutions are qualitative different from those for birth-death updating. We see in Figure 3 that for $k = 4$ (panel A) there is a unique solution with pure Hawk for low τ_{11}, and a mixture with lower Hawk frequency as τ_{11} increases. As k increases (panels B–D) we see regions where there

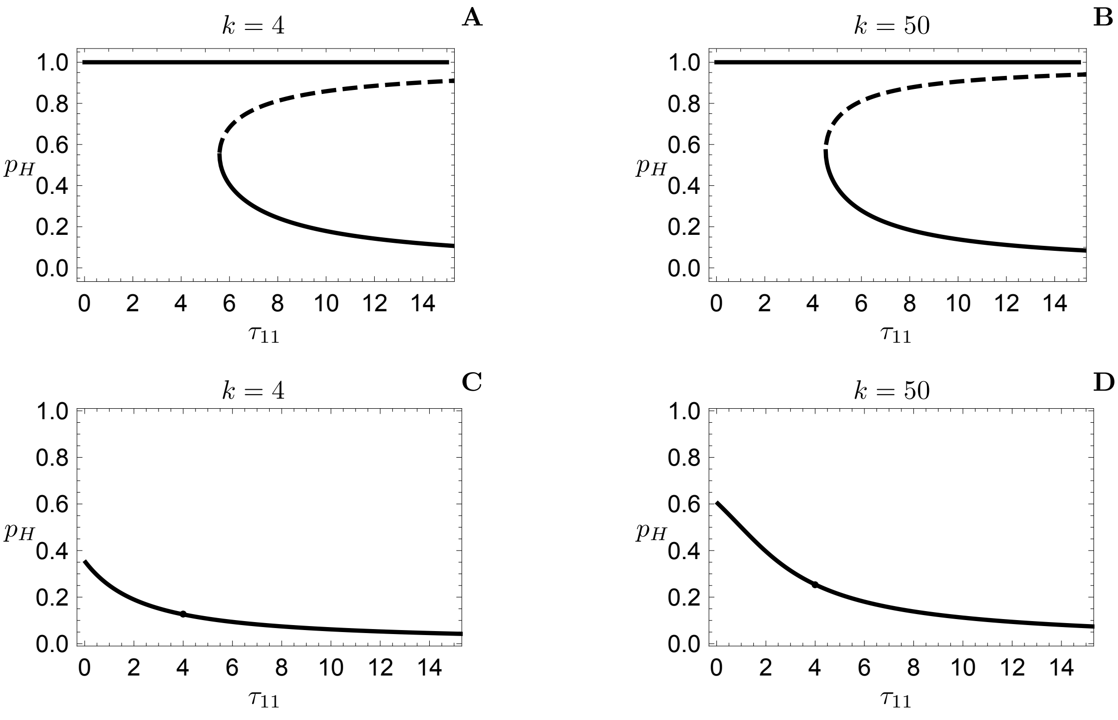

Figure 2: Bifurcation diagram for the Hawk-Dove game for birth-death updating when $V = 2 > 1 = C$ (top panels A, B) and $V = 1 < 2 = C$ (bottom panels C, D) for graph degree $k = 4, 50$. The solid (dashed) line shows the frequency of Hawk p_H at a stable (unstable) NE for the adjusted replicator dynamics (24). In all plots $r = 1$, $\tau_{12} = \tau_{21} = \tau_{22} = 1$.

are two ESSs, pure Hawk and a mixture, and for $k = 50$ we see this over a very large range of τ_{11}s (and this figure is almost identical to the well-mixed population case from Křivan and Cressman (2017)). Note that the case $V > C$ would yield a pure Hawk ESS in the game with a well-mixed population without time constraints, and so the above has yielded a markedly different solution. Panels E and F that assume $V < C$ show a mixed solution as in the equivalent case without time constraints, but again with Hawk frequency declining with τ_{11}. We also observe that as the graph degree decreases, it takes a shorter interaction time τ_{11} for Doves to invade. This suggests that death-birth models are much more sensitive to graph degree than birth-death ones. Contrary to the death-birth updating case, for birth-death updating Doves invade for $k = 4$ at $\tau_{11} \approx 5.6$ and for $k = 50$ at $\tau_{11} \approx 4.5$, i.e., invasion is slightly less likely as τ_{11} decreases.

The main explanation for this is that for the birth-death processes, there is always a direct interaction between replacing and replaced individuals. Thus irrespective of the number of neighbours an individual has, whenever it is possible to replace/be replaced by an individual of the other type, it will always interact with at least one individual of that type. If the other type is rare, as for new invading groups, this will likely be the only such individual, whatever the value of the graph degree, and this pairwise interaction will have a significant effect on the evolutionary outcome. For death-birth processes, a random individual first dies, and those competing for the vacant space are not directly interacting. The number, and proportion (see equation (9) which holds for both processes), of opponents of each type then changes much more with the value of k. We can see this by comparing equations (23), (25) with equations (16), (24). Equations (16), (24) include both the specific individual to be replaced and others in the neighbourhood, but equations (23), (25) contain the other individuals only. Thus for the death-birth model the degree plays a more important role.

4.2. Prisoner's Dilemma

Here we consider the single shot Prisoner's Dilemma game given by the payoff matrix

$$\pi = \begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \left[\begin{array}{cc} b - c & -c \\ b & 0 \end{array} \right] \end{array} \tag{28}$$

where b is the benefit and c is the cost of cooperation. Following Křivan and Cressman (2017) (see also Broom et al., 2019) we consider a repeated PD where individuals are free to decide if they want to play the

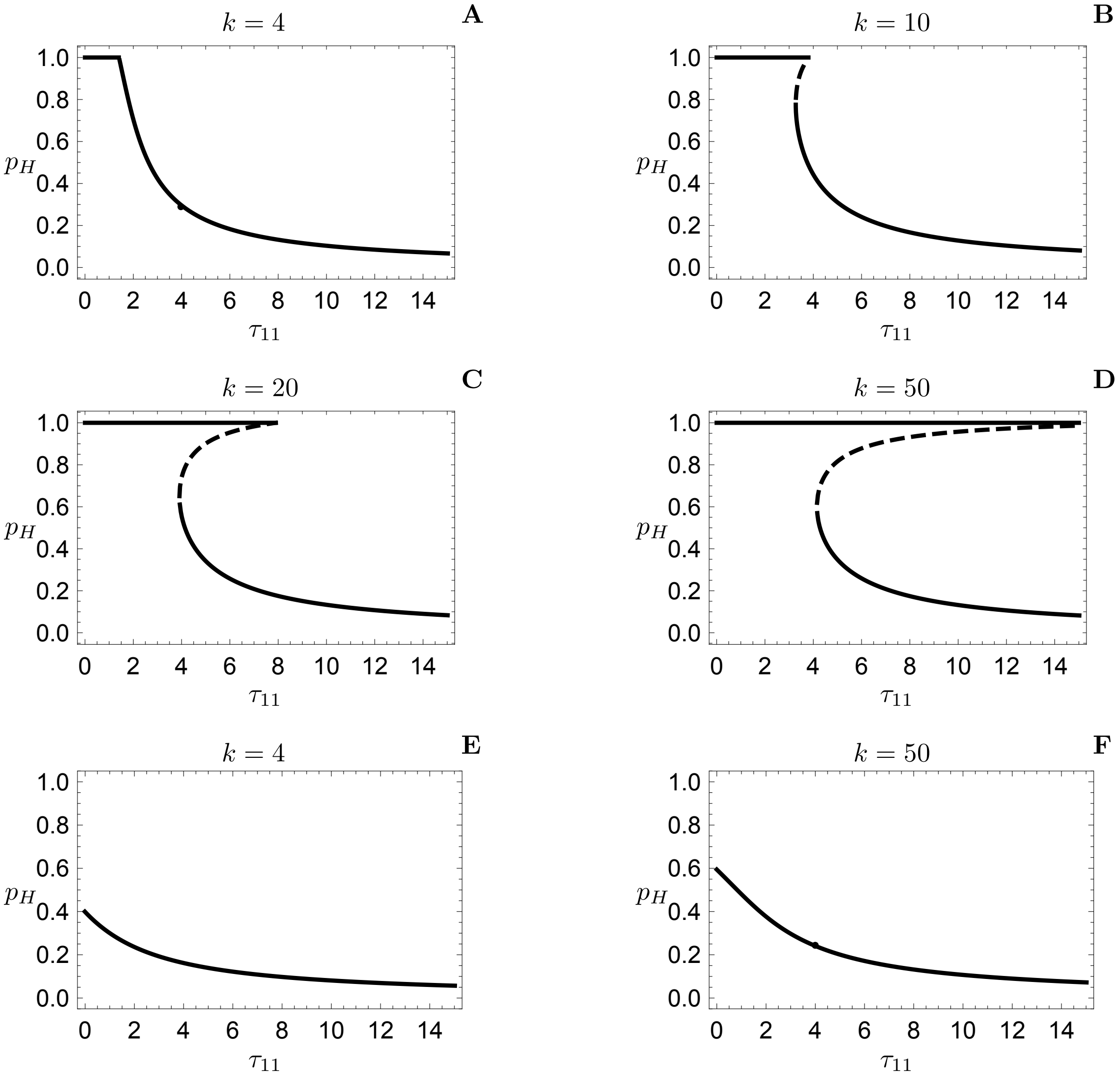

Figure 3: Bifurcation diagram for the Hawk-Dove game for death-birth updating when $V = 2 > 1 = C$ in panels A–D and $V = 1 < 2 = C$ in panels E and F for graph degree $k = 4, 10, 20, 50$. The solid (dashed) line shows the frequency of Hawk p_H at a stable (unstable) NE for the adjusted replicator dynamics (25). In all plots $r = 1$, $\tau_{12} = \tau_{21} = \tau_{22} = 1$.

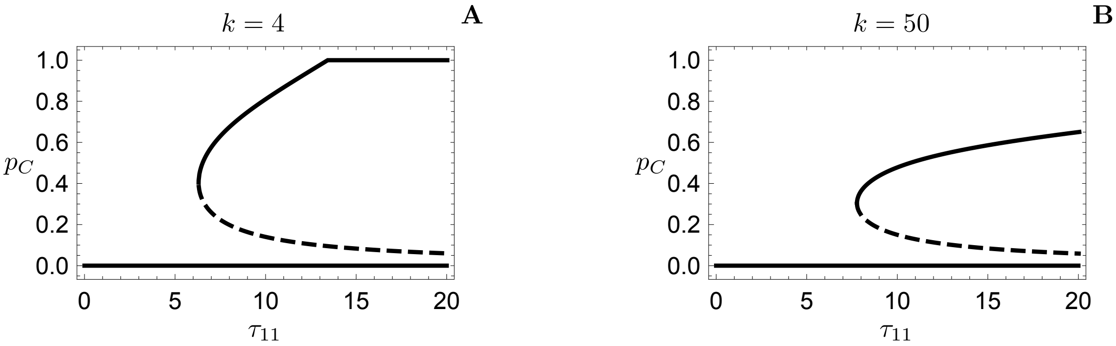

Figure 4: Bifurcation diagram for the PD game for birth-death updating for graph degree $k = 4, 50$. The solid (dashed) line shows the frequency of Cooperate p_C at a stable (unstable) NE for the adjusted replicator dynamics (24). Other parameters used in simulations: $b = 2$, $c = 1$, $r = 1$, $\mu = 1$.

game the next round with the same partner or not. This is the opting out game (Zhang et al., 2016). The entries of interaction matrix (3) are now interpreted as the average number of rounds the two players stay together. Then, the payoff matrix per interaction (which can consist of several rounds) is

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \left[\begin{array}{cc} (b-c)\tau_{11} & -c\tau_{12} \\ b\tau_{12} & 0 \end{array}\right]. \end{array} \tag{29}$$

If p_C denotes the probability with which an individual of type A cooperates, payoffs to a random individual for the birth-death process are

$$\begin{aligned} E(A|B,1) =& r\big(y_{AA}(b-c)p_C(p_C\tau_{11} + (1-p_C)\tau_{12})(k-1) \\ & + y_{AB}((b-c)p_C((p_C+h)\tau_{11} + (1-p_C-h)\tau_{12}) + bh\tau_{12})\big), \\ E(B|A,1) =& r\Big(\big(y_{AB}((b-c)p_C((p_C+h)\tau_{11} + (1-p_C-h)\tau_{12}) - ch\tau_{12})(k-2) \\ & + y_{BB}(b-c)(p_C+h)((p_C+h)\tau_{11} + (1-p_C-h)\tau_{12})\big) \\ & + y_{AB}((b-c)p_C((p_C+h)\tau_{11} + (1-p_C-h)\tau_{12}) - ch\tau_{12})\Big) \end{aligned}$$

while for the death-birth process

$$\begin{aligned} E(A,1) =& y_{AA}rk(b-c)p_C\big(p_C\tau_{11} + (1-p_C)\tau_{12}\big), \\ E(B,1) =& r(k-1)y_{AB}(bp_C((p_C+h)\tau_{11} + (1-p_C-h)\tau_{12}) - c(p_C+h)(p_C\tau_{11} + (1-p_C)\tau_{12})) + \\ & ry_{BB}(b-c)(p_C+h)((p_C+h)\tau_{11} + (1-p_C-h)\tau_{12}). \end{aligned} \tag{30}$$

Here we focus on the case where only interactions between two cooperators take more rounds, i.e., $\tau_{11} \geq 1$ and $\tau_{12} = \tau_{22} = 1$ (note that τ_{22} does not occur in the payoff functions directly, but affects them indirectly through the interaction probabilities y_{XY}). Dependence of p_C on the number of rounds the game is played τ_{11} is shown for birth-death updating in Figure 4 and for death-birth updating in Figure 5. For this model there are significant changes in outcome as k varies for both birth-death and death-birth models, although again those for the death-birth model are much larger. Besides Defect, that is always an ESS for both birth-death and death-birth models, there is also a stable mixed solution for sufficiently large τ_{11} in both models. The difference between the two updating rules is that Cooperation evolves at a lower number of rounds τ_{11} for the death-birth updating when compared with the birth-death model.

5. Discussion

We have developed a new approach to the theory of two-player symmetric evolutionary games with two strategies on regular graphs that explicitly considers duration of interactions between players. We applied this theory to the Hawk-Dove and Prisoner's dilemma games. In the case of the Hawk-Dove game we showed that when the cost of fighting is low in which the classic model predicts all individuals will play the Hawk

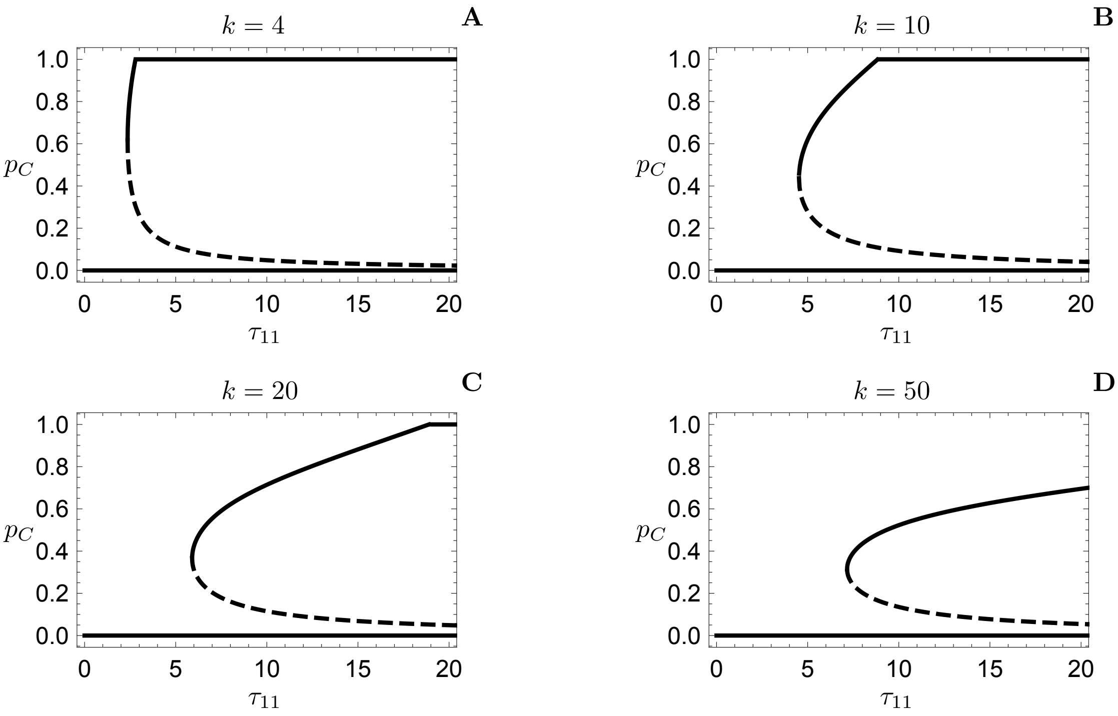

Figure 5: Bifurcation diagram for the PD game for death-birth updating for $k = 4, 10, 20, 50$. The solid (dashed) line shows the frequency of Cooperate p_C at a stable (unstable) NE for the adjusted replicator dynamics (25). Other parameters used in simulations: $b = 2$, $c = 1$, $r = 1$.

strategy, a mixed strategy where individuals play both the Hawk and Dove strategy exists. Similarly, for the repeated Prisoner's dilemma cooperation evolves. In both cases we showed that the results are sensitive to the graph degree and to the updating process that can be either death-birth or birth-death. For the Hawk-Dove model and death-birth updating from Figure 3 we observe that at fixed τ_{11} aggressivity at the interior equilibrium increases with the graph degree. This means that more neighbours an individual has, the more aggressive it will be. However, this prediction changes for birth-death updating. In this case when the cost of fighting is low when compared with the cost of the reward ($C < V$), the level of aggressivity at the interior NE decreases with the graph degree. However, when $C > V$, the effect of the graph degree on the interior equilibrium is almost negligible. For the repeated Prisoner's dilemma game we obtained similar results in that for both updating rules the level of cooperativity at the interior NE decreases with increasing graph degree (Figures 5 and 4).

When graph degree is high, i.e., when everybody can interact with a large number of individuals, our results fit with those obtained for unstructured well mixed populations (e.g., cf. Figure 3B, D vs. Figure 3A,B in Křivan and Cressman, 2017). The difference is that mixed equilibria occur at lower interaction times when graph degree is finite. This makes sense because for example in the case of the repeated Prisoner's dilemma game Hamilton's rule (e.g., Hamilton, 1964; Broom and Křivan, 2018) states that two players must interact long enough for cooperation to evolve. Thus, cooperation is more likely to evolve on graphs where individuals have lower number of neighbours, i.e., the same individuals do interact more often (Pacheco et al., 2006). On the other hand, we observe that at the interior NE for the PD game (Figures 5 and 4) the level of cooperative behaviour decreases with the number of neighbours, i.e., the level of defection increases. An explanation for this is that the more neighbours an individual has, the less time it spends interacting with any given individual, and the lower the contribution to future rewards of interactions from this individual. Thus the penalty for defecting from reciprocal behaviour by any individual is lower, so the temptation to defect is correspondingly higher.

A separation of timescales is central to the models of evolutionary game theory for well-mixed populations that assume that payoffs are calculated at the Hardy-Weinberg distribution of interacting pairs. This is also true for evolutionary models that assume dependence of interaction times on strategies (e.g., Garay et al., 2017; Křivan and Cressman, 2017; Garay et al., 2018; Křivan et al., 2018; Cressman and Křivan, 2019; Broom et al., 2019), and as we wish to compare our work to these, this is how we do this in the current paper too. The introduction of structure, at least for regular graphs as we consider, does not actually make a huge deal of difference per se. We can see this from comparing Figures 2 and 4 for the birth-death process with analogous figures in Křivan and Cressman (2017). It is Figures 3 and 5 for the death-birth process which are really different, and the cause here is that the individuals competing for the vacant space after an individual has died do not interact with each other.

An interesting comparator for our model is the work of Taylor and Nowak (2006) which models an infinite unstructured population with non-constant interaction rates. Given the population is unstructured, the more direct comparison is with Křivan and Cressman (2017), which as we have discussed in Section 4, is a limiting case for our model as k becomes large. The model of Taylor and Nowak (2006) considered two strategies where individuals encountered others at different rates, so that each of the three possible pairs formed at different rates (r_{AA}, r_{AB} and r_{BB}). This is actually the practical consequence of the time constraints in the Křivan and Cressman (2017) paper, where the length of interactions depends on strategies individuals play. Calculation of fitnesses in evolutionary game theory is based on an implicit assumption that the pair distribution corresponds to Hardy-Weinberg equilibrium (e.g., Křivan and Cressman, 2017). When pairing is preferential or pairs take different times, the resulting pair distribution does not correspond to Hardy–Weinberg equilibrium and fitness functions are not linear in strategies. Although fitnesses used in Taylor and Nowak (2006) are also non-linear in strategies, they do not consider the pair distribution. In Taylor and Nowak (2006) the payoffs are simply an average of the payoffs over all of the games played; the main focus is the novel idea that repairing is not random, and so they do not follow the potential underlying dynamical system in detail (there would be lone individuals, and some would get more pairings than others). In contrast, in Křivan and Cressman (2017) payoffs explicitly depend upon the times that interactions take, through explicit calculation of the pair distribution, beyond just through their effect on the relative pairing probabilities (pairing is instantaneous in Křivan and Cressman (2017) and so there are no lone individuals, although these are an important feature of the later work Křivan et al. (2018)). We should also note that the latter paper is perhaps the simplest example in a recent series of articles (Garay et al., 2017; Křivan and Cressman, 2017; Garay et al., 2018; Křivan et al., 2018; Cressman and Křivan, 2019) on a time constraint problem.

We have only considered two dynamics here, birth-death and death-birth, with selection operating at the birth event in each case. In fact there are a number of possible dynamics, and in particular we can consider selection on the death event, so that we have a set of four dynamics BDB (birth-death with selection on the birth), DBB as we have considered, but also BDD and DBD. We have not explicitly included the other two dynamics because for weak selection on regular graphs it is where selection occurs (on the first or second event) that matters, and so BDD is the same as DBB and DBD is the same as BDB (Ohtsuki et al., 2006).

Other researchers have considered the two dynamics that we have considered, and their effect on the evolution of cooperation (when there are no time constraints) in great detail. The population structure allows positive assortment among cooperators (Santos and Pacheco, 2005) which allows cooperators to potentially evolve, and this is particularly true for irregular graphs with heterogenous individuals, allowing hubs of individuals to form (Santos et al., 2008). In general for regular graphs and weak selection, cooperation can be favoured when selection occurs on the second event, but not on the first (Ohtsuki et al., 2006). In our model this corresponds to the death-birth dynamics, but not the birth-death one (see Zukewich et al. (2013) for some exploration of this issue). In more complex scenarios this selection on the first versus second event does not always hold (for example in the structured population framework of (Broom and Rychtář, 2012) the result seems to hold for static structures (Pattni et al., 2017) but not mobile populations (Pattni et al., 2018)). Clearly with the introduction of time constraints in our model, again this result does not hold.

There are a number of ways that mathematical modelling has demonstrated that cooperation can occur (Nowak, 2006); one key way is through the presence of population structure, which can mean that cooperative individuals are more likely to interact with other cooperators, which makes them resistant to exploitation by defectors (Ohtsuki et al., 2006; Santos and Pacheco, 2005). In particular, this is true for structures where individuals are heterogeneous (Santos et al., 2008) allowing hubs or clusters of cooperators to form. The dynamics that one uses are also important; for example Ohtsuki et al. (2006) showed that death-birth or birth-death dynamics with selection on the second event promotes cooperation but not when selection happens in the first event.

There has also been past work on graphs where the interactions depend upon the type of individuals (e.g., Pacheco et al., 2006; Wu et al., 2010). There different pairs of individuals interact at different rates, due to the fact that links can be formed and broken, and individuals have different propensities to form links with individuals of different types. Thus payoffs depend upon a rescaling of the payoff matrix using the long-term distribution of links which is similar to our rescaled payoff matrix (29) for the repeated Prisoner's dilemma game, where the rescaling is with respect to the number of rounds the two individuals stay together. Thus, there are a number of differences between their work and ours, both in terms of assumptions and consequences. Wu et al. (2010) consider two mechanisms. The first mechanism assumes that pairs break with some probabilities denoted by k_{XY} and new pairs are formed at random. The similarity with our work is that our interaction times are inversely proportional to their disbanding probabilities, i.e., $\tau_{XY} \sim 1/k_{XY}$. The crucial difference is that Wu et al. (2010) allow re-wiring of the graph after a pair disbands, i.e., one of the singles from the disbanded pair forms a new pair with any single individual, while this is not possible in our model. Thus, their graph is varying in time and not of fixed degree. This makes it difficult to compare our results with theirs. Their Figure 6 shows that if rewiring happens quite often then (almost) no cooperation evolves. This is quite understandable, because re-wiring happens in their model at random, so with more re-wiring they should tend to the classic PD game where individuals meet at random. The random re-wiring in Wu et al. (2010) leads in their model to Hardy-Weinberg proportions of interacting pairs when disbanding rates are equal. As we show in Section 2 this holds in our model only if we assume the graph degree tends to infinity. When graph degree is finite, distribution of pairs is not in Hardy–Weinberg equilibrium.

In Pacheco et al. (2006) individuals play games with all of their neighbours, and so receive an average over whichever neighbours they have. In our work, only one individual can be played at a time, and this leads to significant differences. For instance if in their model there is an individual that breaks a link to one neighbour at a high rate and to another at a low rate, it will (approximately) simply receive the payoff for the game against the latter individual. This compares to having fights against two individuals that take a very long time or very short time, respectively, for our model. But here, having two such neighbours would lead to a very low payoff, as eventually the first individual will eventually become involved in a long contest, which then prevents it gaining payoffs from a short one; the consideration of interaction times is again fundamental.

Finally, we note that, in common with most work on structured population models, mutations occur rarely, and so at any one time a population only consists of two type, a resident and a mutant, with the contest settled in favour of one or the other before a new mutation event. Most authors assume players are pure-strategists, and this has generally led them to consider two strategy games only. However our population involves mixed strategy players, and so is readily extendable to games with multiple pure strategies, the Rock-Scissors-Paper game being one possible example. Thus we believe that our methodology is widely applicable in situations where both spatial factors and the duration of events are relevant, which we would argue is the case for a large range of biological situations.

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Appendix A. Proof of uniqueness of distributional equilibria (18).

Here we prove uniqueness of the resident distribution (18). The first equation in (14) has a unique solution

$$x_{AA} = \frac{2\tau_{AA}kr - \sqrt{4\tau_{AA}(k-1)r+1}+1}{2\tau_{AA}k^2r+2} \tag{A.1}$$

that satisfies the constraint $0 \leq x_{AA} \leq 1/k$, see (15). From the last equation in (11) it follows that $z_{B|B} = 1-(k-2)x_{AB} - 2x_{BB} \geq 0$ and the second equation in (14) can be written in the form

$$x_{AB} = \frac{1}{k-2}\left(1-2x_{BB}-\sqrt{\frac{x_{BB}(1-x_{BB})}{r\tau_{AA}}}\right) \tag{A.2}$$

and so

$$\frac{\partial x_{AB}}{\partial x_{BB}} = \frac{1}{k-2}\left(-2-\frac{1-2x_{BB}}{2\tau_{AA}r\sqrt{\frac{(1-x_{BB})x_{BB}}{\tau_{AA}r}}}\right).$$

From (15) it follows that for any valid solution we have that $x_{BB} < 1/2$, and so we can write the above as

$$\frac{\partial x_{AB}}{\partial x_{BB}} = -\frac{2}{k-2} - g(x_{BB}) < -\frac{2}{k-2},$$

where $g(x_{BB}) > 0$. We thus have the corresponding derivative of x_{BB} with respect to x_{AB} satisfying

$$0 > \frac{\partial x_{BB}}{\partial x_{AB}} \geq -\frac{k-2}{2}.$$

From the third equation in (14) we calculate

$$x_{BB} = 1-(k-1)x_{AB} - \frac{(1-x_{AB})x_{AB}}{\tau_{AA}r(1-(k-1)x_{AA}-x_{AB})}. \tag{A.3}$$

We know from (15) that the denominator is positive. Similarly from the third inequality in (15), at any valid solution $x_{AB} < 1/2$ (since we assume $k \geq 3$), and so the third term can be rewritten as minus a positive and increasing function of x_{AB}. Thus it will have a positive derivative, and we have

$$\frac{\partial x_{BB}}{\partial x_{AB}} = -(k-1) - f(x_{AB}) < -(k-1).$$

where $f(x_{AB}) > 0$.

A solution to (14) then corresponds to an interesection of lines (A.2) and (A.3). From the above we can see that (A.3) descends faster than (A.2) in the valid region of solutions, and so there can be at most one solution. We have found a solution, and so this must be unique.

Appendix B. Convergence to the distribution equilibria

Here we consider a polymorphic population consisting of types A and B. For any pair distributional dynamics we can assume that equations (11) and (12) hold for any combinations of x_{AA}, x_{AB} and x_{BB}. However equation (14) only holds at the pair distributional equilibrium. In particular the distributional dynamics will satisfy the following differential equations, as fighting pairs are continually formed and broken.

$$\begin{aligned} x'_{AA} &= ry_{AA} - \frac{x_{AA}}{\tau_{AA}}, \\ x'_{AB} &= ry_{AB} - \frac{x_{AB}}{\tau_{AB}}, \\ x'_{BB} &= ry_{BB} - \frac{x_{BB}}{\tau_{BB}}. \end{aligned} \tag{B.1}$$

Substituting for the y_{XY} terms given in (12), we obtain

$$\begin{aligned} x'_{AA} =& r\frac{z^2_{A|A}}{1-x_{AA}} - \frac{x_{AA}}{\tau_{AA}} \\ x'_{AB} =& r\frac{z_{A|B}z_{B|A}}{1-x_{AB}} - \frac{x_{AB}}{\tau_{AB}} \\ x'_{BB} =& r\frac{z^2_{B|B}}{1-x_{BB}} - \frac{x_{BB}}{\tau_{BB}}. \end{aligned} \tag{B.2}$$

Substituting for $z_{A|A}$ from (11) into the equation for x'_{AA} in (B.2) yields

$$x'_{AA} = r\frac{(1-kx_{AA})^2}{1-x_{AA}} - \frac{x_{AA}}{\tau_{AA}}, \tag{B.3}$$

which has the following unique, stable equilibrium

$$x^*_{AA} = \frac{1 + 2kr\tau_{AA} - \sqrt{4(k-1)r\tau_{AA}+1}}{2+2k^2r\tau_{AA}}$$

that satisfies $1/k > x^*_{AA} > 0$.

In addition, the derivative of the right hand-side of (B.3) with respect to x_{AA} evaluated at the equilibrium is

$$\frac{r(1-(k-1)x_{AA})}{(1-x_{AA})^2}\left((k-1)x_{AA}-(2k-3)\right) - \frac{1}{\tau_{AA}} < \frac{r(1-(k-1)x_{AA})}{(1-x_{AA})^2}\left(2(2-k)\right) < 0, \tag{B.4}$$

because of (15) and so the equilibrium is stable.

Thus, x_{AA} converges to this equilibrium, and in the following we will assume that $x_{AA} = x^*_{AA}$. We are thus left with considering the following two dimensional dynamical system:

$$\begin{aligned} x'_{AB} =& r\frac{1-(k-1)x^*_{AA}-x_{AB})(1-(k-1)x_{AB}-x_{BB})}{1-x_{AB}} - \frac{x_{AB}}{\tau_{AB}}, \\ x'_{BB} =& r\frac{(1-(k-2)x_{AB}-2x_{BB})^2}{1-x_{BB}} - \frac{x_{BB}}{\tau_{BB}}. \end{aligned} \tag{B.5}$$

Calculating the Jacobian, we get (for $k \geq 3$)

$$\begin{aligned} \frac{\partial x'_{AB}}{\partial x_{AB}} =& \frac{r(1-(k-1)x^*_{AA}-x_{AB})(1-(k-1)x_{AB}-x_{BB})}{(1-x_{AB})^2} - \frac{(k-1)r(1-(k-1)x^*_{AA}-x_{AB})}{1-x_{AB}} \\ & - \frac{r(1-(k-1)x_{AB}-x_{BB})}{1-x_{AB}} - \frac{1}{\tau_{AB}}, \\ \frac{\partial x'_{AB}}{\partial x_{BB}} =& \frac{-r(1-(k-1)x^*_{AA}-x_{AB})}{1-x_{AB}}, \\ \frac{\partial x'_{BB}}{\partial x_{AB}} =& \frac{-2(k-2)r(1-(k-2)x_{AB}-2x_{BB})}{1-x_{BB}}, \\ \frac{\partial x'_{BB}}{\partial x_{BB}} =& \frac{r(1-(k-2)x_{AB}-2x_{BB})(2x_{BB}-3-(k-2)x_{AB})}{(1-x_{BB})^2} - \frac{1}{\tau_{BB}}. \end{aligned}$$

Setting $\tau_{AA} = \tau_{AB} = \tau_{BB} = \tau$ as we must have for the limiting case $h \to 0$ and $x_{AA} = x_{AB} = x_{BB} = x$ as at the resident-only equilibrium. Let

$$d = \frac{1-kx}{1-x} < 1. \tag{B.6}$$

We remark that from (15) we have $1 - kx > 0$, thus $d > 0$. In addition, $-(3+(k-4)x) < -2$, since $1 + (k-4)x > 0$. Then we have

$$\begin{aligned} \frac{\partial x'_{AB}}{\partial x_{AB}} &= -\frac{r(k-1)(1-kx)}{(1-x)^2} - \frac{1}{\tau} = -\frac{r(k-1)}{1-x}d - \frac{1}{\tau} = -r(k-1)d - \frac{1}{\tau} < -r(k-1)d < 0, \\ \frac{\partial x'_{AB}}{\partial x_{BB}} &= -\frac{r(1-kx)}{1-x} = -rd < 0, \\ \frac{\partial x'_{BB}}{\partial x_{AB}} &= -\frac{2r(k-2)(1-kx)}{1-x} = -2(k-2)rd < 0, \\ \frac{\partial x'_{BB}}{\partial x_{BB}} &= -\frac{r(3+(k-4)x)(1-kx)}{(1-x)^2} - \frac{1}{\tau} = -\frac{r(3+(k-4)x)}{1-x}d - \frac{1}{\tau} < -2rd - \frac{1}{\tau} < -2rd. \end{aligned}$$

Thus the determinant of the Jacobian satisfies

$$\mathrm{Det}(J) > (-(k-1)rd)(-2rd) - (-rd)(-2(k-2)rd) = 2r^2d^2 > 0 \tag{B.7}$$

which implies together with the above that the equilibrium is stable.

Appendix C. Equilibria of replicator equations (24) and (25) are independent of a.

We assume that the mutant strategy is only infinitesimally different from residents so that we have that all $y_{AA} = y_{AB} = y_{BB}$ in (12) for all as. From (16) then

$$\begin{aligned}
E(A|A,a) =& r(k-1)y_{AA}\left((q_{A|A}\Pi_{AA} + q_{B|A}\Pi_{AB}) + \frac{\Pi_{AA}}{k-1}\right),\\
E(A|B,a) =& r(k-1)y_{AA}\left((q_{A|A}\Pi_{AA} + q_{B|A}\Pi_{AB}) + \frac{\Pi_{AB}}{k-1}\right),\\
E(B|A,a) =& r(k-1)y_{AA}\left((q_{A|B}\Pi_{BA} + q_{B|B}\Pi_{BB}) + \frac{\Pi_{BA}}{k-1}\right),\\
E(B|B,a) =& r(k-1)y_{AA}\left((q_{A|B}\Pi_{BA} + q_{B|B}\Pi_{BB}) + \frac{\Pi_{BB}}{k-1}\right).
\end{aligned}$$

Thus

$$E(A|B,a) - E(B|A,a) = r(k-1)y_{AA}(\Pi_{AB}(q_{B|A} + \frac{1}{k-1}) + q_{A|A}\Pi_{AA} - \Pi_{BA}(q_{A|B} + \frac{1}{k-1}) - q_{B|B}\Pi_{BB}).$$

Since from (9) $q_{A|A} = q_{A|B} + \frac{1}{k-1}$ and $q_{B|B} = q_{B|A} + \frac{1}{k-1}$

$$E(A|B,a) - E(B|A,a) = r(k-1)y_{AA}(q_{A|A}(\Pi_{AA} - \Pi_{BA}) + q_{B|B}(\Pi_{AB} - \Pi_{BB})).$$

Since from (2) $\Pi_{AA} - \Pi_{BA} = \Pi_{AB} - \Pi_{BB}$(neglecting terms of order h^2),

$$E(A|B,a) - E(B|A,a) = r(k-1)y_{AA}(q_{A|A} + q_{B|B})(\Pi_{AA} - \Pi_{BA}) = rky_{AA}(\Pi_{AA} - \Pi_{BA}).$$

This is independent of a, so we can just consider $a = 1$ as we have done.

A simlar procedure works for equation (25), where we find that

$$E(A,a) - E(B,a) = ry_{AA}((k-1)(\Pi_{AA} - \Pi_{BA}) + (\Pi_{AA} - \Pi_{BB})).$$

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