Interaction times change evolutionary outcomes: Two-player matrix games

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Abstract

Two most influential models of evolutionary game theory are the Hawk-Dove and Prisoner's dilemma models. The Hawk-Dove model explains evolution of aggressiveness, predicting individuals should be aggressive when the cost of fighting is lower than its benefit. As the cost of aggressiveness increases and outweighs benefits, aggressiveness in the population should decrease. Similarly, the Prisoner's dilemma models evolution of cooperation. It predicts that individuals should never cooperate despite cooperation leading to a higher collective fitness than defection. The question is then what are the conditions under which cooperation evolves? These classic matrix games, which are based on pair-wise interactions between two opponents with player payoffs given in matrix form, do not consider the effect that conflict duration has on payoffs. However, interactions between different strategies often take different amounts of time. In this article, we develop a new approach to an old idea that opportunity costs lost while engaged in an interaction affect individual fitness. When applied to the Hawk-Dove and Prisoner's dilemma, our theory that incorporates general interaction times leads to qualitatively different predictions. In particular, not all individuals will behave as Hawks when fighting cost is lower than benefit, and cooperation will evolve in the Prisoner's dilemma.

Keywords: evolutionary game theory, Hawk-Dove game, pair formation, population dynamics, Prisoner's dilemma

1. Introduction

Most classic evolutionary games (e.g., the Hawk-Dove game (Maynard Smith, 1974) or the Prisoner's Dilemma (Poundstone, 1992)) assume an infinite population where individuals play pairwise games. The outcome of these games is described by a payoff matrix that allows to calculate the Nash equilibrium (NE), or an Evolutionarily Stable Strategy (ESS). The standard assumptions for these games neglect two important components. First, they neglect the opportunity cost of time lost while an individual is engaged in an interaction with its opponent. For example, in the case of the Hawk-Dove game this is the duration of the fight, in the case of the Prisoner's dilemma this is the time two individuals cooperate. One of the earliest articles developing evolutionary game theory (Maynard Smith and Price, 1973) does consider opportunity cost in a Hawk-Dove type game. There, additional payoffs are added to individuals who are engaged in shorter interactions. As we will see and as pointed out in the Discussion, their approach is different than ours.

Second, if we assume that the population is finite, time of the interaction changes the number of individuals that are available to play the game. Thus, to develop more realistic models of evolutionary game theory, one needs to consider changes in numbers of interacting pairs as a function of duration of interactions. So, we need to consider those individuals that are currently engaged in an interaction and those that are free to form new pairs to play the game. This introduces a complex feedback where duration of interactions influences the numbers of interacting pairs which, in turn, influences the game's NE or ESS.

In this article, we extend the matrix game theory by considering explicitly duration of conflicts between opponents. Similarly to the payoff matrix, we define the interaction time matrix that describes the duration of a conflict between any two elementary strategies. Animal fitness for matrix games is defined as the mean payoff an individual gets per interaction. Once duration of interactions is considered, this leads to two possible fitness definitions. First, we will define fitness as mean payoff per time. Second, we define fitness as the mean payoff per mean duration of the interaction. This latter concept of fitness is similar to the one that is used in optimal foraging theory (Charnov, 1976; Stephens and Krebs, 1986). We develop the theory of time-constrained evolutionary games based on symmetric two-player games (i. e. matrix games) with two pure strategies and illustrate our results by applying them to the Hawk-Dove game and the Prisoner's dilemma.

The Hawk-Dove game models the evolution of aggressiveness. Animals are known to solve their conflicts in complex ways that may or may not include various display behaviors before the real fight (Clutton-Brock and Albon, 1979; Sinervo and Lively, 1996). For example, Clutton-Brock and Albon (1979) observed the course of contests between male red deer. Out of 50 cases, only 14 ended in a fight that can be potentially lethal to one or both opponents. Two types of display behavior were observed: Roar contest and parallel walk. In total, no display behavior was observed in 10 cases that resulted in 1 fight. Roar contest only that lead to one stag withdrawal was observed in 16 cases, parallel

walk only was observed in 7 cases (out of which 5 resulted in a fight), and a roar contest followed by the parallel walk was observed in 17 cases (out of which 8 resulted in a fight). This shows that there is a variability among individuals with respect to their aggressiveness. There are aggressive individuals that fight immediately without display, as well as individuals that are aggressive but they do display before fighting. Therefore, we will consider the interactions between two Hawks that can be longer (in the case of display), or shorter (without any display) than are the other interactions (i. e., between two Doves, or between a Hawk and a Dove).

We also consider the repeated Prisoner's dilemma where the expected number of rounds that two individuals interact depends on their strategy choices. For instance, if we assume that individuals can opt out of an interaction that is not beneficial, interactions between two cooperators will last longer (see the opting out game developed by Zhang et al., 2016). We will thus focus on duration of the interaction between two cooperators while we assume that all other interactions take the same amount of time. In particular, we ask here how long the interactions between two cooperators need to last for cooperation to evolve in this model?

We show that explicit consideration of interaction times in the above two games leads to qualitatively new predictions for their evolutionary outcomes. In particular, our approach leads to a different view on the evolution of aggressiveness and cooperation than provided by the classic Hawk-Dove and Prisoner's Dilemma matrix games respectively.

2. Two-strategy game with symmetric interaction times

Consider a symmetric matrix game with two pure strategies e_1 and e_2 and payoffs described by a payoff matrix

$$
\begin{array}{cc}
 & \begin{array}{cc} e_1 & e_2 \end{array} \\
\begin{array}{c} e_1 \\ e_2 \end{array} & \begin{pmatrix} \pi_{11} & \pi_{12} \\ \pi_{21} & \pi_{22} \end{pmatrix}.
\end{array}
\tag{1}
$$

That is, π_{ij} is the expected payoff obtained by e_i in a pair-wise interaction with e_j.

Contrary to standard game models, we assume that all interactions take some time. These times are given by the interaction time matrix

$$
\begin{array}{cc}
 & \begin{array}{cc} e_1 & e_2 \end{array} \\
\begin{array}{c} e_1 \\ e_2 \end{array} & \begin{pmatrix} \tau_{11} & \tau_{12} \\ \tau_{21} & \tau_{22} \end{pmatrix}.
\end{array}
\tag{2}
$$

In what follows, we assume that interaction times are positive and the interaction time matrix is symmetric, i. e., $\tau_{12} = \tau_{21}$. The payoff matrix (1) then provides the payoffs per interaction with each interaction taking time specified in (2).

3

To "solve" the game given by matrices (1) and (2), we need to describe the process of players' pairing as well as how individual fitness is related to payoff received. In this article, we assume that all singles immediately and randomly pair, so all individuals are paired. The numbers of pairs are denoted as n_{11}, n_{12}, and n_{22} where the subindices denote strategies of the two paired individuals. In particular, n_{12} is the number of pairs where one (irrespective if it is the first or the second individual) individual plays strategy e_1 and the other individual plays strategy e_2. The overall (fixed) number of individuals is then $N = 2(n_{11} + n_{12} + n_{22})$.

A pair n_{ij} splits up following a Poisson process with parameter τ_{ij}, i. e., in a unit of time, the number of pairs that disband is n_{ij}/τ_{ij}. So, per unit of time there will be $2n_{11}/\tau_{11} + n_{12}/\tau_{12}$ individuals playing strategy e_1 and $2n_{22}/\tau_{22} + n_{12}/\tau_{12}$ individuals playing strategy e_2 that will immediately form new pairs. The total number of individuals forming new pairs is $2(n_{11}/\tau_{11} + n_{12}/\tau_{12} + n_{22}/\tau_{22})$. Since we assume that singles instantaneously and randomly pair, the proportion of newly formed n_{11} pairs among all newly formed pairs is

$$\left(\frac{2n_{11}/\tau_{11} + n_{12}/\tau_{12}}{2(n_{11}/\tau_{11} + n_{12}/\tau_{12} + n_{22}/\tau_{22})} \right)^2.$$

To obtain the number of newly formed n_{11} pairs we multiply this proportion by the number of all newly formed pairs $n_{11}/\tau_{11} + n_{12}/\tau_{12} + n_{22}/\tau_{22}$. Similar considerations for n_{12} and n_{22} pairs lead to the following pair dynamics

$$
\begin{aligned}
\frac{dn_{11}}{dt} &= -\frac{n_{11}}{\tau_{11}} + \frac{\left(\frac{2n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} \right)^2}{4 \left(\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{22}}{\tau_{22}} \right)} \\[2em]
\frac{dn_{12}}{dt} &= -\frac{n_{12}}{\tau_{12}} + \frac{2 \left(\frac{2n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} \right) \left(\frac{n_{12}}{\tau_{12}} + \frac{2n_{22}}{\tau_{22}} \right)}{4 \left(\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{22}}{\tau_{22}} \right)} \\[2em]
\frac{dn_{22}}{dt} &= -\frac{n_{22}}{\tau_{22}} + \frac{\left(\frac{n_{12}}{\tau_{12}} + \frac{2n_{22}}{\tau_{22}} \right)^2}{4 \left(\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{22}}{\tau_{22}} \right)}.
\end{aligned}
\tag{3}
$$

We observe that at the equilibrium

$$
\frac{n_{11}}{\tau_{11}} = \frac{\left(\frac{2n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}}\right)^2}{4\left(\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{22}}{\tau_{22}}\right)}
$$

$$
\frac{n_{12}}{\tau_{12}} = \frac{2\left(\frac{2n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}}\right)\left(\frac{n_{12}}{\tau_{12}} + \frac{2n_{22}}{\tau_{22}}\right)}{4\left(\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{22}}{\tau_{22}}\right)} \tag{4}
$$

$$
\frac{n_{22}}{\tau_{22}} = \frac{\left(\frac{n_{12}}{\tau_{12}} + \frac{2n_{22}}{\tau_{22}}\right)^2}{4\left(\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{22}}{\tau_{22}}\right)},
$$

$\frac{n_{11}}{\tau_{11}}, \frac{n_{12}}{\tau_{12}}, \frac{n_{22}}{\tau_{22}}$ are in Hardy-Weinberg proportions, i. e.,

$$
\frac{n_{11}}{\tau_{11}}\frac{n_{22}}{\tau_{22}} = \frac{1}{4}\left(\frac{n_{12}}{\tau_{12}}\right)^2.
$$

We remark that because $2(n_{11} + n_{12} + n_{22}) = N$, equations (4) are dependent and to calculate the equilibrium we need to know the number of e_1 (or e_2) strategists in the population. Let $n_1 = n_{12} + 2n_{11}$ and $n_2 = n_{12} + 2n_{22}$ be numbers of e_1 and e_2, respectively, strategists in the population ($n_1 + n_2 = N$). Assuming that $\tau_{12}^2 \neq \tau_{11}\tau_{22}$, equation (4) has two solutions for n_{ij} in terms of n_1 for $0 \leq n_1 \leq N$. However, one solution is never feasible in the sense that some coordinates are negative. The solution that has all coordinates positive is

$$
n_{11} = \frac{n_1\left(\tau_{12}^2 - \tau_{11}\tau_{22}\right) - \tau_{12}^2\frac{N}{2} + \tau_{12}\sqrt{n_1(n_1-N)\left(\tau_{12}^2 - \tau_{11}\tau_{22}\right) + \left(\frac{N}{2}\right)^2\tau_{12}^2}}{2\left(\tau_{12}^2 - \tau_{11}\tau_{22}\right)},
$$

$$
n_{12} = \frac{\tau_{12}^2\frac{N}{2} - \tau_{12}\sqrt{n_1(n_1-N)\left(\tau_{12}^2 - \tau_{11}\tau_{22}\right) + \left(\frac{N}{2}\right)^2\tau_{12}^2}}{\tau_{12}^2 - \tau_{11}\tau_{22}}, \tag{5}
$$

$$
n_{22} = \frac{N}{2} - n_{11} - n_{12}.
$$

When $\tau_{12}^2 = \tau_{11}\tau_{22}$, equation (4) has the unique solution

$$
n_{11} = \frac{n_1^2}{2N}, \quad n_{12} = \frac{n_1 n_2}{N}, \quad n_{22} = \frac{n_2^2}{2N}
$$

satisfying the classic Hardy-Weinberg law

$$
p_{11} = p_1^2, \quad p_{12} = 2p_1 p_2, \quad p_{22} = p_2^2
$$

where $p_i = n_i/N$ are proportions of the two alleles/strategies and $p_{ij} = 2n_{ij}/N$ are genotype/phenotype proportions. In particular, if all interaction times are the same (i. e., $\tau_{ij} = \tau$ for all $i, j = 1, 2$ which corresponds to the implicit assumptions underlying the classic matrix model), the equilibrium is given by random pair formation of all individuals.
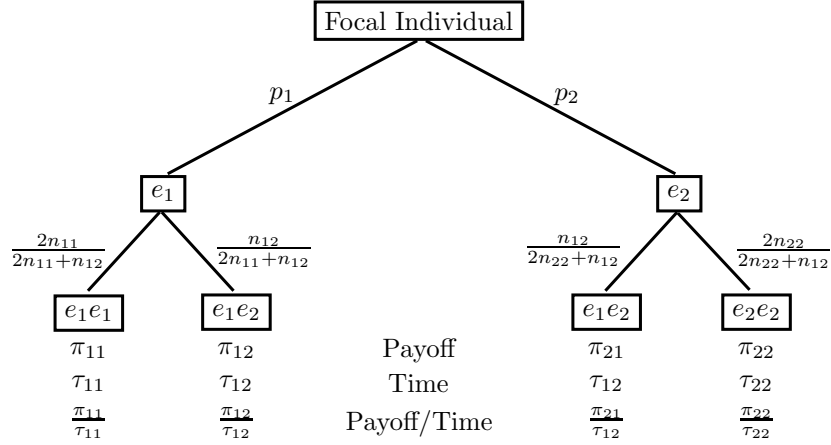
Figure 1: The decision tree for a two strategy game with interaction times. The focal individual plays strategy e_i with probability p_i ($p_1 + p_2 = 1$). The second level shows the probability that the focal individual pairs with an individual playing strategy e_j. The last three lines define payoff obtained from the interaction after the pair disbands, duration of the pairing, and the payoff per time.

3. Payoffs, fitness and evolutionary outcome

In what follows, we consider two methods to define individual fitness in terms of expected payoff. Both methods assume that payoffs are given out only when a pair disbands. The first approach assumes that fitnesses are calculated as the expected payoff per unit of interaction time while the second approach assumes that fitnesses are calculated as the expected payoff per expected interaction time.

3.1. Fitness is calculated as expected payoff per unit of time

This fitness is calculated as the expected payoff per unit of interaction time an individual of a given phenotype obtains. For example, let us consider an individual playing strategy e_1 (Figure 1 with $p_1 = 1$). The probability that this individual is paired with another individual playing the same strategy is $2n_{11}/(2n_{11}+n_{12})$ and with an individual playing strategy e_2 is $n_{12}/(2n_{11}+n_{12})$. When paired with an individual playing strategy e_1, the focal individual receives payoff π_{11}/τ_{11} per unit of time. Similarly, when paired with an individual playing strategy e_2, the focal individual gets payoff π_{12}/τ_{12} per unit of time. Then fitness Π_i of an individual playing strategy e_i ($i = 1, 2$) is calculated as the average payoff per unit of time which leads to

$$
\begin{aligned}
\Pi_1 &= \frac{2n_{11}}{2n_{11} + n_{12}} \frac{\pi_{11}}{\tau_{11}} + \frac{n_{12}}{2n_{11} + n_{12}} \frac{\pi_{12}}{\tau_{12}}, \\
\Pi_2 &= \frac{2n_{22}}{2n_{22} + n_{12}} \frac{\pi_{22}}{\tau_{22}} + \frac{n_{12}}{2n_{22} + n_{12}} \frac{\pi_{21}}{\tau_{12}}.
\end{aligned}
\tag{6}
$$

6

The corresponding time-constrained matrix game is then the two-strategy game with payoffs given by these two fitness functions evaluated at the equilibrium (5). Notice that, unlike the classic matrix games, these fitnesses depend nonlinearly on the proportions of the two pure strategies through the number of pairs.

First, we look for pure strategy solutions to this time-constrained game. For example, suppose all individuals play strategy e_2. Then $n_{11} = n_{12} = 0$ and $\Pi_2 = \frac{\pi_{22}}{\tau_{22}}$. We ask when strategy e_1 can invade? Strategy e_1 can invade provided its invasion fitness is higher than is the fitness of strategy e_2 when alone. As the number of n_{11} pairs tends to 0 much faster (convergence is of order n_1^2) than n_{12} (of order n_1) when n_1 tends to 0, we obtain invasion fitness $\Pi_1 = \frac{\pi_{12}}{\tau_{12}}$.[2] The monomorphic population at e_2 will be stable if $\frac{\pi_{22}}{\tau_{22}} > \frac{\pi_{12}}{\tau_{12}}$. In game-theoretic terms, e_2 is a strict NE as we will see in Section 4. Conversely, if $\frac{\pi_{22}}{\tau_{22}} < \frac{\pi_{12}}{\tau_{12}}$, then e_2 is not a solution since it is not a NE.

Second, we seek a mixed equilibrium consisting of phenotypes e_1 and e_2 in a polymorphic population. (The monomorphic case is discussed in Section 4.) In the polymorphic case, where n_i individuals play strategy e_i ($i = 1, 2$, $n_1 + n_2 = N$), the equilibrium must satisfy $\Pi_1 = \Pi_2$ so that neither phenotype can increase its payoff by switching its strategy. Such an equilibrium corresponds to a mixed strategy NE. Together with (4) the population-distributional equilibria corresponding to a mixed NE are

$$
\begin{aligned}
p_{1\pm} = \frac{n_{1\pm}}{N} = \frac{1}{2B} \Big(& \pm (\pi_{11}\tau_{22} - \pi_{22}\tau_{11})\sqrt{A} + \pi_{22}^2\tau_{11}^2 + \\
& \tau_{22} \left(2\pi_{12}^2\tau_{11} + 2\pi_{12}\pi_{21}\tau_{11} - 3\pi_{11}\pi_{12}\tau_{12} - \pi_{11}\pi_{21}\tau_{12} + \pi_{11}^2\tau_{22}\right) \\
& -\pi_{22}\left(\tau_{12}\left(3\pi_{12}\tau_{11} + \pi_{21}\ \tau_{11} - 4\pi_{11}\tau_{12}\right) + 2\pi_{11}\tau_{11}\tau_{22}\right) \Big)
\end{aligned} \quad (7)
$$

where

$$
\begin{aligned}
A = & (\pi_{22}\tau_{11} - \pi_{11}\tau_{22})^2 + (\pi_{12} - \pi_{21})^2\ \tau_{12}^2 \\
& +4(\pi_{11}\pi_{22}\tau_{12}^2 + \pi_{12}\pi_{21}\tau_{11}\tau_{22}) - 2(\pi_{12} + \pi_{21})\tau_{12}(\pi_{22}\tau_{11} + \pi_{11}\ \tau_{22})
\end{aligned}
$$

and

$$
B = A - (\pi_{12} - \pi_{21})^2(\tau_{12}^2 - \tau_{11}\tau_{22}).
$$

We can analyze stability of the two equilibria $p_{1\pm}$. There are four possible cases classified according to the (in)stability of the pure strategies.

Case 1. Strategy e_1 is stable and e_2 is unstable ($\frac{\pi_{12}}{\tau_{12}} > \frac{\pi_{22}}{\tau_{22}}$, $\frac{\pi_{11}}{\tau_{11}} > \frac{\pi_{21}}{\tau_{12}}$). Then either there is no mixed equilibrium, i. e., both p_{1_+} and p_{1_-} are outside the interval $[0, 1]$ (Figure 2A), or both p_{1_+} and p_{1_-} are in the interval $[0, 1]$ and then the smaller one is stable (Figure 2B).

Case 2. Strategies e_1 and e_2 are unstable ($\frac{\pi_{12}}{\tau_{12}} > \frac{\pi_{22}}{\tau_{22}}$, $\frac{\pi_{11}}{\tau_{11}} < \frac{\pi_{21}}{\tau_{12}}$). In this case, exactly one of p_{1_+} and p_{1_-} is in the interval $[0, 1]$ and it is stable (Figure 2C).

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[2]That is, if there are no e_1 individuals ($n_1 = 0$ and $2n_{11} + n_{12} = 0$), then $n_{12}/(2n_{11} + n_{12})$ and $2n_{11}/(2n_{11} + n_{12})$ are taken as 1 and 0 respectively in Figure 1 and in (6).

Case 3. Strategies e_1 and e_2 are stable ($\frac{\pi_{12}}{\tau_{12}} < \frac{\pi_{22}}{\tau_{22}}$, $\frac{\pi_{11}}{\tau_{11}} > \frac{\pi_{21}}{\tau_{12}}$). In this case, one of p_{1_+} and p_{1_-} is in the interval $[0,1]$ and it is unstable (Figure 2D). There are two stable pure strategy equilibria.

Case 4. Strategy e_1 is unstable and e_2 is stable ($\frac{\pi_{12}}{\tau_{12}} < \frac{\pi_{22}}{\tau_{22}}$, $\frac{\pi_{11}}{\tau_{11}} < \frac{\pi_{21}}{\tau_{12}}$). Then either there is no mixed equilibrium (in the interval $[0,1]$; Figure 2E), or both p_{1_+} and p_{1_-} are in the interval $[0,1]$ and then the larger one is stable (Figure 2F).

We illustrate these general concepts for two important special examples now.

3.2. Hawk–Dove game

Here we apply the above result to the Hawk-Dove game ($e_1 = H$, $e_2 = D$) with the payoff matrix

$$
\begin{array}{cc}
 & \begin{array}{cc} H & D \end{array} \\
\begin{array}{c} H \\ D \end{array} & \begin{pmatrix} V - C & 2V \\ 0 & V \end{pmatrix}
\end{array}
\tag{8}
$$

where the value of the resource is $2V$, the individual cost of fighting is C, and the interaction time matrix is

$$
\begin{array}{cc}
 & \begin{array}{cc} H & D \end{array} \\
\begin{array}{c} H \\ D \end{array} & \begin{pmatrix} \tau_{11} & \tau \\ \tau & \tau \end{pmatrix}.
\end{array}
\tag{9}
$$

This model assumes that all interactions except those between two Hawks take the same time τ. The interaction τ_{11} between two Hawks can be either longer, or shorter that τ. A larger τ_{11} models Hawks that display (for the common time τ) before they fight. A smaller τ_{11} means that Hawks do not display before fighting. Both these situations have been observed and reported in the literature (e. g., Clutton-Brock and Albon, 1979).

We will consider two cases that depend on the parameters C and V.

Case A ($V > C$). Here, the cost of fight is low compared to the value of the resource. In this case, the classical Hawk-Dove model with all interactions times equal predicts that all individuals in the population will be Hawks. Since Doves cannot invade the Hawk only equilibrium because their invasion fitness ($\frac{\pi_{21}}{\tau_{12}} = 0$) is lower than is the fitness of Hawks when alone ($\frac{\pi_{11}}{\tau_{11}} = \frac{V-C}{\tau_{11}} > 0$), the Hawk equilibrium continues to be an equilibrium of our model. Contrary to the classic case we show now there is a mixed equilibrium when τ_{11} is high enough. As $\frac{\pi_{12}}{\tau_{12}} = \frac{2V}{\tau} > \frac{V}{\tau} = \frac{\pi_{22}}{\tau_{22}}$ we are in Case 1 and from (7) we get that for

$$
\tau_{11} > \tau \left(3 - \frac{C}{V} + 2\sqrt{1 - \frac{C}{V}} \right)
$$

there are two equilibria

$$
p_{1_\pm} = \frac{C\tau + V(\tau + \tau_{11}) \pm \sqrt{(C\tau + V(\tau_{11} - \tau))^2 - 4V^2(\tau_{11} - \tau)\tau}}{2(C\tau + V(\tau_{11} - \tau))}
\tag{10}
$$

that are between 0 and 1. These equilibria are shown in Figure 3A. The arrows show directions in which fitness increases. Thus, we observe bi-stability where the all Hawk equilibrium is always locally stable, and provided the interaction time τ_{11} is long enough, the interior equilibrium p_{1_-} is also locally stable. We observe that the region of local stability for the all Hawk equilibrium decreases as the interaction time between two Hawks increases.

Case B ($C > V$). Now assume that the cost of fighting is high compared to the value of the resource. Since $\frac{\pi_{11}}{\tau_{11}} = \frac{V-C}{\tau} < 0$ and $\frac{\pi_{21}}{\tau_{12}} = 0$, Doves can invade the Hawk only equilibrium and so $e_1 = H$ is not a NE. In fact, this shows that we are in Case 2 (Figure 2C), that there is only one NE and that it is a mixed stable equilibrium. From (7) we get that the equilibrium between 0 and 1 is p_{1_-} from (10). Dependence of this equilibrium on interaction time between two Hawks is shown in Figure 3B.

Figure 3B also shows that the equilibrium frequency of Hawks is at its maximum value of V/C when we are in the classic case where all interaction times are the same (i. e. $p_1(\tau_{11})$ as a function of τ_{11} has a maximum at $\tau_{11} = \tau$). In fact, this equilibrium frequency first increases from

$$p_{1_-}(0) = \frac{C + V - \sqrt{C^2 - 2CV + 5V^2}}{2(C - V)}$$

when $\tau_{11} = 0$ to $p_{1_-}(\tau) = V/C$ when $\tau_{11} = \tau$. When τ_{11} is short, Hawk-Hawk pairs will disband fast and these Hawks will quickly pair with another Hawk, which decreases their fitness, or another Dove, which increases their fitness. As can be shown, the balance between these two effects leads to most Hawks involved in Hawk-Dove contests when τ_{11} is short as the frequency of Hawk-Hawk contests, p_{11}, is close to 0. When $\tau_{11} = \tau$, the frequency of Hawks p_1 in the population is V/C, i. e., we recover the standard result of the Hawk-Dove model. As the interaction time increases further on, the proportion of Hawks in the population decreases because Hawks are losing too much time in their fights. For large τ_{11}, p_{1_-} tends to 0 as seen in Figure 3B.

3.2.1. Repeated games (Prisoner's dilemma)

Interaction times also play an important role in repeated two-player games where it is typically assumed that there is a fixed probability ρ that there will be the next round of the game. This probability ρ is not under the players' control. That is, the expected number of rounds is $1/(1-\rho)$. Assume that each player uses the same single-round pure strategy e_i for the entire interaction with its current partner, that the expected number of rounds of the interaction between e_i and e_j is τ_{ij}, and that payoffs from each round are cummulative (i. e., the expected payoff per interaction for strategy e_i against e_j is $\tau_{ij}\pi_{ij}$ where π_{ij} is the payoff in the single-shot game). With random pair formation among free individuals between rounds, the corresponding discrete-time process for the numbers n_{ij} of pairs $e_i e_j$ at round t has the same equilibrium (4) as the continuous-time process (3) of Section 2. The solution to the time-constrained game is then

given by applying the general theory developed above to the adjusted payoff per interaction matrix with interaction time matrix (2).

Consider the repeated Prisoner's dilemma game (PD) where payoffs of co-operators (C) and defectors (D) for a single round are given by the simplified version of the PD game (Pacheco et al., 2006); namely,

$$
\begin{array}{cc}
& \begin{array}{cc} C & D \end{array} \\
\begin{array}{c} C \\ D \end{array} &
\left(\begin{array}{cc} b-c & -c \\ b & 0 \end{array} \right)
\end{array}
\tag{11}
$$

where b is the benefit the cooperator provides a defector at a cost c to himself. Since it is assumed that $b > c > 0$, any player prefers to play against C rather than against D. Thus, if each player can decide whether to continue his inter-action to the next round, he should play only one round against D and as many as possible (i. e. continue until the interaction ends after an expected number of rounds $1/(1-\rho)$) against C. That is, $\tau_{12} = \tau_{22} = 1$ and $\tau_{11} = 1/(1-\rho) > 1$. This models what is known as the opting out game (Zhang et al., 2016).

In fact, we will consider a more general model with symmetric interaction time matrix (2) (with $e_1 = C$ and $e_2 = D$) and corresponding payoff per inter-action matrix

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

The payoffs per unit of time Π_i to strategy e_i are now given by

$$
\begin{aligned}
\Pi_1 &= \frac{2n_{11}}{2n_{11} + n_{12}}(b-c) - \frac{n_{12}}{2n_{11} + n_{12}}c, \\
\Pi_2 &= \frac{n_{12}}{2n_{22} + n_{12}}b
\end{aligned}
\tag{13}
$$

where n_{ij} as functions of the number of cooperators n_1 are from (5).

The monomorphic population e_2 with all individuals being defectors is al-ways stable as cooperators cannot invade ($\frac{\pi_{22}}{\tau_{22}} = 0 > -c = \frac{\pi_{12}}{\tau_{12}}$). On the other hand, a population of all cooperators is unstable since $\frac{\pi_{11}}{\tau_{11}} = b - c < b = \frac{\pi_{21}}{\tau_{12}}$. These stability results match the classic one-shot PD game. However, as we are in Case 4 of Section 3, there is the possibility of two interior equilibria

$$
p_{1\pm} = \frac{1}{2}\left(1 \pm \sqrt{1 + \frac{4\,b\,c\,\tau_{12}^2}{(b-c)^2(\tau_{12}^2 - \tau_{11}\tau_{22})}}\right)
$$

where cooperators survive with defectors. Both p_{1-} and p_{1+} exist and are between 0 and 1 for

$$
\tau_{11} > \frac{(b+c)^2\tau_{12}^2}{(b-c)^2\tau_{22}}.
\tag{14}
$$

Furthermore, in this case, equilibrium p_{1+} is stable (Figure 2F).

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Thus, if the time (i. e., the number of rounds) two cooperators continue to interact is large enough, stable coexistence of cooperators and defectors is possible (Figure 4A). In particular, if interaction times between two defectors and a defector–cooperator pair last for the same time τ, the cooperation evolves provided

$$\frac{\tau_{11}}{\tau} > \frac{(b+c)^2}{(b-c)^2}.$$

This result, which cannot occur in the classic repeated PD game, was also found by Zhang et al. (2016) and related there to the results of game experiments when players were allowed to opt out.

On the other hand, if defectors stay together a shorter time than is the common time the other interactions last (i. e., $\tau_{11} = \tau_{12} = \tau_{21} > \tau_{22}$) inequality (14) does not hold and there is no interior equilibrium. In this case, defection is the only ESS of the game.

3.3. Fitness is calculated as expected payoff per expected time

This fitness is calculated as the average payoff an individual of a given phenotype obtains per expected time of the interaction. For example, let us consider an individual playing strategy e_1. From the decision tree in Figure 1, the average payoff this individual gets is $\frac{2n_{11}}{2n_{11}+n_{12}}\pi_{11} + \frac{n_{12}}{2n_{11}+n_{12}}\pi_{12}$. The average time of an interaction is $\frac{2n_{11}}{2n_{11}+n_{12}}\tau_{11} + \frac{n_{12}}{2n_{11}+n_{12}}\tau_{12}$. To obtain an individual fitness we divide the average payoff by the average time, which yields

$$\Pi_1 = \frac{2n_{11}\pi_{11} + n_{12}\pi_{12}}{2n_{11}\tau_{11} + n_{12}\tau_{12}} \quad \text{and} \quad \Pi_2 = \frac{2n_{22}\pi_{22} + n_{12}\pi_{21}}{2n_{22}\tau_{22} + n_{12}\tau_{12}}. \qquad (15)$$

Once again, strategy e_i will be a strict NE provided $\pi_{ii}/\tau_{ii} > \pi_{ji}/\tau_{ji}$ ($i,j = 1, 2$, $i \neq j$). That is, (in)stability of the pure strategies are given by the four cases of Section 3.1. The interior population-distributional equilibrium can be analytically calculated using e. g., `Solution` function of Mathematica 11 which provides up to two solutions p_1 in $[0, 1]$. Qualitatively, their stability is again given by Figure 2 with the same four cases as in Section 3.1. These expressions are too complex for analysis but they simplify for the Hawk-Dove and the Prisoner's dilemma games.

3.3.1. Hawk–Dove game

The analogue of the interior equilibria (10) for the Hawk-Dove game when fitness is given by (15) are

$$p_{1\pm} = \frac{\pm\sqrt{F}(C\tau + V\tau_{11}) + \left(2CV\tau^3 + C(C-V)\tau^2\tau_{11} + (2C-V)V\tau\tau_{11}^2 + V^2\tau_{11}^3\right)}{2\tau_{11}\left(C^2\tau^2 + 2CV\tau(\tau_{11}-\tau) + V^2\tau_{11}(\tau_{11}-\tau)\right)},$$
$$(16)$$

where

$$F = 4V^2\tau^4 + (C-3V)(C+V)\tau^2\tau_{11}^2 + 2(C-V)V\tau\tau_{11}^3 + V^2\tau_{11}^4.$$

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Qualitatively, this follows the two cases where fitness function is given as the payoff per interaction time of Section 3.2. For $C < V$ (Case A), Doves cannot invade the all Hawk population, so that all Hawk is a stable NE. Moreover, provided interaction time between two Hawks is long enough, there are again two interior equilibria with the smaller one being stable (Figure 3C).

For $C > V$ (Case B), solution p_{1_+} is outside the interval $[0, 1]$ and the only stable solution is p_{1_-}. Figure 3D shows the dependence of p_{1_-} on the fighting time τ_{11}. We observe that as τ_{11} tends to 0, p_{1_-} tends to $(V + C)/(2C)$ which is a higher equilibrium frequency of Hawks than the standard model (i. e. when all interaction times are equal). The equilibrium frequency of Hawks is now a decreasing function for all $\tau_{11} > 0$. In particular, in contrast to Case B of Section 3.1.1, it can be shown that the frequency of Hawk-Hawk pairs no longer approaches 0 as τ_{11} decreases. Also, as the interaction time between two Hawks increases beyond $\tau_{11} = \tau$, the proportion of Hawks in the population decreases much faster when compared to Case B of Section 3.1.1 (Figure 3, panel D compared to panel B).

3.3.2. Repeated Prisoner's dilemma

For payoffs (12), the formula for $p_{1_\pm}$ when interaction times are arbitrary is more complex under fitnesses (15) than under (13) and so is omitted here. However, it can be shown that $p_{1_\pm}$ are both between 0 and 1 if and only if

$$\tau_{11} > \frac{(b + c)\tau_{12}^2}{(b - c)\tau_{22}}.$$

When applied to the special case corresponding to the opting out game (i.e., $\tau_{12} = \tau_{22} = \tau$, the two interior equilibria exist when

$$\frac{\tau_{11}}{\tau} > \frac{b + c}{b - c}$$

and are given by

$$p_{1\pm} = A \pm \frac{(c\tau_{11} - b(\tau + \tau_{11}))\sqrt{\tau + \tau_{11}}\sqrt{(b - c)^2\tau_{11}^2 - (b + c)^2\tau^2}}{2\sqrt{\tau_{11} - \tau}\left(-2bc\tau_{11}(\tau + \tau_{11}) + b^2(\tau + \tau_{11})^2 + c^2(-\tau^2 + \tau\tau_{11} + \tau_{11}^2)\right)}$$

where

$$A = \frac{\left(c(\tau - \tau_{11}) + b(\tau + \tau_{11})\right)\left(b(\tau + \tau_{11}) - c(2\tau + \tau_{11})\right)}{2\left(b^2(\tau + \tau_{11})^2 - 2bc\tau_{11}(\tau + \tau_{11}) + c^2(\tau\tau_{11} + \tau_{11}^2 - \tau^2)\right)}.$$

As we are in Case 4 of Section 3 and it can be proved that $0 < p_{1_+} < p_{1_-} < 1$, p_{1_+} and p_{1_-} are unstable and stable respectively (Figure 2F).

Qualitatively, the effect of interaction time in the opting out game is similar whether fitness is calculated as expected payoff per unit time (Figure 4A) or as expected payoff per expected time (Figure 4B), in that sufficiently long interactions τ_{11} between two cooperators lead to the stable coexistence of cooperation

and defection. On the other hand, for the latter fitness calculation, the onset of stable coexistence occurs for smaller values of τ_{11} with a correspondingly larger basin of attraction that suggests it is easier for cooperative behavior to evolve in this scenario.

So far we have considered a polymorphic population consisting of two phenotypes. In the next section we consider a monomorphic population where individuals play mixed strategies.

4. Monomorphic population

Assume all individuals in the population are playing a mixed strategy (p_1^*, p_2^*). That is, on average, with probability p_1^* each individual plays e_1 and with probability p_2^* plays e_2. This means that there will be $n_i = p_i^* N$ individuals playing strategy e_i. With instantaneous random pair formation, the number of pairs n_{ij} at time t will again satisfy the dynamics (3) whose equilibrium is given by (5). Substituting these equilibrium values into the decision tree of Figure 1, we can then calculate the fitness $\Pi_{(p_1^*, p_2^*)}(p_1, p_2)$ of a focal individual using mixed strategy (p_1, p_2) when the monomorphic population plays strategy (p_1^*, p_2^*). Similar to the polymorphic case of Section 3, this leads to two different fitness functions.

4.1. Fitness is calculated as expected payoff per time

From the Payoff/Time given in the last line of Figure 1, $\Pi_{(p_1^*, p_2^*)}(p_1, p_2)$ is linear in the focal individual mixed strategy (p_1, p_2). That is,

$$\Pi_{(p_1^*, p_2^*)}(p_1, p_2) = p_1 \Pi_1 + p_2 \Pi_2 \tag{17}$$

where Π_1 and Π_2 are given by (6) evaluated at (p_1^*, p_2^*). An interior mixed strategy (p_1^*, p_2^*) is a NE (i. e. $\Pi_{(p_1^*, p_2^*)}(p_1, p_2) \leq \Pi_{(p_1^*, p_2^*)}(p_1^*, p_2^*)$ for all (p_1, p_2)) if and only if $\Pi_1 = \Pi_2$ (see Appendix A). In particular, interior NE correspond to circles (either empty or solid) with $0 < p_1 < 1$ in Figure 2 from the pure strategy model of Sections 2 and 3.

Also shown in Appendix A is that (p_1^*, p_2^*) is a local ESS (Hofbauer and Sigmund, 1998) if and only if $(\Pi_1 - \Pi_2)(p_1^* - p_1) > 0$ for all (p_1, p_2) sufficiently close but not equal to (p_1^*, p_2^*) where Π_1 and Π_2 are given by (6) evaluated at (p_1, p_2). Furthermore, a pure strategy is a local ESS if and only if it is a strict NE.[3] Thus, (p_1^*, p_2^*) is a local ESS if and only if it corresponds to a solid circle in Figure 2.

In fact, local ESSs correspond to the locally asymptotically stable equilibria for standard evolutionary game dynamics that model the evolution of monomorphic populations. For instance, this is clear for the canonical equation of the adaptive dynamics (Hofbauer and Sigmund, 1998)

$$\frac{dp_1}{dt} = \sigma \frac{d\Pi_{(p_1^*, p_2^*)}(p_1, p_2)}{dp_1}\bigg|_{p_1 = p_1^*} = \sigma(\Pi_1 - \Pi_2), \tag{18}$$

---

[3]Here we ignore the non generic case where $\Pi_1 = \Pi_2$ at the pure strategy.

where $\sigma > 0$ is a proportionality constant that describes the speed of adaptation. When $\sigma \ll 1$ ($\sigma \gg 1$), adaptation operates on a much slower (faster) time scale than pair dynamics.

The local ESSs also correspond to the locally asymptotically stable equilibria for standard evolutionary game dynamics that model the evolution of polymorphic populations such as the replicator dynamics (Taylor and Jonker, 1978)

$$\frac{dp_1}{dt} = \sigma p_1 (1 - p_1)(\Pi_1 - \Pi_2) \tag{19}$$

where each individual is a pure strategist as in Sections 2 and 3.

4.2. Fitness is calculated as expected payoff per expected time

From the Payoff and Time lines given in Figure 1, the average payoff the focal individual gets is

$$E = p_1 \left(\frac{2n_{11}\pi_{11} + n_{12}\pi_{12}}{2n_{11} + n_{12}} \right) + p_2 \left(\frac{n_{12}\pi_{21} + 2n_{22}\pi_{22}}{n_{12} + 2n_{22}} \right)$$

and the expected time is

$$T = p_1 \left(\frac{2n_{11}\tau_{11} + n_{12}\tau_{12}}{2n_{11} + n_{12}} \right) + p_2 \left(\frac{n_{12}\tau_{12} + 2n_{22}\tau_{22}}{n_{12} + 2n_{22}} \right).$$

Fitness of the focal individual playing mixed strategy (p_1, p_2) in a monomorphic population playing strategy (p_1^*, p_2^*) is then defined as the average payoff per the average time

$$\Pi_{(p_1^*, p_2^*)}(p_1, p_2) = \frac{E}{T} \tag{20}$$

where all pairs n_{ij} are calculated at (p_1^*, p_2^*). This fitness function is no longer equal to $p_1 \Pi_1 + p_2 \Pi_2$, i. e., is not linear in the focal individual strategy.

Once again, from Appendix A, strategy (p_1^*, p_2^*) is an interior NE if and only if $\Pi_1 = \Pi_2$ where Π's are given by (15) and the local ESSs correspond to the solid circles in Figure 2.

5. Discussion

We developed a new approach to the theory of two-player symmetric evolutionary games with two strategies that explicitly considers duration of interactions between players. When applied to the Hawk-Dove and Prisoner's dilemma games, this theory makes new evolutionary predictions. In particular, it shows that in the Hawk-Dove game non-aggressiveness can evolve even when the cost of fighting is low provided interactions between two Hawks take long enough time. Similarly, for the Prisoner's dilemma, when interaction time between two cooperators is long enough, cooperation can evolve. These novel predictions will change our way of thinking about evolution of aggressiveness and cooperation.

The theory developed in this article is based on symmetric two-player games (i. e., matrix games) with two pure strategies with symmetric interaction times, i. e., interaction time of a couple where the first individual plays strategy 1 and the second individual plays strategy 2 is the same as is the interaction time for a couple where first individual plays strategy 2 and the second strategy 1. In this article, we assume that pairing between individuals is random and instantaneous, so all individuals are paired. This assumption simplifies bookkeeping and leads to analytic results (most of calculations were done in Mathematica 11). Fitness is gained upon pair disbanding. For classic matrix games, fitness is defined as the average payoff an individual receives in an infinite population of players. There are two complications that must be dealt with once interaction times are explicitly considered. First, one needs to define fitness anew. In this article, we consider two fitness functions, one assuming that fitness is measured instantaneously (i. e., per unit of time), the other, motivated by the optimal foraging theory (Charnov, 1976; Stephens and Krebs, 1986; Křivan, 1996), assumes that fitness is measured as the average payoff an individual obtains from a random interaction divided by the average time spent in a random interaction. Second, as interaction times are considered explicitly, one needs to keep track of the number of all couples. In this article, we describe these dynamics by differential equations assuming that pair disbanding is described by a Poisson process. In principle, this means that pairing is asynchronous in time.

In the classical Hawk-Dove model (Maynard Smith and Price, 1973), the prominent example to model and explain evolution of aggressiveness, fights are assumed to be time consuming, but this is not captured by the model, where all interactions take the same time. However, there are many documented examples where interactions between two individuals take different times that depend on the individuals' phenotypes. In particular, Clutton-Brock and Albon (1979, see also (Maynard Smith, 1974)) provide an example of contests between male red deer. In that contest, some individuals do display while some others do not which changes the time individuals interact. Similarly, Sinervo and Lively (1996) observe three phenotypes of side-blotched lizard with different territorial behaviors. While orange-throated males are aggressive and often fight without any display, blue-throated males spend a lot of time challenging and displaying, before a possible fight. It is thus clear that these phenotypes spend different times in their interactions, which has an effect on their fitness. Indeed, in this article, we show that varying the time two Hawks interact crucially influences the evolutionary outcome for the Hawk-Dove model. In particular, Figure 3 shows that when cost of fighting is smaller than the reward of winning a fight, and the fighting time is long enough, there are two locally stable equilibria. The first equilibrium at which all individuals play Hawk strategy corresponds to the classic model with all interaction times equal. However, the other, mixed equilibrium, corresponds to the case where both Hawks and Doves coexist in the population. As the time of fight increases, the region of attractivity of this interior equilibrium increases so it is more likely to occur. This result provides a new explanation why non-aggressive behavior occurs among individuals even when the cost of fighting is small.

As mentioned in the Introduction, Maynard Smith and Price (1973) also incorporate opportunity cost into a Hawk-Dove type game. Specifically, in their computer simulations of multi-round interactions between pairs of individuals, these individuals receive a payoff from the interaction as well as an additional payoff that decreases as the number of rounds increase. Thus, in contrast to our model, the opportunity cost in their model is independent of the strategy that the individual uses in future interactions. Moreover, in our terminology, their fitness is payoff per interaction and so does not take account of the interaction time. Despite these differences with our approach, it is noteworthy that they also find that the population does not consist entirely of Hawks when the probability of serious injury in a fight is low.

In the case of the repeated Prisoner's dilemma, we show that, provided cooperators stay together for enough rounds of the game while the other possible pairs disband quickly, cooperation does evolve (Figure 4). These assumptions are quite realistic, especially if players can choose whether to continue the game to the next round with the same opponent, since it is always better to play against a cooperator than a defector in the Prisoner's dilemma game. Our model thus provides a different mechanism than others (Nowak, 2006) that lead to the evolution of cooperation. On the other hand, our mechanism is similar to models based on direct reciprocity that require the probability of next encounter between two cooperators is higher than the cost to benefit ratio. This probability condition is often satisfied through non random pair formation processes in a well-mixed population (Taylor and Nowak, 2006) or in a structured population where individuals interact with neighbors in a graph (Pacheco et al., 2006). In our model with random pair formation, provided the interaction time between two cooperators is long enough when compared to common interaction times between other pairs, cooperation evolves. We also analyzed the case where all interactions except those between defectors take the same time. These two situations are substantially different, because while the first case assumes that both individuals must be willing to pair, the second approach assumes that a pair will continue their interaction unless both want to disband. The evolutionary outcomes are substantially different as well. While in the first case we showed that high enough cooperation times lead to cooperative behavior in the population, in the second case this is not so.

Acknowledgement

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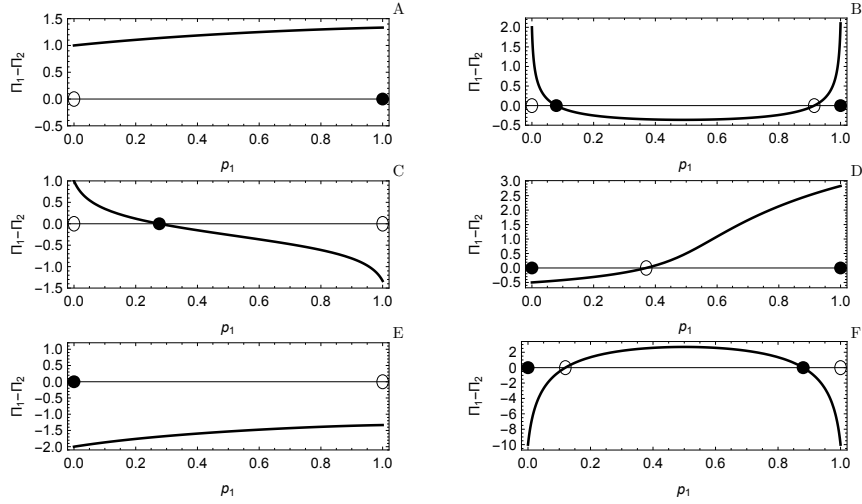
Figure 2: Stability analysis of population-distributional equilibria (7) for two-strategy matrix games with interaction times. Solid circles at the endpoints (i. e., at $p_1 = 0$ or 1) are strict NE and so ESS whereas empty circles are unstable. Interior circles are NE that are either stable and local ESS (solid) or unstable NE (empty). The four cases in Section 3 correspond to panels A and B (Case 1), panel C (Case 2), panel D (Case 3) and panels E and F (Case 4).
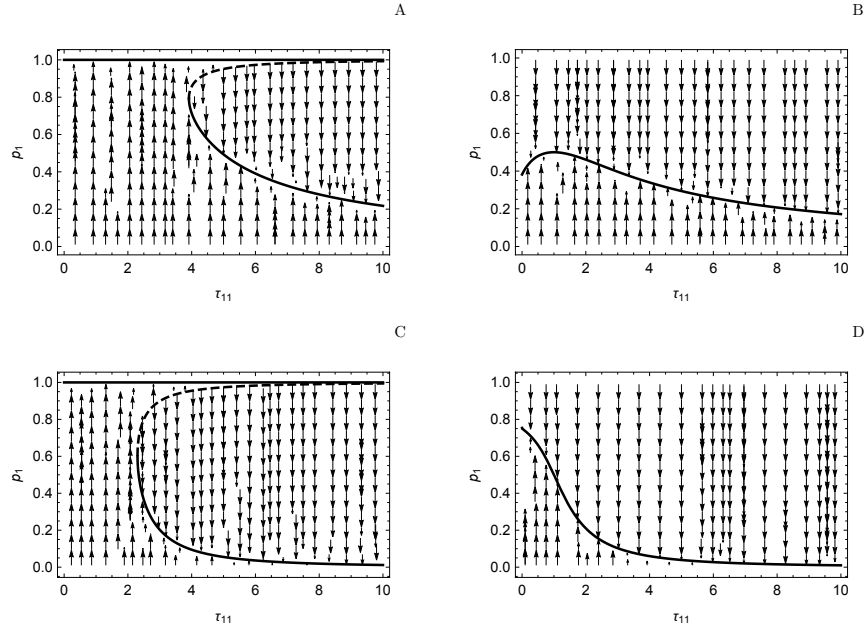
Figure 3: Equilibrium frequencies of Hawks for the Hawk-Dove game as a function of the expected Hawk-Hawk interaction time τ_{11} when fitnesses are given by (6) (Panels A,B) and by (15) (Panels C,D). The left panels assume a relatively low cost ($V > C$, $V = 2$, $C = 1$), while the right panels assume a relatively high cost ($C > V$, $V = 1$, $C = 2$). The solid (respectively, dashed) curve shows the stable (respectively, unstable) NE of this game. Other parameters: $\tau_{12} = \tau_{22} = \tau = 1$.
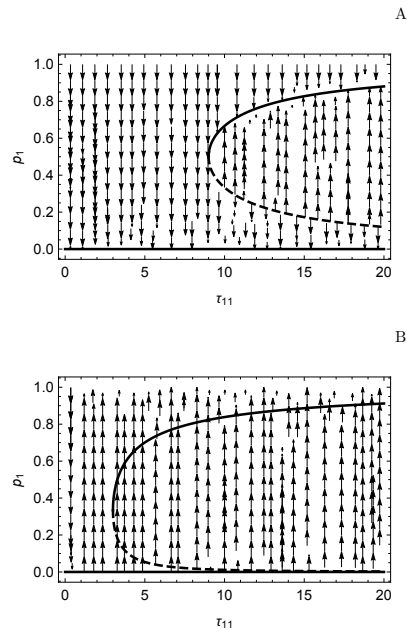
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Figure 4: Equilibrium frequencies of cooperation for the repeated Prisoner's dilemma game with opting out when fitnesses are given by (6) (Panel A) and by (15) (Panel B) as a function of the expected number of rounds τ_{11} played by a cooperative pair. The solid (respectively, dashed) curve shows the stable (respectively, unstable) NE of this game. Other parameters: $b = 2$, $c = 1$, $\tau_{12} = \tau_{22} = \tau = 1$.

Appendix A. NE of the monomorphic population

Here we prove that strategy (p_1^*, p_2^*) is a NE for fitness function (17) iff $\Pi_1 = \Pi_2$, where Π's are given by (6) and are evaluated at (p_1^*, p_2^*). An interior mixed strategy (p_1^*, p_2^*) is a NE if and only if $\Pi_{(p_1^*, p_2^*)}(p_1, p_2) \leq \Pi_{(p_1^*, p_2^*)}(p_1^*, p_2^*)$ for all (p_1, p_2) which is equivalent to $(p_1 - p_1^*)(\Pi_1 - \Pi_2) \leq 0$ for all $0 \leq p_1 \leq 1$. This leads to the result given in the main text. The NE (p_1^*, p_2^*) is a local ESS if and only if $\Pi_{(p_1, p_2)}(p_1, p_2) < \Pi_{(p_1^*, p_2^*)}(p_1, p_2)$ for all (p_1, p_2) sufficiently close but not equal to (p_1^*, p_2^*) if and only if $(p_1 - p_1^*)(\Pi_1 - \Pi_2) < 0$ for all $0 \leq p_1 \leq 1$ that are close to p_1^* where Π_i are evaluated at (p_1, p_2). It follows that an interior NE (p_1^*, p_2^*) is a local ESS iff $\Pi_1 > \Pi_2$ when $p_1 < p_1^*$ is close to p_1^*. We see this is true at those NE with $0 < p_1 < 1$ that correspond to solid circles in Figure 2.

Here we prove that strategy (p_1^*, p_2^*) is a NE for fitness function (20) iff $\Pi_1 = \Pi_2$, where Π's are evaluated at (p_1^*, p_2^*). To prove this we rewrite (20) as

$$\Pi_{(p_1^*, p_2^*)}(p_1, p_2) = \frac{p_1 A^* + p_2 B^*}{p_1 C^* + p_2 D^*} \tag{A.1}$$

where A^* to D^* are evaluated at (p_1^*, p_2^*). Then

$$\Pi_{(p_1^*, p_2^*)}(p_1, p_2) = \frac{p_1 A^* + p_2 B^*}{p_1 C^* + p_2 D^*} \leq \frac{p_1^* A^* + p_2^* B^*}{p_1^* C^* + p_2^* D^*} = \Pi_{(p_1^*, p_2^*)}(p_1^*, p_2^*)$$

iff

$$(p_1 - p_1^*)\left(\frac{A^*}{C^*} - \frac{B^*}{D^*}\right) \leq 0 \tag{A.2}$$

for every (p_1, p_2). This means that $\frac{A^*}{C^*} = \frac{B^*}{D^*}$ and $\Pi_1 = \Pi_2$.

Now we prove that (p_1^*, p_2^*) is a local ESS. We need to show that

$$\Pi_{(p_1, p_2)}(p_1, p_2) = \frac{p_1 A + p_2 B}{p_1 C + p_2 D} < \frac{p_1^* A + p_2^* B}{p_1^* C + p_2^* D} = \Pi_{(p_1, p_2)}(p_1^*, p_2^*)$$

where A to D are now evaluated at (p_1, p_2). This inequality is equivalent to strict inequality in (A.2) with A^* to D^* replaced by A to D. It follows that a NE (p_1^*, p_2^*) is a local ESS iff $\Pi_1 > \Pi_2$ evaluated at (p_1, p_2) for all $p_1 < p_1^*$ close to p_1^*. We see this is true at those NE with $0 < p_1 < 1$ that correspond to solid circles in Figure 2.