Interaction times change evolutionary outcomes: Two-player matrix games

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\begin{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.

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.

\end{abstract}

Keywords:
Evolutionary game theory
Hawk-Dove game
Population dynamics
Prisoner’s dilemma
nτ nτ nτ

N

nnn

N

nτ nτ

individuals playing strategy n

nn

n.

)n

(2)

individuals playing strategy j

However, one solution is never

+/ +/ +/ +1 11 11 12 1
2
2
2
ττ ττ ττ

and 2. Two-strategy game with symmetric interaction times

interaction with strategy

π

interaction time matrix is symmetric, i.e., 

2. Two-strategy game with symmetric interaction times

Contrary to standard game models, we assume that all interactions

consider the repeated Prisoner’s dilemma where the

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 di-
e
erent

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 e1 and

e2 and payoffs described by a payoff matrix

\[
\begin{pmatrix}
e_1 & e_2 \\
e_1' & e_2' \\
e_1' & e_2' \\
e_1' & e_2' \\
e_1' & e_2'
\end{pmatrix}
\]

That is, πij is the expected payoff obtained by ei in a pair-wise
interaction with ej.

Contrary to standard game models, we assume that all interactions

take some time. These times are given by the interaction time matrix

\[
\begin{pmatrix}
e_1 & e_2 \\
e_1' & e_2' \\
e_1' & e_2' \\
e_1' & e_2'
\end{pmatrix}
\]

In what follows, we assume that interaction times are positive and the
interaction time matrix is symmetric, i.e., τ12 = τ21. The payoff matrix
(1) then provides the payoffs per interaction with each interaction
taking time specified in (2).

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 n11, n12, and n22 where the subindices
denote strategies of the two paired individuals. In particular, n12 is the
number of pairs where one (irrespective if it is the first or the second
individual) plays strategy e1 and the other individual plays
strategy e2. The overall (fixed) number of individuals is then

N = 2(n11 + n12 + n22).

A pair n2 splits up following a Poisson process with parameter τij,
i.e., in a unit of time, the number of pairs that disband is nτij. So, per
unit of time there will be 2n11/τ11 + n12/τ12 individuals playing strategy e1
and 2n12/τ12 + n22/τ22 individuals playing strategy e2 that will immedi-
ately form new pairs. The total number of individuals forming new
pairs is 2(n11/τ11 + n12/τ12 + n22/τ22). Since we assume that singles
instantaneously and randomly pair, the proportion of newly formed
n11 pairs among all newly formed pairs is

\[
\frac{2n11/τ11 + n12/τ12}{2(n11/τ11 + n12/τ12 + n22/τ22)}
\]

To obtain the number of newly formed n11 pairs we multiply this
proportion by the number of all newly formed pairs

n11 = n11/τ11 + n12/τ12 + n22/τ22. Similar considerations for n12 and n22 pairs
lead to the following pair dynamics

\[
\begin{align*}
\frac{dn_{11}}{dt} &= -\frac{n_{11}}{\tau_{11}} + \frac{2n_{11}}{\tau_{11}} \left(\frac{n_{11} + n_{12}}{\tau_{11} + \tau_{12}} + \frac{n_{22}}{\tau_{22}}\right) \\
\frac{dn_{12}}{dt} &= -\frac{n_{12}}{\tau_{12}} + \frac{2n_{12}}{\tau_{12}} \left(\frac{n_{11} + n_{12}}{\tau_{11} + \tau_{12}} + \frac{n_{22}}{\tau_{22}}\right) \\
\frac{dn_{22}}{dt} &= -\frac{n_{22}}{\tau_{22}} + \frac{n_{22}}{\tau_{12}} \left(\frac{n_{11} + n_{2}}{\tau_{11} + \tau_{12}} + \frac{n_{22}}{\tau_{22}}\right) \\
\end{align*}
\]

We observe that at the equilibrium

\[
\begin{align*}
n_{11} &= \frac{2n_{11} + n_{12}}{\tau_{11}} \\
n_{12} &= \frac{2n_{12}}{\tau_{12}} \left(\frac{n_{11} + n_{12}}{\tau_{11} + \tau_{12}} + \frac{n_{22}}{\tau_{22}}\right) \\
n_{22} &= \frac{n_{22}}{\tau_{22}} \left(\frac{n_{11} + n_{12}}{\tau_{11} + \tau_{12}} + \frac{n_{22}}{\tau_{22}}\right)
\end{align*}
\]

are in Hardy-Weinberg proportions, i.e.,

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

We remark that because 2(n11 + n12 + n22) = N, Eq. (4) are dependent
and to calculate the equilibrium we need to know the number of e1 (or
e2) strategists in the population. Let n1 = n11 + n12 and n2 = n12 + n22
be numbers of e1 and e2, respectively, strategists in the population
(n1 + n2 = N). Assuming that τ12 ≠ τ12, Eq. (4) has two solutions for
n11 in terms of n1 for 0 ≤ n1 ≤ N. However, one solution is never
feasible in the sense that some coordinates are negative. The solution
that has all coordinates positive is
When paired with an individual playing strategy $e_1$ (Fig. 1 with $p_1 = 1$). The probability that this individual is paired with another individual playing the same strategy is $2n_1/(2n_1 + n_2)$ and with an individual playing strategy $e_2$ is $n_2/(2n_1 + n_2)$ when paired with an individual playing strategy $e_1$, the focal individual receives payoff $x_{i} e_{i} n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 n_2 n_1 

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

3.1.1. Hawk–Dove game

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

\[
\begin{pmatrix}
H & D \\
V - C & 2V
\end{pmatrix}
\]

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

\[
\begin{pmatrix}
H & D \\
\tau_{11} & \tau_{12} \\
\tau_{21} & \tau_{22}
\end{pmatrix}
\]

This model assumes that all interactions except those between two Hawks take the same time \(\tau\). The interaction \(\tau_{11}\) between two Hawks can be either longer, or shorter that \(\tau\). A larger \(\tau_{11}\) models Hawks that display (for the common time \(\tau\)) before they fight. A smaller \(\tau_{11}\) 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 fighting is low compared to the value of the resource. In this case, the classical Hawk-Dove model with all interaction times equal predicts that all individuals in the population will be Hawks. Since Doves cannot invade the Hawk only equilibrium because their invasion fitness \(\frac{2V}{V-C} = 0\) is lower than the fitness of Hawks when alone \(\frac{2V}{V-C} > 0\), 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 \(\tau_{11}\) is high enough. As \(\frac{2V}{V-C} > \frac{V}{\tau} = \frac{2V}{\tau_{12}}\) we are in Case 1 and from (7) we get that for

\[
\tau_{11} > \sqrt{\frac{V}{\tau} + 2\sqrt{1 - \frac{V}{V-C}}}
\]

there are two equilibria

\[
p_h = \frac{Cr + V(r + \tau_{11}) \pm \sqrt{(Cr + V(\tau_{11} - r))^2 - 4V^2(\tau_{11} - r)^2}}{2(Cr + V(\tau_{11} - r))}
\]

that are between 0 and 1. These equilibria are shown in Fig. 3A. The arrows show directions in which fitness increases. Thus, we observe bistability where the all Hawk equilibrium is always locally stable, and provided the interaction time \(\tau_{11}\) is long enough, the interior equilibrium \(p_h\) 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 \(\frac{2V}{V-C} = \frac{V}{\tau} < 0\) and \(\frac{2V}{\tau} = 0\), 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 (Fig. 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 \(p_h\) from (10). Dependence of this equilibrium on interaction time between two Hawks is shown in Fig. 3B.

Fig. 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. \(p_h(\tau_{11})\) as a function of \(\tau_{11}\) has a maximum at \(\tau_{11} = \tau\)). In fact, this equilibrium frequency first increases from

\[
p_h(0) = \frac{C + V - \sqrt{C^2 - 2CV + 5V^2}}{2(C - V)}
\]

when \(\tau_{11} = 0\) to \(p_h(\tau) = V/C\) when \(\tau_{11} = \tau\). When \(\tau_{11}\) 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 \(\tau_{11}\) is short as the frequency of Hawk-Hawk contests, \(p_{11}\), is close to 0.
When \( r_1 = r \), 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 \( r_1 \), \( p_{1-} \) tends to 0 as seen in Fig. 3B.

### 3.1.2. 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 \( \rho \) that will be the next round of the game. This probability \( \rho \) 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 \( \tau_{ij} \), and that payoffs from each round are cumulative (i.e., the expected payoff per interaction for strategy \( e_i \) against \( e_j \) is \( \tau_{ij} \pi_{ij} \), where \( \pi_{ij} \) 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 cooperators (C) and defectors (D) for a single round are given by the simplified version of the PD game (Pacheco et al., 2006); namely,

\[
\begin{pmatrix}
C & D \\
C & b - c & -c \\
D & b & 0
\end{pmatrix}
\]

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 interaction 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, \( r_{12} = r_{21} = 1 \) and \( r_{11} = 1/(1 - \rho) > 1 \). 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 \( e_i = C \) and \( e_j = D \)) and corresponding payoff per interaction matrix

\[
\begin{pmatrix}
C & D \\
C & (b - c)\tau_{11} & -c\tau_{12} \\
D & b\tau_{12} & 0
\end{pmatrix}
\]

The payoffs per unit of time \( \Pi_{ij} \) to strategy \( e_i \) are now given by

\[
\Pi_i = \frac{2n_{11}}{2n_{11} + n_{12}}(b - c) - \frac{n_{12}}{2n_{11} + n_{12}}c,
\]

\[
\Pi_j = \frac{n_{12}}{2n_{12} + n_{11}}b
\]

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 always stable as cooperators cannot invade (\( \frac{n_{11}}{n_{12}} = 0 > -c = \frac{n_{11}}{n_{12}} \)). On the other hand, a population of all cooperators is unstable since \( \frac{n_{11}}{n_{12}} = b - c < b = \frac{n_{11}}{n_{12}} \). 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

\[
p_{1+} = \frac{1}{2} \left[ 1 - \frac{1}{\sqrt{1 + \frac{4b}{(b-c)^2}\tau_{12}^2}} \right]
\]

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

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Fig. 3. Equilibrium frequencies of Hawks for the Hawk-Dove game as a function of the expected Hawk-Hawk interaction time \( r_{11} \), 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: \( r_{12} = r_{21} = r = 1 \).
Once again, strategy $e_i$ will be a strict NE provided $x_i/e_i > x_j/e_j$ (i, j=1,2, i ≠ 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 Fig. 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.

3.2.1. Hawk–Dove game

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

$$p_1 = \pm \sqrt{F(Cr + V\tau_1) + (2CV + 1)(C - V)\tau^2\tau_1 + (2C - V)\tau^2\tau_1 + V^2\tau^4},$$

where

$$F = 4V^2\tau^4 + (C - 3V)(C + V)\tau^2\tau_1 + 2(C - V)V\tau^2\tau_1 + V^2\tau^4.$$

Qualitatively, this follows the two cases where fitness function is given as the payoff per interaction time of Section 3.1.1. 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 (Fig. 3C).

For $C > V$ (Case B), solution $p_1$ is outside the interval [0, 1] and the only stable solution is $p_1$. Fig. 3D shows the dependence of $p_1$ on the fighting time $\tau_1$. We observe that as $\tau_1$ 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 $\tau_1 > 0$. 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 $\tau_1$ decreases. Also, as the interaction time between two Hawks increases beyond $\tau_1 = \tau$, the proportion of Hawks in the population decreases much faster when compared to Case B of Section 3.1.1 (Fig. 3, panel D compared to panel B).

3.2.2. Repeated Prisoner’s dilemma

For payoffs (12), the formula for $p_1$ 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 $p_1$ is both between 0 and 1 if and only if

$$\frac{(b + c)\tau_1}{\tau} > \frac{b + c}{b - c}.$$

When applied to the special case corresponding to the opting out game (i.e., $\tau_1 = \tau_2 = \tau$), the two interior equilibria exist when

$$\frac{\tau_1}{\tau} > \frac{b + c}{b - c}$$

and are given by

$$p_1 = A \pm \frac{\sqrt{\tau_1 \tau_2 + \frac{\tau_1}{\tau} - \frac{\tau_1}{\tau} - \frac{\tau_1}{\tau} - \frac{\tau_1}{\tau} + (b + c)^2 \tau^2}}{\tau_1 \tau_2 - \frac{\tau_1}{\tau} - \frac{\tau_1}{\tau} - \frac{\tau_1}{\tau} - \frac{\tau_1}{\tau} - \frac{\tau_1}{\tau} + (b + c)^2 \tau^2}$$

where

$$A = (b + c)^2 \tau^2 + \frac{\tau_1}{\tau} \tau_2 - \frac{\tau_1}{\tau} \tau_2 - \frac{\tau_1}{\tau} \tau_2 - \frac{\tau_1}{\tau} \tau_2 + (b + c)^2 \tau^2.$$

As we are in Case 4 of Section 3 and it can be proved that
0 < p₁ < p⁺₁ < 1, p₂⁺ and p₁⁺ are unstable and stable respectively (Fig. 2F).

Qualitatively, the effect of interaction time in the opting out game is similar whether fitness is calculated as expected payoff per unit time (Fig. 4A) or as expected payoff per expected time (Fig. 4B), in that sufficiently long interactions T₁₂ 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 T₁₂ 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 (p₁⁺, p₂⁺). That is, on average, with probability p₁⁺ each individual plays e₁ and with probability p₂⁺ plays e₂. This means that there will be Np₁⁺N individuals playing strategy e₁. With instantaneous random pair formation, the number of pairs nij at time t will again satisfy the dynamics (3) whose equilibrium is given by (5). Substituting these equilibrium values into the decision tree of Fig. 1, we can then calculate the fitness \( \Pi_{p₁⁺, p₂⁺}^{*}(p₁, p₂) \) of a focal individual using mixed strategy (p₁, p₂) when the monomorphic population plays strategy (p₁⁺, p₂⁺). 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 Fig. 1, \( \Pi_{p₁⁺, p₂⁺}^{*}(p₁, p₂) \) is linear in the focal individual mixed strategy (p₁, p₂). That is,

\[
\Pi_{p₁⁺, p₂⁺}^{*}(p₁, p₂) = p₁\Pi₁ + p₂\Pi₂
\]  

(17)

where \( \Pi₁ \) and \( \Pi₂ \) are given by (6) evaluated at (p₁⁺, p₂⁺). An interior mixed strategy (p₁⁺, p₂⁺) is a NE (i.e. \( \Pi_{p₁⁺, p₂⁺}(p₁, p₂) ≤ \Pi_{p₁⁺, p₂⁺}(p₁⁺, p₂⁺) \) for all (p₁, p₂)) if and only if \( \Pi₁ = \Pi₂ \) (see Appendix A). In particular, interior NE correspond to circles (either empty or solid) with 0 < p₁ < 1 in Fig. 2 from the corresponding fitness of the focal individual per average per time.

Also shown in Appendix A is that (p₁⁺, p₂⁺) is a local ESS (Hofbauer and Sigmund, 1998) if and only if \( (\Pi₁ - \Pi₂)(p₁⁺ - p₁) > 0 \) for all (p₁, p₂) sufficiently close but not equal to (p₁⁺, p₂⁺) where \( \Pi₁ \) and \( \Pi₂ \) are given by (6) evaluated at (p₁, p₂). Furthermore, a pure strategy is a local ESS if and only if it is a strict NE. Thus, (p₁⁺, p₂⁺) is a local ESS and if only if it corresponds to a solid circle in Fig. 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)

\[
\frac{dp₁}{dt} = \sigma \frac{\Pi_{p₁⁺, p₂⁺}(p₁, p₂) - p₁\Pi₁}{p₁ - p₁⁺} = \sigma(\Pi₁ - \Pi₂),
\]  

(18)

where \( \sigma > 0 \) is a proportionality constant that describes the speed of adaptation. When \( \sigma \epsilon \epsilon (\sigma = 1) \), 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)

\[
\frac{dp₁}{dt} = \sigma p₁(1 - p₁)(\Pi₁ - \Pi₂),
\]  

(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 Fig. 1, the average payoff the focal individual gets is

\[
E = p₁\left( \frac{2n₁s₁₁ + n₁s₁₂}{2n₁₁ + n₁₂} \right) + p₂\left( \frac{n₁s₂₁ + 2n₁s₂₂}{n₁₁ + 2n₁₂} \right)
\]

and the expected time is

\[
T = p₁\left( \frac{2n₁s₁₁ + n₁s₁₂}{2n₁₁ + n₁₂} \right) + p₂\left( \frac{n₁s₂₁ + 2n₁s₂₂}{n₁₁ + 2n₁₂} \right).
\]

Fitness of the focal individual playing mixed strategy (p₁⁺, p₂⁺) in a monomorphic population playing strategy (p₁⁺, p₂⁺) is then defined as the average payoff per the average time

\[
\Pi_{p₁⁺, p₂⁺}^{*}(p₁, p₂) = \frac{E}{T}
\]  

(20)

where all pairs nij are calculated at (p₁⁺, p₂⁺). This fitness function is no longer equal to \( p₁\Pi₁ + p₂\Pi₂ \), i.e., is not linear in the focal individual strategy.

Once again, from Appendix A, strategy (p₁⁺, p₂⁺) is an interior NE if and only if \( \Pi₁ = \Pi₂ \) where \( \Pi's \) are given by (15) and the local ESSs correspond to the solid circles in Fig. 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; Krivan, 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.

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Footnote:

2 Here we ignore the non generic case where \( \Pi₁ = \Pi₂ \) at the pure strategy.
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, Siviero 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, Fig. 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 (Fig. 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.

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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 \(\Pi_s\) 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 \(\Pi_{p_1^*}^\tau_{p_2^*}(p_1, p_2) = \Pi_{p_1^*}^\tau_{p_2^*}(p_1, p_2)\) for all \((p_1, p_2)\) which is equivalent to \((p_1 - p_1^*)\gamma(H_1 - H_2) \leq 0\) 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 \(\Pi_{p_1^*}^\tau_{p_2^*}(p_1, p_2) < \Pi_{p_1^*}^\tau_{p_2^*}(p_1, p_2)\) for all \((p_1, p_2)\) sufficiently close but not equal to \((p_1^*, p_2^*)\) if and only if \((p_1 - p_1^*)\gamma(H_1 - H_2) < 0\) for all \(0 \leq p_1 \leq 1\) that are close to \(p_1^*\) where \((p_1, p_2)\) 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 Fig. 2.

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

\[
P_{p_1^*}^\tau_{p_2^*}(p_1, p_2) = \frac{p_1 A^* + p_2 B^*}{p_1 C^* + p_2 D^*}
\]

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

\[
P_{p_1^*}^\tau_{p_2^*}(p_1, p_2) = \frac{p_1 A^* + p_2 B^*}{p_1 C^* + p_2 D^*} \leq \frac{p_1 A^* + p_2 B^*}{p_1 C^* + p_2 D^*} = \Pi_{p_1^*}^\tau_{p_2^*}(p_1^*, p_2^*)
\]

iff

\[
(p_1 - p_1^*)\left(\frac{A^*}{C^*} - \frac{B^*}{D^*}\right) \leq 0
\]

(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 if \(\Pi_1 > \Pi_2\) 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 Fig. 2.

References

Charnov, E.L., 1976. Optimal foraging: attack strategy of a mantid. Am. Nat. 110, 141–151.
Clutton-Brock, T.H., Albon, S.D., 1979. The roaring of red deer and the evolution of honest advertisement. Behaviour 69, 145–170.
Hofbauer, J., Sigmund, K., 1998. Evolutionary Games and Population Dynamics. Cambridge University Press, Cambridge, UK.
Křivan, V., 1996. Optimal foraging and predator-prey dynamics. Theor. Popul. Biol. 49, 265–290.
Maynard Smith, J., 1974. The theory of games and the evolution of animal conflicts. J. Theor. Biol. 47, 209–221.
Maynard Smith, J., Price, G.R., 1973. The logic of animal conflict. Nature 246, 15–18.
Nowak, M.A., 2006. Five rules for the evolution of cooperation. Science 314, 1560–1563.
Pacheco, J.M., Traulsen, A., Nowak, M.A., 2006. Active linking in evolutionary games. J. Theor. Biol. 243, 437–443.
Poundstone, W., 1992. Prisoner’s Dilemma. Oxford University Press, Oxford, UK.
Sinervo, B., Lively, C.M., 1996. The rock-paper-scissors game and the evolution of alternative male strategies. Nature 380, 240–243.
Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University Press, Princeton, NJ.
Taylor, C., Nowak, M.A., 2006. Evolutionary game dynamics with non-uniform interaction rates. Theor. Popul. Biol. 69, 243–252.
Taylor, P.D., Jonker, L.B., 1978. Evolutionary stable strategies and game dynamics. Math. Biosci. 40, 145–156.
Zhang, B.-Y., Fan, S.-J., Li, C., Zheng, X.-D., Yao, J.-Z., Cressman, R., Tao, Y., 2016. Opting out against defection leads to stable coexistence with cooperation. Sci. Rep. 6 (35902),