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The asymmetric Hawk-Dove game with costs measured as time lost

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ABSTRACT

The classic Hawk-Dove game is a symmetric game in that it does not distinguish between the winners and losers of Hawk-Hawk or Dove-Dove contests. Either of the two interacting Hawks or the two interacting Doves have the same probability to win/lose the contest. In addition, all pairwise interactions take the same time and after disbanding, the individuals pair instantaneously again. This article develops an asymmetric version of the Hawk-Dove model where all costs are measured by the time lost. These times are strategy dependent and measure the length of the conflict and, when a fight occurs between two interacting Hawks, the time an individual needs to recover and pair again. These recovery times depend on whether the Hawk won or lost the contest so that we consider an asymmetric Hawk-Dove game where we distinguish between winners and losers. However, the payoff matrix for this game does not correspond to the standard bimatrix game, because some entries are undefined. To calculate strategy payoffs we consider not only costs and benefits obtained from pairwise contests but also costs when individuals are disbanded. Depending on the interacting and recovery times, the evolutionary outcomes are: Hawk only, both Hawk and Dove, and a mixed strategy. This shows that measuring the cost in time lost leads to a new prediction since, in the classic (symmetric) Hawk-Dove model that does assume positive cost ($C > 0$), both Hawk and Dove strategy is never an evolutionary outcome.

1. Introduction

In evolutionary ecology, the classic Hawk-Dove model (Maynard Smith and Price, 1973) plays an important role to explain, from the Darwinian point of view, the evolution of aggressiveness. The model, which is one of the most celebrated in evolutionary game theory (e.g., Hofbauer and Sigmund, 1998; Broom and Rychtář, 2013; McNamara and Leimar, 2020), assumes that individuals behave either aggressively (Hawk strategy), or cooperatively (Dove strategy) and they compete for some benefit of value V. The winner obtains the benefit and the loser pays a cost C if they fight.[1] The model predicts that, if the cost is higher than the benefit ($C > V$), individuals should play a mixed strategy where they use the aggressive strategy with probability V/C while, when fighting is not costly ($C < V$), individuals should be aggressive. Although the model proved very instrumental to explain evolution of aggressiveness (e.g., Sirot, 2000; Hsu et al., 2006; Kokko et al., 2014), it is difficult to imagine how to measure the benefits and costs in the same units. E.g., two stags can compete for females and the benefit of winning the contest can be measured by the number of females a stag gets, while the cost of a fight can lead to injuries of one or both stags, or even to death. Expressing these two in a common currency seems to be impossible. This makes applications of game theory in biology more difficult when compared to economic applications where utility theory allows one to define a preference relation on possible outcomes of the game. Utilities are often expressed in money with the natural preference order.

The Hawk-Dove game is also one of the models often used to describe cultural evolution of social behavior and structure (e.g., Molleman et al., 2014; Herold and Kuzmics, 2020; Perepelitsa, 2021) where it stands as a prototype of an evasion game (Molleman et al., 2013) in which the relative payoff of each pure strategy decreases with the frequency of this strategy in the population which results in a unique mixed evolutionarily stable equilibrium or an evolutionarily stable state.

Two-player games assume that players obtain payoffs through pairwise interactions that last the same time, irrespective of strategies the players use. This is an important assumption, because it leads to an equilibrium pair distribution that corresponds to the

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[1] Interestingly, the classic model is symmetric in the sense that if both contestants are of the same behavioral type, they equally share both reward and cost, i.e., this symmetrised model does not distinguish between the winner and the loser of a fight.

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Hardy–Weinberg distribution of population genetics (Hofbauer and Sigmund, 1998; Broom and Rychtář, 2013). Game theory assumes that pairs are formed instantaneously and payoffs are evaluated at the equilibrium pair distribution. Křivan and Cressman (2017) (see also Garay et al., 2017) extended this approach by assuming that interaction length is strategy dependent. This leads to distributional dynamics that are much more complicated when compared to the case of uniform interaction times. This theory has been applied to the Hawk-Dove model (Křivan and Cressman, 2017; Broom and Křivan, 2020), the Prisoner's dilemma game (Křivan and Cressman, 2017; Broom and Křivan, 2020; Křivan and Cressman, 2020), the Battle of the Sexes (Cressman and Křivan, 2020), and the Owner-Intruder game (Cressman and Křivan, 2019). These applications show that differences in interaction times lead to novel predictions for the evolutionary outcomes for these games when compared to the classic model outcomes (e.g., in the case of the repeated Prisoner's dilemma game, cooperation can evolve if pairs of cooperators stay together for enough rounds). For the Hawk-Dove model (Křivan and Cressman, 2017), a mixed strategy evolutionary outcome exists even when the cost of the fight is low and the interaction time between two Hawks is high enough. The classic model that assumes all interactions take the same time predicts that Hawk is the evolutionary outcome in this case.

The classic (symmetric) Hawk-Dove game as well as the asymmetric version called the Owner-Intruder game (Broom and Rychtář, 2013) assume that a Hawk wins a contest with a Dove, but they do not distinguish between winners and losers in Hawk-Hawk and Dove-Dove interactions where individual payoffs are equally shared between the two contestants. This is because standard two-player game theory assumes payoffs are obtained only through pairwise interactions and all individuals are paired, i.e., single individuals that are disbanded from a pair find partners instantaneously. In this article, we consider a more realistic scenario, where disbanded individuals do not pair instantaneously and fitness of each strategy depends on costs and benefits (also called "payoffs") not only obtained from pairwise interactions but also obtained when individuals are single. Because these costs and benefits when single can depend on whether the individual won or lost the contest, we need to keep track of who is the winner and who is the loser. Thus, we need to consider an asymmetric game where an individual is either in the position of the winner or the loser. However, unlike the payoff bimatrix of a standard two-player asymmetric game (e.g., the Owner-Intruder game; Broom and Rychtář, 2013), our asymmetric game does not have all entries defined. For example, in the case of the Hawk-Dove game, payoff to loser playing Hawk and winner playing Dove is undefined (see payoff bimatrix (1) below) since this event never occurs.

In this article, we assume that when two Hawks fight, the individuals need some resting time when the pair disbands. E.g., when the fight is for some food, the winner of the contest receives the resource and needs some time to "process" it. In this case, the resting time can be viewed as the handling time a predator needs when it captures a prey after a dispute with another predator. In this analogy, it is important to mention that considering handling times led to more general functional responses (Holling, 1959) with strong implications for predator–prey coexistence (Gause, 1934) when compared to the Lotka-Volterra predator–prey model (Volterra, 1926). In another context, if two stags playing Hawk fight for females, the loser may require a longer time to recover from the contest when compared to the winner.

One novelty of this article is that it considers costs, measured in time lost, of singles in the Hawk-Dove game. Thus, we consider two types of times (see time bimatrix (4) below). The first is the strategy-dependent time lost in contest between two individuals and this time is the same for both contestants, resulting in a time interaction matrix that is symmetric in strategies. When these are the only times considered in the game, Křivan and Cressman (2017) showed that strategy-dependent interaction times can change predictions of the classic Hawk-Dove model. In this article, we are also interested in the so called "recovery time" which is the time an individual needs after it is disbanded from a pair and before it can form a new pair. It is natural to assume that this time depends on whether the individual won or lost the contest, so that we need to track winners and losers of the game without averaging payoffs as in the classic Hawk-Dove game. All costs in this article are measured by time lost, i.e., $C = 0$ in the classic model. Thus, we separate units in which benefits are measured from units in which costs are measured. From the time bimatrix, we are able to calculate the equilibrium pair distribution of our asymmetric Hawk-Dove game in different model scenarios (Sections 2.1 and 2.3) and analyze what effect these have on the evolutionary outcome (Section 2.2) when the payoff bimatrix is given by (3) below.

2. Models

In this article, we consider a contest competition between two individuals with two phenotypes called Hawk and Dove. In the classical model (Maynard Smith and Price, 1973) the benefit of winning a contest is V and the cost to the loser in a fight, which only occur in Hawk-Hawk contests, is C. Hawks always win contests with Doves and in the symmetric game, individual payoffs in Hawk-Hawk or Dove-Dove contests are equally shared between the two contestants, as there is no distinction between the winner and the loser.

For our purposes, it is necessary to consider an asymmetric version of the Hawk-Dove game where we distinguish between the winner and the loser in the Hawk-Hawk and Dove-Dove contests. We denote by H_w (H_ℓ) a Hawk individual who wins (loses) the contest. Similarly, D_w (D_ℓ) denotes a Dove individual who wins (loses) the contest. The game is then represented by the following payoff bimatrix

$$\begin{array}{c} \\ H_w \\ D_w \end{array} \begin{array}{c} \begin{array}{cc} H_\ell & D_\ell \end{array} \\ \left[\begin{array}{cc} (V,-C) & (V,0) \\ \text{NDF} & (V,0) \end{array}\right] \end{array}. \tag{1}$$

That is, when two Hawks meet, a fight occurs and the winner receives the benefit and the loser bears the cost. Moreover, when a Hawk and Dove encounter each other, the Hawk always wins the contest without a fight. For this reason, the entry in the payoff matrix when a Dove who wins encounters a Hawk who loses is not defined (NDF). Finally, when two Doves meet, one wins the benefit without a fight.

We remark that the above winner-loser game defined by payoff matrix (1) does not correspond to the standard asymmetric (bimatrix) game. Asymmetric games (Maynard Smith and Parker, 1976) assume either there are real differences between the two contestants (e.g., different sexes in the Battle of the Sexes; Dawkins, 1976), different species in predator–prey games (Vincent and Brown, 2005; Broom et al., 2016), or the two individuals are identical, but play different roles (e.g., the Owner-Intruder game as an asymmetric version of the Hawk-Dove game; Broom and Rychtář, 2013). In particular, in the standard asymmetric game, all row strategies interact with all column strategies so that all entries in the bimatrix are defined. The game defined by (1) does not consider any such differences between the players. The winner gets payoff V irrespective of the strategy it plays while the loser does better when it plays Dove.

If, in the Hawk-Hawk and Dove-Dove encounters, each player is equally likely to be in the position of the winner or the loser, the expected payoff to the row player is then given by the standard payoff matrix for the symmetric Hawk-Dove game (Maynard Smith and Price, 1973); namely,

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

This standard payoff matrix does not distinguish between the winner and the loser of the game. However, there may be other costs/benefits that may be different for winners and losers. For example, if individuals do not pair instantaneously after they disband, they may accrue some payoff as singles and this payoff may depend on whether the individual won or lost the contest. Thus, to calculate the average fitness for each strategy, we need to consider winners and losers explicitly without averaging the payoff matrix first (as is done to obtain the above standard payoff matrix).

In this article, we take another approach which assumes all costs to an individual (e.g., the cost of fighting or the cost of recovery) are measured as the time taken in these activities. In particular, we set $C = 0$ in the payoff bimatrix (1) to obtain

$$\begin{array}{c|cc} & H_\ell & D_\ell \\ H_w & (V,0) & (V,0) \\ D_w & \text{NDF} & (V,0) \end{array} = \begin{array}{c|cc} & H_\ell & D_\ell \\ & (\pi^w_{HH}, \pi^\ell_{HH}) & (\pi_{HD}, \pi_{DH}) \\ & \text{NDF} & (\pi^w_{DD}, \pi^\ell_{DD}) \end{array}. \tag{3}$$

The payoff matrix (3) then provides the payoffs per interaction, where the payoff of either player does not depend on the strategy it plays, as the winner always receives full benefit V while the loser does not get anything.

The classic Hawk-Dove model assumes that all interactions take the same amount of time and there is no recovery time. The change in the individual fitness after each interaction is then given directly by the payoff. In this article, individual fitness is defined as the expected payoff received per unit of time spent in interaction and in recovery activities (see Section 2.2) when distribution of players in the population is at an equilibrium (see Section 2.1). Contrary to the classic result where the only evolutionary outcome when $C = 0$ is the population consisting of all Hawks, Křivan and Cressman (2017) showed that an interior stable mixed strategy (i.e., a coexistence equilibrium of Hawks and Doves) exists when interaction times between Hawks last long enough.

In this article, besides costs associated with time lost due to interactions, we focus on the case where a fight between two Hawks leads to a period of recovery during which individuals cannot enter new contests. Moreover, our model includes the situation where the recovery times for the winner Hawk and the loser Hawk are different. For example, the loser Hawk may need more time to recover from a fight if it is injured than the winner Hawk, or the winner Hawk may need more time to process contested resource. Interaction and recovery times are given by the time bimatrix

$$\begin{array}{c|cc} & H_\ell & D_\ell \\ H_w & (\tau_{HH}+\tau_w, \tau_{HH}+\tau_\ell) & (\tau_{HD}, \tau_{HD}) \\ D_w & \text{NDF} & (\tau_{DD}, \tau_{DD}) \end{array} \tag{4}$$

where τ_{ij} $(i,j \in \{H, D\})$ measures interaction time between two individuals and τ_w (τ_ℓ) is the resting time the winner (loser) Hawk needs to recover before pairing with a new individual. Following the usual assumption of the classic Hawk-Dove model, we assume that pairs are formed instantaneously, i.e., all individuals that are ready to pair find their partner immediately. Thus, the searching time is neglected and there are no searching individuals.

In the following, we consider the two cases where Hawk losers and winners both have recovery times (Section 2.1) and where only the losing Hawks require a recovery time (Section 2.3). Since our model includes recovering individuals, we must consider singles explicitly. We consider very fast pairing so that the distribution of pairs and recovering singles is at equilibrium. In the next section, we calculate this equilibrium.

2.1. Pair distribution when both the loser and the winner Hawk need recovery time

In order to investigate the evolutionary outcome(s) of our model, individual fitness functions need to be determined at the equilibrium activity distribution for the current numbers of Hawks and Doves. To this end, we first describe the pair formation dynamics in (5) below when these numbers are fixed and then calculate its equilibrium distribution.

The numbers of pairs are denoted as n_{HH}, n_{HD}, and n_{DD} where the subindices denote strategies of the two paired individuals, and n_{H_w} (n_{H_ℓ}) is the number of recovering Hawks that won (lost) their Hawk-Hawk contest and are not yet ready to pair.[2] In general, we assume these two recovery times can differ. Thus, per unit of time, there will be $\frac{n_{HD}}{\tau_{HD}} + \frac{n_{H_w}}{\tau_w} + \frac{n_{H_\ell}}{\tau_\ell}$ single Hawk individuals ready to pair immediately, $2\frac{n_{DD}}{\tau_{DD}} + \frac{n_{HD}}{\tau_{HD}}$ single Dove individuals that will immediately form new pairs, and $2\frac{n_{HH}}{\tau_{HH}}$ Hawk individuals that enter the recovery period.[3] The total number of individuals forming new pairs is $2\frac{n_{HD}}{\tau_{HD}} + 2\frac{n_{DD}}{\tau_{DD}} + \frac{n_{H_w}}{\tau_w} + \frac{n_{H_\ell}}{\tau_\ell}$. The proportion of newly formed n_{HH} pairs among all newly formed pairs is

$$\left(\frac{\frac{n_{HD}}{\tau_{HD}} + \frac{n_{H_w}}{\tau_w} + \frac{n_{H_\ell}}{\tau_\ell}}{2\frac{n_{HD}}{\tau_{HD}} + 2\frac{n_{DD}}{\tau_{DD}} + \frac{n_{H_w}}{\tau_w} + \frac{n_{H_\ell}}{\tau_\ell}} \right)^2 .$$

To obtain the number of newly formed n_{HH} pairs, we multiply this proportion by the number of all newly formed pairs $(\frac{n_{HD}}{\tau_{HD}} + \frac{n_{DD}}{\tau_{DD}} + \frac{n_{H_w}}{2\tau_w} + \frac{n_{H_\ell}}{2\tau_\ell})$. Similar considerations for n_{HD} and n_{DD} pairs lead to the following dynamics of pairs and recovering winner and loser Hawks

$$\begin{aligned}
\frac{dn_{HH}}{dt} &= -\frac{n_{HH}}{\tau_{HH}} + \frac{\left(\frac{n_{HD}}{\tau_{HD}} + \frac{n_{H_w}}{\tau_w} + \frac{n_{H_\ell}}{\tau_\ell}\right)^2}{4\left(\frac{n_{HD}}{\tau_{HD}} + \frac{n_{DD}}{\tau_{DD}} + \frac{n_{H_w}}{2\tau_w} + \frac{n_{H_\ell}}{2\tau_\ell}\right)} \\
\frac{dn_{HD}}{dt} &= -\frac{n_{HD}}{\tau_{HD}} + \frac{2\left(\frac{n_{HD}}{\tau_{HD}} + \frac{n_{H_w}}{\tau_w} + \frac{n_{H_\ell}}{\tau_\ell}\right)\left(\frac{n_{HD}}{\tau_{HD}} + \frac{2n_{DD}}{\tau_{DD}}\right)}{4\left(\frac{n_{HD}}{\tau_{HD}} + \frac{n_{DD}}{\tau_{DD}} + \frac{n_{H_w}}{2\tau_w} + \frac{n_{H_\ell}}{2\tau_\ell}\right)} \\
\frac{dn_{DD}}{dt} &= -\frac{n_{DD}}{\tau_{DD}} + \frac{\left(\frac{n_{HD}}{\tau_{HD}} + \frac{2n_{DD}}{\tau_{DD}}\right)^2}{4\left(\frac{n_{HD}}{\tau_{HD}} + \frac{n_{DD}}{\tau_{DD}} + \frac{n_{H_w}}{2\tau_w} + \frac{n_{H_\ell}}{2\tau_\ell}\right)} \\
\frac{dn_{H_w}}{dt} &= -\frac{n_{H_w}}{\tau_w} + \frac{n_{HH}}{\tau_{HH}} \\
\frac{dn_{H_\ell}}{dt} &= -\frac{n_{H_\ell}}{\tau_\ell} + \frac{n_{HH}}{\tau_{HH}}.
\end{aligned} \tag{5}$$

Since the total numbers of Hawks $(N_H = 2n_{HH} + n_{HD} + n_{H_w} + n_{H_\ell})$ and Doves $(N_D = 2n_{DD} + n_{HD})$ do not change in dynamics (5), this reduces to a three-dimensional system, e.g., in variables n_{HD}, n_{H_w}, and n_{H_ℓ}. Indeed, substituting $n_{HH} = (N_H - n_{HD} - n_{H_w} - n_{H_\ell})/2$ and

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[2] In particular, individuals who interact with a Dove require no recovery time since these individuals do not engage in a fight. This is consistent with the story behind the classic Hawk-Dove model. However, Appendix A shows that our methods can be extended to include resting times for winner Hawks (Doves) and resting times for loser Hawks (Doves). When these times are independent of the pairs from which individuals disbanded, the extended model again has a unique positive equilibrium of the pair formation dynamics generalizing (5) below and qualitatively the same evolutionary outcomes found in Section 2.2 where it is assumed that individuals who interact with a Dove require no recovery time. Our methods are general enough to treat other models, but in this article we focus on those that are consistent with the classic Hawk-Dove model assumptions.

[3] We assume that both winners and losers enter recovery periods whose lengths depend on whether the Hawk is a loser or a winner.

$n_{DD} = (N_D - n_{HD})/2$ in (5), we obtain the following reduced system of differential equations

$$\begin{aligned}
\frac{dn_{HD}}{dt} &= \frac{(N_D - n_{HD})\tau_{HD}^2(n_{H_\ell}\tau_w + n_{H_w}\tau_\ell) - n_{HD}^2\tau_{DD}\tau_\ell\tau_w}{\tau_{HD}(\tau_\ell\tau_w(N_D\tau_{HD} + 2n_{HD}\tau_{DD} - n_{HD}\tau_{HD}) + n_{H_\ell}\tau_{DD}\tau_{HD}\tau_w + n_{H_w}\tau_{DD}\tau_{HD}\tau_\ell)}\\
\frac{dn_{H_w}}{dt} &= \frac{N_H - n_{HD} - n_{H_\ell} - n_{H_w}}{2\tau_{HH}} - \frac{n_{H_w}}{\tau_w}\\
\frac{dn_{H_\ell}}{dt} &= \frac{N_H - n_{HD} - n_{H_\ell} - n_{H_w}}{2\tau_{HH}} - \frac{n_{H_\ell}}{\tau_\ell}.
\end{aligned} \tag{6}$$

Provided $\tau_{DD} \neq \frac{2\tau_{HD}^2}{2\tau_{HH}+\tau_\ell+\tau_w}$, there exists a unique positive equilibrium[4] of system (6) (and, consequently, unique equilibrium of system (5))

$$\begin{aligned}
n_{HD}^* &= \frac{\tau_{HD}^2(N_D + N_H) - \tau_{HD}\sqrt{N_D^2\tau_{HD}^2 + 2N_DN_H\left(\tau_{DD}(2\tau_{HH} + \tau_\ell + \tau_w) - \tau_{HD}^2\right) + N_H^2\tau_{HD}^2}}{2\tau_{HD}^2 - \tau_{DD}(2\tau_{HH} + \tau_\ell + \tau_w)}\\
n_{H_w}^* &= \frac{\tau_w\left(\tau_{HD}^2(N_D - N_H) + N_H\tau_{DD}(2\tau_{HH} + \tau_\ell + \tau_w) - \tau_{HD}\sqrt{N_D^2\tau_{HD}^2 + 2N_DN_H\left(\tau_{DD}(2\tau_{HH} + \tau_\ell + \tau_w) - \tau_{HD}^2\right) + N_H^2\tau_{HD}^2}\right)}{(2\tau_{HH} + \tau_\ell + \tau_w)\left(\tau_{DD}(2\tau_{HH} + \tau_\ell + \tau_w) - 2\tau_{HD}^2\right)}\\
n_{H_\ell}^* &= \frac{\tau_\ell\left(\tau_{HD}^2(N_D - N_H) + N_H\tau_{DD}(2\tau_{HH} + \tau_\ell + \tau_w) - \tau_{HD}\sqrt{N_D^2\tau_{HD}^2 + 2N_DN_H\left(\tau_{DD}(2\tau_{HH} + \tau_\ell + \tau_w) - \tau_{HD}^2\right) + N_H^2\tau_{HD}^2}\right)}{(2\tau_{HH} + \tau_\ell + \tau_w)\left(\tau_{DD}(2\tau_{HH} + \tau_\ell + \tau_w) - 2\tau_{HD}^2\right)}.
\end{aligned} \tag{7}$$

This unique equilibrium is plotted as a function of the proportion of Hawks $p_H = \frac{N_H}{N_H+N_D}$ in Fig. 1A for a particular choice of model parameters. When $\tau_{DD} = \frac{2\tau_{HD}^2}{2\tau_{HH}+\tau_\ell+\tau_w}$, the unique equilibrium simplifies to

$$\begin{aligned}
n_{HD}^* &= \frac{N_DN_H}{N_D + N_H}\\
n_{H_w}^* &= \frac{N_H^2\tau_w}{(N_D + N_H)(2\tau_{HH} + \tau_\ell + \tau_w)}\\
n_{H_\ell}^* &= \frac{N_H^2\tau_\ell}{(N_D + N_H)(2\tau_{HH} + \tau_\ell + \tau_w)}.
\end{aligned} \tag{8}$$

We observe that in this special case, the number of n_{HD}^* and n_{DD}^* pairs do not depend on the interaction times. Note that (7) or (8) also determine n_{HH}^* and n_{DD}^*.

In order to determine individual fitness functions, we conjecture that the distribution of pairs and singles converges to this equilibrium. Unfortunately, we are not able to show this analytically or to verify its local asymptotic stability for arbitrary time bimatrix (4) and positive resting times τ_w and τ_ℓ. As we are especially interested in this article on the effect of resting times, we were able to show local asymptotic stability of the distributional equilibrium when $\tau_{HH} = \tau_{HD} = \tau_{DD}$.[5] On the other hand, our extensive numerical simulations of the distributional dynamics support this conjecture for general positive interaction times too.

2.2. Payoffs and evolutionary outcomes

Following Křivan and Cressman (2017), we define fitnesses as the expected payoff per unit of time an individual obtains when the pair distribution is at the unique equilibrium (7). The probability that a Hawk is paired with another Hawk is $\frac{2n_{HH}}{2n_{HH}+n_{HD}+n_{H_w}+n_{H_\ell}}$ and the payoff per unit of time in this case is $\frac{\pi_{HH}^w}{\tau_{HH}+\tau_w}$ for the winning Hawk and $\frac{\pi_{HH}^\ell}{\tau_{HH}+\tau_\ell}$ for the losing Hawk. We assume that each Hawk is equally likely to win or lose the contest so that the average payoff per unit of time for a Hawk paired with another Hawk is $\frac{n_{HH}}{2n_{HH}+n_{HD}+n_{H_w}+n_{H_\ell}}\left(\frac{\pi_{HH}^w}{\tau_{HH}+\tau_w} + \frac{\pi_{HH}^\ell}{\tau_{HH}+\tau_\ell}\right)$. Similar calculations hold also for Doves, i.e., probability that a Dove is paired with another Dove is $\frac{2n_{DD}}{2n_{DD}+n_{HD}}$ as we assume that Doves do not need any resting time, and the payoff per unit of time in this case is $\frac{\pi_{DD}^w}{\tau_{DD}}$ for the winning Dove and $\frac{\pi_{DD}^\ell}{\tau_{DD}}$ for the losing Dove. Again, we assume that each Dove is equally likely to win or lose the contest so that the average payoff per unit of time for a Dove paired with another Dove is $\frac{n_{DD}}{2n_{DD}+n_{HD}}\left(\frac{\pi_{DD}^w}{\tau_{DD}} + \frac{\pi_{DD}^\ell}{\tau_{DD}}\right)$. If π_{DD} denotes the average of π_{DD}^w and π_{DD}^ℓ, we get that the average payoff per unit of time for a Dove paired with another Dove is $\frac{2n_{DD}}{2n_{DD}+n_{HD}}\frac{\pi_{DD}}{\tau_{DD}}$. A Hawk is paired with a Dove with probability $\frac{n_{HD}}{2n_{DD}+n_{HD}}$ and the payoff per unit of time in this case is

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[4] We calculated and verified this equilibrium is the only positive solution using Mathematica computer algebra software. We observe that, at the equilibrium, the number of pairs satisfies

$$\frac{n_{HH}}{\tau_{HH}}\frac{n_{DD}}{\tau_{DD}} = \frac{1}{4}\left(\frac{n_{HD}}{\tau_{HD}}\right)^2.$$

This is a generalization of the classic Hardy–Weinberg equilibrium proportions that assumes $\tau_{HH} = \tau_{HD} = \tau_{DD}$.

[5] Using command `Reduce` of Wolfram Mathematica, we verified the Routh-Hurwitz stability criteria applied to system (6) at equilibrium (7).

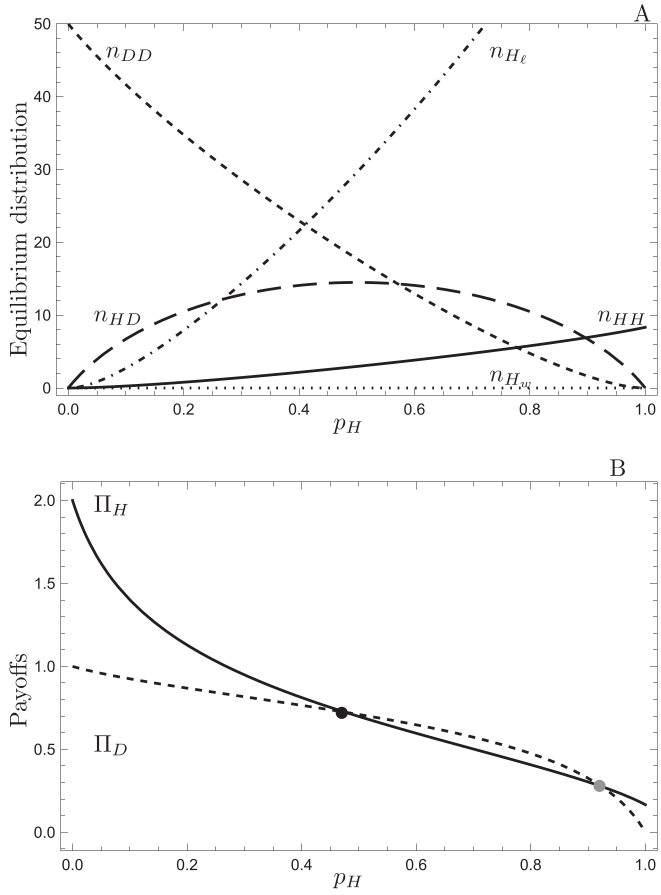

Fig. 1. Pair and singles equilibrium distribution (5) as a function of proportion of Hawks p_H in the population of fixed size $N = 100$ (Panel A). Solid (dashed) curve in Panel B is Hawk (Dove) payoff (9) as a function of p_H in the population of fixed size $N = 100$. Interior NE occur when Π_H intersects Π_D; namely, a stable NE (black dot) at $p_H \approx 0.48$ and an unstable one (gray dot) at $p_H \approx 0.92$. Parameters: $V = 2$, $\pi^w_{HH} = \pi_{HD} = V = 2$, $\pi^\ell_{HH} = 0$, $\pi_{DH} = 0$, $\pi_{DD} = V/2 = 1$, $\tau_{HH} = 1$, $\tau_{DD} = 1$, $\tau_{HD} = 1$, $\tau_w = 0$, $\tau_\ell = 10$.

$\frac{\pi_{HD}}{\tau_{HD}}$ for the Hawk and $\frac{\pi_{DH}}{\tau_{HD}}$ for the Dove. When fitnesses Π_H and Π_D for Hawks and Doves, respectively, are defined as average payoffs calculated at the equilibrium pair distribution we obtain

$$\begin{aligned}\Pi_H &= \frac{n^*_{HH}}{2n^*_{HH}+n^*_{HD}+n^*_{H_w}+n^*_{H_\ell}}\left(\frac{\pi^w_{HH}}{\tau_{HH}+\tau_w}+\frac{\pi^\ell_{HH}}{\tau_{HH}+\tau_\ell}\right)+\frac{n^*_{HD}}{2n^*_{HH}+n^*_{HD}+n^*_{H_w}+n^*_{H_\ell}}\frac{\pi_{HD}}{\tau_{HD}}\\ \Pi_D &= \frac{2n^*_{DD}}{2n^*_{DD}+n^*_{HD}}\frac{\pi_{DD}}{\tau_{DD}}+\frac{n^*_{HD}}{2n^*_{DD}+n^*_{HD}}\frac{\pi_{DH}}{\tau_{HD}}\end{aligned} \tag{9}$$

as we assume that resting Hawks do not accrue any fitness. These fitnesses (cf. Figure 1B) are evaluated at the unique equilibrium distribution $(n^*_{HH}, n^*_{HD}, n^*_{DD}, n^*_{H_w}, n^*_{H_\ell})$ (cf. Figure 1A) given in (7). By p_H ($p_D = 1 - p_H$), we denote the proportion of Hawks (Doves) in the population, i.e., $N_H = p_H N$ and $N_D = (1 - p_H)N$ where $N = N_H + N_D$ is the total population.

First, suppose that the population consists entirely of Hawks, i.e., $p_H = 1$. The equilibrium pair distribution is then

$$\begin{aligned}&(n^*_{HH}, n^*_{HD}, n^*_{DD}, n^*_{H_w}, n^*_{H_\ell})\\ &= \left(\frac{N_H\tau_{HH}}{2\tau_{HH}+\tau_\ell+\tau_w}, 0, 0, \frac{N_H\tau_w}{2\tau_{HH}+\tau_\ell+\tau_w}, \frac{N_H\tau_\ell}{2\tau_{HH}+\tau_\ell+\tau_w}\right).\end{aligned}$$

At this equilibrium, Hawk fitness is

$$\Pi_H = \frac{\tau_{HH}(\pi^\ell_{HH}(\tau_{HH}+\tau_w)+\pi^w_{HH}(\tau_{HH}+\tau_\ell))}{(\tau_{HH}+\tau_\ell)(\tau_{HH}+\tau_w)(2\tau_{HH}+\tau_\ell+\tau_w)}.$$

Let us consider a Dove mutant in the Hawk only population. The mutant will interact only with Hawks, i.e., there will be no Dove pairs, and fitness of such Dove mutant is $\Pi_D = \frac{\pi_{DH}}{\tau_{HD}}$. Thus, the Dove mutant can invade the Hawk only population when $\Pi_D > \Pi_H$ which yields

$$\frac{\pi_{DH}}{\tau_{HD}}\left(2+\frac{\tau_\ell+\tau_w}{\tau_{HH}}\right) > \frac{\pi^\ell_{HH}}{\tau_{HH}+\tau_\ell}+\frac{\pi^w_{HH}}{\tau_{HH}+\tau_w}.$$

We observe that, for our asymmetric Hawk-Dove game given by bimatrix (3) where $\pi_{DH} = \pi^\ell_{HH} = 0$ and $\pi^w_{HH} = V$, the above inequality simplifies to $V < 0$. As we assume that $V > 0$, Doves cannot invade the Hawk only population in our game, i.e., Hawk is always a Nash equilibrium (NE) as illustrated in Fig. 2.

Similarly, we consider when a Hawk mutant can invade the Dove only population. In a Dove only population, average fitness is $\Pi_D = \frac{\pi_{DD}}{\tau_{DD}}$ and fitness of a Hawk mutant that can be paired only with Doves is $\Pi_H = \frac{\pi_{HD}}{\tau_{HD}}$ as there are no resting Hawks. Thus, from (3) with $\pi_{DD} = \frac{1}{2}(\pi^w_{DD} + \pi^\ell_{DD})$, Hawks can invade provided

$$\frac{V}{\tau_{HD}} = \frac{\pi_{HD}}{\tau_{HD}} > \frac{\pi_{DD}}{\tau_{DD}} = \frac{V/2}{\tau_{DD}}, \tag{10}$$

i.e., when $\tau_{HD} < 2\tau_{DD}$ (Fig. 2A,B). In the classic Hawk-Dove game which assumes $\tau_{HD} = \tau_{DD}$, this inequality always holds. Fig. 2C, D shows the case where $\tau_{HD} > 2\tau_{DD}$ and Hawks cannot invade a Dove only population. This is because the cost of time lost when a Hawk interacts with a Dove is too high. All four panels of Fig. 2 (but especially Panels B and D) show that, as the resting time of the Hawk losers gets large, the domain of attraction of the Hawk NE becomes quite small. Then, even if the initial proportion of Hawks is high (i.e., above the dashed curve), random perturbations to the evolutionary dynamics or stochastic effects due to finite population size are likely to bring the population distribution below the dashed curve, from where the population will tend to the mixed NE (solid curve in Fig. 2A,B) or the Dove only NE (Fig. 2C,D).

The interior (i.e. mixed) NE are obtained by solving $\Pi_H = \Pi_D$. In particular, Fig. 2A, B shows that when Hawks can invade a Dove only population (i.e., when $\tau_{HD} < 2\tau_{DD}$), there exist two interior NE when the loser resting time is high enough. One of these interior NE is stable (shown by the solid curve) and the other unstable (shown as the dashed curve).[6] Since panel A assumes that winner Hawks do not need any resting time ($\tau_w = 0$), we observe that when loser Hawk resting time is long enough, Hawks do not take over the population

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[6] Stability of NE is typically considered to be dynamic stability (e.g., local asymptotic stability) with respect to an evolutionary dynamics such as the replicator equation (Taylor and Jonker, 1978; Hofbauer and Sigmund, 1998; Broom and Rychtář, 2013). For two-strategy games, an interior NE is stable if and only if the fitness of a strategy whose frequency is slightly less (more) than at the NE is larger (smaller) than the fitness of the other strategy. Thus, for the parameters of Figure 1, panel B shows there are two interior NE, one stable at $p_H \approx 0.48$ and one unstable at $p_H \approx 0.92$. This panel also shows the Hawk only population is a stable NE since the fitness of Hawks there is larger than the fitness of Doves (i.e., Doves cannot invade). A stable NE is then considered to be an evolutionary outcome.

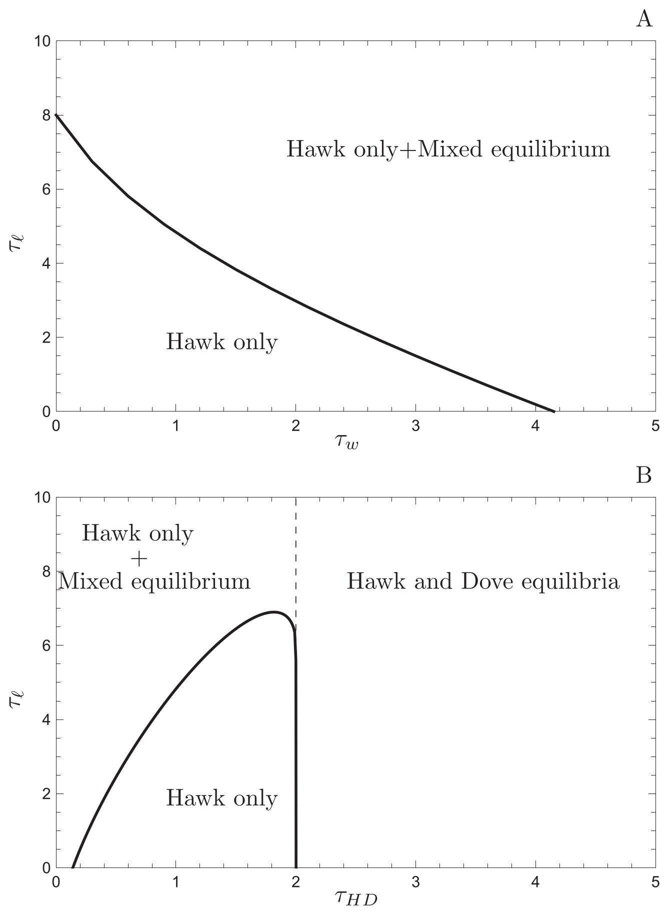

Fig. 3. Continuation of fold points in τ_w–τ_ℓ (Panel A) and τ_{HD}–τ_ℓ (Panel B) parameter space. The three possible structures to the evolutionary outcomes are: Hawk only, both Hawk only and Dove only (denoted as Hawk and Dove equilibria), and coexistence of a mixed evolutionary outcome with Hawk only (denoted as Hawk only + Mixed equilibrium). Panel A assumes $\tau_{HD} = 1$ and panel B assumes $\tau_w = 1$. Other parameters: $V = 2$, $\pi^w_{HH} = \pi_{HD} = V = 2$, $\pi^\ell_{HH} = 0$, $\pi_{DH} = 0$, $\pi_{DD} = V/2 = 1$, $\tau_{HH} = 1$, $\tau_{DD} = 1$.

when they invade the Dove only population. Instead, the evolutionary outcome is then the interior stable NE. In fact, as loser Hawks spend more time resting, the proportion of Doves increases at this evolutionary outcome and the domain of attraction of this evolutionary outcome also increases until it eventually attracts almost all initial distributions consisting of a mixture of Hawk and Dove individuals.

Panel B in Fig. 2 is similar to panel A except that it assumes that winner Hawks spend some time resting ($\tau_w = 5$). This further promotes the Dove strategy in the population. We stress that since $\tau_{HH} = \tau_{HD} = \tau_{DD} = 1$ in panels A and B, the classic Hawk-Dove model that does not consider resting times predicts the Hawk only population is the unique evolutionary outcome. In fact, when all

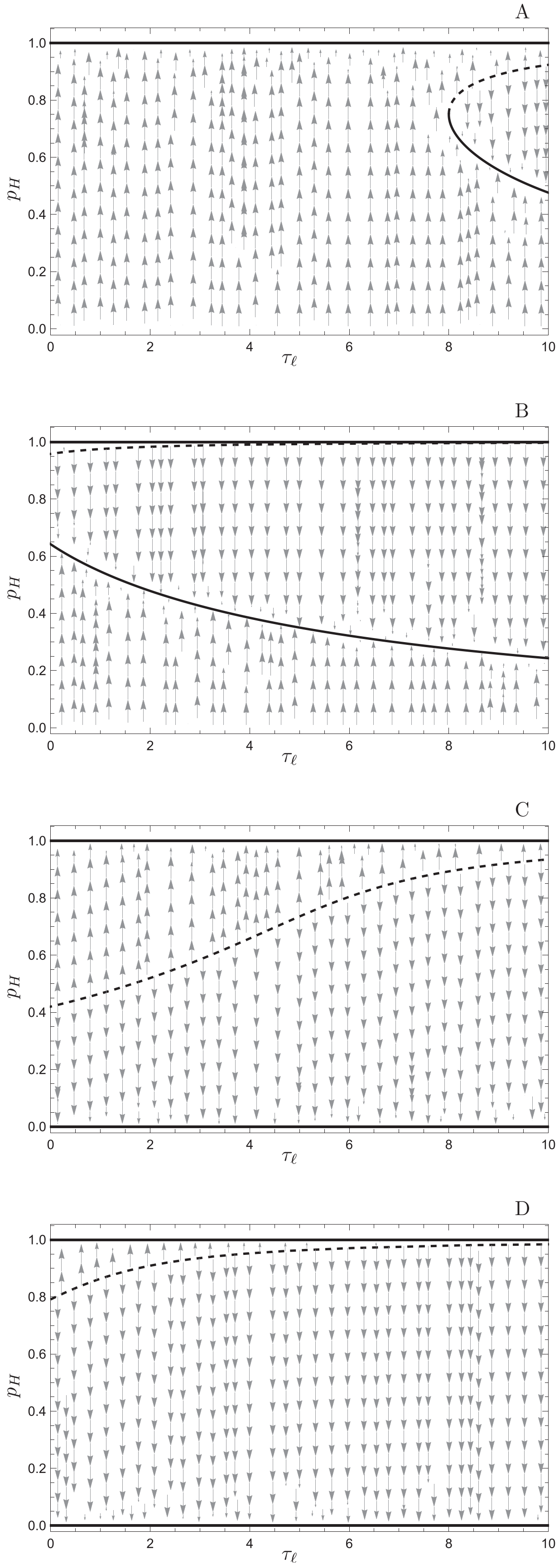

Fig. 2. Proportion of Hawks at Nash equilibria as a function of the recovery time for the loser Hawk τ_ℓ for distributional dynamics (5) with payoffs (9). Solid (dashed) curves indicate stable (unstable) NE. Arrows indicate the direction of the evolutionary dynamics at fixed τ_ℓ. Panel A assumes $\tau_{HD} = 1, \tau_w = 0$, panel B $\tau_{HD} = 1, \tau_w = 5$, panel C assumes $\tau_{HD} = 3, \tau_w = 5$, and panel D assumes $\tau_{HD} = 3, \tau_w = 10$. Other parameters: $V = 2$, $\pi^w_{HH} = \pi_{HD} = V = 2$, $\pi^\ell_{HH} = 0$, $\pi_{DH} = 0$, $\pi_{DD} = V/2 = 1$, $\tau_{HH} = 1$, $\tau_{DD} = 1$.

interaction times are equal as in the classic Hawk-Dove model, inequality $\tau_{HD} < 2\tau_{DD}$ holds and our results show that resting times have a strong effect on evolution of aggressivity because as resting times increase (cf. panel C vs. panel D), the proportion of Hawk strategy at the interior equilibrium decreases and the domain of attraction of the Hawk only strategy diminishes.

Panels C and D show the situation where Hawks cannot invade the Dove only population because they spend too much time interacting with Doves (i.e., $\tau_{HD} > 2\tau_{DD}$). In this case, there is one interior NE, which is unstable, and both Hawk only and Dove only are evolutionary outcomes depending on the initial distribution. Again we observe that as loser Hawks spend more time while resting, the domain of attraction of Dove only equilibrium increases. So, when resting times are high, it is more likely that the Dove only population will be achieved.

Fig. 3A considers the case where all interaction times are equal (when $\tau_{HH} = \tau_{HD} = \tau_{DD} = 1$), i.e., the Hawk only equilibrium is the only evolutionary outcome in the classic Hawk-Dove game. As shown in Fig. 2A there may be two interior NE in this case. Fig. 3A shows the dependence of the fold point where the two interior NE coincide as a function of τ_ℓ and τ_w. Above the curve, the stable interior NE (i.e., a mixed equilibrium of Hawk and Dove strategies) exists while, below the curve, Hawk only is the unique evolutionary outcome. This shows that provided the resting time(s) are long enough, Hawks can coexist with Doves even when there is no payoff cost (i.e., $C = 0$). The cost is now in time lost after the fight. Fig. 3B shows all three possible structures to the evolutionary outcomes in $\tau_{HD} - \tau_\ell$ parameter space. These structures are (i) Hawk only, (ii) Hawk only and Dove only and (iii) Hawk only plus mixed strategy evolutionary outcome.

Although distributional dynamics (5) assume that all interaction and resting times are positive, Figs. 2 and 3 include cases when some resting times are 0, e.g., when winner Hawk does not need any recovery time. The following section examines the distributional dynamics in this case.

2.3. Distributional dynamics when only the loser Hawk needs recovery time

In this section, we assume that only the loser Hawk needs some recovery time to pair again while all other individuals pair instantaneously after a contest, i.e., $\tau_w = 0$ and $\tau_\ell > 0$. As we cannot set $\tau_w = 0$ in distributional dynamics (5), we derive distributional dynamics for this case anew. Since winning Hawks are ready to pair immediately after a contest, there will be $\frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}} + \frac{n_{H_\ell}}{\tau_\ell}$ single Hawk individuals and $2\frac{n_{DD}}{\tau_{DD}} + \frac{n_{HD}}{\tau_{HD}}$ single Dove individuals per unit of time that will immediately form new pairs, and $\frac{n_{HH}}{\tau_{HH}}$ loser Hawk individuals that enter the recovery period. The total number of individuals forming new pairs is $\frac{n_{HH}}{\tau_{HH}} + 2\frac{n_{HD}}{\tau_{HD}} + 2\frac{n_{DD}}{\tau_{DD}} + \frac{n_{H_\ell}}{\tau_\ell}$. The proportion of newly formed n_{HH} pairs among all newly formed pairs is

$$\left(\frac{\frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}} + \frac{n_{H_\ell}}{\tau_\ell}}{\frac{n_{HH}}{\tau_{HH}} + 2\frac{n_{HD}}{\tau_{HD}} + 2\frac{n_{DD}}{\tau_{DD}} + \frac{n_{H_\ell}}{\tau_\ell}}\right)^2.$$

To obtain the number of newly formed n_{HH} pairs we multiply this proportion by the number of all newly formed pairs $\left(\frac{n_{HH}}{2\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}} + \frac{n_{DD}}{\tau_{DD}} + \frac{n_{H_\ell}}{2\tau_\ell}\right)$. Similar considerations for n_{HD} and n_{DD} pairs lead to the following pair dynamics

$$\begin{aligned}
\frac{dn_{HH}}{dt} &= -\frac{n_{HH}}{\tau_{HH}} + \frac{\left(\frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}} + \frac{n_{H_\ell}}{\tau_\ell}\right)^2}{4\left(\frac{n_{HH}}{2\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}} + \frac{n_{DD}}{\tau_{DD}} + \frac{n_{H_\ell}}{2\tau_\ell}\right)}\\
\frac{dn_{HD}}{dt} &= -\frac{n_{HD}}{\tau_{HD}} + \frac{2\left(\frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}} + \frac{n_{H_\ell}}{\tau_\ell}\right)\left(\frac{n_{HD}}{\tau_{HD}} + \frac{2n_{DD}}{\tau_{DD}}\right)}{4\left(\frac{n_{HH}}{2\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}} + \frac{n_{DD}}{\tau_{DD}} + \frac{n_{H_\ell}}{2\tau_\ell}\right)}\\
\frac{dn_{DD}}{dt} &= -\frac{n_{DD}}{\tau_{DD}} + \frac{\left(\frac{n_{HD}}{\tau_{HD}} + \frac{2n_{DD}}{\tau_{DD}}\right)^2}{4\left(\frac{n_{HH}}{2\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}} + \frac{n_{DD}}{\tau_{DD}} + \frac{n_{H_\ell}}{2\tau_\ell}\right)}\\
\frac{dn_{H_\ell}}{dt} &= -\frac{n_{H_\ell}}{\tau_\ell} + \frac{n_{HH}}{\tau_{HH}}.
\end{aligned} \tag{11}$$

Since the total number of Hawks $N_H = 2n_{HH} + n_{HD} + n_{H_\ell}$, and Doves $N_D = 2n_{DD} + n_{HD}$ do not change, system (11) reduces to a two-dimensional system, e.g., in variables n_{HD} and n_{H_ℓ}

$$\begin{aligned}
\frac{dn_{HD}}{dt} &= \frac{\tau_{HD}^2\tau_\ell(N_D - n_{HD})(N_H - n_{HD} - n_{H_\ell}) + 2n_{H_\ell}\tau_{HD}^2\tau_{HH}(N_D - n_{HD}) - 2n_{HD}^2\tau_{DD}\tau_{HH}\tau_\ell}{\tau_{HD}(\tau_\ell(2\tau_{HH}(N_D\tau_{HD} + n_{HD}(2\tau_{DD} - \tau_{HD})) + \tau_{DD}\tau_{HD}(N_H - n_{HD} - n_{H_\ell})) + 2n_{H_\ell}\tau_{DD}\tau_{HD}\tau_{HH})}\\
\frac{dn_{H_\ell}}{dt} &= \frac{N_H - n_{HD} - n_{H_\ell}}{2\tau_{HH}} - \frac{n_{H_\ell}}{\tau_\ell}.
\end{aligned} \tag{12}$$

For $\tau_\ell \neq 2\frac{\tau_{HD}^2}{\tau_{DD}} - \tau_{HH}$, system (12) has a unique positive distributional equilibrium

$$\begin{aligned}
n_{HD}^* &= \frac{\tau_{HD}\left(\sqrt{\tau_{HD}^2(N_D^2 + N_H^2) - 2N_DN_H\left(\tau_{HD}^2 - 2\tau_{DD}(\tau_{HH} + \tau_\ell)\right)} + \tau_{HD}\ (N_D + N_H)\right)}{2\tau_{HD}^2 - 2\tau_{DD}(\tau_{HH} + \tau_\ell)},\\
n_{H_\ell}^* &= \frac{\tau_\ell\left(\tau_{HD}\sqrt{\tau_{HD}^2(N_D^2 + N_H^2) - 2N_DN_H\left(\tau_{HD}^2 - 2\tau_{DD}(\tau_{HH} + \tau_\ell)\right)} + \tau_{HD}^2(N_D - N_H) + 2N_H\tau_{DD}(\tau_{HH} + \tau_\ell)\right)}{2(\tau_{HH} + \tau_\ell)\left(\tau_{DD}(\tau_{HH} + \tau_\ell) - \tau_{HD}^2\right)}.
\end{aligned} \tag{13}$$

When $\tau_{DD} = 2\frac{\tau_{HD}^2}{\tau_{HH}+\tau_\ell}$, the equilibrium is

$$\begin{aligned} n_{HD}^{*} &= \frac{N_D N_H}{N_D + N_H}, \\ n_{H_\ell}^{*} &= \frac{N_H^2 \tau_\ell}{(N_D + N_H)(2\tau_{HH} + \tau_\ell)}. \end{aligned} \tag{14}$$

In contrast to Section 2.1 where we are unable to verify analytically local asymptotic stability of equilibrium (7), equilibrium (13) is asymptotically stable in the positive part of the phase space.[7]

3. Discussion

In this article, we analysed a Hawk-Dove model under the assumption that all costs are measured by time lost. These costs comprise the time spent in interactions and the time fighting Hawks need to recover and form new pairs. We focus on the time a fighting Hawk needs to recover and start a new interaction. Such time can be needed due to possible injuries, or fatigue after a fight. In the case of predators competing for a prey, the recovery time can also capture the handling time the winner of the fight needs to handle the resource. As the recovery time depends on whether the Hawk won or lost the fight, we must distinguish between the winner and the loser of the contest. Such differences in recovery times between winners and loser lead to an asymmetric evolutionary game. As there are also payoff consequences when individuals are resting, we cannot use the usual approach of symmetrising the payoff matrix by assuming that each individual is equally like to be in the position of the winner or the loser. Instead, we have to deal with the asymmetric payoff bimatrix (with some undefined entries) to calculate payoffs for both winners and losers and then calculate fitnesses of Hawks and Doves as average payoffs (averaging over winners and losers payoffs).

In this article, we do not consider any other payoff costs associated with the fight which corresponds to setting $C = 0$ in the classic Hawk-Dove game. We also do not consider any additional payoffs for resting individuals, although these could be easily included in our general setup. All costs are given by time lost either in interacting or resting state. To calculate probabilities with which individuals interact with other individuals (i.e., probabilities of the four possible interacting pairs), we define distributional dynamics that describe changes in the numbers of pairs and of single loser and winner Hawks. Following the implicit assumption of evolutionary game theory, we assume that distributional dynamics operate on a fast time scale when compared with evolution and calculate the unique distributional equilibrium. We then calculate Nash equilibria for the game at this distributional equilibrium and equate stable NE with evolutionary outcomes.

We focus on the effect that resting time has on these evolutionary outcomes and show that, depending on parameters, there are three possible structures to the evolutionary outcomes (Figs. 2 and 3). First, Hawk only may be the unique evolutionary outcome. Second, both elementary strategies (i.e., Hawk, Dove) are evolutionary outcomes. Third, a mixed strategy evolutionary outcome exists together with the Hawk only evolutionary outcome. Fig. 3A shows that the mixed strategy exists when the resting times are long enough. In particular, Fig. 2A, B and Fig. 3A assume that all interaction times are the same, which, if there were no resting times, correspond to the classic Hawk-Dove game with cost set to zero (i.e., $C = 0$). The classic model predicts that Hawk strategy is the only evolutionary outcome in this case. In fact, the classic model with any nonnegative value of C never exhibits the second or third possible structures of the evolutionary outcomes. However, as we see, considering positive resting times leads to novel prediction because, as resting times increase, aggressivity in population decreases for two reasons. First, there is a mixed evolutionary outcome at which individuals play both Hawk and Dove strategy and the proportion of Dove strategy at this equilibrium increases with increased resting times. Second, although the strategy Hawk only is still an evolutionary outcome, its domain of attraction decreases with increased resting times. Fig. 3B shows the three possible structures of the evolutionary outcomes with respect to parameters τ_{HD} and τ_ℓ.

In the main body of the article, we do not consider recovery times of singles arising from interactions involving Doves, because in these interactions there is no fight. Recovery or resting times for single individuals who have interacted with a Dove can be incorporated into our model. One such extension, analysed in Appendix A, assumes that both Hawks and Doves have positive resting times which are independent of the pairs from which individuals disbanded. The extended model again has a unique positive equilibrium of the pair formation dynamics and qualitatively the same structures to evolutionary outcomes found in Section 2.2 where it is assumed that individuals who interact with a Dove require no recovery time. Our methods are general enough to treat other situations as well, but in this article we focus on those that are consistent with the classic Hawk-Dove model assumptions.

Although Dove only is never the unique evolutionary outcome, our analysis shows that when both Dove and Hawk are evolutionary outcomes, the domain of attraction of the Hawk equilibrium can be very small (e.g. Fig. 2D). In such cases, e.g., due to random perturbations or stochastic effects due to finite populations, it is likely that the population will end at the Dove only equilibrium.

The story behind the Hawk-Dove game provides an obvious example where interaction times (e.g., fighting time between two Hawks) play an integral part of the model. Our approach incorporates these times as well as times for other activities (e.g., recovery time) as costs due to time lost. We want to emphasize that these other activities are the result of the interactions and strategy of the individual, but they also consider the fitness of an individual who is no longer in a pair. The classic game theory does not consider the fitness of unpaired individuals. Clearly, other evolutionary games also have underlying times associated to different activities when individuals are unpaired. E.g., the Battle of the Sexes game (Dawkins, 1976) where philandering males when mated with fast females immediately desert and look for a new mate while the female cares for the offspring before mating again. In such circumstances, our novel concept of integrating these times into the evolutionary game theory model can be applied. In particular, we hope that this approach will find applications in the theory of biological, social and cultural evolution.

CRediT authorship contribution statement

Vlastimil Křivan: Conceptualization, Writing - review & editing. **Ross Cressman:** Conceptualization, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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[7] We calculated the trace and determinant of the Jacobian of system (12) evaluated at equilibrium (13). These are quite complex expressions but using command `Reduce` of Wolfram Mathematica we verified that for positive values of parameters the trace is negative and the determinant is positive, i.e., distributional equilibrium (13) is locally asymptotically stable.

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Appendix A. Both Hawks and Doves have resting times

In the main body of the article, we assumed that only Hawks need some resting times after a fight. One possible extension of the model is to assume that both Hawks and Doves need resting times after an interaction which leads to the following interaction time bimatrix

$$\begin{array}{c|cc} & H_\ell & D_\ell \\ \hline H_w & (\tau_{HH}+\tau_{Hw}, \tau_{HH}+\tau_{H\ell}) & (\tau_{HD}+\tau_{Hw}, \tau_{HD}+\tau_{D\ell}) \\ D_w & \text{NDF} & (\tau_{DD}+\tau_{Dw}, \tau_{DD}+\tau_{D\ell}) \end{array} \tag{A.1}$$

where we assume that winner Hawks (Doves) have resting time τ_{Hw} (τ_{Dw}) and loser Hawks (Doves) have resting time $\tau_{H\ell}$ ($\tau_{D\ell}$) independently from which pair they disbanded. Then the distributional dynamics are

$$\begin{aligned}
\frac{dn_{HH}}{dt} &= -\frac{n_{HH}}{\tau_{HH}} + \frac{\left(\frac{n_{Hw}}{\tau_{Hw}}+\frac{n_{H_\ell}}{\tau_{H\ell}}\right)^2}{2\left(\frac{n_{Hw}}{\tau_{Hw}}+\frac{n_{H_\ell}}{\tau_{H\ell}}+\frac{n_{Dw}}{\tau_{Dw}}+\frac{n_{D_\ell}}{\tau_{D\ell}}\right)} \\
\frac{dn_{HD}}{dt} &= -\frac{n_{HD}}{\tau_{HD}} + \frac{\left(\frac{n_{Hw}}{\tau_{Hw}}+\frac{n_{H_\ell}}{\tau_{H\ell}}\right)\left(\frac{n_{Dw}}{\tau_{Dw}}+\frac{n_{D_\ell}}{\tau_{D\ell}}\right)}{\left(\frac{n_{Hw}}{\tau_{Hw}}+\frac{n_{H_\ell}}{\tau_{H\ell}}+\frac{n_{Dw}}{\tau_{Dw}}+\frac{n_{D_\ell}}{\tau_{D\ell}}\right)} \\
\frac{dn_{DD}}{dt} &= -\frac{n_{DD}}{\tau_{DD}} + \frac{\left(\frac{n_{Dw}}{\tau_{Dw}}+\frac{n_{D_\ell}}{\tau_{D\ell}}\right)^2}{2\left(\frac{n_{Hw}}{\tau_{Hw}}+\frac{n_{H_\ell}}{\tau_{H\ell}}+\frac{n_{Dw}}{\tau_{Dw}}+\frac{n_{D_\ell}}{\tau_{D\ell}}\right)} \\
\frac{dn_{Hw}}{dt} &= -\frac{n_{Hw}}{\tau_{Hw}} + \frac{n_{HH}}{\tau_{HH}} + \frac{n_{HD}}{\tau_{HD}} \\
\frac{dn_{H_\ell}}{dt} &= -\frac{n_{H_\ell}}{\tau_{H\ell}} + \frac{n_{HH}}{\tau_{HH}} \\
\frac{dn_{Dw}}{dt} &= -\frac{n_{Dw}}{\tau_{Dw}} + \frac{n_{DD}}{\tau_{DD}} \\
\frac{dn_{D_\ell}}{dt} &= -\frac{n_{D_\ell}}{\tau_{D\ell}} + \frac{n_{DD}}{\tau_{DD}} + \frac{n_{HD}}{\tau_{HD}}.
\end{aligned} \tag{A.2}$$

System (A.2) has a unique positive equilibrium.[8] Payoffs evaluated at this unique equilibrium distribution are then

$$\begin{aligned}
\Pi_H &= \frac{n^*_{HH}}{2n^*_{HH}+n^*_{HD}+n^*_{Hw}+n^*_{H_\ell}}\left(\frac{\pi^w_{HH}}{\tau_{HH}+\tau_{Hw}}+\frac{\pi^\ell_{HH}}{\tau_{HH}+\tau_{H\ell}}\right)+\frac{n^*_{HD}}{2n^*_{HH}+n^*_{HD}+n^*_{Hw}+n^*_{H_\ell}}\frac{\pi_{HD}}{\tau_{HD}+\tau_{Hw}} \\
\Pi_D &= \frac{n^*_{DD}}{2n^*_{DD}+n^*_{HD}+n^*_{Dw}+n^*_{D_\ell}}\left(\frac{\pi^w_{DD}}{\tau_{DD}+\tau_{Dw}}+\frac{\pi^\ell_{DD}}{\tau_{DD}+\tau_{D\ell}}\right)+\frac{n^*_{HD}}{2n^*_{DD}+n^*_{HD}+n^*_{Dw}+n^*_{D\ell}}\frac{\pi_{DH}}{\tau_{HD}+\tau_{D\ell}}
\end{aligned} \tag{A.3}$$

where $n^*_{D_w}$ ($n^*_{D_\ell}$) is the number of single Dove winners (losers) at the equilibrium.First, suppose that the population consists entirely of Hawks, i.e., $p_H = 1$. The equilibrium pair distribution is then

$$(n^*_{HH}, n^*_{HD}, n^*_{DD}, n^*_{Hw}, n^*_{H_\ell}, n^*_{Dw}, n^*_{D_\ell}) = \left(\frac{N_H\tau_{HH}}{2\tau_{HH}+\tau_{H\ell}+\tau_{Hw}}, 0, 0, \frac{N_H\tau_{Hw}}{2\tau_{HH}+\tau_{H\ell}+\tau_{Hw}}, \frac{N_H\tau_{H\ell}}{2\tau_{HH}+\tau_{H\ell}+\tau_{Hw}}, 0, 0\right).$$

At this equilibrium, Hawk fitness is

$$\Pi_H = \frac{\tau_{HH}(\pi^\ell_{HH}(\tau_{HH}+\tau_{Hw})+\pi^w_{HH}(\tau_{HH}+\tau_{H\ell}))}{(\tau_{HH}+\tau_{H\ell})(\tau_{HH}+\tau_{Hw})(2\tau_{HH}+\tau_{H\ell}+\tau_{Hw})}.$$

Let us consider a Dove mutant in the Hawk only population. The mutant will interact only with Hawks, i.e., there will be no Dove pairs, and fitness of such Dove mutant is $\Pi_D = \frac{\pi_{DH}}{\tau_{HD}+\tau_{D\ell}}$. Thus, the Dove mutant can invade the Hawk only population when $\Pi_D > \Pi_H$, which yields

$$\frac{\pi_{DH}(2\tau_{HH}+\tau_{H\ell}+\tau_{Hw})}{\tau_{HH}(\tau_{D\ell}+\tau_{HD})} > \frac{\pi^\ell_{HH}}{\tau_{HH}+\tau_{H\ell}} + \frac{\pi^w_{HH}}{\tau_{HH}+\tau_{Hw}}.$$

We observe that, for our asymmetric Hawk-Dove game given by bimatrix (3) where $\pi_{DH} = \pi^\ell_{HH} = 0$ and $\pi^w_{HH} = V$, the above inequality simplifies to $V < 0$. As we assume that $V > 0$, Doves cannot invade the Hawk only population in our game, i.e., Hawk is always an evolutionary outcome.

Second, suppose that the population consists entirely of Doves, i.e., $p_H = 0$. The equilibrium pair distribution is then

$$(n^*_{HH}, n^*_{HD}, n^*_{DD}, n^*_{Hw}, n^*_{H_\ell}, n^*_{Dw}, n^*_{D_\ell}) = \left(0, 0, \frac{N_D\tau_{DD}}{2\tau_{DD}+\tau_{D\ell}+\tau_{Dw}}, 0, 0, \frac{N_D\tau_{Dw}}{2\tau_{DD}+\tau_{D\ell}+\tau_{Dw}}, \frac{N_D\tau_{D\ell}}{2\tau_{DD}+\tau_{D\ell}+\tau_{Dw}}\right).$$

At this equilibrium, Dove fitness is

$$\Pi_D = \frac{\tau_{DD}(\pi^\ell_{DD}(\tau_{DD}+\tau_{Dw})+\pi^w_{DD}(\tau_{DD}+\tau_{D\ell}))}{(\tau_{DD}+\tau_{D\ell})(\tau_{DD}+\tau_{Dw})(2\tau_{DD}+\tau_{D\ell}+\tau_{Dw})}.$$

Let us consider a Hawk mutant in the Dove only population. The mutant will interact only with Doves, i.e., there will be no Hawk pairs, and fitness of such Hawk mutant is $\Pi_H = \frac{\pi_{HD}}{\tau_{HD}+\tau_{Hw}}$. Thus, the Hawk mutant can invade the Dove only population when $\Pi_H > \Pi_D$, which yields

$$\frac{\pi_{HD}(2\tau_{DD}+\tau_{D\ell}+\tau_{Dw})}{\tau_{DD}(\tau_{Dw}+\tau_{HD})} > \frac{\pi^\ell_{DD}}{\tau_{DD}+\tau_{D\ell}} + \frac{\pi^w_{DD}}{\tau_{DD}+\tau_{Dw}}.$$

We observe that, for our asymmetric Hawk-Dove game given by bimatrix (3) where $\pi_{HD} = \pi^w_{DD} = V$ and $\pi^\ell_{DD} = 0$, the above inequality simplifies to

$$\frac{2\tau_{DD}+\tau_{D\ell}+\tau_{Dw}}{\tau_{DD}(\tau_{Dw}+\tau_{HD})} > \frac{1}{\tau_{DD}+\tau_{Dw}}.$$

This formula generalizes a similar result in (10).

From these results and our numerical simulations, we observe the evolutionary outcomes for the model in this Appendix are the same three types as for the model in the main text.

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[8] We calculated this equilibrium in Mathematica and verified its positivity. We do not give the formula here as it is quite complex.

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