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Bimatrix games that include interaction times alter the evolutionary outcome: The Owner–Intruder game

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ABSTRACT

Classic bimatrix games, that are based on pair-wise interactions between two opponents in two different roles, do not consider the effect that interaction duration has on payoffs. However, interactions between different strategies often take different amounts of time. In this article, we further develop a new approach to an old idea that opportunity costs lost while engaged in an interaction affect individual fitness. We consider two scenarios: (i) individuals pair instantaneously so that there are no searchers, and (ii) searching for a partner takes positive time and populations consist of a mixture of singles and pairs. We describe pair dynamics and calculate fitnesses of each strategy for a two-strategy bimatrix game that includes interaction times. Assuming that distribution of pairs (and singles) evolves on a faster time scale than evolutionary dynamics described by the replicator equation, we analyze the Nash equilibria (NE) of the time-constrained game. This general approach is then applied to the Owner–Intruder bimatrix game where the two strategies are Hawk and Dove in both roles. While the classic Owner–Intruder game has at most one interior NE and it is unstable with respect to replicator dynamics, differences in pair duration change this prediction in that up to four interior NE may exist with their stability depending on whether pairing is instantaneous or not. The classic game has either one (all Hawk) or two ((Hawk,Dove) and (Dove,Hawk)) stable boundary NE. When interaction times are included, other combinations of stable boundary NE are possible. For example, (Dove,Dove), (Dove,Hawk), or (Hawk,Dove) can be the unique (stable) NE if interaction time between two Doves is short compared to some other interactions involving Doves.

1. Introduction

Classic evolutionary game theoretical models in normal form consider two players with a finite number of strategies and a payoff matrix. Players in a large (infinite) population meet at random, interact pair-wise, and obtain their corresponding (individual) fitnesses. There are three important and somewhat hidden assumptions: (i) interaction times between two strategies are not considered, i.e., they are all assumed to be the same, (ii) the distribution of strategy pairs corresponds to random pair formation among all individuals and (iii) individual fitness accrues only through pair interactions. These assumptions fit genetic population models with two (or more) alleles at a single locus. In the genetic model, the alleles pair randomly during meiosis and the resulting distribution of genotypes is given by the Hardy–Weinberg equation. When alone, alleles cannot gain any fitness. For many phenotypic models (e.g., the Hawk–Dove, or Prisoner's dilemma), these assumptions are likely not satisfied. For example, when two aggressive individuals are in a fight, their interaction can be much longer when compared to the situation where one individual (a Dove) exits from an interaction with a Hawk (in which case the Hawk will win the contest). Because contests between different strategies can take different times, the resulting equilibrium distribution of pairs does not correspond to the Hardy–Weinberg equation.

Křivan and Cressman (2017) showed that, when individuals pair instantaneously but the interaction times are strategy dependent, the Hawk–Dove model may have a mixed ESS (i.e., an evolutionarily stable state that consists of a mixture of Hawks and Doves) when the cost of a fight is lower than the value of the contested resource. For this to happen, the interaction time between two Hawks must be long enough relative to interaction times between other strategies. Such an outcome is not possible in the

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classic Hawk–Dove game that does not consider interaction times. Similarly, for the repeated Prisoner's dilemma, provided cooperators stay together for enough rounds of the game while pairs with at least one defector disband quickly, cooperation does evolve (Křivan and Cressman, 2017). This situation arises naturally 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 (see also the opting-out game (Zhang et al., 2016)).

Moreover, individuals can gain/lose fitness when alone (e.g., individuals with different strategies may have different mortalities). While the above games do not consider singles, Křivan et al. (2018) assumed that pairing between individuals is not immediate and being single has fitness consequences. They showed that distributional dynamics alone can lead to density dependence in models (e.g., the Hawk–Dove model) that are only frequency dependent when pairing is instantaneous and all interaction times are the same.

All the models considered above are based on symmetric games (in particular, matrix games), where the two contestants are assumed to be drawn from the same population and can differ only in their choice of strategy. It is well known that various asymmetries (Broom and Rychtář, 2013) in contestants lead to qualitatively different outcomes when interaction times are not considered. A class of asymmetric games, bimatrix games, where the two contestants are drawn from two different types of individuals (e.g., two populations or two roles) was studied thoroughly in the literature (e.g., Broom and Rychtář, 2013; Cressman, 2003; Hofbauer and Sigmund, 1998). A well-known result of classic evolutionary game theory for these games is that no interior evolutionarily stable strategy exists (Selten, 1980) (i.e., no ESS where each population is a mixture of pure strategies). Furthermore, bimatrix games may have an interior Nash equilibrium (NE) but it cannot be asymptotically stable under the (bimatrix) replicator equation, the standard game dynamics of evolutionary game theory (Hofbauer and Sigmund, 1998). In particular, ESSs and asymptotically stable equilibria correspond to strict NEs of the bimatrix game (i.e., pure strategy pairs where both players do strictly worse by unilaterally changing their strategy).

Given the conceptual differences between the evolutionary outcomes of classic matrix and bimatrix games, it is important to understand the consequences of strategy-dependent interaction times by extending the analysis beyond the matrix games considered by Křivan and Cressman (2017). To this end, in this article, we study the effect of interaction time on the evolutionary outcome of bimatrix games when both populations have two strategies. We consider two pair formation processes based on the assumption that the number of individuals of each population are the same. In Section 2, as existing pairs disband, these individuals instantaneously form new pairs randomly among themselves. From the analytic expression of the equilibrium distribution of pairs at a given number of each strategy in both populations, we analyze the resulting game (i.e., investigate its NEs and their stability) when individual fitness is defined as expected payoff per unit time. When interaction times are all the same, we recover the classic results. Otherwise, more complicated evolutionary outcomes emerge such as multiple interior NEs (some of which are stable and some unstable) as well as strict NE that differ from the classic game. These possibilities are illustrated there by a thorough analysis of the Owner–Intruder game (Broom and Rychtář, 2013), the bimatrix version of the Hawk–Dove game where individuals assume one of the two roles, owner or intruder.

In Section 3, when pairs disband, the resulting singles form new pairs at random through the mass action principle with a finite encounter rate. Since the analytic expression of the equilibrium distribution of pairs at a given number of each strategy in both populations is no longer tractable unless all interaction times are the same, we analyze the Owner–Intruder game, with unequal interaction times, numerically.

2. Instantaneous pair formation

We consider a bimatrix game with two strategies denoted by e_i $(i = 1, 2)$ for the row player in population 1 and f_j $(j = 1, 2)$ for the column player in population 2. The payoff bimatrix is

$$\begin{array}{c} \\ e_1 \\ e_2 \end{array} \begin{array}{c} \begin{array}{cc} f_1 & f_2 \end{array} \\ \begin{bmatrix} \pi^e_{11}, \pi^f_{11} & \pi^e_{12}, \pi^f_{12} \\ \pi^e_{21}, \pi^f_{21} & \pi^e_{22}, \pi^f_{22} \end{bmatrix} \end{array} \tag{1}$$

where π^e_{ij} (respectively, π^f_{ij}) is the payoff to e_i (respectively f_j) when interacting with f_j (respectively e_i). In contrast to classic evolutionary game theory, we explicitly incorporate the duration of interactions into the game through the time interaction matrix

$$\begin{array}{c} \\ e_1 \\ e_2 \end{array} \begin{array}{c} \begin{array}{cc} f_1 & f_2 \end{array} \\ \begin{bmatrix} \tau_{11} & \tau_{12} \\ \tau_{21} & \tau_{22} \end{bmatrix} \end{array} \tag{2}$$

where τ_{ij} is the expected time two players using strategy e_i and f_j stay together.

In this section, we assume that, when pairs split, all these newly single individuals immediately form new pairs at random. We are interested in the equilibrium distribution of strategy pairs (e_i, f_j) for given numbers of the different strategies. Let n_{ij} be the number of strategy pair (e_i, f_j). As shown in Appendix A, pair dynamics are

$$\begin{aligned}
\frac{dn_{11}}{dt} &= -\frac{n_{11}}{\tau_{11}} + \frac{\left(\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}}\right)\left(\frac{n_{11}}{\tau_{11}} + \frac{n_{21}}{\tau_{21}}\right)}{\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{21}}{\tau_{21}} + \frac{n_{22}}{\tau_{22}}} \\
\frac{dn_{12}}{dt} &= -\frac{n_{12}}{\tau_{12}} + \frac{\left(\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}}\right)\left(\frac{n_{12}}{\tau_{12}} + \frac{n_{22}}{\tau_{22}}\right)}{\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{21}}{\tau_{21}} + \frac{n_{22}}{\tau_{22}}} \\
\frac{dn_{21}}{dt} &= -\frac{n_{21}}{\tau_{21}} + \frac{\left(\frac{n_{21}}{\tau_{21}} + \frac{n_{22}}{\tau_{22}}\right)\left(\frac{n_{11}}{\tau_{11}} + \frac{n_{21}}{\tau_{21}}\right)}{\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{21}}{\tau_{21}} + \frac{n_{22}}{\tau_{22}}} \\
\frac{dn_{22}}{dt} &= -\frac{n_{22}}{\tau_{22}} + \frac{\left(\frac{n_{21}}{\tau_{21}} + \frac{n_{22}}{\tau_{22}}\right)\left(\frac{n_{12}}{\tau_{12}} + \frac{n_{22}}{\tau_{22}}\right)}{\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{21}}{\tau_{21}} + \frac{n_{22}}{\tau_{22}}}
\end{aligned} \tag{3}$$

and the equilibrium distribution satisfies

$$\frac{n_{ij}}{\tau_{ij}} = \frac{\left(\frac{n_{i1}}{\tau_{i1}} + \frac{n_{i2}}{\tau_{i2}}\right)\left(\frac{n_{1j}}{\tau_{1j}} + \frac{n_{2j}}{\tau_{2j}}\right)}{\left(\frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} + \frac{n_{21}}{\tau_{21}} + \frac{n_{22}}{\tau_{22}}\right)} \quad \text{for } i, j = 1, 2. \tag{4}$$

Intuitively, at equilibrium, the number of disbanding (e_i, f_j) pairs per unit time (i.e., the left-hand side $\frac{n_{ij}}{\tau_{ij}}$ of (4)) must equal the number of newly formed (e_i, f_j) pairs from the newly single e_i strategists $\left(\frac{n_{i1}}{\tau_{i1}} + \frac{n_{i2}}{\tau_{i2}}\right)$ and f_j strategists $\left(\frac{n_{1j}}{\tau_{1j}} + \frac{n_{2j}}{\tau_{2j}}\right)$.

We observe that at the equilibrium distribution, $\frac{n_{ij}}{\tau_{ij}}$ satisfy the generalized Hardy–Weinberg equation, i.e.,

$$\frac{n_{11}}{\tau_{11}}\frac{n_{22}}{\tau_{22}} = \frac{n_{12}}{\tau_{12}}\frac{n_{21}}{\tau_{21}}. \tag{5}$$

Given the number of e_1 and f_1 strategists ($N_{e_1} = n_{11} + n_{12}$ and $N_{f_1} = n_{11} + n_{21}$, respectively) as well as the total number of individuals $N = n_{11} + n_{12} + n_{21} + n_{22}$ in either population, Appendix A shows that the unique nonnegative solution to (4) and

(5) is (assuming $\tau_{12}\tau_{21} \neq \tau_{11}\tau_{22}$)

$$
\begin{aligned}
n_{11} &= \frac{\sqrt{A} + (N_{e_1} + N_{f_1})(\tau_{12}\tau_{21} - \tau_{11}\tau_{22}) - N\tau_{12}\tau_{21}}{2(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})},\\
n_{12} &= \frac{-\sqrt{A} + (N_{e_1} - N_{f_1})(\tau_{12}\tau_{21} - \tau_{11}\tau_{22}) + N\tau_{12}\tau_{21}}{2(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})},\\
n_{21} &= \frac{-\sqrt{A} - (N_{e_1} - N_{f_1})(\tau_{12}\tau_{21} - \tau_{11}\tau_{22}) + N\tau_{12}\tau_{21}}{2(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})},\\
n_{22} &= \frac{\sqrt{A} - (N_{e_1} + N_{f_1})(\tau_{12}\tau_{21} - \tau_{11}\tau_{22}) + N(\tau_{12}\tau_{21} - 2\tau_{11}\tau_{22})}{2(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})},
\end{aligned}
\tag{6}
$$

where

$$
\begin{aligned}
A = {} & (N\tau_{12}\tau_{21} - (N_{e_1} + N_{f_1})(\tau_{12}\tau_{21} - \tau_{11}\tau_{22}))^2\\
& + 4N_{e_1}N_{f_1}\tau_{11}\tau_{22}(\tau_{12}\tau_{21} - \tau_{11}\tau_{22}).
\end{aligned}
\tag{7}
$$

When $\tau_{12}\tau_{21} = \tau_{11}\tau_{22}$ the above distributional equilibrium corresponds to the standard Hardy–Weinberg distribution

$$
(n_{11}, n_{12}, n_{21}, n_{22}) = \left(\frac{N_{e_1}N_{f_1}}{N}, \frac{N_{e_1}N_{f_2}}{N}, \frac{N_{e_2}N_{f_1}}{N}, \frac{N_{e_2}N_{f_2}}{N}\right) \tag{8}
$$

where $N_{e_2} \equiv N - N_{e_1}$ and $N_{f_2} \equiv N - N_{f_1}$. This is an important special case since it includes the classic situation, i.e., all interaction times are the same ($\tau_{11} = \tau_{12} = \tau_{21} = \tau_{22}$).

2.1. Fitness and evolutionary outcomes

Following Křivan and Cressman (2017), we define fitness as the expected payoff that an individual of a given phenotype obtains per unit of interaction time. For example, let us consider an individual playing strategy e_1 in population 1. The probability that this individual is paired with an individual playing strategy f_1 is $n_{11}/(n_{11} + n_{12})$ and with an individual playing strategy f_2 is $n_{12}/(n_{11} + n_{12})$. When paired with an individual playing strategy f_1, the focal individual receives payoff π^e_{11}/τ_{11} per unit of time. Similarly, when paired with an individual playing strategy f_2, the focal individual gets payoff π^e_{12}/τ_{12} per unit of time. Thus, the focal individual has expected payoff (i.e., fitness) Π_{e_1} given by the first equation in (9). The fitness for individuals playing e_2 and those in the second population are calculated analogously, which leads to ($i, j = 1, 2$)

$$
\begin{aligned}
\Pi_{e_i} &= \frac{n_{i1}}{n_{i1} + n_{i2}}\frac{\pi^e_{i1}}{\tau_{i1}} + \frac{n_{i2}}{n_{i1} + n_{i2}}\frac{\pi^e_{i2}}{\tau_{i2}}\\
\Pi_{f_j} &= \frac{n_{1j}}{n_{1j} + n_{2j}}\frac{\pi^f_{1j}}{\tau_{1j}} + \frac{n_{2j}}{n_{1j} + n_{2j}}\frac{\pi^f_{2j}}{\tau_{2j}}.
\end{aligned}
\tag{9}
$$

The corresponding time-constrained bimatrix game based on payoff bimatrix (1) and time interaction matrix (2) is then the two-strategy game with payoffs given by the fitness functions (9) evaluated at the distributional equilibrium (6) for fixed size N of each population.[1]

To analyze this time-constrained bimatrix game, we examine how its NE structure depends on model parameters. We start by looking for NE in pure strategies (i.e., both populations are monomorphic) before considering NE where both populations are polymorphic (i.e., the interior NE later in this section) and boundary NE (where exactly one population is polymorphic) in Section 2.3. Let us consider the equilibrium where all individuals of population 1 play strategy e_1 while all individuals of the second population play strategy f_1. Then $n_{11} = N$ and fitnesses of residents are $\Pi_{e_1} = \frac{\pi^e_{11}}{\tau_{11}}$ and $\Pi_{f_1} = \frac{\pi^f_{11}}{\tau_{11}}$. Now consider a mutant of the first population playing strategy e_2 in the resident system. This mutant can pair only with f_1−strategists in which case its fitness is $\Pi_{e_2} = \frac{\pi^e_{21}}{\tau_{21}}$. Similarly, $\Pi_{f_2} = \frac{\pi^f_{12}}{\tau_{12}}$. Thus, the strategy (e_1, f_1) cannot be invaded if $\frac{\pi^e_{21}}{\tau_{21}} < \frac{\pi^e_{11}}{\tau_{11}}$ and $\frac{\pi^f_{12}}{\tau_{12}} < \frac{\pi^f_{11}}{\tau_{11}}$, in which case (e_1, f_1) is a strict NE.[2] Similar considerations for other pure strategy pairs show that a strategy (e_i, f_j) is a strict NE for the fitness functions given in (9) if it is a strict NE of the classic game given by a time-adjusted payoff bimatrix

$$
\begin{array}{c} \\ e_1 \\ e_2 \end{array}
\begin{array}{c} \begin{array}{cc} f_1 & f_2 \end{array} \\
\begin{bmatrix} \left(\frac{\pi^e_{11}}{\tau_{11}}, \frac{\pi^f_{11}}{\tau_{11}}\right) & \left(\frac{\pi^e_{12}}{\tau_{12}}, \frac{\pi^f_{12}}{\tau_{12}}\right) \\ \left(\frac{\pi^e_{21}}{\tau_{21}}, \frac{\pi^f_{21}}{\tau_{21}}\right) & \left(\frac{\pi^e_{22}}{\tau_{22}}, \frac{\pi^f_{22}}{\tau_{22}}\right) \end{bmatrix}
\end{array}. \tag{10}
$$

We remark that the inequality conditions for a strict NE are independent of population size. Furthermore, the fitness functions (9) when the populations are not monomorphic are convex combinations of the appropriate entries in the time-adjusted payoff bimatrix (e.g., $\Pi_{e_1} = \alpha\frac{\pi^e_{11}}{\tau_{11}} + (1-\alpha)\frac{\pi^e_{12}}{\tau_{12}}$ for some $0 \le \alpha \le 1$). It is the same for the classic bimatrix game except that for us α is no longer a linear function of the strategy frequencies of the other population since the distributional equilibrium is not the standard Hardy–Weinberg distribution. In fact, α depends on population size N as well.

A strict NE can be pictured as corresponding to a particular vertex of the unit square (cf. Fig. 2 with the axes scaled to be frequencies of the first strategy in each population instead of numbers and with vertices given as solid dots corresponding to strict NE). It is well-known (see Figs. 10.1, 10.2, 11.1 in Hofbauer and Sigmund, 1998, or Figs. 3.3.1, 3.3.2, 3.3.3 in Cressman, 2003) that a classic two-strategy bimatrix game may have no strict NE, exactly one strict NE (e.g., Fig. 2A), or exactly two strict NE that are diagonally opposite each other (e.g., Fig. 2E). Furthermore, the classic two-strategy bimatrix game (with nondegenerate payoff bimatrix) can be classified by its strict NE and its interior NE (i.e., its unique NE where both populations are polymorphic) if it exists.

By examining interior NE, we will see this classification method fails for two-strategy time-constrained bimatrix games (see Section 2.2). These equilibria must satisfy $\Pi_{e_1} = \Pi_{e_2}$ and $\Pi_{f_1} = \Pi_{f_2}$ so that neither phenotype can increase its payoff by unilaterally switching its strategy. Unfortunately, obtaining analytic formulas for interior NE seems to be out of reach except in two special cases.

One special case is when interaction times satisfy $\tau_{12}\tau_{21} = \tau_{11}\tau_{22}$. Then the payoffs (9) evaluated at the equilibrium distribution (8) are the same as the payoffs for the classic bimatrix game with payoff matrix given by the time adjusted payoff matrix (10), i.e.,

$$
\begin{aligned}
\Pi_{e_i} &= \frac{N_{f_1}}{N}\frac{\pi^e_{i1}}{\tau_{i1}} + \frac{N_{f_2}}{N}\frac{\pi^e_{i2}}{\tau_{i2}}\\
\Pi_{f_j} &= \frac{N_{e_1}}{N}\frac{\pi^f_{1j}}{\tau_{1j}} + \frac{N_{e_2}}{N}\frac{\pi^f_{2j}}{\tau_{2j}},
\end{aligned}
\tag{11}
$$

[1] We will use the phrase “fitness functions” rather than “payoffs” for these time-constrained games from now on to avoid confusion with payoffs in (1).

[2] If (e_1, f_1) is a strict NE, it must also resist invasion by mutants in population 1 that use any other strategy (including a mixed strategy) besides e_1. However, since the fitness of the focal mutant is linear in the components of its mixed strategy, it is enough to verify (e_1, f_1) cannot be invaded by the pure strategy e_2 (and by f_2 in population 2).

where $i, j = 1, 2$, and the interior NE simplifies to

$$(N_{e_1}, N_{f_1}) = \left(\frac{N\tau_{12}(\pi^f_{22}\tau_{21} - \pi^f_{21}\tau_{22})}{\tau_{22}(\pi^f_{11}\tau_{22} - \pi^f_{12}\tau_{21}) + \tau_{12}(\pi^f_{22}\tau_{21} - \pi^f_{21}\tau_{22})}, \frac{N\tau_{21}(\pi^e_{22}\tau_{12} - \pi^e_{12}\tau_{22})}{\tau_{22}(\pi^e_{11}\tau_{22} - \pi^e_{12}\tau_{21}) + \tau_{12}(\pi^e_{22}\tau_{21} - \pi^e_{21}\tau_{22})} \right) \quad (12)$$

whenever both components are strictly between 0 and N. In fact, this is the interior NE of the classic bimatrix game with time-adjusted bimatrix (10).

The other special case is interior symmetric NE (i.e., those on the main diagonal where $N_{e_1} = N_{f_1}$) for role-independent time constrained bimatrix games. As discussed in Section 2.2, there are up to two such diagonal interior symmetric NE and the formulas for these are given in Křivan and Cressman (2017).

To find interior NE in the general case, we can instead consider the replicator equation at fixed population size N. This dynamics is given by[3]

$$\frac{dN_{e_1}}{dt} = \frac{N_{e_1}(N - N_{e_1})}{N}(\Pi_{e_1}(N_{e_1}, N_{f_1}) - \Pi_{e_2}(N_{e_1}, N_{f_1}))$$
$$\frac{dN_{f_1}}{dt} = \frac{N_{f_1}(N - N_{f_1})}{N}(\Pi_{f_1}(N_{e_1}, N_{f_1}) - \Pi_{f_2}(N_{e_1}, N_{f_1})) \quad (13)$$

where $\Pi_{e_i}(N_{e_1}, N_{f_1})$ and $\Pi_{f_i}(N_{e_1}, N_{f_1})$ are fitnesses (9) evaluated at the equilibrium distribution (6) for a given (N_{e_1}, N_{f_1}). Rest points of the replicator equation with N_{e_1} and N_{f_1} strictly between 0 and N are the interior NE of the underlying game (Hofbauer and Sigmund, 1998). Moreover, when all $\tau_{ij} = \tau$ are equal, the dynamics (13) is the replicator equation of the classic bimatrix game (up to the factor τ that only affects the speed along trajectories and not the evolutionary outcome).

Through the Owner-Intruder game with time-constraints, we illustrate the two special cases mentioned above (i.e., either $\tau_{12}\tau_{21} = \tau_{11}\tau_{22}$ or interior symmetric NE) as well as the replicator method for the general case.

2.2. Owner–Intruder game

The classic owner intruder game (Broom and Rychtář, 2013; Cressman, 2003; Hofbauer and Sigmund, 1998; Maynard Smith, 1982) is the two-role extension of the symmetric Hawk–Dove game (i.e., matrix game) that models the situation in which an individual either owns a site or is an intruder trying to seize a site. An individual can either be a Hawk (strategy e_1 if owner and f_1 if intruder) or a Dove (strategy e_2 if owner and f_2 if intruder) in either of the two roles. The payoff bimatrix of the game is

Owner\Intruder	Hawk	Dove
Hawk	$\frac{V-C}{2}, \frac{V-C}{2}$	$V, 0$
Dove	$0, V$	$\frac{V}{2}, \frac{V}{2}$

where V (the value attached to the site) and C (the cost of fighting) are positive. It is an example of a role-independent bimatrix game since an individual's payoff depends only on the strategies used in the interaction and not on whether the individual is the owner or the intruder.[4]

When the cost of fighting is low ($C < V$), the classic game has a single NE $(e_1, f_1) = (H, H)$ where individuals in both positions behave as hawks. When the cost of fighting is high ($C > V$) there are two strict NE $(e_2, f_1) = (D, H)$ and $(e_1, f_2) = (H, D)$ as well as a mixed NE $(p_1, q_1) = (V/C, V/C)$, where Hawk strategy is played with probability V/C in both roles. This mixed NE cannot be a (two-species) ESS, because bimatrix games can have ESSs only in pure strategies (Selten, 1980).[5]

For the time-constrained bimatrix game, we first analyze its strict NE through the following time-adjusted bimatrix (cf. (10))

Owner\Intruder	Hawk	Dove
Hawk	$\frac{V-C}{2\tau_{11}}, \frac{V-C}{2\tau_{11}}$	$\frac{V}{\tau_{12}}, 0$
Dove	$0, \frac{V}{\tau_{21}}$	$\frac{V}{2\tau_{22}}, \frac{V}{2\tau_{22}}$

The following list contains all strict NE of the time-constrained Owner–Intruder game (Fig. 1). After each item in this list, the panels in Fig. 2 that have this strict NE are indicated in parentheses.

- If $V > C$, then strategy (H, H) is a NE (e.g., Fig. 2A–D).
- If $\tau_{12} > 2\tau_{22}$ and $\tau_{21} > 2\tau_{22}$, then strategy (D, D) is a NE (e.g., Fig. 2B, F, G, H).
- If $V < C$ and $\tau_{12} < 2\tau_{22}$, then strategy (H, D) is a NE (e.g., Fig. 2E, J).
- If $V < C$ and $\tau_{21} < 2\tau_{22}$, then strategy (D, H) is a NE (e.g., Fig. 2E, I).

Dependence of strict NEs as a function of model parameters are shown in Fig. 1. There is at least one strict NE for all parameter values except in the degenerate situations where $V = C$, $\tau_{12} = 2\tau_{22}$, or $\tau_{21} = 2\tau_{22}$ (these are the dashed lines in Fig. 1) that are discussed in Section 2.3.

Of particular note is that, although strategy pair (Dove, Dove) is never an ESS (i.e. a strict NE) for the classic Owner–Intruder game (since Dove is never an ESS for the Hawk–Dove matrix game), this pair is a strict NE when $2\tau_{22} < \min\{\tau_{12}, \tau_{21}\}$. This analysis shows that when compared with the classical model, the model that considers duration of interactions can have strategy (D, D) as a NE provided the interaction time between Doves is small.

In the special case where interaction times satisfy $\tau_{12}\tau_{21} = \tau_{11}\tau_{22}$, the interior NE (provided it exists) is given by (12) as

$$(N_{e_1}, N_{f_1}) = \left(\frac{N\tau_{12}V(\tau_{21} - 2\tau_{22})}{\tau^2_{22}(V - C) + \tau_{12}V(\tau_{21} - 2\tau_{22})}, \frac{N\tau_{21}V(\tau_{12} - 2\tau_{22})}{(V - C)\tau^2_{22} + \tau_{21}V(\tau_{12} - 2\tau_{22})} \right).$$

We observe that when all interaction times are the same, the interior equilibrium is $(N_{e_1}, N_{f_1}) = (NV/C, NV/C)$ exactly as in the classical Owner–Intruder game.

To investigate interior NE further for the Owner–Intruder game, fitness functions (9) are now

$$\Pi_{e_1} = \frac{n_{11}(V - C)}{2\tau_{11}(n_{11} + n_{12})} + \frac{n_{12}V}{\tau_{12}(n_{11} + n_{12})},$$
$$\Pi_{e_2} = \frac{n_{22}V}{2\tau_{22}(n_{21} + n_{22})},$$
$$\Pi_{f_1} = \frac{n_{11}(V - C)}{2\tau_{11}(n_{11} + n_{21})} + \frac{n_{21}V}{\tau_{21}(n_{11} + n_{21})}, \quad (14)$$
$$\Pi_{f_2} = \frac{n_{22}V}{2\tau_{22}(n_{12} + n_{22})}.$$

[3] Replicator dynamics at fixed population size assume that frequencies of e_1 strategists p_1 are described by $\frac{dp_1}{dt} = p_1(1 - p_1)(\Pi_{e_1}(N_{e_1}, N_{f_1}) - \Pi_{e_2}(N_{e_1}, N_{f_1}))$ (Hofbauer and Sigmund, 1998). Because $N_{e_1} = p_1 N$ and the overall size N of population 1 is assumed to be fixed, we obtain $\frac{dN_{e_1}}{dt} = \frac{dp_1}{dt}N$ which yields the first equation in (13).

[4] Broom and Rychtář (2013) refer to role independence as an "uncorrelated asymmetry" (see also the role games of Hofbauer and Sigmund (1998)). Mathematically, role independence is equivalent to the second payoff entries in the bimatrix forming the transpose of the matrix of first entries. It is assumed that the pure strategy sets for both roles are the same as well as the ordering of their elements. Typically, the strategies are given the same name in both roles (e.g., Hawk and Dove) and the same order. Every role-independent bimatrix game is the two-role extension of a symmetric matrix game and has NE where both populations use the same strategy; namely, a NE of the matrix game. In addition, there may be other NE.

[5] In fact, a strategy pair is an ESS for a classic bimatrix game if and only if it is a strict NE.

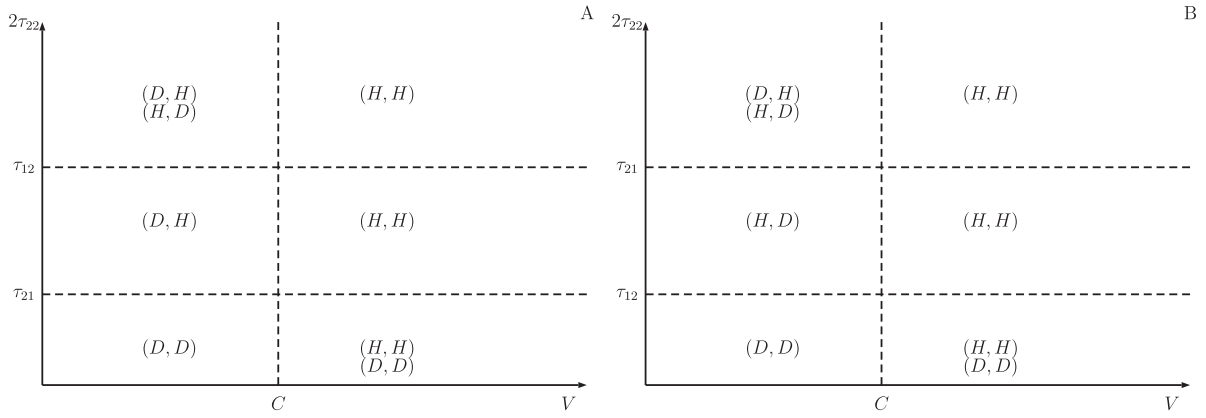

Fig. 1. Strict NE of the Owner–Intruder game as functions of V and $2\tau_{22}$ parameters. Panel A assumes that $\tau_{21} < \tau_{12}$ and panel B assumes the opposite inequality.

Evaluating these at the equilibrium distribution (6) yields

$$\Pi_{e_1} = \frac{(C\tau_{12} + (2\tau_{11} - \tau_{12})V)\left(\sqrt{A} - N\tau_{12}\tau_{21}\right)}{4N_{e_1}\tau_{11}\tau_{12}(\tau_{11}\tau_{22} - \tau_{12}\tau_{21})} + \frac{\tau_{12}(V-C)\left(N_{e_1} + N_{f_1}\right) + 2\tau_{11}V\left(N_{e_1} - N_{f_1}\right)}{4N_{e_1}\tau_{11}\tau_{12}}$$

$$\Pi_{e_2} = -\frac{V\left(\sqrt{A} + N(\tau_{12}\tau_{21} - 2\tau_{11}\tau_{22}) - \left(N_{e_1} + N_{f_1}\right)(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})\right)}{4\tau_{22}(N - N_{e_1})(\tau_{11}\tau_{22} - \tau_{12}\tau_{21})}$$

$$\Pi_{f_1} = -\frac{\sqrt{A}(C\tau_{21} + (2\tau_{11} - \tau_{21})V)}{4N_{f_1}\tau_{11}\tau_{21}(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})} + \frac{N\tau_{12}(C\tau_{21} + 2\tau_{11}V - \tau_{21}V)}{4N_{f_1}\tau_{11}(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})} - \frac{(C-V)\left(N_{e_1} + N_{f_1}\right)}{4N_{f_1}\tau_{11}} + \frac{2\tau_{11}V\left(N_{f_1} - N_{e_1}\right)}{4N_{f_1}\tau_{11}\tau_{21}}$$

$$\Pi_{f_2} = -\frac{V\left(\sqrt{A} + N(\tau_{12}\tau_{21} - 2\tau_{11}\tau_{22}) - \left(N_{e_1} + N_{f_1}\right)(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})\right)}{4\tau_{22}\left(N - N_{f_1}\right)(\tau_{11}\tau_{22} - \tau_{12}\tau_{21})},$$

where A is given in (7). To find interior NE, we need to solve $\Pi_{e_1} = \Pi_{e_2}$ and $\Pi_{f_1} = \Pi_{f_2}$.

Two-strategy, bimatrix games that are role-independent have role-independent interaction times if and only if $\tau_{12} = \tau_{21}$ (i.e., the length of Hawk–Dove interactions does not depend on whether the Hawk is the owner or the intruder).[6] Symmetric NE of the role-independent time-constrained Owner–Intruder game are then those of the time-constrained Hawk–Dove matrix game, which are found analytically in Křivan and Cressman (2017) using `Solve` command of Mathematica 11.

Since attempts to use this method to find interior NE when the time-constrained bimatrix game was not role-independent or interaction times did not satisfy $\tau_{12}\tau_{21} = \tau_{11}\tau_{22}$ failed, we now analyze the NE of the Owner–Intruder game numerically through the replicator equation, focusing on the cases where $V > C$ and $V < C$ separately.

First, assume that $V > C$ (Fig. 2, panels A–D). Then (H, H) is always a strict NE. When the time-constrained Owner–Intruder game is role-independent, the replicator equation is invariant along the main diagonal of the unit square and its trajectories in the unit square are reflections in the main diagonal (Fig. 2A,B,C). Furthermore, on the diagonal, the dynamics (13) restricts to the replicator equation for the time-constrained Hawk–Dove matrix game, which was analyzed by Křivan and Cressman (2017). They showed that, when interaction times between two Hawks are long enough (and all other interaction times are the same), there exist two (symmetric) interior NEs and the one with fewer Hawks is locally asymptotically stable while the other one is unstable. However, numerical simulations (e.g., Fig. 2C) show that both interior symmetric NE (i.e., those gray points that are on the main diagonal) are saddles (i.e., unstable) for the bimatrix replicator dynamics.[7]

Simulations of the replicator equation for the role-independent time-constrained Owner–Intruder game with $V > C$ show that long interaction times between Hawks now lead to two new asymmetric interior NE (i.e., those off the main diagonal shown as black interior dots in Fig. 2C). Numerical simulations suggest that these two equilibria are neutrally stable as they appear to be surrounded by a family of closed trajectories. The domain of the phase space filled by these closed curves is separated from the rest by two heteroclinic orbits that join the two symmetric NE. In particular, the symmetric strict NE (H, H) where all individuals play Hawk is not globally asymptotically stable.

The neutral stability of the asymmetric NE disappears when the time interaction matrix is role dependent. For example, it is reasonable to assume that interaction time between intruding Hawk and owning Dove is longer than that between intruding Dove and owning Hawk (i.e., $\tau_{21} > \tau_{12}$) because an owning Dove tries to defend its site against attacking Hawk. This role-dependent interaction time makes one of the two interior asymmetric NE unstable while the other becomes locally asymptotically stable (Fig. 2D).

Now assume that $V < C$ (Fig. 2, panels E–K). Hawk is no longer an ESS for the classic Hawk–Dove game and the only NE is the interior ESS where the population plays Hawk with probability $\frac{V}{C}$. On the other hand, the classic Owner–Intruder game has two strict NE (H, D) and (D, H)[8] and the unstable interior NE where both populations plays Hawk with probability $\frac{V}{C}$. This corresponds to the time-constrained game with all interaction times equal (Fig. 2E). When Hawk–Dove interactions are sufficiently long compared to Dove–Dove interactions (specifically, $\tau_{21} > 2\tau_{22}$ and $\tau_{12} > 2\tau_{22}$), then (D, D) is the only NE (Fig. 2F). With a lower cost (Fig. 2G), two symmetric interior NE appear (they are both saddles) along with two neutrally stable asymmetric interior NE that are surrounded by a family of closed trajectories. Furthermore, a small perturbation of these NE by introducing a slight role dependence in interaction times makes one of them locally asymptotically stable and

[6] We call a multi-strategy time-constrained bimatrix game "role-independent" if both its payoff bimatrix and its time interaction matrix are role-independent. This last requirement is equivalent to the time interaction matrix being symmetric (i.e., $\tau_{ij} = \tau_{ji}$ for all i, j).

[7] From extensive simulations of the replicator equation, it seems likely that any interior symmetric NE of two-strategy role-independent time-constrained bimatrix games are always saddles but we have no proof of this conjecture. In the special case where $\tau_{12}\tau_{21} = \tau_{11}\tau_{22}$ (and $\tau_{12} = \tau_{21}$), interior symmetric NE are saddles since, from (11), Π_{e_1} (and Π_{f_1}) depends only on the strategy frequency of the other population, implying that the Jacobian of replicator dynamics (13) evaluated at interior equilibrium (12) has zeros on the main diagonal. This extends the same well-known result for classic role-independent bimatrix games (Hofbauer and Sigmund, 1998).

[8] The second strict NE is often called the "paradoxical ESS" (Maynard Smith, 1982) since it corresponds to the intruder always taking over the site and becoming the owner.

the other unstable (panel H). Larger differences for role dependent interaction times (panels I and J respectively) eliminate interior NE altogether and make the paradoxical ESS (D, H) (respectively, (H, D)) globally asymptotically stable. Panel K is a degenerate case where $\tau_{12} = \tau_{21} = 2\tau_{22}$ and so has boundary NE as discussed in the following section.

Finally, panel L assumes $V = C = 1$, $\tau_{11} = 3$ and all other interaction times are 1. This parametrization corresponds to the situation where sets of the NE along the boundary of square $[0, N] \times [0, N]$ exist. As calculated in the following section, the sets of NE are $0 \le N_{e_1} < \frac{3}{4}N$ when $N_{f_1} = N$ and $0 \le N_{f_1} < \frac{3}{4}N$ when $N_{e_1} = N$.

2.3. Boundary NE

The previous two sections analyzed the strict NE and interior NE for two-strategy time-constrained bimatrix games. These games may also have NE on an edge of the square that are not at a vertex (i.e., partially mixed NE where only one of the two populations is polymorphic). For example, suppose that population 1 is polymorphic and population 2 is monomorphic at pure strategy f_1, i.e., $N_{f_1} = N$. Then, at a NE on this edge, the fitnesses of both strategies of population 1 must be equal, i.e., $\Pi_{e_1} = \Pi_{e_2}$. Since $n_{12} = n_{22} = 0$, $\Pi_{e_1} = \frac{\pi^e_{11}}{\tau_{11}}$ and $\Pi_{e_2} = \frac{\pi^e_{21}}{\tau_{21}}$ from (9).[9] In this degenerate case where $\frac{\pi^e_{11}}{\tau_{11}} = \frac{\pi^e_{21}}{\tau_{21}}$, a point along the edge $N_{f_1} = N$ is a NE if and only if $\Pi_{f_1} \ge \Pi_{f_2}$. Since $n_{21} = N_{e_2}$, $n_{11} = N_{e_1}$ and $N = N_{e_1} + N_{e_2}$,

$$\Pi_{f_1} = \frac{N_{e_1}}{N}\frac{\pi^f_{11}}{\tau_{11}} + \frac{N_{e_2}}{N}\frac{\pi^f_{21}}{\tau_{21}}. \tag{15}$$

On the other hand, the invasion fitness of strategy f_2 when there are no individuals playing this strategy is (see Appendix B)

$$\Pi_{f_2} = \frac{N_{e_1}\pi^f_{12}\tau_{21} + N_{e_2}\pi^f_{22}\tau_{11}}{N\tau_{11}\tau_{22} + N_{e_1}(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})}. \tag{16}$$

Solving $\Pi_{f_1} = \Pi_{f_2}$ gives us, in general, up to two roots for N_{e_1} satisfying $0 \le N_{e_1} \le N$. These roots divide the edge into closed subintervals, on each of which $\Pi_{f_1} - \Pi_{f_2}$ does not change sign. Each such subinterval with this difference nonnegative is then a connected set of NE.[10] However, since each point on this edge is a rest point of the replicator equation, none can be asymptotically stable under this dynamics.

For the Owner–Intruder game, boundary NE emerge on the top edge of the square $[0, N] \times [0, N]$ where $N_{f_1} = N$ when $V = C$ since $\frac{\pi^e_{11}}{\tau_{11}} = \frac{\pi^e_{21}}{\tau_{21}} = 0$ along this edge. By evaluating when $\Pi_{f_1} \ge \Pi_{f_2}$ along this edge, we find the following three cases for sets of NE of the form (N_{e_1}, N):

1. $\tau_{11} \le 2\tau_{12}$ and $\tau_{21} < 2\tau_{22}$ and $0 \le N_{e_1} \le N$
2. $\tau_{11} > 2\tau_{12}$ and $\tau_{21} < 2\tau_{22}$ and $0 \le N_{e_1} \le \frac{N\tau_{11}(\tau_{21} - 2\tau_{22})}{2(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})}$
3. $\tau_{11} < 2\tau_{12}$ and $\tau_{21} \ge 2\tau_{22}$ and $\frac{N\tau_{11}(\tau_{21} - 2\tau_{22})}{2(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})} \le N_{e_1} \le N$.

Similarly, let us consider the right edge of the square where all individuals of the first species play strategy Hawk, i.e., $N_{e_1} = N$. When $V = C$, this leads to the following sets of NE for the Owner–Intruder game:

1. $\tau_{11} \le 2\tau_{21}$ and $\tau_{12} < 2\tau_{22}$ and $0 \le N_{f_1} \le N$
2. $\tau_{11} > 2\tau_{21}$ and $\tau_{12} < 2\tau_{22}$ and $0 \le N_{f_1} \le \frac{N\tau_{11}(\tau_{12} - 2\tau_{22})}{2(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})}$
3. $\tau_{11} < 2\tau_{21}$ and $\tau_{12} > 2\tau_{22}$ and $\frac{N\tau_{11}(\tau_{12} - 2\tau_{22})}{2(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})} \le N_{f_1} \le N$.

[9] In classic two-strategy bimatrix games, the pure strategy pair (e_1, f_1) may be a NE in this situation but not a strict NE. We have ignored this degenerate case in the classification of pure strategy NE in Sections 2.1 and 2.2 of our time-constrained bimatrix game through (10) above.

[10] In classical games, this set is called a NE component (Cressman, 2003).

These sets of NE on the boundary are illustrated in Fig. 2L for the role-independent time-constrained Owner–Intruder game with $V = C$. From Křivan and Cressman (2017) the interior NE in this figure appears for $\tau_{11} > \tau(3 - C/V + 2\sqrt{1 - C/V}) = 2\tau$ (assuming $\tau_{12} = \tau_{22} = \tau$). In this case the NEs on the edges form two disconnected components. Since $\tau_{12} = \tau_{21}$, the NE component on the upper edge is then the reflection in the main diagonal of the component on the right-hand edge.

We note that sets of NE also appear (Fig. 2K) on the lower (respectively, left-hand) edges of the square when $\tau_{12} = 2\tau_{22}$ (respectively, $\tau_{21} = 2\tau_{22}$). By other choices of interaction time τ_{11} we can also get disconnected components along these edges.

3. Non instantaneous pair formation

So far we have assumed that pair formation is instantaneous, i.e., there are no singles. This assumption is natural in population genetics, where alleles exist as singles only during meiosis but otherwise they are always paired in diploid individuals. However, since it may be more realistic in general to assume that it takes some time for singles to form pairs, we consider both singles and paired individuals in this section. We also assume that, when a pair disbands, these new singles are ready immediately to start searching for new partners with encounter rate λ and new pairs are formed by random encounters between one single from each population.[11]

The number of singles of the two strategies for population 1 are denoted by n_{e_i} for $i = 1, 2$ and for population 2 by n_{f_j} for $j = 1, 2$. Then

$$\begin{aligned} N_{e_i} &= n_{e_i} + n_{i1} + n_{i2} \\ N_{f_j} &= n_{f_j} + n_{1j} + n_{2j} \end{aligned} \tag{17}$$

are the total number of individuals playing a given strategy. We continue to assume that the total number of individuals in each population is N (i.e., $N_{e_1} + N_{e_2} = N = N_{f_1} + N_{f_2}$).

Distributional dynamics of singles and pairs when pair formation is described by the mass action law are then

$$\begin{aligned}
\frac{dn_{e_1}}{dt} &= -\lambda n_{e_1}(n_{f_1} + n_{f_2}) + \frac{n_{11}}{\tau_{11}} + \frac{n_{12}}{\tau_{12}} \\
\frac{dn_{e_2}}{dt} &= -\lambda n_{e_2}(n_{f_1} + n_{f_2}) + \frac{n_{21}}{\tau_{21}} + \frac{n_{22}}{\tau_{22}} \\
\frac{dn_{f_1}}{dt} &= -\lambda n_{f_1}(n_{e_1} + n_{e_2}) + \frac{n_{11}}{\tau_{11}} + \frac{n_{21}}{\tau_{21}} \\
\frac{dn_{f_2}}{dt} &= -\lambda n_{f_2}(n_{e_1} + n_{e_2}) + \frac{n_{12}}{\tau_{12}} + \frac{n_{22}}{\tau_{22}} \\
\frac{dn_{11}}{dt} &= \lambda n_{e_1} n_{f_1} - \frac{n_{11}}{\tau_{11}} \\
\frac{dn_{12}}{dt} &= \lambda n_{e_1} n_{f_2} - \frac{n_{12}}{\tau_{12}} \\
\frac{dn_{21}}{dt} &= \lambda n_{e_2} n_{f_1} - \frac{n_{21}}{\tau_{21}} \\
\frac{dn_{22}}{dt} &= \lambda n_{e_2} n_{f_2} - \frac{n_{22}}{\tau_{22}}.
\end{aligned} \tag{18}$$

Appendix C shows that (18) has a unique distributional equilibrium for a fixed N and given N_{e_1} and N_{f_1}.

[11] These last assumptions rule out applying the methods to bimatrix games where newly single individuals may wait after disbanding before they are ready to form new pairs. For example, in the model for parental care of offspring known as the Battle of the Sexes (Dawkins, 1976), when fast females mate with philandering males to produce offspring, it is assumed that the male immediately deserts and begins searching for a new mate whereas the female remains and cares for the offspring for a certain amount of time before searching for a new mate.

Assuming that singles do not get any payoffs, the fitnesses (i.e., the expected payoff to an individual per unit time) of the four strategies evaluated at the unique equilibrium of (18) are ($i, j = 1, 2$)

$$\begin{aligned}\Pi_{e_i} &= \frac{n_{i1}}{N_{e_i}}\frac{\pi^e_{i1}}{\tau_{i1}} + \frac{n_{i2}}{N_{e_i}}\frac{\pi^e_{i2}}{\tau_{i2}},\\ \Pi_{f_j} &= \frac{n_{1j}}{N_{f_j}}\frac{\pi^f_{1j}}{\tau_{1j}} + \frac{n_{2j}}{N_{f_j}}\frac{\pi^f_{2j}}{\tau_{2j}}.\end{aligned} \tag{19}$$

These fitness functions depend on N, N_{e_1} and N_{f_1}. Since, at the unique distributional equilibrium of (18),

$$n_{ij} = \lambda n_{e_i} n_{f_i} \tau_{ij}, \quad i, j = 1, 2 \tag{20}$$

fitnesses (19) simplify to ($i, j = 1, 2$)

$$\begin{aligned}\Pi_{e_i} &= \frac{\lambda(n_{f_1}\pi^e_{i1} + n_{f_2}\pi^e_{i2})}{\lambda n_{f_1}\tau_{i1} + \lambda n_{f_2}\tau_{i2} + 1},\\ \Pi_{f_j} &= \frac{\lambda(n_{e_1}\pi^f_{1j} + n_{e_2}\pi^f_{2j})}{\lambda n_{e_1}\tau_{1j} + \lambda n_{e_2}\tau_{2j} + 1}.\end{aligned} \tag{21}$$

The time-constrained bimatrix game with non instantaneous pair formation based on payoff bimatrix (1) and time interaction matrix (2) is then the two-strategy game with payoffs given by the fitness functions (21) evaluated at the distributional equilibrium of (18) for fixed size N of each population and encounter rate λ. As in Section 2, we are interested in the NE of this game and its evolutionary outcome.

3.1. Classic bimatrix game with non instantaneous pair formation

The classic model implicitly assumes all interaction times are equal (i.e., $\tau_{ij} = \tau$ for all $i, j = 1, 2$). However, since the classic model also assumes that individuals are always interacting (i.e., always in pairs), the question arises whether the classic predictions remain valid when pair formation requires time. This section examines the question.

The equilibrium distribution of (18) is

$$\begin{aligned}n_{e_i} &= \frac{N_{e_i}}{N}\frac{\left(\sqrt{4\lambda N\tau + 1} - 1\right)}{2\lambda N\tau}\\ n_{f_j} &= \frac{N_{f_j}}{N}\frac{\left(\sqrt{4\lambda N\tau + 1} - 1\right)}{2\lambda N\tau}.\end{aligned}$$

Substituting these expressions to (21) leads to

$$\begin{aligned}\Pi_{e_i} &= \frac{4N\lambda}{(1+\sqrt{1+4\lambda\tau N})^2}\left(\pi^e_{i1}\frac{N_{f_1}}{N} + \pi^e_{i2}\frac{N_{f_2}}{N}\right),\\ \Pi_{f_j} &= \frac{4N\lambda}{(1+\sqrt{1+4\lambda\tau N})^2}\left(\pi^f_{1j}\frac{N_{e_1}}{N} + \pi^f_{2j}\frac{N_{e_2}}{N}\right).\end{aligned} \tag{22}$$

Thus, up to the positive factor $\frac{4N\lambda}{(1+\sqrt{1+4\lambda\tau N})^2}$, these are the payoffs of the classic bimatrix game with payoff matrix (1). From this it follows that the NE of the classic bimatrix game with non instantaneous pair formation is the same as the the classic bimatrix game and, moreover, the trajectories of the replicator equation are the same (up to the speed along the trajectory). Thus, the two games have the same evolutionary outcomes.

To rephrase, standard evolutionary game theory models of bimatrix games can explicitly incorporate time constraints without affecting the game-theoretic analysis as long as all interaction times are the same. It is then irrelevant whether pair formation is instantaneous or requires some time.

3.2. Evolutionary outcomes with non instantaneous pair formation

As we saw in Section 2, evolutionary outcomes of time-constrained bimatrix games with instantaneous pair formation depend heavily on pair interaction times when these are not all the same (e.g., Fig. 2). This section analyzes the same phenomena when pair formation is not instantaneous.

We start by characterizing the strict NE of these games. From (21), at strategy pair (e_1, f_1),

$$\Pi_{e_1} = \frac{\lambda n_{f_1}\pi^e_{11}}{\lambda n_{f_1}\tau_{11} + 1}, \quad \Pi_{f_1} = \frac{\lambda n_{e_1}\pi^f_{11}}{\lambda n_{e_1}\tau_{11} + 1},$$

since $n_{e_2} = n_{f_2} = 0$. Note that the fitness Π_{e_1} (Π_{f_1}) does not depend on distributional equilibrium of population 1 (2). Thus, the invasion fitnesses of strategy e_2 and f_2 are

$$\Pi_{e_2} = \frac{\lambda n_{f_1}\pi^e_{21}}{\lambda n_{f_1}\tau_{21} + 1}$$

and

$$\Pi_{f_2} = \frac{\lambda n_{e_1}\pi^f_{12}}{\lambda n_{e_1}\tau_{12} + 1}$$

as given in (21) with $n_{e_2} = n_{f_2} = 0$. Furthermore, at this strategy pair, $N = n_{e_1} + n_{11} = n_{e_1} + \lambda n_{e_1} n_{f_1}\tau_{11} = n_{f_1} + n_{11}$. Thus, $n_{e_1} = n_{f_1}$ and so $N = \lambda\tau_{11}n^2_{e_1} + n_{e_1}$ and

$$n_{e_1} = \frac{-1 + \sqrt{1 + 4N\lambda\tau_{11}}}{2\lambda\tau_{11}} = n_{f_1}.$$

Strategy pair (e_1, f_1) is a strict NE provided $\Pi_{e_1} > \Pi_{e_2}$ and $\Pi_{f_1} > \Pi_{f_2}$, i.e.,

$$\begin{aligned}\frac{\pi^e_{11}}{\tau_{11}(\sqrt{4\lambda N\tau_{11} + 1} + 1)} &> \frac{\pi^e_{21}}{\tau_{21}\left(\sqrt{4\ \lambda N\tau_{11} + 1} - 1\right) + 2\tau_{11}}\\ \frac{\pi^f_{11}}{\tau_{11}(\sqrt{4\lambda N\tau_{11} + 1} + 1} &> \frac{\pi^f_{12}}{\tau_{12}\left(\sqrt{4\lambda N\tau_{11} + 1} - 1\right) + 2\tau_{11}}.\end{aligned} \tag{23}$$

Similarly, we can obtain conditions for other strict NE. Contrary to the case of instantaneous pairing where these conditions are given by the adjusted payoff matrix (10), we cannot write these conditions in a similar form when pairing is non-instantaneous. This is seen from expressions (23), where the invasion fitness for strategy e_2 (f_2) depends not only on interaction time τ_{21} (τ_{12}), but also on interaction time τ_{11}.

As λ increases to infinity, payoff Π_{e_1} (Π_{f_1}) converges to π^e_{11}/τ_{11} (π^f_{11}/τ_{11}) and invasion fitness Π_{e_2} (Π_{f_2}) converges to π^e_{21}/τ_{21} (π^f_{12}/τ_{12}). Thus, when the encounter rate of singles is large, the strict NE of the time-constrained bimatrix game with non instantaneous pair formation are the same as the strict NE of the time-constrained bimatrix game of Section 2 (i.e., with instantaneous pair formation). In fact, for large λ, the interior NE match as well since there are essentially no singles in the system.

The next section illustrates these general results for the Owner–Intruder game.

3.3. The Owner–Intruder game with non instantaneous pair formation

When all interaction times equal to τ as in Section 3.1, there is an interior NE if and only if $V < C$. As a function of λ and τ, it is

given by

$$n_{e_1} = n_{f_1} = \frac{V(-1+\sqrt{1+4\lambda N\tau})}{2C\lambda\tau}$$
$$n_{e_2} = n_{f_2} = \frac{(C-V)(-1+\sqrt{4\lambda N\tau})}{2C\lambda\tau} \quad (24)$$
$$N_{e_1} = N_{f_1} = \frac{NV}{C},$$

which is the classic result for the case when $V < C$.

However, for a general time interaction matrix, an analytic expression for the interior NE is not available. Our recourse is to apply the replicator equation (13) with payoffs (21) when pairing is non-instantaneous. On contrary to the case of instantaneous pairing, we cannot now express the distributional equilibrium at the current strategy numbers explicitly. Thus, we have to solve replicator equation (13) together with the system of algebraic equations

$$N_{e_1} = n_{e_1}(1+\lambda n_{f_1}\tau_{11}+\lambda n_{f_2}\tau_{12})$$
$$N_{f_1} = n_{f_1}(1+\lambda n_{e_1}\tau_{11}+\lambda n_{e_2}\tau_{21}). \quad (25)$$

This is a semi-explicit index 1 differential-algebraic equation (Ascher and Petzold, 1998) that we solve numerically using Mathematica 11.

Fig. 3 shows the results for two encounter rates. Panels A–H use the same parameter values (i.e., V, C, τ_{ij}) as corresponding panels in Fig. 2. For the role-independent time-constrained cases (panels A–C, E–G), trajectories remain reflections of each other with respect to the main diagonal. We see that for large enough encounter rate ($\lambda = 10$ in panels A–H) the strict NE still match those of Section 2. However, there are differences in stability of interior NE between Figs. 2 and 3. The neutral stability of the two off-diagonal equilibria in Fig. 2C and G is lost and the two equilibria become unstable. Fig. 3C and G show two trajectories that start close to the two equilibria and that converge to equilibrium $(N_{e_1}, N_{f_1}) = (100, 100)$ and $(N_{e_1}, N_{f_1}) = (0, 0)$, respectively. Panels C', D', G', and H' show numerical simulations for yet smaller encounter rate ($\lambda = 1$). We observe that this leads to disappearance of interior NE in panels C' and D', and to destabilization of the interior stable NE in panel H that is replaced by a locally stable limit cycle in panel H'. These numerical simulations, for the parameter values used, show that small and intermediate encounter rates make coexistence of both strategies in polymorphic state less likely.

4. Discussion

This article extends to two-strategy bimatrix games the new approach to evolutionary game theory developed by Křivan and Cressman (2017) for two-player, two-strategy, symmetric normal form games (i.e., matrix games) that incorporates the effect pair interaction times that depend on the players' strategies have on the evolutionary outcome. Evolutionary game theory applied to bimatrix games is based on two populations (or two roles) where individuals interact in pairs, one from each population. Classical bimatrix games, similarly to matrix games, assume that individuals get payoffs when paired, pairing is random and instantaneous, and the number of different types of pairs is given by the Hardy–Weinberg distribution. The evolutionary outcome of the bimatrix game is then predicted through an analysis of the NE structure of its payoff bimatrix and how this is connected to the eventual behavior of the game dynamics (e.g., the replicator equation). A complete analysis of the evolutionary outcome is well-known for all classical two-strategy bimatrix games (Cressman, 2003; Hofbauer and Sigmund, 1998).

When interaction times depend on strategies used by the pair, the Hardy–Weinberg distribution of pairs is no longer relevant and expected individual payoff is now a nonlinear function of the numbers using each strategy in the two populations whether the pair formation process among disbanded pairs is instantaneous (Section 2) or not (Section 3). However, in both cases, we show the existence of a unique distribution as a function of these numbers at the beginning of these respective sections,[12] although we are only able to provide an analytic expression for it when pair formation is instantaneous (see Eq. (6)). Nevertheless, this allows us to define a time-constrained, bimatrix game in Section 2 and in Section 3 where payoff (which we call the fitness function) is given as expected individual payoff per unit time. As pointed out in Sections 2 and 3.1, this new formulation reduces to the classic bimatrix game when all interaction times are the same.

What is then of interest is how different interaction times affect the evolutionary outcome. To this end, we completely characterized strict NE for all two-strategy, time-constrained, bimatrix games (Sections 2.1 and 3.2 respectively). When pairing is instantaneous (Sections 2.1) strict NE are characterized through their time-adjusted payoff matrices (10). A strict NE corresponds to a locally asymptotically stable rest point of the replicator equation where both populations use one of their pure strategies as indicated by solid dots at vertices of the squares of Figs. 2 and 3 respectively.

Unfortunately, other NE of the time-constrained bimatrix game are more difficult to analyze. In particular, the analytic formula for interior NE is not available except in special circumstances due to the complicated distribution that replaces the Hardy–Weinberg distribution in these games. Since interior NE correspond to interior rest points of the replicator equation, they can be approximated by simulating this dynamics for particular games. No attempt is made for a complete analysis of all two-strategy time-constrained bimatrix games.[13] Instead, we focus on the time-constrained Owner–Intruder game. This classic role-independent bimatrix game has an easily understood evolutionary outcome.

When the cost of fighting over a resource C is less than its value V, both the owner of the resource and the intruder should fight for it (i.e., both play Hawk) even though their payoff by doing so is less than if they split the resource without fighting (i.e., both play Dove) in the classic bimatrix game.[14] The reason is that Hawk strictly dominates Dove in each population. Although (Hawk, Hawk) remains a strict NE in the time-constrained bimatrix game, other NE emerge as interaction times change. From panel B of Figs. 2 and 3, we see that (Dove, Dove) can also be a strict NE (in which case there is also an interior NE) when their interaction time is short enough compared to the equal time of the other interactions. Furthermore, while (Dove, Dove) is not a strict NE if only (Hawk, Hawk) interaction time changes, up to four interior NE can appear if this interaction time is large enough, some of which are (neutrally) stable and some unstable (panels C and D).

When $V < C$, (Hawk, Hawk) is never a strict NE. In the classic bimatrix game, there are two strict NE; namely, (Hawk, Dove) and the paradoxical ESS (Dove, Hawk) where the intruder always wins the resource (i.e., the owner and intruder switch roles through each interaction) as well as one unstable saddle symmetric interior NE where both populations play the ESS of the classic symmetric Hawk–Dove matrix game. The replicator equation predicts the paradoxical ESS will be the evolutionary outcome if and only

[12] In Section 3, this includes the distribution of pairs and singles.

[13] The difficulty of doing such an analysis can be appreciated by considering the complete analysis for the two-locus two-allele viability selection model of population genetics. Pontz et al. (2018) show that this two-dimensional dynamics on the unit square has at least 192 different phase portraits. We feel our model will have a comparable (or even higher) number of different cases.

[14] The same result occurs for the bimatrix version of the Prisoner's Dilemma game where both players Defect at the evolutionary outcome even though they would be better off if both Cooperate.

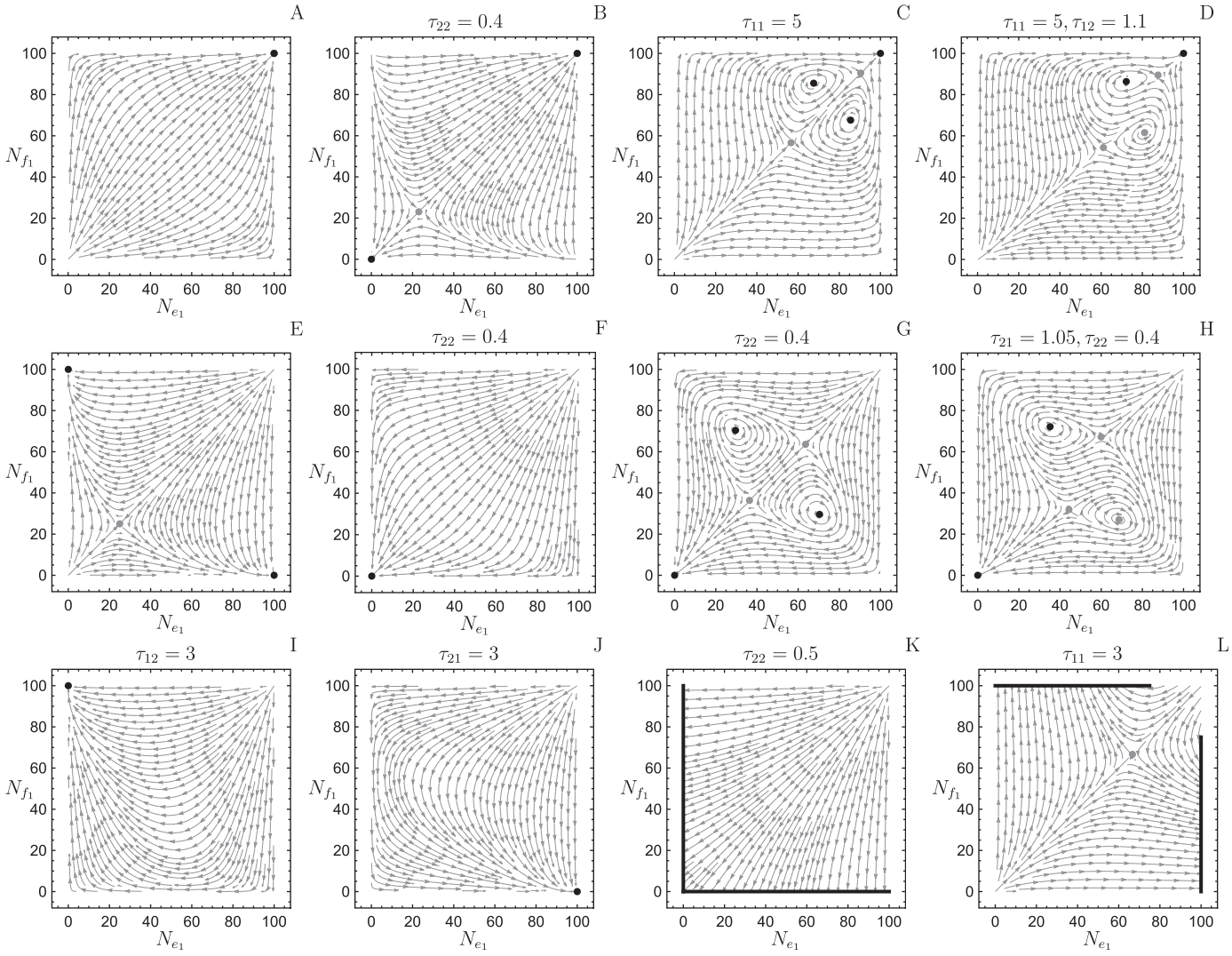

Fig. 2. The replicator dynamics for the Owner–Intruder game depending on V, C and interaction times when pairing is instantaneous. The first four panels (i.e., panels A, B, C, and D) assume $V > C$ (in fact, $V = 4$ and $C = 1$). The other panels assume $V = 1 \leq C$ with $C = 4$ (panels E, F, I, J, K), $C = 1.5$ (panels G, H) and $C = 1$ (panel L). All interaction times not equal to 1 are indicated in each panel. Thus, panels A and E respectively are the replicator dynamics of the classic Owner–Intruder game for $V > C$ and $V < C$ respectively since all interaction times are the same. In particular, the main diagonal is invariant in these two panels since the time-constrained game is role-independent. For the same reason, this invariance holds in panels B, C, F, G, K, L but not in the other four panels (D, H, I, J) that have role dependent interaction times (i.e., $\tau_{12} \neq \tau_{21}$). In panel B, strategy pairs (H, H) and (D, D) are strict NE (since $\min\{\tau_{12}, \tau_{21}\} > 2\tau_{22}$ and $V > C$) and an unstable saddle symmetric interior NE appears. In panel C, Hawk-Hawk interaction time is long enough ($\tau_{11} = 5$) that two unstable saddle symmetric interior NE emerge along with two neutrally stable asymmetric ones. Panel D is an asymmetric perturbation of the interaction time matrix from panel C (specifically τ_{12} shifts from 1 to 1.1) that perturbs the two asymmetric NE to a stable and unstable one. Since $\min\{\tau_{12}, \tau_{21}\} > 2\tau_{22}$ and $V < C$ in panels F, G, H, (D, D) is the only strict NE. It may be globally asymptotically stable (panel F) or only locally asymptotically stable when there are four interior NE with two unstable saddles and two neutrally stable (the role-independent case of panel G) or two unstable saddles together with one unstable and one stable NE (panel H with perturbed interaction matrix compared to panel G). In the role-dependent interaction matrices of panels I and J, τ_{12} (respectively τ_{21}) is large enough that the paradoxical ESS (D, H) (respectively (H, D)) is the only strict NE and it is globally asymptotically stable. Finally, panels K and L illustrate that sets of boundary NE emerge (thick black line segments) when $V = 1$, $C = 4$, $\tau_{11} = \tau_{12} = \tau_{21} = 2\tau_{22} = 1$ (panel K), and $V = C$ (panel L).

if the initial population distribution has more Hawks as intruders than as owners. As shown in Fig. 2, panels I and J, either one of these strict NE can disappear by introducing a role dependence into the time interaction matrix (2). In fact, both must disappear when (Dove, Dove) becomes a strict NE through their interaction time being short enough compared to the equal time of the other interactions in Figs. 2 and 3, in which case interior NE may (panels G and H) or may not appear (panel F). There are also marked differences between the evolutionary outcomes when pair formation is instantaneous compared to when it is non instantaneous, as detailed in the main text.

In this article, although we have relaxed the implicit assumption of classic evolutionary game theory that all interactions take the same amount of time, we have assumed that newly single individuals are immediately available to form pairs. This rules out straightforward application of our methods to models where some single individuals from a disbanded pair wait before joining the pair formation process. For instance, this occurs in parental care models, e.g., Battle of the Sexes (Broom and Rychtář, 2013; Cressman, 2003; Dawkins, 1976; Hofbauer and Sigmund, 1998; Mylius, 1999) when males are immediately available to mate after a couple disbands whereas females will not mate immediately but stay to care for offspring if abandoned by their mate. We also assume that both populations have the same number of individuals, which is required when pair formation is instantaneous. On the other hand, when pair formation is non-instantaneous, all calculations can be

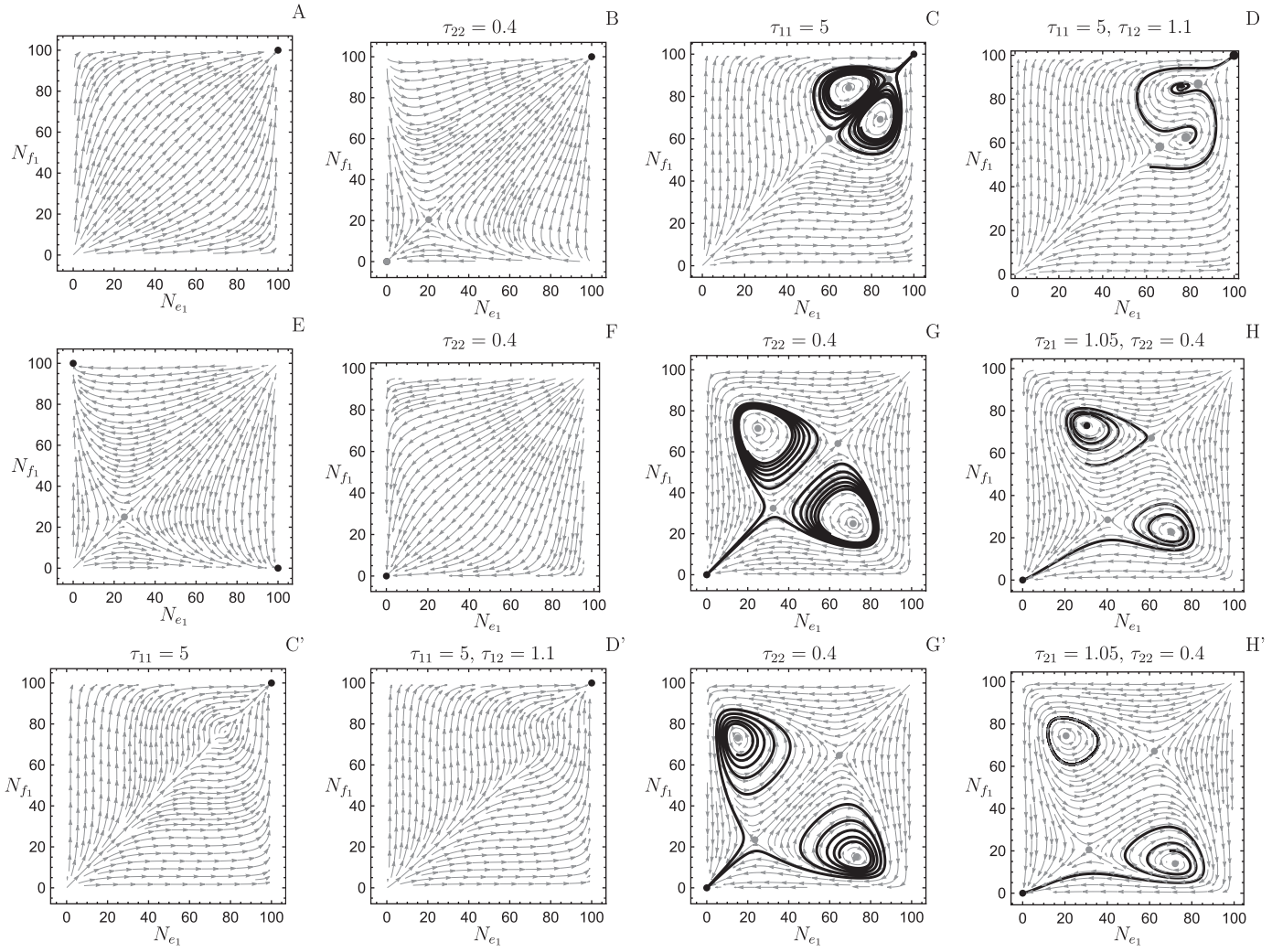

Fig. 3. The replicator dynamics for the Owner–Intruder game when pairing is not instantaneous. For role-independent time-constrained bimatrix games (panels A, B, C, E, F, G, C', G'), the main diagonal remains invariant. The encounter rate between singles is $\lambda = 10$ in panels A–H and $\lambda = 1$ in panels C'–H'. Other parameters are the same as in the corresponding panels of Fig. 2. Panels A and E are identical to their corresponding panels in Fig. 2 since these are all equivalent to the classic bimatrix game. There are also no noticeable differences between panels B and F compared to Fig. 2. The differences with Fig. 2 (which emerges for very large λ) are as follows. For long interaction times between Hawks when $V > C$, the four interior NE of Fig. 2 disappear completely when $\lambda = 1$ (panels C' and D') whereas the two asymmetric interior NE become unstable for intermediate λ (panel C). When the interaction time between Doves is short and $V < C$, the asymmetric interior NE of the role-independent time-constrained bimatrix game lose stability and the two symmetric interior shift apart as λ decreases (panels G and G'). With role-dependent interaction times, the asymptotically stable interior NE of Fig. 2H eventually becomes unstable when λ decreases and a stable limit cycle emerges.

generalized to population 1 having a different size than population 2, although the formulas are more complex.[15]

In this article, we have generalized two-strategy bimatrix games by explicitly including interaction times when pure strategists from each population are paired. When applied to the classic Owner-Intruder game where each individual, at given interaction, is either a Hawk or a Dove, we have a model where owners and intruders have a choice between two levels of effort when engaged in a conflict (Hawks are willing to expend a great deal of time and effort to obtain the resource while Doves are not). Another approach to this conflict situation is to allow intermediate levels of effort, resulting in a time-constrained Owner-Intruder game with a continuum of pure strategies. In the classic game with continuous strategy sets (for a recent review see Cressman and Apaloo, 2018), the analysis of NE that have additional properties such as Continuously Stable Strategy (CSS) or Neighborhood Invader Strategy (NIS) are particularly important. Although beyond the scope of this article, it is then essential to first understand the effect of interaction times on these concepts of CSS and NIS.

The results of this article show that the evolutionary outcome for bimatrix games becomes more complex when interaction times are incorporated into the game-theoretic model. The results are also more complex than those reported by Křivan and Cressman (2017) for matrix games with strategy-dependent interaction times as is to be expected given the conceptual differences between classic matrix and bimatrix games. It is our contention that these added complexities are often unavoidable to make the evolutionary model more realistic. This is especially true when the model purports to describe a behavioral system where pairs interact for different amounts of time.

[15] With unequal population size, the time-constrained bimatrix game with all τ_{ij} equal is no longer the classic bimatrix game as in Section 3.1.

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Appendix A. Pairs distributional dynamics when pairing is instantaneous

Here we derive pair dynamics (3). Let us consider a small time interval Δ. Because pairs n_{ij} split up following a Poisson process with parameter τ_{ij}, in this time interval a proportion $\frac{\Delta}{\tau_{ij}}$ of the n_{ij} pairs disbands and there will be $(\frac{n_{i1}}{\tau_{i1}}+\frac{n_{i2}}{\tau_{i2}})\Delta$ singles playing strategy e_i and $(\frac{n_{1j}}{\tau_{1j}}+\frac{n_{2j}}{\tau_{2j}})\Delta$ singles playing strategy f_j. The total number of disbanded singles in each population in time interval Δ is

$$\left(\frac{n_{11}}{\tau_{11}}+\frac{n_{12}}{\tau_{12}}+\frac{n_{21}}{\tau_{21}}+\frac{n_{22}}{\tau_{22}}\right)\Delta. \tag{A.1}$$

If these singles immediately and randomly pair, the proportion of newly formed n_{ij} pairs among all newly formed pairs will be

$$\frac{(\frac{n_{i1}}{\tau_{i1}}+\frac{n_{i2}}{\tau_{i2}})\Delta}{\left(\frac{n_{11}}{\tau_{11}}+\frac{n_{12}}{\tau_{12}}+\frac{n_{21}}{\tau_{21}}+\frac{n_{22}}{\tau_{22}}\right)\Delta}\quad\frac{(\frac{n_{1j}}{\tau_{1j}}+\frac{n_{2j}}{\tau_{2j}})\Delta}{\left(\frac{n_{11}}{\tau_{11}}+\frac{n_{12}}{\tau_{12}}+\frac{n_{21}}{\tau_{21}}+\frac{n_{22}}{\tau_{22}}\right)\Delta}. \tag{A.2}$$

To obtain the number of newly formed (e_i, f_j) pairs in the time interval Δ we multiply (A.2) by the number of newly formed pairs (which equals the number of disbanded singles because we assume instantaneous pairing) in time interval Δ and we obtain

$$\frac{\left(\frac{n_{i1}}{\tau_{i1}}+\frac{n_{i2}}{\tau_{i2}}\right)\left(\frac{n_{1j}}{\tau_{1j}}+\frac{n_{2j}}{\tau_{2j}}\right)}{\frac{n_{11}}{\tau_{11}}+\frac{n_{12}}{\tau_{12}}+\frac{n_{21}}{\tau_{21}}+\frac{n_{22}}{\tau_{22}}}\Delta.$$

Writing difference equations for pairs

$$n_{ij}(t+\Delta)=n_{ij}(t)-\frac{n_{ij}(t)}{\tau_{ij}}\Delta+\frac{\left(\frac{n_{i1}(t)}{\tau_{i1}}+\frac{n_{i2}(t)}{\tau_{i2}}\right)\left(\frac{n_{1j}(t)}{\tau_{1j}}+\frac{n_{2j}(t)}{\tau_{2j}}\right)}{\frac{n_{11}(t)}{\tau_{11}}+\frac{n_{12}(t)}{\tau_{12}}+\frac{n_{21}(t)}{\tau_{21}}+\frac{n_{22}(t)}{\tau_{22}}}\Delta \tag{A.3}$$

and letting $\Delta\longrightarrow 0_+$, we obtain the pair dynamics (3) in the main text.

From

$$\begin{aligned}N_{e_1}&=n_{11}+n_{12}\\ N_{f_1}&=n_{11}+n_{21}\\ N_{e_2}&=N-N_{e_1}\\ N_{f_2}&=N-N_{f_1}\end{aligned} \tag{A.4}$$

and the generalized Hardy–Weinberg Eq. (5), Mathematica provides two equilibrium solutions for n_{ij} in terms of N, N_{e_1} and N_{f_1}. However, only the one given in (6) is non-negative when $0\le N_{e_1}, N_{f_1}\le N$.

It is not immediately clear that $A\ge 0$ where A is given in (7). To see this, expand A as the following quadratic expression in N_{e_1}

$$\begin{aligned}A=&{N_{e_1}}^2(\tau_{12}\tau_{21}-\tau_{11}\tau_{22})^2-2N_{e_1}(\tau_{12}\tau_{21}-\tau_{11}\tau_{22})\\ &(N\tau_{12}\tau_{21}-N_{f_1}(\tau_{11}\tau_{22}+\tau_{12}\tau_{21}))\\ &+(\tau_{12}\tau_{21}(N-N_{f_1})+N_{f_1}\tau_{11}\tau_{22})^2={aN_{e_1}}^2+bN_{e_1}+c.\end{aligned}$$

The minimum value of this upward parabola is

$$c-\frac{b^2}{2a}=4N_{f_1}\tau_{11}\tau_{12}\tau_{21}\tau_{22}(N-N_{f_1}).$$

Since $0\le N_{f_1}\le N$, this minimum is non-negative and so $A\ge 0$.

Appendix B. Calculation of the invasion fitness (16)

The fitness of strategy f_2, Π_{f_2}, given in (9) calculated at the distributional equilibrium (6) is

$$\begin{aligned}\Pi_{f_2}=&\frac{\sqrt{A}(\pi^f_{22}\tau_{12}-\pi^f_{12}\tau_{22})+N\tau_{12}(\pi^f_{12}\tau_{21}\tau_{22}-2\pi^f_{22}\tau_{11}\tau_{22}+\pi^f_{22}\tau_{12}\tau_{21})}{2\tau_{12}\tau_{22}(N-N_{f_1})(\tau_{12}\tau_{21}-\tau_{11}\tau_{22})}\\ &-\frac{(\tau_{12}\tau_{21}-\tau_{11}\tau_{22})(\pi^f_{12}\tau_{22}(N_{f_1}-N_{e_1})+\pi^f_{22}\tau_{12}(N_{e_1}+N_{f_1}))}{2\tau_{12}\tau_{22}(N-N_{f_1})(\tau_{12}\tau_{21}-\tau_{11}\tau_{22})},\end{aligned}$$

where A is given in (7). The invasion fitness of strategy f_2 when there are no individuals playing this strategy is then $\lim_{N_{f_1}\to N}\Pi_{f_2}$. We observe that

$$\lim_{N_{f_1}\to N}A=(N\tau_{11}\tau_{22}+N_{e_1}(\tau_{12}\tau_{21}-\tau_{11}\tau_{22}))^2.$$

Since $N\ge N_{e_1}$, $N\tau_{11}\tau_{22}+N_{e_1}(\tau_{12}\tau_{21}-\tau_{11}\tau_{22})\ge 0$,

$$\lim_{N_{f_1}\to N}\sqrt{A}=N\tau_{11}\tau_{22}+N_{e_1}(\tau_{12}\tau_{21}-\tau_{11}\tau_{22})$$

and the numerator of Π_{f_2} simplifies to

$$(N-N_{f_1})(\pi^f_{12}\tau_{22}+\pi^f_{22}\tau_{12})(\tau_{12}\tau_{21}-\tau_{11}\tau_{22}).$$

Thus, both the numerator and denominator of Π_{f_2} converge to 0 when $N_{f_1}\to N$ and we calculate the limit using L'Hospital's rule

$$\lim_{N_{f_1}\to N}\Pi_{f_2}=\frac{N_{e_1}\pi^f_{12}\tau_{21}+N_{e_2}\pi^f_{22}\tau_{11}}{N\tau_{11}\tau_{22}+N_{e_1}(\tau_{12}\tau_{21}-\tau_{11}\tau_{22})}. \tag{B.1}$$

Similarly, the fitness of strategy e_2, Π_{e_2}, given in (9) calculated at the distributional equilibrium (6) is

$$\begin{aligned}\Pi_{e_2}=&\frac{\sqrt{A}(\pi^e_{22}\tau_{21}-\pi^e_{21}\tau_{22})+N\tau_{21}(\pi^e_{21}\tau_{12}\tau_{22}-2\pi^2_{22}\tau_{11}\tau_{22}+\pi^2_{22}\tau_{12}\tau_{21})}{2\tau_{21}\tau_{22}(N-N_{2_1})(\tau_{12}\tau_{21}-\tau_{11}\tau_{22})}\\ &-\frac{(\tau_{12}\tau_{21}-\tau_{11}\tau_{22})(\pi^e_{21}\tau_{22}(N_{e_1}-N_{f_1})+\pi^e_{22}\tau_{21}(N_{e_1}+N_{f_1}))}{2\tau_{21}\tau_{22}(N-N_{e_1})(\tau_{12}\tau_{21}-\tau_{11}\tau_{22})}.\end{aligned}$$

The invasion fitness of strategy e_2 when there are no individuals playing this strategy is

$$\lim_{N_{e_1}\to N}\Pi_{e_2}=\frac{N_{f_1}\pi^e_{21}\tau_{12}+N_{f_2}\pi^e_{22}\tau_{11}}{N\tau_{11}\tau_{22}+N_{f_1}(\tau_{12}\tau_{21}-\tau_{11}\tau_{22})} \tag{B.2}$$

by again applying L'Hospital's rule.

Appendix C. Uniqueness of distributional equilibrium of (25)

Fix N_{e_i} and N_{f_j} $(i,j=1,2)$ and define $q_{e_i}=\frac{n_{e_i}}{N_{e_i}}$ $\left(q_{f_j}=\frac{n_{f_j}}{N_{f_j}}\right)$ as the proportion of e_i (f_j) strategists in the population who are single. From (25) it follows that

$$\begin{aligned}q_{e_1}&=\frac{1}{1+\lambda N_{f_1}q_{f_1}\tau_{11}+\lambda N_{f_2}q_{f_2}\tau_{12}}\\ q_{e_2}&=\frac{1}{1+\lambda N_{f_1}q_{f_1}\tau_{21}+\lambda N_{f_2}q_{f_2}\tau_{22}}\\ q_{f_1}&=\frac{1}{1+\lambda N_{e_1}q_{e_1}\tau_{11}+\lambda N_{e_2}q_{e_2}\tau_{21}}\\ q_{f_2}&=\frac{1}{1+\lambda N_{e_1}q_{e_1}\tau_{12}+\lambda N_{e_2}q_{e_2}\tau_{22}}.\end{aligned} \tag{C.1}$$

By Lemma 2 in Garay et al. (2017), there is a unique solution with q_{e_i} and q_{f_j} between 0 and 1.

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