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**Highlights**

- A new approach to the theory of two-player bimatrix evolutionary games where pairs are formed by the mass action principle is developed and compared to models with instantaneous pair formation.
- This theory explicitly considers the duration of interactions between the two players and their status as singles between interactions.
- When applied to the bimatrix Hawk-Dove game (called the Owner-Intruder game), this theory shows that differences in interaction times lead to new interior and boundary Nash equilibria.
- Existence and stability of these Nash equilibria depend on whether pairing is instantaneous or not.

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

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9 **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.

10 *Keywords:* Evolutionary game theory, Hawk–Dove game, Pair formation, Time-scale  
 11 separation, Time-constrained games

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## 12 1. Introduction

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

30 Krivan and Cressman (2017) showed that, when individuals pair instantaneously but  
31 the interaction times are strategy dependent, the Hawk–Dove model may have a mixed  
32 ESS (i.e., an evolutionarily stable state that consists of a mixture of Hawks and Doves)  
33 when the cost of a fight is lower than the value of the contested resource. For this  
34 to happen, the interaction time between two Hawks must be long enough relative to  
35 interaction times between other strategies. Such an outcome is not possible in the classic  
36 Hawk–Dove game that does not consider interaction times. Similarly, for the repeated  
37 Prisoner’s dilemma, provided cooperators stay together for enough rounds of the game  
38 while pairs with at least one defector disband quickly, cooperation does evolve (Krivan  
39 and Cressman, 2017). This situation arises naturally if players can choose whether to  
40 continue the game to the next round with the same opponent, since it is always better to  
41 play against a cooperator than a defector in the Prisoner’s dilemma game (see also the  
42 opting-out game (Zhang et al., 2016)).

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

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

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

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

87 **2. Instantaneous pair formation**

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

$$\begin{array}{cc} & \begin{array}{cc} f_1 & f_2 \end{array} \\ \begin{array}{c} e_1 \\ e_2 \end{array} & \begin{bmatrix} \pi_{11}^e, \pi_{11}^f & \pi_{12}^e, \pi_{12}^f \\ \pi_{21}^e, \pi_{21}^f & \pi_{22}^e, \pi_{22}^f \end{bmatrix} \end{array} \quad (1)$$

91 where  $\pi_{ij}^e$  (respectively,  $\pi_{ij}^f$ ) is the payoff to  $e_i$  (respectively,  $f_j$ ) when interacting with  $f_j$   
92 (respectively  $e_i$ ). In contrast to classic evolutionary game theory, we explicitly incorporate  
93 the duration of interactions into the game through the time interaction matrix

$$\begin{array}{cc} & \begin{array}{cc} f_1 & f_2 \end{array} \\ \begin{array}{c} e_1 \\ e_2 \end{array} & \begin{pmatrix} \tau_{11} & \tau_{12} \\ \tau_{21} & \tau_{22} \end{pmatrix} \end{array} \quad (2)$$

94 where  $\tau_{ij}$  is the expected time two players using strategy  $e_i$  and  $f_j$  stay together.

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

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

99 and the equilibrium distribution satisfies

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

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

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

$$\frac{n_{11}}{\tau_{11}} \frac{n_{22}}{\tau_{22}} = \frac{n_{12}}{\tau_{12}} \frac{n_{21}}{\tau_{21}}. \quad (5)$$

105 Given the number of  $e_1$  and  $f_1$  strategists ( $N_{e_1} = n_{11} + n_{12}$  and  $N_{f_1} = n_{11} + n_{21}$ , respec-  
 106 tively) as well as the total number of individuals  $N = n_{11} + n_{12} + n_{21} + n_{22}$  in either  
 107 population, Appendix A shows that the unique nonnegative solution to (4) and (5) is  
 108 (assuming  $\tau_{12}\tau_{21} \neq \tau_{11}\tau_{22}$ )

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

109 where

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

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

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

112 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  
 113 includes the classic situation, i.e., all interaction times are the same ( $\tau_{11} = \tau_{12} = \tau_{21} = \tau_{22}$ ).

### 114 2.1. Fitness and evolutionary outcomes

115 Following Krivan and Cressman (2017), we define fitness as the expected payoff that  
 116 an individual of a given phenotype obtains per unit of interaction time. For example, let

117 us consider an individual playing strategy  $e_1$  in population 1. The probability that this  
 118 individual is paired with an individual playing strategy  $f_1$  is  $n_{11}/(n_{11} + n_{12})$  and with an  
 119 individual playing strategy  $f_2$  is  $n_{12}/(n_{11} + n_{12})$ . When paired with an individual playing  
 120 strategy  $f_1$ , the focal individual receives payoff  $\pi_{11}^e/\tau_{11}$  per unit of time. Similarly, when  
 121 paired with an individual playing strategy  $f_2$ , the focal individual gets payoff  $\pi_{12}^e/\tau_{12}$  per  
 122 unit of time. Thus, the focal individual has expected payoff (i.e., fitness)  $\Pi_{e_1}$  given by  
 123 the first equation in (9). The fitness for individuals playing  $e_2$  and those in the second  
 124 population are calculated analogously, which leads to  $(i, j = 1, 2)$

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

125 The corresponding time-constrained bimatrix game based on payoff bimatrix (1) and time  
 126 interaction matrix (2) is then the two-strategy game with payoffs given by the fitness  
 127 functions (9) evaluated at the distributional equilibrium (6) for fixed size  $N$  of each  
 128 population.<sup>1</sup>

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

<sup>1</sup>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).

<sup>2</sup>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).



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

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

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

169 The other special case is interior symmetric NE (i.e., those on the main diagonal where  
170  $N_{e_1} = N_{f_1}$ ) for role-independent time constrained bimatrix games. As discussed in Section  
171 2.2, there are up to two such diagonal interior symmetric NE and the formulas for these  
172 are given in Křivan and Cressman (2017).

173 To find interior NE in the general case, we can instead consider the replicator equation  
174 at fixed population size  $N$ . This dynamics is given by<sup>3</sup>

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

175 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 dis-  
176 tribution (6) for a given  $(N_{e_1}, N_{f_1})$ . Rest points of the replicator equation with  $N_{e_1}$  and  
177  $N_{f_1}$  strictly between 0 and  $N$  are the interior NE of the underlying game (Hofbauer and  
178 Sigmund, 1998). Moreover, when all  $\tau_{ij} = \tau$  are equal, the dynamics (13) is the replicator  
179 equation of the classic bimatrix game (up to the factor  $\tau$  that only affects the speed along  
180 trajectories and not the evolutionary outcome).

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

## 184 2.2. Owner-Intruder game

185 The classic owner intruder game (Maynard Smith, 1982; Hofbauer and Sigmund, 1998;  
186 Cressman, 2003; Broom and Rychtář, 2013) is the two-role extension of the symmetric

<sup>3</sup>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  $N_{e_1} = p_1N$  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).

187 Hawk–Dove game (i.e., matrix game) that models the situation in which an individual  
 188 either owns a site or is an intruder trying to seize a site. An individual can either be a  
 189 Hawk (strategy  $e_1$  if owner and  $f_1$  if intruder) or a Dove (strategy  $e_2$  if owner and  $f_2$  if  
 190 intruder) in either of the two roles. The payoff bimatrix of the game is

$$\begin{array}{c|cc} \text{Owner} \backslash \text{Intruder} & \text{Hawk} & \text{Dove} \\ \hline \text{Hawk} & \left[ \frac{V-C}{2}, \frac{V-C}{2} \right] & [V, 0] \\ \text{Dove} & [0, V] & \left[ \frac{V}{2}, \frac{V}{2} \right] \end{array}$$

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

195 When the cost of fighting is low ( $C < V$ ), the classic game has a single NE  $(e_1, f_1) =$   
 196  $(H, H)$  where individuals in both positions behave as hawks. When the cost of fighting is  
 197 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  
 198 mixed NE  $(p_1, q_1) = (V/C, V/C)$ , where Hawk strategy is played with probability  $V/C$  in  
 199 both roles. This mixed NE cannot be a (two-species) ESS, because bimatrix games can  
 200 have ESSs only in pure strategies (Selten, 1980).<sup>5</sup>

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

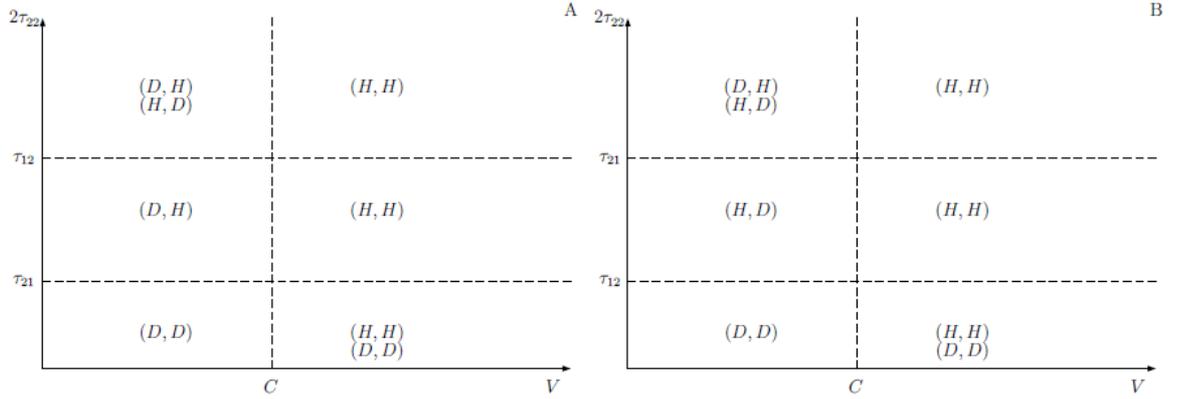
$$\begin{array}{c|cc} \text{Owner} \backslash \text{Intruder} & \text{Hawk} & \text{Dove} \\ \hline \text{Hawk} & \left[ \frac{V-C}{2\tau_{11}}, \frac{V-C}{2\tau_{11}} \right] & \left[ \frac{V}{\tau_{12}}, 0 \right] \\ \text{Dove} & \left[ 0, \frac{V}{\tau_{21}} \right] & \left[ \frac{V}{2\tau_{22}}, \frac{V}{2\tau_{22}} \right] \end{array}.$$

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

- 206 • If  $V > C$ , then strategy  $(H, H)$  is a NE (e.g., Figure 2A–D).

<sup>4</sup>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.

<sup>5</sup>In fact, a strategy pair is an ESS for a classic bimatrix game if and only if it is a strict NE.



**Figure 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.

- 207 • If  $\tau_{12} > 2\tau_{22}$  and  $\tau_{21} > 2\tau_{22}$ , then strategy  $(D, D)$  is a NE (e.g., Figure 2B, F, G,  
208 H).
- 209 • If  $V < C$  and  $\tau_{12} < 2\tau_{22}$ , then strategy  $(H, D)$  is a NE (e.g., Figure 2E, J).
- 210 • If  $V < C$  and  $\tau_{21} < 2\tau_{22}$ , then strategy  $(D, H)$  is a NE (e.g., Figure 2E, I).

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

215 Of particular note is that, although strategy pair (Dove, Dove) is never an ESS (i.e.  
216 a strict NE) for the classic Owner–Intruder game (since Dove is never an ESS for the  
217 Hawk–Dove matrix game), this pair is a strict NE when  $2\tau_{22} < \min\{\tau_{12}, \tau_{21}\}$ . This analysis  
218 shows that when compared with the classical model, the model that considers duration  
219 of interactions can have strategy  $(D, D)$  as a NE provided the interaction time between  
220 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

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

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

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

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

225 Evaluating these at the equilibrium distribution (6) yields

$$\begin{aligned}\Pi_{e_1} &= \frac{(C\tau_{12} + (2\tau_{11} - \tau_{12})V)(\sqrt{A} - N\tau_{12}\tau_{21})}{4N_{e_1}\tau_{11}\tau_{12}(\tau_{11}\tau_{22} - \tau_{12}\tau_{21})} + \frac{\tau_{12}(V-C)(N_{e_1} + N_{f_1}) + 2\tau_{11}V(N_{e_1} - N_{f_1})}{4N_{e_1}\tau_{11}\tau_{12}} \\ \Pi_{e_2} &= -\frac{V\left(\sqrt{A} + N(\tau_{12}\tau_{21} - 2\tau_{11}\tau_{22}) - (N_{e_1} + N_{f_1})(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})\right)}{4\tau_{22}(N - N_{e_1})(\tau_{11}\tau_{22} - \tau_{12}\tau_{21})} \\ \Pi_{f_1} &= -\frac{\sqrt{A}(C\tau_{21} + (2\tau_{11} - \tau_{21})V)}{4N_{f_1}\tau_{11}\tau_{21}(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})} + \frac{N\tau_{12}(C\tau_{21} + 2\tau_{11}V - \tau_{21}V)}{4N_{f_1}\tau_{11}(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})} - \\ &\quad \frac{(C-V)(N_{e_1} + N_{f_1})}{4N_{f_1}\tau_{11}} + \frac{2\tau_{11}V(N_{f_1} - N_{e_1})}{4N_{f_1}\tau_{11}\tau_{21}} \\ \Pi_{f_2} &= -\frac{V\left(\sqrt{A} + N(\tau_{12}\tau_{21} - 2\tau_{11}\tau_{22}) - (N_{e_1} + N_{f_1})(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})\right)}{4\tau_{22}(N - N_{f_1})(\tau_{11}\tau_{22} - \tau_{12}\tau_{21})},\end{aligned}$$

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

227 Two-strategy, bimatrix games that are role-independent have role-independent inter-  
 228 action times if and only if  $\tau_{12} = \tau_{21}$  (i.e., the length of Hawk–Dove interactions does  
 229 not depend on whether the Hawk is the owner or the intruder).<sup>6</sup> Symmetric NE of  
 230 the role-independent time-constrained Owner–Intruder game are then those of the time-  
 231 constrained Hawk–Dove matrix game, which are found analytically in Krivan and Cress-  
 232 man (2017) using `Solve` command of Mathematica 11.

<sup>6</sup>We call a multi-strategy time-constrained bimatrix game “role-independent” if both its payoff bima-  
 trix 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  $i, j$ ).

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

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

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

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

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<sup>7</sup>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),  $\Pi_{e_1}$  (and  $\Pi_{f_1}$ ) 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).

263 2D).

264 Now assume that  $V < C$  (Figure 2, panels E–K). Hawk is no longer an ESS for the  
 265 classic Hawk–Dove game and the only NE is the interior ESS where the population plays  
 266 Hawk with probability  $\frac{V}{C}$ . On the other hand, the classic Owner–Intruder game has two  
 267 strict NE  $(H, D)$  and  $(D, H)$ <sup>8</sup> and the unstable interior NE where both populations plays  
 268 Hawk with probability  $\frac{V}{C}$ . This corresponds to the time-constrained game with all in-  
 269 teraction times equal (Figure 2E). When Hawk–Dove interactions are sufficiently long  
 270 compared to Dove–Dove interactions (specifically,  $\tau_{21} > 2\tau_{22}$  and  $\tau_{12} > 2\tau_{22}$ ), then  $(D, D)$   
 271 is the only NE (Figure 2F). With a lower cost (Figure 2G), two symmetric interior NE  
 272 appear (they are both saddles) along with two neutrally stable asymmetric interior NE  
 273 that are surrounded by a family of closed trajectories. Furthermore, a small perturbation  
 274 of these NE by introducing a slight role dependence in interaction times makes one of  
 275 them locally asymptotically stable and the other unstable (panel H). Larger differences  
 276 for role dependent interaction times (panels I and J respectively) eliminates interior NE  
 277 altogether and make the paradoxical ESS  $(D, H)$  (respectively,  $(H, D)$ ) globally asymp-  
 278 totically stable. Panel K is a degenerate case where  $\tau_{12} = \tau_{21} = 2\tau_{22}$  and so has boundary  
 279 NE as discussed in the following section. Finally, panel L assumes  $V = C = 1$ ,  $\tau_{11} = 3$   
 280 and all other interaction times are 1. This parametrization corresponds to the situation  
 281 where sets of the NE along the boundary of square  $[0, N] \times [0, N]$  exist. As calculated in  
 282 the following section, the sets of NE are  $0 \leq N_{e_1} < \frac{3}{4}N$  when  $N_{f_1} = N$  and  $0 \leq N_{f_1} < \frac{3}{4}N$   
 283 when  $N_{e_1} = N$ .

### 284 2.3. Boundary NE

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

<sup>8</sup>The second strict NE is often called the “paradoxical ESS” (Maynard Smith, 1982) since it corre-  
 sponds to the intruder always taking over the site and becoming the owner.

<sup>9</sup>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.

293  $n_{21} = N_{e_2}$ ,  $n_{11} = N_{e_1}$  and  $N = N_{e_1} + N_{e_2}$ ,

$$\Pi_{f_1} = \frac{N_{e_1}}{N} \frac{\pi_{11}^f}{\tau_{11}} + \frac{N_{e_2}}{N} \frac{\pi_{21}^f}{\tau_{21}}. \quad (15)$$

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

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

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

301 For the Owner–Intruder game, boundary NE emerge on the top edge of the square  
302  $[0, N] \times [0, N]$  where  $N_{f_1} = N$  when  $V = C$  since  $\frac{\pi_{11}^e}{\tau_{11}} = \frac{\pi_{21}^e}{\tau_{21}} = 0$  along this edge. By  
303 evaluating when  $\Pi_{f_1} \geq \Pi_{f_2}$  along this edge, we find the following three cases for sets of  
304 NE of the form  $(N_{e_1}, N)$

- 305 1.  $\tau_{11} \leq 2\tau_{12}$  and  $\tau_{21} < 2\tau_{22}$  and  $0 \leq N_{e_1} \leq N$
- 306 2.  $\tau_{11} > 2\tau_{12}$  and  $\tau_{21} < 2\tau_{22}$  and  $0 \leq N_{e_1} \leq \frac{N\tau_{11}(\tau_{21}-2\tau_{22})}{2(\tau_{12}\tau_{21}-\tau_{11}\tau_{22})}$
- 307 3.  $\tau_{11} < 2\tau_{12}$  and  $\tau_{21} \geq 2\tau_{22}$  and  $\frac{N\tau_{11}(\tau_{21}-2\tau_{22})}{2(\tau_{12}\tau_{21}-\tau_{11}\tau_{22})} \leq N_{e_1} \leq N$

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

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

314 These sets of NE on the boundary are illustrated in Figure 2L for the role-independent  
315 time-constrained Owner–Intruder game with  $V = C$ . From Krivan and Cressman (2017)  
316 the interior NE in this figure appears for  $\tau_{11} > \tau(3 - C/V + 2\sqrt{1 - C/V}) = 2\tau$  (assuming  
317  $\tau_{12} = \tau_{22} = \tau$ ). In this case the NEs on the edges form two disconnected components.

<sup>10</sup>In classical games, this set is called a NE component (Cressman, 2003).

318 Since  $\tau_{12} = \tau_{21}$ , the NE component on the upper edge is then the reflection in the main  
 319 diagonal of the component on the right-hand edge.

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

### 323 3. Non instantaneous pair formation

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

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

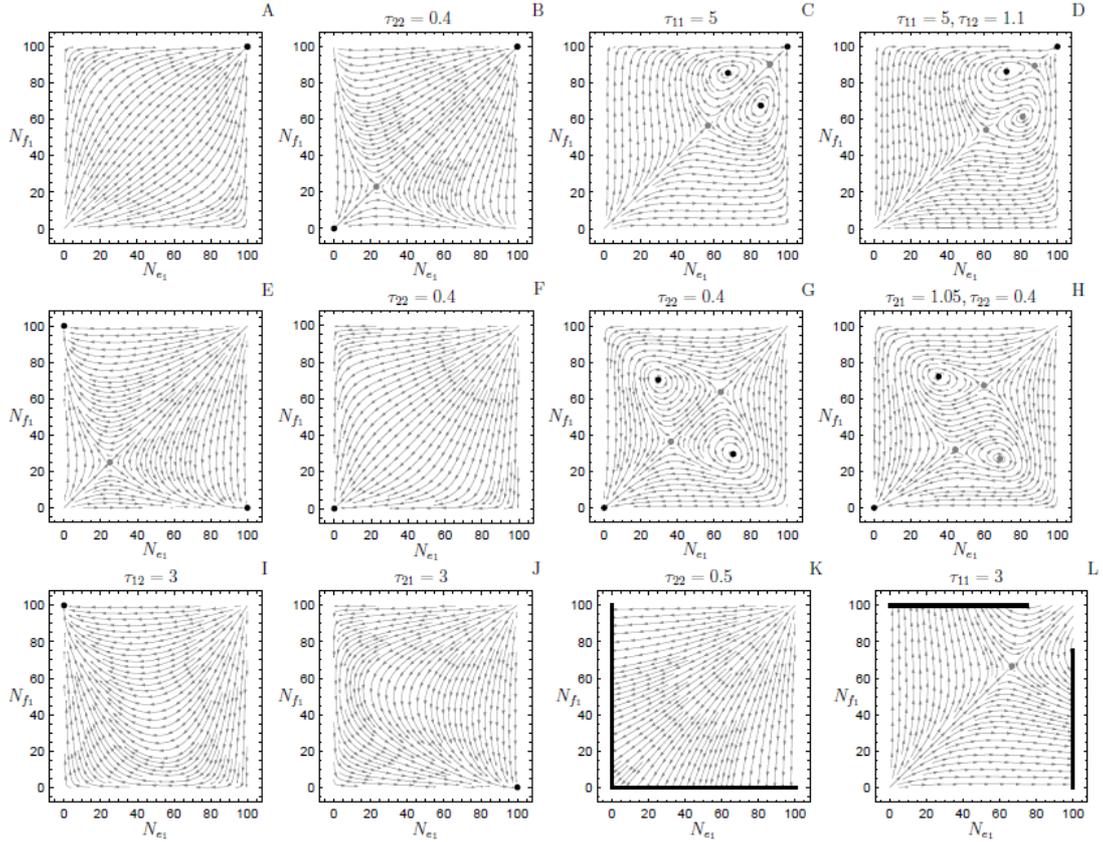
$$\begin{aligned} N_{e_i} &= n_{e_i} + n_{i1} + n_{i2} \\ N_{f_j} &= n_{f_j} + n_{1j} + n_{2j} \end{aligned} \quad (17)$$

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

336 Distributional dynamics of singles and pairs when pair formation is described by the

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<sup>11</sup>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.



**Figure 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  $\tau_{12}$  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,  $\tau_{12}$  (respectively  $\tau_{21}$ ) 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

337 mass action law are then

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

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

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

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

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

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

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

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

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

### 351 3.1. Classic bimatrix game with non instantaneous pair formation

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

356 The equilibrium distribution of (18) is

$$n_{e_i} = \frac{N_{e_i} (\sqrt{4\lambda N\tau + 1} - 1)}{N \cdot 2\lambda N\tau}$$

$$n_{f_j} = \frac{N_{f_j} (\sqrt{4\lambda N\tau + 1} - 1)}{N \cdot 2\lambda N\tau}.$$

357 Substituting these expressions to (21) leads to

$$\Pi_{e_i} = \frac{4N\lambda}{(1 + \sqrt{1 + 4\lambda\tau N})^2} \left( \pi_{i1}^e \frac{N_{f_1}}{N} + \pi_{i2}^e \frac{N_{f_2}}{N} \right),$$

$$\Pi_{f_j} = \frac{4N\lambda}{(1 + \sqrt{1 + 4\lambda\tau N})^2} \left( \pi_{1j}^f \frac{N_{e_1}}{N} + \pi_{2j}^f \frac{N_{e_2}}{N} \right).$$
(22)

358 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  
 359 game with payoff matrix (1). From this it follows that the NE of the classic bimatrix  
 360 game with non instantaneous pair formation is the same as the the classic bimatrix game  
 361 and, moreover, the trajectories of the replicator equation are the same (up to the speed  
 362 along the trajectory). Thus, the two games have the same evolutionary outcomes.

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

### 367 3.2. Evolutionary outcomes with non instantaneous pair formation

368 As we saw in Section 2, evolutionary outcomes of time-constrained bimatrix games  
 369 with instantaneous pair formation depend heavily on pair interaction times when these

370 are not all the same (e.g., Figure 2). This section analyzes the same phenomena when  
371 pair formation is not instantaneous.

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

$$\Pi_{e_1} = \frac{\lambda n_{f_1} \pi_{11}^e}{\lambda n_{f_1} \tau_{11} + 1}, \quad \Pi_{f_1} = \frac{\lambda n_{e_1} \pi_{11}^f}{\lambda n_{e_1} \tau_{11} + 1},$$

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

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

376 and

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

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

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

379 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.,

$$\begin{aligned} \frac{\pi_{11}^e}{\tau_{11}(\sqrt{4\lambda N\tau_{11}} + 1 + 1)} &> \frac{\pi_{21}^e}{\tau_{21}(\sqrt{4\lambda N\tau_{11}} + 1 - 1) + 2\tau_{11}} \\ \frac{\pi_{11}^f}{\tau_{11}(\sqrt{4\lambda N\tau_{11}} + 1 + 1)} &> \frac{\pi_{12}^f}{\tau_{12}(\sqrt{4\lambda N\tau_{11}} + 1 - 1) + 2\tau_{11}}. \end{aligned} \quad (23)$$

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

385 As  $\lambda$  increases to infinity, payoff  $\Pi_{e_1}$  ( $\Pi_{f_1}$ ) converges to  $\pi_{11}^e/\tau_{11}$  ( $\pi_{11}^f/\tau_{11}$ ) and invasion  
386 fitness  $\Pi_{e_2}$  ( $\Pi_{f_2}$ ) converges to  $\pi_{21}^e/\tau_{21}$  ( $\pi_{12}^f/\tau_{12}$ ). Thus, when the encounter rate of singles  
387 is large, the strict NE of the time-constrained bimatrix game with non instantaneous pair  
388 formation are the same as the strict NE of the time-constrained bimatrix game of Section  
389 2 (i.e., with instantaneous pair formation). In fact, for large  $\lambda$ , the interior NE match as  
390 well since there are essentially no singles in the system.

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

392 *3.3. The Owner–Intruder game with non instantaneous pair formation*

393 When all interaction times equal to  $\tau$  as in Section 3.1, there is an interior NE if and  
 394 only if  $V < C$ . As a function of  $\lambda$  and  $\tau$ , it is given by

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

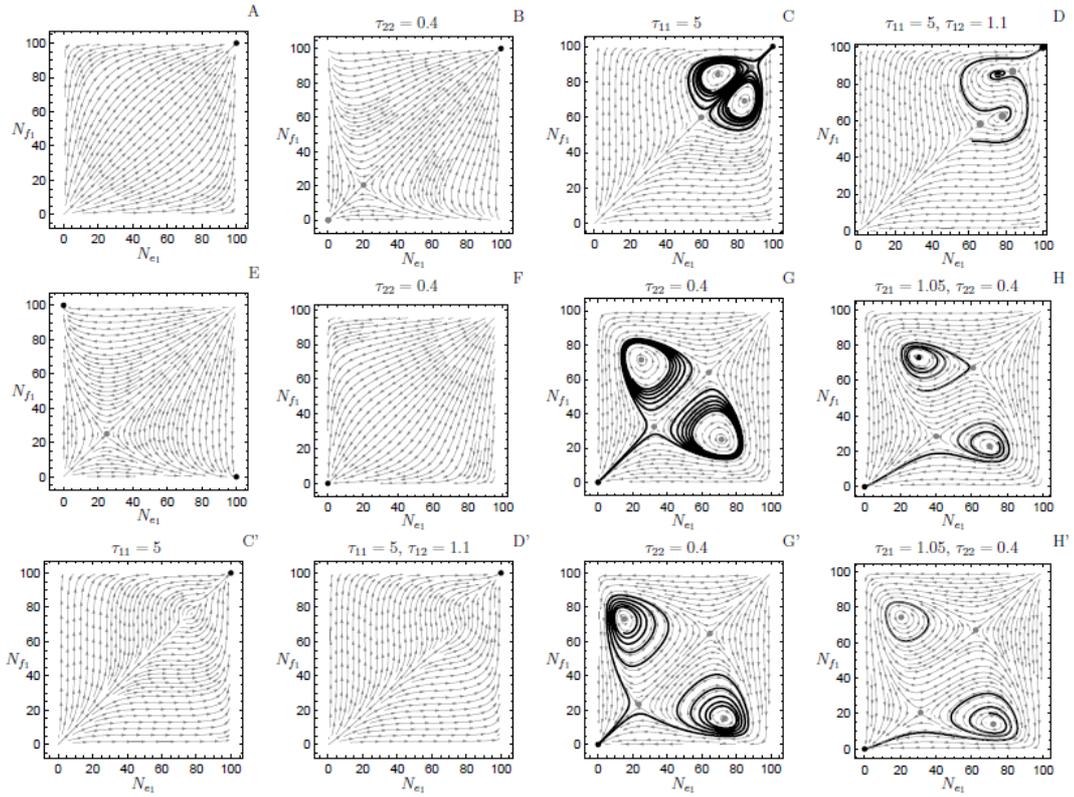
395 which is the classic result for the case when  $V < C$ .

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

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

402 This is a semi-explicit index 1 differential-algebraic equation (Ascher and Petzold, 1998)  
 403 that we solve numerically using Mathematica 10.

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



**Figure 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 Figure 2. Panels A and E are identical to their corresponding panels in Figure 2 since these are all equivalent to the classic bimatrix game. There are also no noticeable differences between panels B and F compared to Figure 2. The differences with Figure 2 (which emerges for very large  $\lambda$ ) are as follows. For long interaction times between Hawks when  $V > C$ , the four interior NE of Figure 2 disappear completely when  $\lambda = 1$  (panels C' and D') whereas the two asymmetric interior NE become unstable for intermediate  $\lambda$  (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  $\lambda$  decreases (panels G and G'). With role-dependent interaction times, the asymptotically stable interior NE of Figure 2H eventually becomes unstable when  $\lambda$  decreases and a stable limit cycle emerges.

419 **4. Discussion**

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

433 When interaction times depend on strategies used by the pair, the Hardy–Weinberg  
 434 distribution of pairs is no longer relevant and expected individual payoff is now a nonlinear  
 435 function of the numbers using each strategy in the two populations whether the pair  
 436 formation process among disbanded pairs is instantaneous (Section 2) or not (Section 3).  
 437 However, in both cases, we show the existence of a unique distribution as a function of  
 438 these numbers at the beginning of these respective sections,<sup>12</sup> although we are only able  
 439 to provide an analytic expression for it when pair formation is instantaneous (see equation  
 440 (6)). Nevertheless, this allows us to define a time-constrained, bimatrix game in Section  
 441 2 and in Section 3 where payoff (which we call the fitness function) is given as expected  
 442 individual payoff per unit time. As pointed out in Sections 2 and 3.1, this new formulation  
 443 reduces to the classic bimatrix game when all interaction times are the same.

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

451 Unfortunately, other NE of the time-constrained bimatrix game are more difficult  
 452 to analyze. In particular, the analytic formula for interior NE is not available except  
 453 in special circumstances due to the complicated distribution that replaces the Hardy–

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<sup>12</sup>In Section 3, this includes the distribution of pairs and singles

454 Weinberg distribution in these games. Since interior NE correspond to interior rest points  
 455 of the replicator equation, they can be approximated by simulating this dynamics for  
 456 particular games. No attempt is made for a complete analysis of all two-strategy time-  
 457 constrained bimatrix games.<sup>13</sup> Instead, we focus on the time-constrained Owner–Intruder  
 458 game. This classic role-independent bimatrix game has an easily understood evolutionary  
 459 outcome.

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

472 When  $V < C$ , (Hawk, Hawk) is never a strict NE. In the classic bimatrix game,  
 473 there are two strict NE; namely, (Hawk, Dove) and the paradoxical ESS (Dove, Hawk)  
 474 where the intruder always wins the resource (i.e., the owner and intruder switch roles  
 475 through each interaction) as well as one unstable saddle symmetric interior NE where  
 476 both populations play the ESS of the classic symmetric Hawk–Dove matrix game. The  
 477 replicator equation predicts the paradoxical ESS will be the evolutionary outcome if and  
 478 only if the initial population distribution has more Hawks as intruders than as owners.  
 479 As shown in Figure 2, panels I and J, either one of these strict NE can disappear by  
 480 introducing a role dependence into the time interaction matrix (2). In fact, both must  
 481 disappear when (Dove, Dove) becomes a strict NE through their interaction time being  
 482 short enough compared to the equal time of the other interactions in Figures 2 and 3,  
 483 in which case interior NE may (panels G and H) or may not appear (panel F). There  
 484 are also marked differences between the evolutionary outcomes when pair formation is

<sup>13</sup>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.

<sup>14</sup>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.

485 instantaneous compared to when it is non instantaneous, as detailed in the main text.

486 In this article, although we have relaxed the implicit assumption of classic evolution-  
 487 ary game theory that all interactions take the same amount of time, we have assumed  
 488 that newly single individuals are immediately available to form pairs. This rules out  
 489 straightforward application of our methods to models where some single individuals from  
 490 a disbanded pair wait before joining the pair formation process. For instance, this occurs  
 491 in parental care models, e.g., Battle of the Sexes (Dawkins, 1976; Hofbauer and Sigmund,  
 492 1998; Mylius, 1999; Cressman, 2003; Broom and Rychtář, 2013) when males are immedi-  
 493 ately available to mate after a couple disbands whereas females will not mate immediately  
 494 but stay to care for offspring if abandoned by their mate. In this article, we assume that  
 495 both populations have the same number of individuals, which is required when pair for-  
 496 mation is instantaneous. On the other hand, when pair formation is non-instantaneous,  
 497 all calculations can be generalized to population 1 having a different size than population  
 498 2, although the formulas are more complex.<sup>15</sup>

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

512 The results of this article show that the evolutionary outcome for bimatrix games  
 513 becomes more complex when interaction times are incorporated into the game-theoretic  
 514 model. The results are also more complex than those reported by Křivan and Cressman  
 515 (2017) for matrix games with strategy-dependent interaction times as is to be expected  
 516 given the conceptual differences between classic matrix and bimatrix games. It is our  
 517 contention that these added complexities are often unavoidable to make the evolutionary  
 518 model more realistic. This is especially true when the model purports to describe a

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<sup>15</sup>With unequal population size, the time-constrained bimatrix game with all  $\tau_{ij}$  equal is no longer the classic bimatrix game as in Section 3.1.

519 behavioral system where pairs interact for different amounts of time.

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526 **Appendix A. Pairs distributional dynamics when pairing is instantaneous**

527 Here we derive pair dynamics (3). Let us consider a small time interval  $\Delta$ . Because  
 528 pairs  $n_{ij}$  split up following a Poisson process with parameter  $\tau_{ij}$ , in this time interval  
 529 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  
 530 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  
 531 singles in each population in time interval  $\Delta$  is

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

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

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

534 To obtain the number of newly formed  $(e_i f_j)$  pairs in the time interval  $\Delta$  we multiply  
 535 (A.2) by the number of newly formed pairs (which equals the number of disbanded singles  
 536 because we assume instantaneous pairing) in time interval  $\Delta$  and we obtain

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

537 Writing difference equations for pairs

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

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

539 From

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

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

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

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

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

545 The minimum value of this upward parabola is

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

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

## 547 Appendix B. Calculation of the invasion fitness (16)

548 The fitness of strategy  $f_2$ ,  $\Pi_{f_2}$ , given in (9) calculated at the distributional equilibrium  
 549 (6) is

$$\Pi_{f_2} = \frac{\sqrt{A}(\pi_{22}^f\tau_{12} - \pi_{12}^f\tau_{22}) + N\tau_{12}(\pi_{12}^f\tau_{21}\tau_{22} - 2\pi_{22}^f\tau_{11}\tau_{22} + \pi_{22}^f\tau_{12}\tau_{21})}{2\tau_{12}\tau_{22}(N - N_{f_1})(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})} -$$

$$\frac{(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})(\pi_{12}^f\tau_{22}(N_{f_1} - N_{e_1}) + \pi_{22}^f\tau_{12}(N_{e_1} + N_{f_1}))}{2\tau_{12}\tau_{22}(N - N_{f_1})(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})},$$

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

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

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

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

553 and the numerator of  $\Pi_{f_2}$  simplifies to

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

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

$$\lim_{N_{f_1} \rightarrow N} \Pi_{f_2} = \frac{N_{e_1}\pi_{12}^f\tau_{21} + N_{e_2}\pi_{22}^f\tau_{11}}{N\tau_{11}\tau_{22} + N_{e_1}(\tau_{12}\tau_{21} - \tau_{11}\tau_{22})}. \quad (\text{B.1})$$

556 Similarly, the fitness of strategy  $e_2$ ,  $\Pi_{e_2}$ , given in (9) calculated at the distributional  
557 equilibrium (6) is

$$\Pi_{e_2} = \frac{\sqrt{A}(\pi_{22}^e \tau_{21} - \pi_{21}^e \tau_{22}) + N \tau_{21}(\pi_{21}^e \tau_{12} \tau_{22} - 2\pi_{22}^2 \tau_{11} \tau_{22} + \pi_{22}^2 \tau_{12} \tau_{21})}{2\tau_{21} \tau_{22} (N - N_{21})(\tau_{12} \tau_{21} - \tau_{11} \tau_{22})} - \frac{(\tau_{12} \tau_{21} - \tau_{11} \tau_{22})(\pi_{21}^e \tau_{22} (N_{e_1} - N_{f_1}) + \pi_{22}^e \tau_{21} (N_{e_1} + N_{f_1}))}{2\tau_{21} \tau_{22} (N - N_{e_1})(\tau_{12} \tau_{21} - \tau_{11} \tau_{22})}.$$

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

$$\lim_{N_{e_1} \rightarrow N} \Pi_{e_2} = \frac{N_{f_1} \pi_{21}^e \tau_{12} + N_{f_2} \pi_{22}^e \tau_{11}}{N \tau_{11} \tau_{22} + N_{f_1} (\tau_{12} \tau_{21} - \tau_{11} \tau_{22})} \quad (\text{B.2})$$

559 by again applying L'Hospital's rule.

### 560 Appendix C. Uniqueness of distributional equilibrium of (25)

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

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

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

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