



Reducing courtship time promotes marital bliss: The Battle of the Sexes game revisited with costs measured as time lost

Ross Cressman^a, Vlastimil Křivan^{b,c,*}

^a Department of Mathematics, Wilfrid Laurier University, Waterloo, Ontario, Canada

^b Department of Mathematics, Faculty of Science, University of South Bohemia, Branišovská 1760, 370 05 České Budějovice, Czech Republic

^c Czech Academy of Sciences, Biology Centre, Institute of Entomology, Branišovská 31, 370 05 České Budějovice, Czech Republic

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ABSTRACT

Classic bimatrix games, that are based on pair-wise interactions between two opponents belonging to different populations, do not consider the cost of time. In this article, we build on an old idea that lost opportunity costs affect individual fitness. We calculate fitnesses of each strategy for a two-strategy bimatrix game at the equilibrium distribution of the pair formation process that includes activity times. This general approach is then applied to the Battle of the Sexes game where we analyze the evolutionary outcome by finding the Nash equilibria (NE) of this time-constrained game when courtship and child rearing costs are measured by time lost. While the classic Battle of the Sexes game has either a unique strict NE (specifically, all males exhibit Philanderer behavior and either all females are Coy or all are Fast depending on model parameters), or a unique interior NE where both sexes exhibit mixed behavior, including time costs for courtship and child rearing changes this prediction. First, (Philanderer, Coy) is never a NE. Second, if the benefit of having offspring is independent of parental strategies, (Philanderer, Fast) is the unique strict NE but a second stable interior NE emerges when courtship time is sufficiently short. In fact, as courtship time becomes shorter, this mixed NE (where most males are Faithful and the Coy female population is increasing) attracts almost all initial population configurations. Third, this latter promotion of marital bliss also occurs when parents who share in child rearing receive a higher benefit from their offspring than those that don't. Finally, for courtship time of moderate duration, the same phenomenon occurs when the population size increases.

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1. Introduction

Classic evolutionary game theoretical models based on two-player normal form games implicitly assume that all interactions between pairs take the same time and individuals pair randomly and instantaneously. As argued in a recent series of articles (Garay et al., 2017; Křivan and Cressman, 2017; Garay et al., 2018; Křivan et al., 2018; Cressman and Křivan, 2019), these assumptions are suspect for many classic evolutionary games (e.g., the Hawk–Dove game where interactions between two Hawks involve fights that take a different amount of time than other interactions where no fights arise and the repeated Prisoner's Dilemma game when each player can choose to opt out of the interaction (Zhang et al., 2016)). The assumptions are patently untrue for the classic Battle of the Sexes (BoS) game that models

parental care of offspring (Broom and Rychtář, 2013) introduced by Dawkins (1976) who assumed, using his names for male/female behavior, that philandering males when mated with fast females immediately desert and look for a new mate while the female cares for the offspring before mating again. Besides being crucial for understanding evolution of parental care and sexual conflict (e.g., Tregenza et al., 2006), this game has been used to model particular biological systems (e.g., Magurran and Nowak, 1991; Webster et al., 2003).

None of the recent series of articles cited above, which show that including different activity times qualitatively change the game's evolutionary outcome, apply directly to the BoS game. The main purpose of this article is then to extend their methods in order to develop a game-theoretic model of the BoS based on lost opportunity cost and show how measuring costs in terms of time affects the evolutionary outcome of Dawkins' parental care model.

For instance, in the BoS model of Dawkins (1976) (see also Cressman, 1992), females always care for their offspring but can

* Corresponding author.

E-mail addresses: rcressman@wlu.ca (R. Cressman), vlastimil.krivan@gmail.com (V. Křivan).

either be coy (insist on a long courtship before mating) or fast (mate immediately) while males are either faithful (willing to engage in long courtships and also care for offspring) or philandering (will not engage in courtship nor care for offspring). When the benefits of offspring and costs of having and caring for them are given by the payoffs considered by Dawkins (1976), the classic model predicts the population will consist of a mixture of these behaviors for both sexes (see Section 2). The problem with this classic model (as well as with many other behavioral models based on (bi) matrix games) is how to use a single currency to measure benefits and costs that define the payoff matrix (see also Mylius, 1999; Argasinski, 2006; Argasinski and Broom, 2013; Argasinski and Broom, 2018). To address this problem, the article allows a second currency besides payoff; namely, the time that interactions and other activities take (see also Křivan et al., 2018).

In Section 3, we use this approach for a general two-player, two-strategy game that includes the time that different activities take. Here we consider three possible individual states: individuals are either free to form pairs (e.g., to mate), they are paired, and they are single but not yet ready to pair (e.g., gestation or lactation period, time to care for offspring on their own). The time-constrained game is then defined by a payoff bimatrix together with a time-bimatrix, from which we are able to formulate the individual fitness of each strategy as a function of the population state.

We apply this general theory to the time-constrained Battle of the Sexes game in Section 4. We consider two parametrizations of the payoff matrix. First, in keeping with the original description by Dawkins (1976), Section 4.1 assumes that all strategies that lead to offspring production have the same benefit given by a payoff to both parents. However, the cost is now measured by time spent in courtship, rearing offspring, and searching for a new mate. When couples that stay together spend less time caring for offspring than females who provide this care on their own, this model makes a strikingly different prediction when compared to the Dawkins model. For instance, regardless of model parameters, the population configuration where all females are fast and all males philander, denoted by (Philanderer, Fast), is an evolutionary outcome whereas in Dawkins' model this requires the benefit from offspring to be greater than the cost of rearing them. A second evolutionary outcome consisting of a mixture of their two behaviors for both sexes emerges whenever courtship time is short enough. Moreover, by reducing courtship time further, this mixed evolutionary outcome promotes marital bliss¹ in that almost all males are faithful and the frequency of coy females increases. In fact, when courtship time is close to zero, almost all initial population configurations evolve to the mixed evolutionary outcome.

For the second parametrization, Section 4.2 assumes the time spent caring for offspring is the same for couples that stay together as for females on their own but now the benefit to the couples is greater. These assumptions are motivated by McNamara et al. (2009) (see also Broom and Rychtář, 2013) "coyness game" that models females who inspect the males they encounter as to whether they are helpful or non-helpful. In our setting, couples with Faithful males obtaining a higher payoff models situations where females paired with Faithful males mate several times while raising their offspring as they do not need to search for a new partner, or where having both partners increases the probability of offspring survival. As we will see, reducing courtship time promotes

marital bliss in this model as well. Moreover, depending on how much greater the benefit to couples is, this may be the only evolutionary outcome. In particular, there may no longer be an evolutionary outcome where all females are Fast.

2. The classic Battle of the Sexes game

The Battle of the Sexes (Dawkins, 1976; Maynard Smith, 1974; Hofbauer and Sigmund, 1998; Broom and Rychtář, 2013; Broom and Křivan, 2018) is a classical bimatrix game that aims to model the conflict between males (the first population) and females (the second population) over the care of their offspring. Here, we briefly summarize the classic BoS game to provide the foundation to include courtship time, time to rear offspring and time to find mates in the time-constrained version analyzed in Section 4.

In the classic parameterization (Dawkins, 1976), males are either faithful (m_1) or philandering (m_2) and females are either coy (f_1) or fast (f_2). A coy female demands a period of courtship before mating, whereas a fast female will mate with a male as soon as they meet. Faithful males are willing to engage in long courtships and will help care for the offspring after mating while a philanderer will not engage in courtship, and so cannot mate with a coy female, and also leaves immediately without helping care for offspring after mating with a fast female. The payoff bimatrix for the Battle of the Sexes is

$$\begin{array}{c|cc} \text{Male} \backslash \text{Female} & \text{Coy} & \text{Fast} \\ \hline \text{Faithful} & \left(B - \frac{C_c}{2} - C_c, B - \frac{C_c}{2} - C_c \right) & \left(B - \frac{C_c}{2}, B - \frac{C_c}{2} \right) \\ \text{Philanderer} & (0, 0) & (B, B - C_r) \end{array} \quad (1)$$

where $B > 0$ is the fitness gained by having offspring, $C_r > 0$ is the (potentially shared) cost of raising the offspring and $C_c > 0$ is the cost of engaging in courtship. In (1), matrix entries are payoff pairs where the first (respectively, second) payoff is that of the male (respectively, female) when this pair plays their respective strategies.

In Dawkins (1976), these costs and benefits were based on the numerical values (given in brackets) in the following assumptions:

1. the total cost of raising offspring ($C_r = 20$)
2. the individual payoff gain from offspring ($B = 15$)
3. the individual cost of courtship ($C_c = 3$)
4. the payoff of not mating (0).

That is, the payoff bimatrix from Dawkins (1976) is then

$$\begin{array}{c|cc} \text{Male} \backslash \text{Female} & \text{Coy} & \text{Fast} \\ \hline \text{Faithful} & (2, 2) \rightarrow (5, 5) \\ & \uparrow \quad \quad \downarrow \\ \text{Philanderer} & (0, 0) \leftarrow (15, -5) \end{array} \quad (2)$$

To see that an evolutionary outcome must involve a mixture of behaviors for both sexes, notice that fast females would do better than coy females when the population consists of faithful males and coy females (i.e., fast females can invade this system). Similarly, when the population has only fast females and faithful males, philandering males can invade. Next, in a population of fast females and philandering males, coy females can invade. Finally, when all females are coy and males philandering, faithful males can invade. That is, there is a cyclic pattern to how the mixture of behaviors is expected to evolve as indicated by the arrows in (2) and reflected in the trajectories of such evolutionary dynamics as the replicator equation (see Fig. 1B and Appendix A). In this figure, there is a unique rest point of the dynamics in the interior of the unit square where $\frac{5}{8}$ (respectively $\frac{5}{6}$) of the males (respectively, females) are faithful (respectively, coy). This corresponds to the game's only Nash equilibrium (i.e., a strategy pair where neither males nor females can increase their payoff by unilaterally changing their strategy).

¹ We call (Faithful, Coy) the marital bliss state in keeping with Dawkins (1976) describing Coy as the domestic-bliss strategy whereby females encourage males to invest in courtship and remain in the marriage. Dawkins goes on to state that the domestic-bliss strategy works in the sense that, for his payoff choices, males (respectively, females) are predominantly Faithful (respectively, Coy) at the mixed (interior) Nash equilibrium (NE).

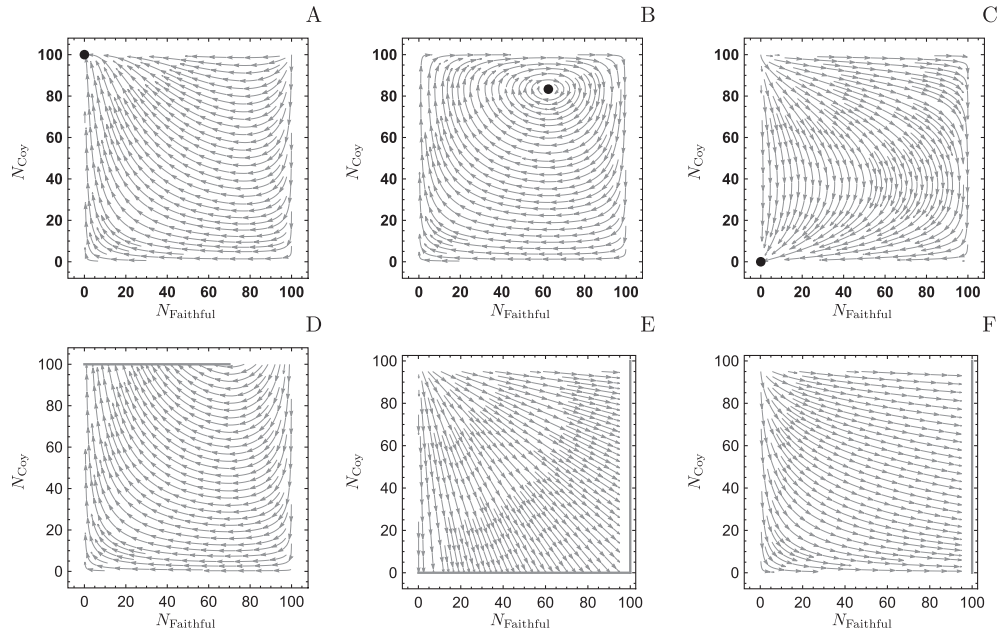


Fig. 1. Phase portrait of the replicator equation for the classic bimatrix games related to BoS. Panels A–D are the classic BoS game with payoff matrix (1) where all payoffs, except the benefit B for offspring, are taken from Dawkins (1976) (i.e., $C_c = 3$, $C_r = 20$). Panel A assumes that $B = 10 \leq \min\{C_c + \frac{C_r}{2}, C_r\}$, panel B assumes $\min\{C_c + \frac{C_r}{2}, C_r\} < B = 15 < C_r$, and panel C assumes $C_r < B = 30$. Panel D is the threshold case where $B = C_c + \frac{C_r}{2} = 13$. Panel E corresponds to the payoff matrix given by (14) with $B = 1$ and no cost of courtship ($C_c = 0$) or of raising offspring ($C_r = 0$). Panel F corresponds to the payoff matrix given by (18) with $B_1 = 1$ and $B_2 = 2$. Nash equilibria are indicated by black dots or line segments. In this and subsequent figures, $N_{Faithful}$ is the same as N_{m1} and N_{Coy} is N_{f1} used in the text. Values of other parameters: $N_m = 100$, $N_f = 100$.

For other payoff parameters (B, C_c, C_r), different Nash equilibria (NE) arise. The complete characterization (Broom and Rychtář, 2013), except in the threshold cases considered at the end of this section, shows that this NE is unique for each payoff parameter set and given by:

- If $B < \min\{C_c + \frac{C_r}{2}, C_r\}$, strategy $(m_2, f_1) = (\text{Philanderer}, \text{Coy})$ is the NE (Fig. 1A).
- If $B > C_r$, strategy $(m_2, f_2) = (\text{Philanderer}, \text{Fast})$ is the NE (Fig. 1C).
- For intermediate benefits satisfying $\frac{C_r}{2} + C_c < B < C_r$, the classic case has an interior mixed NE, where the proportion of males that are faithful (respectively, females that are coy) is $\frac{C_r - B}{C_r + C_c - B}$ (respectively, $\frac{C_r}{2(B - C_c)}$), which is surrounded by a family of closed curves for the replicator equation (Fig. 1B).

In cases (a) and (b), the unique NE is globally asymptotically stable (i.e., the NE is locally asymptotically stable and all interior trajectories converge to it) under the replicator equation (as well as many other evolutionary dynamics, e.g., Sandholm, 2010). This result can also be deduced directly when considering payoffs in (1) since, in case (a) for example, Philanderer strictly dominates Faithful for males (since male payoff entries in (1) satisfy $B - \frac{C_r}{2} - C_c < 0$ and $B - \frac{C_r}{2} < B$) and, once there are no faithful males in the population, Coy strictly dominates Fast (i.e., $B - C_r < 0$). In game-theoretic terms, the games in cases (a) and (b) are strictly dominance solvable to their unique NE. In this article, we consider such a NE as the evolutionary outcome since it is globally asymptotically stable.

Interestingly, in Dawkins' classic model, the marital-bliss state (Faithful, Coy) is never the evolutionary outcome even though this may be the socially preferred solution. From this perspective, the institution of marriage combined with an initial courtship period could be viewed as forming a binding agreement to enforce the (Faithful, Coy) outcome which otherwise would not evolve in society. On the other hand, that (Philanderer, Coy) societies evolve

when $B < \min\{C_c + \frac{C_r}{2}, C_r\}$ is also a questionable consequence of the classic model in that no offspring are produced (see also Section 4) and such a society will disappear.

In the threshold cases where $B = C_r$ or $B = C_c + C_r/2 < C_r$, there is a set of NE where one sex plays only one of its pure strategies and the other sex may play different mixtures of its two strategies. Moreover, each interior trajectory of the replicator equation converges to a single point in this set that depends on the initial point of the trajectory. For instance, when $B = C_c + C_r/2 < C_r$ as in Fig. 1D, the NE set has all females Coy and at most $\frac{2C_c}{C_r} < 1$ of the males Faithful.²

3. The two-player, two-strategy time-constrained game

From a recent series of articles (Garay et al., 2017, 2018; Křivan and Cressman, 2017; He et al., 2018; Křivan et al., 2018; Cressman and Křivan, 2019), it is clear that including the time that activities take into game-theoretic models alters the expected evolutionary outcome. Since the theory developed in these articles does not directly apply to the time-constrained BoS game of Section 4, we first extend their methods to general bimatrix games that include the BoS. To this end, consider the two-strategy, two-player, asymmetric game given by the payoff bimatrix (Hofbauer and Sigmund, 1998; Cressman, 2003; Broom and Rychtář, 2013)

² To see this, notice that when $B = C_c + C_r/2 < C_r$, payoff bimatrix (1) is

Male\Female	Coy	Fast
Faithful	(0, 0)	(C_c, C_c)
Philanderer	(0, 0)	($C_c + C_r/2, C_c - C_r/2$)

Because $C_c + C_r/2 > C_c$, philandering males receive higher payoff than faithful males if the population contains any fast females (implying all trajectories in Fig. 1D move to the left except those on the upper boundary of the square). Moreover, if there are no faithful males, the payoff to coy females is higher than to fast females (i.e., $C_c - C_r/2 < 0$), accounting for the upward movement along the left-hand boundary of the square. Thus, all females must be Coy at any NE. Finally, on the upper boundary where all females are Coy, the payoff to coy (respectively, fast) females is 0 (respectively, $C_c p_1 + (C_c - C_r/2)p_2 = C_c - (C_r/2)p_2$), where p_i is the proportion of males playing strategy m_i . Thus, a point on this boundary is a NE if and only if $C_c - (C_r/2)p_2 \leq 0$ (i.e., $p_2 \leq \frac{2C_c}{C_r} < 1$).

$$\begin{matrix} & f_1 & f_2 \\ m_1 & \left[\begin{matrix} \pi_{11}^m, \pi_{11}^f & \pi_{12}^m, \pi_{12}^f \end{matrix} \right] \\ m_2 & \left[\begin{matrix} \pi_{21}^m, \pi_{21}^f & \pi_{22}^m, \pi_{22}^f \end{matrix} \right] \end{matrix} \quad (3)$$

where the (pure) strategies of player 1 (respectively, player 2) are m_1 and m_2 (respectively, f_1 and f_2) and π_{ij}^m (respectively π_{ij}^f) is the payoff to m_i (respectively, f_j) when paired with f_j (respectively, m_i). The NE structure of these games without time constraints (i.e., of classic two-strategy bimatrix games) is well-known (e.g., Hofbauer and Sigmund, 1998; Cressman, 2003) as well as their stability properties under such evolutionary dynamics as the replicator equation.

In the time-constrained game, individuals require some time to form pairs when they are ready to do so (e.g., a time to encounter an individual of the opposite sex who is ready to mate) as well as time they spend when in pairs (e.g., time as a couple) or disbanded from a pair but not yet ready to form new pairs (e.g., time to care for offspring on their own). In this article, we assume that these latter times (i.e., couple and caring time) together are determined by the pair formed and so can be modeled by the following “time-bimatrix”

$$\begin{matrix} & f_1 & f_2 \\ m_1 & \left[\begin{matrix} \tau_{11} + \tau_{m_1}^{f_1}, \tau_{11} + \tau_{f_1}^{m_1} & \tau_{12} + \tau_{m_1}^{f_2}, \tau_{12} + \tau_{f_2}^{m_1} \end{matrix} \right] \\ m_2 & \left[\begin{matrix} \tau_{21} + \tau_{m_2}^{f_1}, \tau_{21} + \tau_{f_1}^{m_2} & \tau_{22} + \tau_{m_2}^{f_2}, \tau_{22} + \tau_{f_2}^{m_2} \end{matrix} \right] \end{matrix} \quad (4)$$

Here, for example, τ_{ij} is the time an m_i strategist paired with an f_j strategist stays together and $\tau_{m_i}^{f_j}$ is the time an m_i strategist that was disbanded from a pair with an f_j strategist needs before it is ready to form a new pair.

The two-strategy, time-constrained bimatrix game is then given by payoff bimatrix (3) and time-bimatrix (4). To solve this game, we need to calculate individual fitness as a function of the number of individuals using each strategy.

3.1. Fitnesses in the time-constrained game

Let n_{m_i} be the number of individuals in the first population playing strategy m_i and n_{f_j} be the number of individuals of the second population playing strategy f_j that are ready to pair. We call these individuals “searchers”. Also, by $n_{m_i f_j}$, we denote the number of (m_i, f_j) pairs, and by $n_{m_i}^{f_j}$ the number of m_i strategists that were disbanded from a pair with an f_j strategist, but are not yet ready to pair again. Similarly, $n_{f_j}^{m_i}$ denotes the number of f_j strategists that were disbanded from a pair with an m_i strategist, but are not yet ready to pair again.

Assuming that individuals who are ready to form pairs encounter each other randomly at a constant encounter rate λ , then at the distributional equilibrium

$$\begin{aligned} \lambda n_{m_i} n_{f_j} \tau_{ij} &= n_{m_i f_j} \\ \lambda n_{m_i} n_{f_j} \tau_{m_i}^{f_j} &= n_{m_i}^{f_j} \\ \lambda n_{m_i} n_{f_j} \tau_{f_j}^{m_i} &= n_{f_j}^{m_i} \end{aligned} \quad (5)$$

for $i, j = 1, 2$. The first equation in (5) says that the rate with which new pairs are formed equals the rate with which existing pairs disband,³ and the second and the third equations say that the rate with which disbanded individuals become searchers must be the same as is the rate with which new pairs are formed.

We follow the approach of Křivan and Cressman (2017) by defining fitness as the expected payoff per unit time at the equilibrium distribution (which is well-defined by Appendix B) of the pair formation process. These fitnesses, which assume that pay-

offs are obtained through interaction only (i.e., searchers and disbanded individuals do not gain any extra payoff), are given by (see Appendix C)

$$\begin{aligned} \Pi_{m_1} &= \frac{\lambda(n_{f_1} \pi_{11}^m + n_{f_2} \pi_{12}^m)}{1 + \lambda n_{f_1} (\tau_{11} + \tau_{m_1}^{f_1}) + \lambda n_{f_2} (\tau_{12} + \tau_{m_1}^{f_2})} \\ \Pi_{m_2} &= \frac{\lambda(n_{f_1} \pi_{21}^m + n_{f_2} \pi_{22}^m)}{1 + \lambda n_{f_1} (\tau_{21} + \tau_{m_2}^{f_1}) + \lambda n_{f_2} (\tau_{22} + \tau_{m_2}^{f_2})} \\ \Pi_{f_1} &= \frac{\lambda(n_{m_1} \pi_{11}^f + n_{m_2} \pi_{21}^f)}{1 + \lambda n_{m_1} (\tau_{11} + \tau_{f_1}^{m_1}) + \lambda n_{m_2} (\tau_{21} + \tau_{f_1}^{m_2})} \\ \Pi_{f_2} &= \frac{\lambda(n_{m_1} \pi_{12}^f + n_{m_2} \pi_{22}^f)}{1 + \lambda n_{m_1} (\tau_{12} + \tau_{f_2}^{m_1}) + \lambda n_{m_2} (\tau_{22} + \tau_{f_2}^{m_2})} \end{aligned} \quad (6)$$

4. The Battle of the Sexes game where cost is time

In this section, we model the Battle of the Sexes as a two-player, two-strategy time-constrained game where costs are measured by times taken for different activities. We start by defining time-bimatrix (4). Based on the classic BoS story (Dawkins, 1976), let τ_{2r} be the time spent caring for offspring by each member of a couple that stays together, τ_{1r} the time spent caring for offspring by a female on her own, and τ_c the time spent in courtship (if there is one). We assume that $\tau_{1r} \geq \tau_{2r}$ (i.e., females on their own spend at least as much time caring for their offspring as males or females do when they stay together). Since faithful males stay together with their mate during both courtship (when applicable) and caring of offspring, $\tau_{11} = \tau_{2r} + \tau_c$ and $\tau_{12} = \tau_{2r}$ in (4). On the other hand, philandering males spend no time in courtship or child rearing and so $\tau_{21} = \tau_{22} = 0$. Furthermore, all individuals from disbanded pairs are immediately ready to form new pairs except for fast females paired with philanderers. That is, $\tau_{f_2}^{m_2} = \tau_{1r}$ and all other $\tau_{m_i}^{f_j} = \tau_{f_j}^{m_i} = 0$ in (4). This leads to the following time-bimatrix

$$\begin{matrix} \text{Male} \backslash \text{Female} & \text{Coy} & \text{Fast} \\ \text{Faithful} & \left[\begin{matrix} \tau_{2r} + \tau_c, \tau_{2r} + \tau_c & \tau_{2r}, \tau_{2r} \end{matrix} \right] \\ \text{Philanderer} & \left[\begin{matrix} 0, 0 & 0, \tau_{1r} \end{matrix} \right] \end{matrix} \quad (7)$$

Furthermore, benefits of having offspring continue to be measured in terms of payoffs. Let B_1 (respectively, B_2) be the benefit to each member of a couple of having offspring if the male deserts (respectively, is faithful). We assume $B_1 \leq B_2$ to reflect that individual benefits are at least as high when both parents care for offspring compared to when only a single parent (i.e., the mother) does. Thus, the payoff bimatrix is

$$\begin{matrix} \text{Male} \backslash \text{Female} & \text{Coy} & \text{Fast} \\ \text{Faithful} & \left[\begin{matrix} (B_2, B_2) & (B_2, B_2) \end{matrix} \right] \\ \text{Philanderer} & \left[\begin{matrix} (0, 0) & (B_1, B_1) \end{matrix} \right] \end{matrix} \quad (8)$$

The time-constrained BoS is then the game based on payoff bimatrix (8) and time-bimatrix (7).⁴

The evolutionary outcomes for these games are determined through their fitness functions which, from (6), are

$$\begin{aligned} \Pi_{m_1} &= \frac{\lambda B_2 (n_{f_1} + n_{f_2})}{1 + \lambda n_{f_1} (\tau_c + \tau_{2r}) + \lambda n_{f_2} \tau_{2r}} \\ \Pi_{m_2} &= \lambda B_1 n_{f_2} \\ \Pi_{f_1} &= \frac{\lambda B_2 n_{m_1}}{1 + \lambda n_{m_1} (\tau_c + \tau_{2r})} \\ \Pi_{f_2} &= \frac{\lambda (B_2 n_{m_1} + B_1 n_{m_2})}{1 + \lambda (n_{m_1} \tau_{2r} + n_{m_2} \tau_{1r})} \end{aligned} \quad (9)$$

³ That is, when $\tau_{ij} > 0$, $\lambda n_{m_i} n_{f_j} = \frac{n_{m_i f_j}}{\tau_{ij}}$. When $\tau_{ij} = 0$, there are no (m_i, f_j) pairs.

⁴ We assume all model parameters $(B_1, B_2, \tau_{1r}, \tau_{2r}, \tau_c, \lambda)$ are positive.

where the population state given by N_{m_i} and N_{f_j} determines uniquely the numbers of searchers n_{m_i} and n_{f_j} .

One immediate result is that (Philanderer, Coy) is never the evolutionary outcome when cost is measured as time. To see this, when all males are Philanderers, $n_{m_1} = 0$ and so $\Pi_{f_1} = 0$ and $\Pi_{f_2} = \frac{\lambda B_1 n_{m_2}}{\lambda n_{m_2} \tau_{1r} + 1} > 0$. Thus, Fast females can invade and so (Philanderer, Coy) is not an evolutionary outcome.⁵ In particular, the time-constrained game avoids the unrealistic scenario pointed out by (Broom and Rychtář (2013), page 325) that the evolutionary outcome can be that no mating (and so no offspring) occur for the classic BoS game (1) when B is sufficiently low (Fig. 1A).

An important technique to determine evolutionary outcomes in general is to examine dominance relationships among the strategies. However, since fitness functions for time-constrained games are no longer linear in the population state, dominance cannot be determined by only comparing entries in a payoff matrix as is done for classic bimatrix games (e.g., Section 2). Instead, fitness comparisons are needed at all population states.⁶ For instance, from (9), it is straightforward to show that in general

$$\Pi_{f_2} - \Pi_{f_1} = \frac{\lambda \left(\lambda n_{m_1}^2 B_2 \tau_c + \lambda n_{m_1} n_{m_2} (B_1 (\tau_c + \tau_{2r}) - B_2 \tau_{1r}) + B_1 n_{m_2} \right)}{(1 + \lambda n_{m_1} (\tau_c + \tau_{2r})) (1 + \lambda (n_{m_1} \tau_{2r} + n_{m_2} \tau_{1r}))}. \quad (10)$$

Thus, if

$$\frac{B_1}{\tau_{1r}} \geq \frac{B_2}{\tau_c + \tau_{2r}}, \quad (11)$$

then Fast strictly dominates Coy in the female population since $\Pi_{f_2} - \Pi_{f_1} > 0$ at all population states (i.e., for all possible n_{m_i}).⁷ That is, under (11), all females are Fast at any evolutionary outcome. Furthermore, when all females are Fast (i.e., $N_{f_1} = n_{f_1} = 0$),

$$\Pi_{m_2} - \Pi_{m_1} = \frac{\lambda n_{f_2} (\lambda B_1 n_{f_2} \tau_{2r} + B_1 - B_2)}{1 + \lambda n_{f_2} \tau_{2r}}. \quad (12)$$

Notice that, if $B_1 = B_2$, then $\Pi_{m_2} - \Pi_{m_1} > 0$ when all females are Fast and so the male population evolves to Philanderer. In particular, if Coy females have no advantage over Fast females either in terms of benefits (i.e., $B_1 = B_2$) or in terms of time costs (i.e., $\tau_{1r} = \tau_{2r}$), then (Philanderer, Fast) is the only evolutionary outcome of the time-constrained BoS game and trajectories of the replicator dynamics are qualitatively the same as those shown in Fig. 2E.⁸

In general, from (10), $\Pi_{f_2} - \Pi_{f_1} > 0$ if the male population consists of all Philanderer (i.e., $n_{m_1} = 0$) or all Faithful (i.e., $n_{m_2} = 0$).

⁵ Alternatively, when all females are Coy, $n_{f_2} = 0$ and so $\Pi_{m_2} = 0$ and $\Pi_{m_1} = \frac{\lambda B_2 n_{f_1}}{\lambda n_{f_1} (\tau_c + \tau_{2r}) + 1} > 0$ and so Faithful males can invade the (Philanderer, Coy) population. In fact, since both Faithful males and Fast females can invade the (Philanderer, Coy) population, NE near this population configuration as well as cycling behavior similar to Fig. 1B are both excluded.

⁶ However, fitness of a focal individual using a mixed strategy remains linear in the components of this strategy. For example, if the focal female plays Coy with probability q_1 and Fast with probability $q_2 = 1 - q_1$ then her fitness is $q_1 \Pi_{f_1} + q_2 \Pi_{f_2}$. Thus, if fast females strictly dominate Coy, then Fast also strictly dominates any mixed female strategy with a positive probability of playing Coy.

⁷ Cressman and Křivan (2019) define $\frac{B_1}{\tau_{1r}}$ (respectively, $\frac{B_2}{\tau_c + \tau_{2r}}$) in (11) as the time-adjusted payoff to Fast (respectively, Coy) females when interacting with Philanderer (respectively, Faithful) males for the bimatrix game based on payoff matrix (8) and time-bimatrix (7). It was shown there that comparisons of time-adjusted payoffs is closely connected to the game's evolutionary outcome when pairs are formed instantaneously.

⁸ In game-theoretic terminology, this game is strictly dominance solvable to the strategy pair (Philanderer, Fast). It is well-known (Sandholm, 2010) that such a pair is then globally asymptotically stable for standard evolutionary dynamics such as the replicator equation. This also occurs in Fig. 2E since the number of Coy females is always decreasing and, when all females are Fast, the number of Faithful males always decreases. There are other choices of model parameters for which the time-constrained game is strictly dominance solvable to (Philanderer, Fast).

That is, Fast females dominate Coy on both the left and right edges of the square as depicted by downward arrows in the phase portraits of Figs. 2 and 3. Furthermore, if all females are Coy (i.e., $n_{f_2} = 0$), then

$$\Pi_{m_2} - \Pi_{m_1} = -\frac{\lambda B_2 n_{f_1}}{1 + \lambda n_{f_1} (\tau_c + \tau_{2r})} \quad (13)$$

and so Faithful males dominate Philanderer on the top edge of the square (i.e., arrows are to the right along this edge). Thus, all evolutionary outcomes where either females or males exhibit a single strategy must have all females Fast (i.e., the only NE on the boundary of the square are on the bottom edge).

In the remainder of Section 4, we use these facts to analyze the evolutionary outcome of the time-constrained BoS game in the following two situations. First, Section 4.1 assumes any advantage for Coy females is based on time costs (i.e., $\tau_{2r} < \tau_{1r}$) and so the payoff gain from offspring (i.e., the benefit in bimatrix (8)) is strategy independent (i.e., $B_1 = B_2 \equiv B$). This model may describe the case where all male–female pairs that have offspring, produce the same number and only the time taken in this endeavor depends on the strategies used. Second, in Section 4.2, all individuals who engage in child rearing spend the same amount of time on this activity (i.e., $\tau_{1r} = \tau_{2r}$) but the benefits are strategy dependent (e.g., pairs involving faithful males produce more offspring) and so $B_2 > B_1$.

4.1. Cost is time and the benefits of offspring are strategy independent

When benefits of offspring are strategy independent, the payoff bimatrix (8) is

$$\begin{array}{c|cc} \text{Male} \backslash \text{Female} & \text{Coy} & \text{Fast} \\ \hline \text{Faithful} & (B, B) & (B, B) \\ \text{Philanderer} & (0, 0) & (B, B) \end{array} \quad (14)$$

where B is the payoff of having offspring. We recall that Philanderer males do not mate with Coy females so there are no offspring and the corresponding payoff entry is (0, 0). Without time constraints, this game corresponds to the classic BoS payoff matrix (1) where we set $C_r = C_c = 0$. Due to the ties in bimatrix payoffs, the classic BoS game (i.e., the game where interaction times are independent of strategies) based on (14) now has infinitely many NE that are formed by the bottom and the right-hand edges of the square in Fig. 1E. That is, the evolutionary outcome is either that all males are Faithful (right edge) or all females are Fast (bottom edge). As we will see, adding costs as time lost in (7) has a drastic effect on the evolutionary outcome in the time-constrained game.

First, from Appendix D, (Philanderer, Fast) is a strict NE and the only NE on the boundary of the unit square.⁹ In fact, for long courtship time, (Philanderer, Fast) is the only NE (e.g., if $\tau_c \geq \tau_{1r} - \tau_{2r}$, then the game is dominance solvable to (Philanderer, Fast) by (11) and (12)). However, as shown in the following section, when courtship time is short and $\tau_{2r} < \tau_{1r}$, there may be other evolutionary outcomes where both sexes exhibit a mixture of their strategies (corresponding to a NE in the interior of the square).

4.1.1. Mixed (interior) evolutionary outcomes

At an interior evolutionary outcome (N_{m_i}, N_{f_j}), both sexes are polymorphic with some males (respectively, females) Faithful and others Philanderer (respectively, Coy and others Fast) as seen in Fig. 2. Such an outcome must satisfy the NE conditions; namely, $\Pi_{m_1} = \Pi_{m_2}, \Pi_{f_1} = \Pi_{f_2}$. Unfortunately, unlike classic bimatrix

⁹ For two-strategy bimatrix games without time constraints, this behavior on the boundary guarantees that the only evolutionary outcome is (Philanderer, Fast) (in particular, there are no interior NE). However, the nonlinearity of the fitness functions leaves open the possibility that interior NE exist for the time-constrained game.

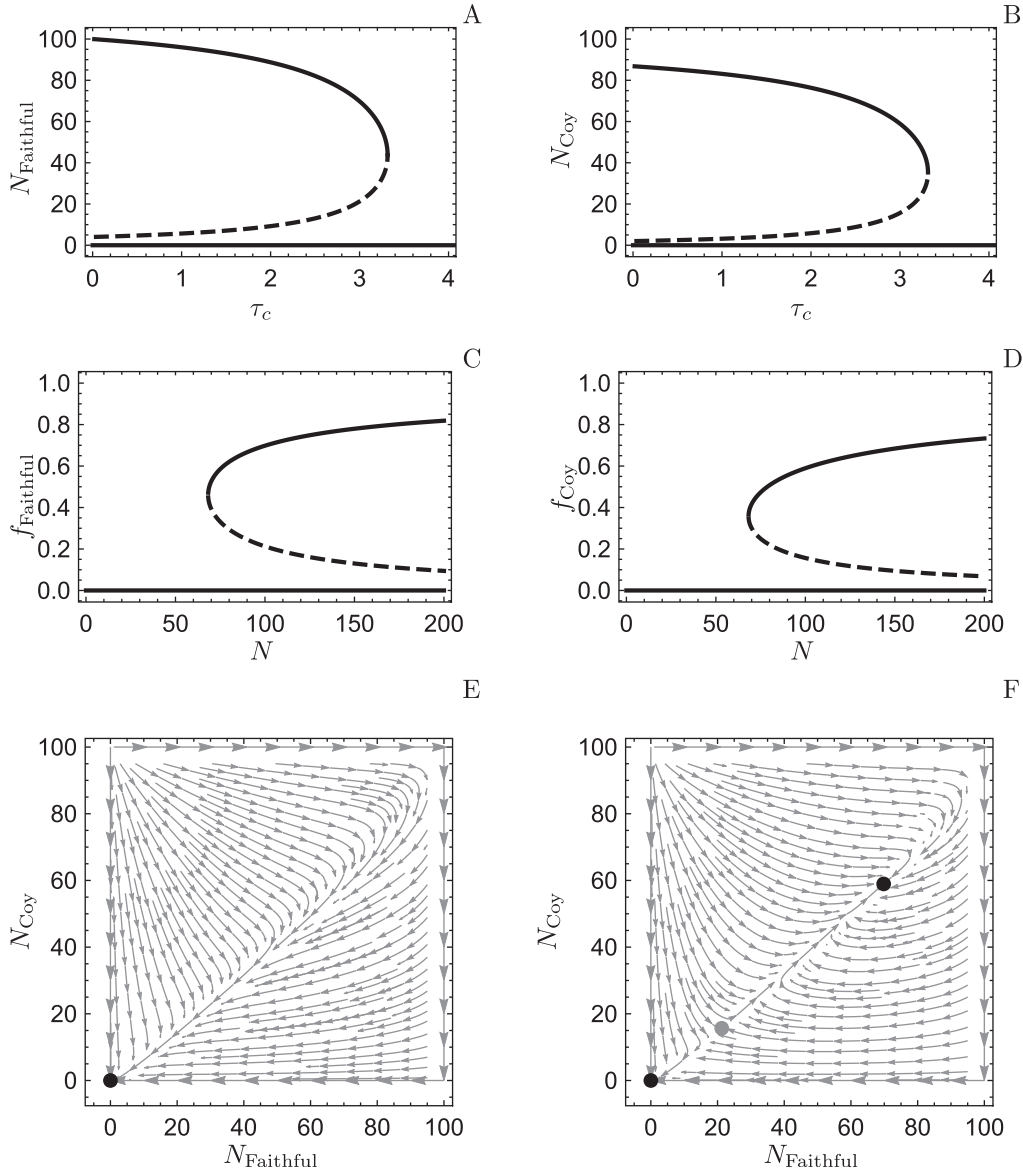


Fig. 2. The time-constrained BoS game with payoff bimatrix (14) and time-bimatrix (17). Panels A and B show the dependence of NE on courtship time τ_c for $N_m = N_f = 100$, displayed in terms of $N_{\text{Faithful}} \equiv N_{m_1}$ (panel A) and $N_{\text{Coy}} \equiv N_{f_1}$ (panel B). Panels C and D show the dependence of NE on population size N for $\tau_c = 3$ displayed in terms of frequencies $f_{\text{Faithful}} \equiv N_{m_1}/N$ (panel C) and $f_{\text{Coy}} \equiv N_{f_1}/N$ (panel D). Thick solid curves show stable NE while thick dashed curves show the unstable interior NE of the replicator equation. Panels E and F show corresponding phase portraits of the replicator equation for $\tau_c = 4$ (Panel E) and $\tau_c = 3$ (Panel F). Solid black (respectively, grey) dots indicate stable (respectively, unstable) NE. Other parameters used in simulations: $B = 1$, $\tau_{1r} = 10$, $\tau_{2r} = 5$, $\lambda = 0.1$, $N_m = N_f = 100$.

games without time-constraints, interior NE cannot be calculated analytically for a general time interaction bimatrix of the form (4).

Instead of calculating mixed NE directly, we consider numerical analysis of the replicator equation (Appendix A)

$$\begin{aligned} \frac{dN_{m_1}}{dt} &= \frac{N_{m_1}(N_m - N_{m_2})}{N_m} (\Pi_{m_1}(N_{m_1}, N_{m_2}, N_{f_1}, N_{f_2}) \\ &\quad - \Pi_{m_2}(N_{m_1}, N_{m_2}, N_{f_1}, N_{f_2})) \\ \frac{dN_{f_1}}{dt} &= \frac{N_{f_1}(N_f - N_{f_2})}{N_f} (\Pi_{f_1}(N_{m_1}, N_{m_2}, N_{f_1}, N_{f_2}) \\ &\quad - \Pi_{f_2}(N_{m_1}, N_{m_2}, N_{f_1}, N_{f_2})) \end{aligned} \quad (15)$$

where Π_{m_i} and Π_{f_i} are fitnesses (6) evaluated at the unique equilibrium distribution of (5) for strategy numbers $(N_{m_1}, N_{m_2}, N_{f_1}, N_{f_2})$. As we cannot express this equilibrium distribution analytically, we have to solve, together with (15), a system of algebraic equations

$$\begin{aligned} N_{m_i} &= n_{m_i} + n_{m_{f_1}} + n_{m_{f_2}} + n_{m_i}^{f_1} + n_{m_i}^{f_2} \\ N_{f_j} &= n_{f_j} + n_{f_{m_1}} + n_{f_{m_2}} + n_{f_j}^{m_1} + n_{f_j}^{m_2} \end{aligned}$$

for $i, j = 1, 2$. At the equilibrium distribution (5), we can express these total numbers in terms of n_{m_i} and n_{f_j} as

$$\begin{aligned} N_{m_i} &= n_{m_i} \left(1 + \lambda n_{f_1} (\tau_{i1} + \tau_{m_i}^{f_1}) + \lambda n_{f_2} (\tau_{i2} + \tau_{m_i}^{f_2}) \right) \\ N_{f_j} &= n_{f_j} \left(1 + \lambda n_{m_1} (\tau_{1j} + \tau_{f_j}^{m_1}) + \lambda n_{m_2} (\tau_{2j} + \tau_{f_j}^{m_2}) \right). \end{aligned} \quad (16)$$

System (15) and (16) is a differential-algebraic equation (DAE) that can be solved numerically in Mathematica, or XPPAUT bifurcation software (Ermentrout, 2002). Mixed NE that correspond to stable rest points of the replicator equation are considered to be evolutionary outcomes of the time-constrained BoS game.

To illustrate this approach, we apply it to the special case where $\tau_{1r} = 2\tau_{2r}$ in keeping with the story behind the original BoS model.

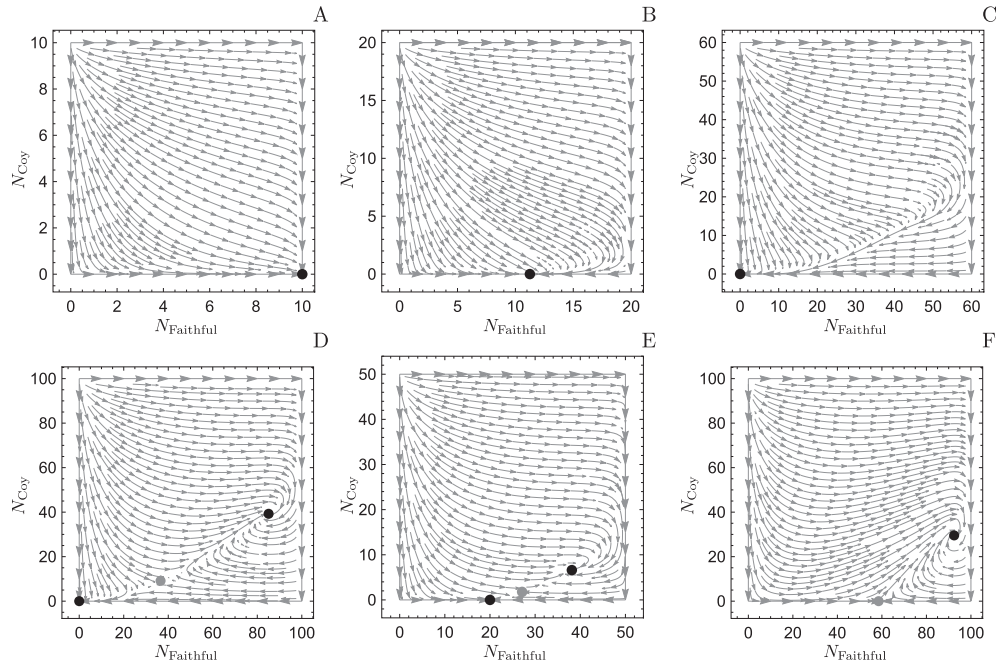


Fig. 3. Phase portraits of the replicator equation for the BoS game given by payoff matrix (18) and time-bimatrix (19). The first four panels (A,B,C,D) assume $B_2 = 1.8 < 2B_1$ (cf., Figs. 4A, B and 5A, B). Population size is $N = 10 < N_1$ (panel A), $N_1 < N = 20 < N_2$ (panel B), $N = 60 > N_2$ (panel C) and $N = 100 > N_2$ (panel D). Panel E assumes the threshold value for benefit $B_2 = 2 = 2B_1$ and $N = 50 > N_1$ (cf., Figs. 4C, D and 5C, D). Panel F assumes $B_2 = 2.3 > 2B_1$ and $N = 100 > N_3$ (cf., Figs. 4E, F and 5E, F) where the unstable rest point on the bottom edge is not a NE since this population configuration can be invaded by Coy females. Solid black (respectively, grey) dots are stable (respectively, unstable) rest points of the replicator Eq. (15). Other parameters used in simulations: $B_1 = 1, \lambda = 0.1, \tau_c = 0.1, \tau_r = 1$.

That is, a couple that stays together splits the cost of rearing offspring (an assumption underlying the classic payoff bimatrix (1)). The time-bimatrix (7) is then

$$\begin{array}{c|cc} \text{Male} \backslash \text{Female} & \text{Coy} & \text{Fast} \\ \hline \text{Faithful} & \begin{bmatrix} \tau_{2r} + \tau_c, \tau_{2r} + \tau_c \\ \tau_{2r}, \tau_{2r} \end{bmatrix} & \begin{bmatrix} \tau_{2r}, \tau_{2r} \\ \tau_{2r}, \tau_{2r} \end{bmatrix} \\ \text{Philanderer} & \begin{bmatrix} 0, 0 \\ 0, 2\tau_{2r} \end{bmatrix} & \begin{bmatrix} 0, 2\tau_{2r} \\ 0, 2\tau_{2r} \end{bmatrix} \end{array} \quad (17)$$

When $\tau_c \geq \tau_{1r} - \tau_{2r} = \tau_{2r}$, the game is strictly dominance solvable to (Philanderer, Fast). However, for short courtship time, there are other possibilities (Fig. 2). There may be no mixed NE, or two in which case one is stable (solid lines in Fig. 2A,B and black interior dot in Fig. 2F) and the other unstable (dashed lines in Fig. 2A,B and grey dot in Fig. 2F). Numerical simulations given in these figures show mixed NE do coexist together with the strict NE (Philanderer, Fast) equilibrium.¹⁰

It is interesting to observe in Fig. 2A,B that, as courtship time (τ_c) decreases, the frequencies of strategies Faithful and Coy increase in the population at the stable interior equilibrium and the domain of attraction of this evolutionary outcome increases too. In fact, when τ_c is short enough, almost all males will eventually be Faithful and the large majority of females Coy for most initial population configurations (Fig. 2F). That is, to increase the level of marital bliss in the population, the institution of courtship is required but the courtship period should be kept as short as possible. This result is reflected in the article title. Moreover, while most couples go through a courtship period at this evolutionary outcome, some females are willing to have offspring immediately on encountering a mate, secure in the knowledge that almost all males will do their share of rearing the offspring.

In the classic BoS game with bimatrix (1), the proportion of Faithful males at an interior NE (if it exists) also increases to 1 as the courtship costs (C_c) decreases to 0. However, the proportion of Coy females actually decreases to $\frac{C_c}{2B}$.¹¹ So reducing courtship cost again promotes marital-bliss behavior in the male population but it is not as clear in the female population. Moreover, the stability of the interior evolutionary outcome in the time-constrained game is unlike that of the interior NE of the classic BoS model with Dawkins' payoffs. Although this latter NE may be close to the (Faithful, Coy) population, evolutionary cycles around it takes the population far away from marital bliss. This contrasts with stability in the time-constrained game where the population evolves to the interior NE near the marital-bliss population configuration.

4.2. Benefits of offspring are strategy dependent but offspring rearing time is not

In this section, the time-constrained BoS game with equal times for rearing offspring (i.e., $\tau_{2r} = \tau_{1r} \equiv \tau_r$) is investigated. If there is no benefit advantage for couples to stay together, we already know that the game is strictly dominance solvable to the unique evolutionary outcome (Philanderer, Fast). Thus, here we will assume that payoffs for couples that stay together (i.e., when females mate with Faithful males) have a higher fitness compared to the case where a Fast female mates with a Philanderer male (i.e., $B_2 > B_1$). For example, females paired with Faithful males can mate several times while raising their offspring as they do not need to search for a new partner whereas females paired with Philanderer males do not have a partner to mate with while caring for offspring, or have less opportunities to mate. This leads to an alternative parameterization of the time-constrained Battle of the Sexes game with payoff bimatrix

¹⁰ These simulations assume the male and female populations are of equal size. Qualitatively similar results emerge from other simulations (not shown) where $N_m \neq N_f$.

¹¹ Here we assume that $\frac{C_c}{2} < B < C_r$ so that the interior NE exists for all C_c .

$$\begin{array}{c|cc} \text{Male} \backslash \text{Female} & \text{Coy} & \text{Fast} \\ \hline \text{Faithful} & (B_2, B_2) & (B_2, B_2) \\ \text{Philanderer} & (0, 0) & (B_1, B_1) \end{array} \quad (18)$$

and time-bimatrix

$$\begin{array}{c|cc} \text{Male} \backslash \text{Female} & \text{Coy} & \text{Fast} \\ \hline \text{Faithful} & \tau_r + \tau_c, \tau_r + \tau_c & \tau_r, \tau_r \\ \text{Philanderer} & 0, 0 & 0, \tau_r \end{array} \quad (19)$$

Payoff bimatrix (18) was considered by McNamara et al. (2009) (see also Broom and Rychtář, 2013) in their “coyness game” that models females who inspect the males they encounter as to whether they are helpful or non-helpful. When time constraints are not considered, the arrows in (18) show that Faithful strictly dominates Philanderer in the male population and so, at any evolutionary outcome all males must be Faithful. In fact, there are infinitely many NE with all males Faithful and any mix of Coy and Fast females (Fig. 1F).

For the time-constrained game, it is shown at the beginning of Section 4 that all females cannot be Coy at an evolutionary outcome (i.e., there must be some Fast females) since there are no NE on the upper edge of the square in Fig. 3. Of particular interest is whether there are interior evolutionary outcomes similar to Section 4.1 with short courtship time that are close to the marital-bliss state for some choices of model parameters. Before addressing this question in Section 4.2.1, we first consider the existence of evolutionary outcomes on the boundary of the square. As we will see, the analysis of these evolutionary outcomes for the time-constrained game (which must be NE on the bottom edge) with payoff bimatrix (18) and time-bimatrix (19) becomes quite complicated. In order to simplify the discussion in the main text, we will assume for the remainder of this section that the male and female populations have the same size (i.e., $n_m = n_f \equiv N$).¹² The results are summarized in Table 1 which shows that there can be at most one NE on the boundary.

First, we observe that (Faithful, Fast), which was not a NE when payoffs were strategy independent and given by (14), can be a NE provided the population size is not too large (Fig. 3A). Indeed, because $B_2 > B_1$ then for small n_{f_2} , $\Pi_{m_1} = \frac{\lambda B_2 n_{f_2}}{1 + \lambda \tau_r n_{f_2}} > \lambda B_1 n_{f_2} = \Pi_{m_2}$ when $n_{f_1} = 0$ and so Philanderer males cannot invade a small population configured at (Faithful, Fast). Furthermore, Fast females always dominate Coy when all males are Faithful. Thus, (Faithful, Fast) is a strict NE at low population densities (specifically $N < N_1$ where N_1 is given in the legend of Table 1).

Second, (Philanderer, Fast) can also be a strict NE (Fig. 3C, D), as it is for the time-constrained game with payoff bimatrix (14). It is now enough to determine when Faithful males cannot invade since Fast females strictly dominate Coy when all males are Philanderer. In order to prevent invasion, a Philanderer male must use the opportunity to produce more offspring than a Faithful male per unit time by not “wasting” time caring for these offspring. At low population size, the payoff from these extra offspring is not enough to compensate for the lower payoff per offspring since Faithful males can invade exactly as in the previous paragraph. Moreover, for higher population size, Appendix D.2 (see also Table 1) shows this extra opportunity for Philanderer males can only compensate if the benefit to Faithful males is less than twice that of Philanderer males (i.e., $B_2 < 2B_1$) and population size is large enough (specifically, $N > N_2$ where N_2 is given in the legend of Table 1).

Finally, depending on courtship time and population size as well as on these benefits (see Table 1), a boundary NE may occur in the interior of the bottom edge where the male population is a

mixture of Faithful and Philanderer behaviors (Fig. 3B, E). In fact, if $B_2 < 2B_1$, then such a boundary NE exists for all intermediate population sizes, $N_1 < N < N_2$.¹³ On the other hand, if $B_2 > 2B_1$, these boundary NE exist for all population sizes $N > N_1$ if courtship time is long enough (specifically, $\tau_c > \frac{B_1 \tau_r}{B_2 - B_1}$) but only for intermediate population size when courtship time is shorter. In this latter case, there is no boundary NE for large population size as shown in Fig. 3F where a mixed NE in the interior of the square emerges (see the following section).

Our analyses clearly show that population size has a strong effect on evolutionary outcomes when time constraints are considered. This is to say that, contrary to the classic BoS game (or any other bimatrix game) whose evolutionary outcomes are independent of the population size (i.e., classic games are only frequency dependent), the time constrained BoS game is density dependent.

4.2.1. Mixed (interior) evolutionary outcomes

From the above analytic results on boundary NE for the BoS game based on payoff bimatrix (18) and time-bimatrix (19), there must be interior NE when $B_2 > 2B_1$ and $\tau_c < \frac{B_1 \tau_r}{B_2 - B_1}$.¹⁴ In fact, by following the same numerical methods as in Section 4.1, simulations suggest this interior NE is then globally asymptotically stable and so the only evolutionary outcome as in Fig. 3F.

Furthermore, as illustrated by the simulations in Fig. 4, interior NE exist for all BoS games based on (18) and (19) when courtship time is short enough. At least one such NE is then a stable evolutionary outcome although another evolutionary outcome may co-exist on the boundary where all females are Fast. Also, as in Section 4.1, as τ_c decreases to 0, almost all males are Faithful at the stable interior NE, the frequency of Coy females is increasing, and this evolutionary outcome attracts most initial population configurations. That is, reducing courtship time continues to promote marital bliss in these time-constrained BoS games.

From Table 1, it is also apparent that population size has an important effect on the evolutionary outcomes of these games. These effects are especially interesting when courtship time is short enough (as in Fig. 5) so that Fast female behavior does not strictly dominate Coy behavior in the female population. By Fig. 5, we see that (Faithful, Fast) is the unique evolutionary outcome for small population size. As population size increases, this boundary evolutionary outcome first moves along the bottom edge of the square and then either continues to (Philanderer, Fast) (Fig. 5A–D) or disappears (Fig. 5E,F). Moreover, an interior evolutionary outcome emerges that attracts most initial population configurations as population size increases. In fact, almost all males are Faithful (Fig. 5A,C,E) and the frequency of Coy females is increasing (Fig. 5B,D,F) when population size is large. That is, population size also promotes marital bliss.

Increasing population size also promotes marital bliss for short courtship times when benefits from offspring are strategy independent as in Section 4.1 (see Fig. 2C, D). On the other hand, the dependence of boundary evolutionary outcomes on population size is much simpler for this model in that (Philanderer, Fast) is always a strict NE and the only NE on the boundary. Of course, the advantages to couples where the male is Faithful considered separately in Section 4.1 ($\tau_{2r} < \tau_{1r}$) and Section 4.2 ($B_2 > B_1$) can be assumed to hold simultaneously. Combining both these assumptions lead to

¹³ Thus, if $B_2 < 2B_1$, exactly one boundary NE exists for a given population size; namely, (Faithful, Fast) for small populations ($N < N_1$), (Philanderer, Fast) for large populations ($N > N_2$) and mixed male behavior for intermediate population size ($N_1 < N < N_2$). Here, and throughout Section 4, we have ignored threshold values of parameters such as $N = N_1$ and $\tau_c = \frac{B_1 \tau_r}{B_2 - B_1}$.

¹⁴ This follows from the fact that all our population games, which have continuous payoff functions, must have at least one NE (Nash, 1951). Notice that the boundary rest point (grey dot) in Fig. 3F is not a NE since this population configuration can be invaded by Coy females. That is, the only NE is interior (black dot) for this game.

¹² The general case where the sex-ratio is not even (and $\tau_{1r} \geq \tau_{2r}$) is analyzed in Appendix D.

Table 1

Evolutionary outcomes for the classic and time-constrained Battle of the Sexes game. Asterisks indicate evolutionary outcomes that correspond to strict NE. For the game without time constraints as well as for τ_c large enough in the time-constrained game (e.g., those for which inequality (11) holds), the game is strictly dominance solvable to these strict NE. For the time-constrained games, the sex-ratio is assumed to be equal, $N_m = N_f = N$. For the time-constrained games based on (18) and (19), $N_1 = \frac{B_2(B_2-B_1)}{\lambda B_1^2 \tau_r}$, $N_2 = \frac{B_2-B_1}{\lambda(2B_1-B_2)\tau_r}$, and $N_3 = \frac{(B_2-B_1)(B_1^2 \tau_c + B_1 B_2(2\tau_r - \tau_c) - B_2^2 \tau_r)}{\lambda B_1(2B_1-B_2)(B_1(\tau_r + \tau_c) - B_2 \tau_c) \tau_r}$ are the threshold population densities taken from D.3. Cases (i)-(iii) have qualitatively the same phase portraits as in Fig. 3B in a vicinity of the boundary equilibrium.

Model	Nash Equilibria	Conditions on Model Parameters	Figure
Classic BoS game (1) without time constraints	(Philander, Coy)*	$B < \min\{C_c + \frac{C_r}{2}, C_r\}$	Fig. 1A
	(Philander, Fast)*	$B > C_r$	Fig. 1C
	Interior NE	$\frac{C_r}{2} + C_c < B < C_r$	Fig. 1B
Time constrained BoS game with payoff bimatrix (14) and time-bimatrix (7)	(Philanderer, Fast)*	always	Fig. 2E,F
	Stable interior NE	when τ_c is not too long and $\tau_{2r} < \tau_{1r}$	Fig. 2F
Time constrained BoS game with payoff bimatrix (18) and time-bimatrix (19)	(Faithful, Fast)*	$N < N_1$	Fig. 3A
	(Philanderer, Fast)*	$B_2 < 2B_1, N > N_2$	Fig. 3C,D
	NE on boundary with all females Fast and	any of the following three conditions	Fig. 3B
	$N_{m_1} = \frac{B_2(\lambda N(B_2 - 2B_1)\tau_r - B_1 + B_2)}{\lambda(B_1 - B_2)^2 \tau_r}$	(i) $B_2 < 2B_1$ and $N_1 < N < N_2$ (ii) $2B_1 < B_2$, $\tau_c > \frac{\tau_r B_1}{B_2 - B_1}$, $N > N_1$	
	Stable interior NE	(iii) $2B_1 < B_2$, $\tau_c < \frac{\tau_r B_1}{B_2 - B_1}$, $N_1 < N < N_3$ when τ_c is not too long	Fig. 3D,E,F

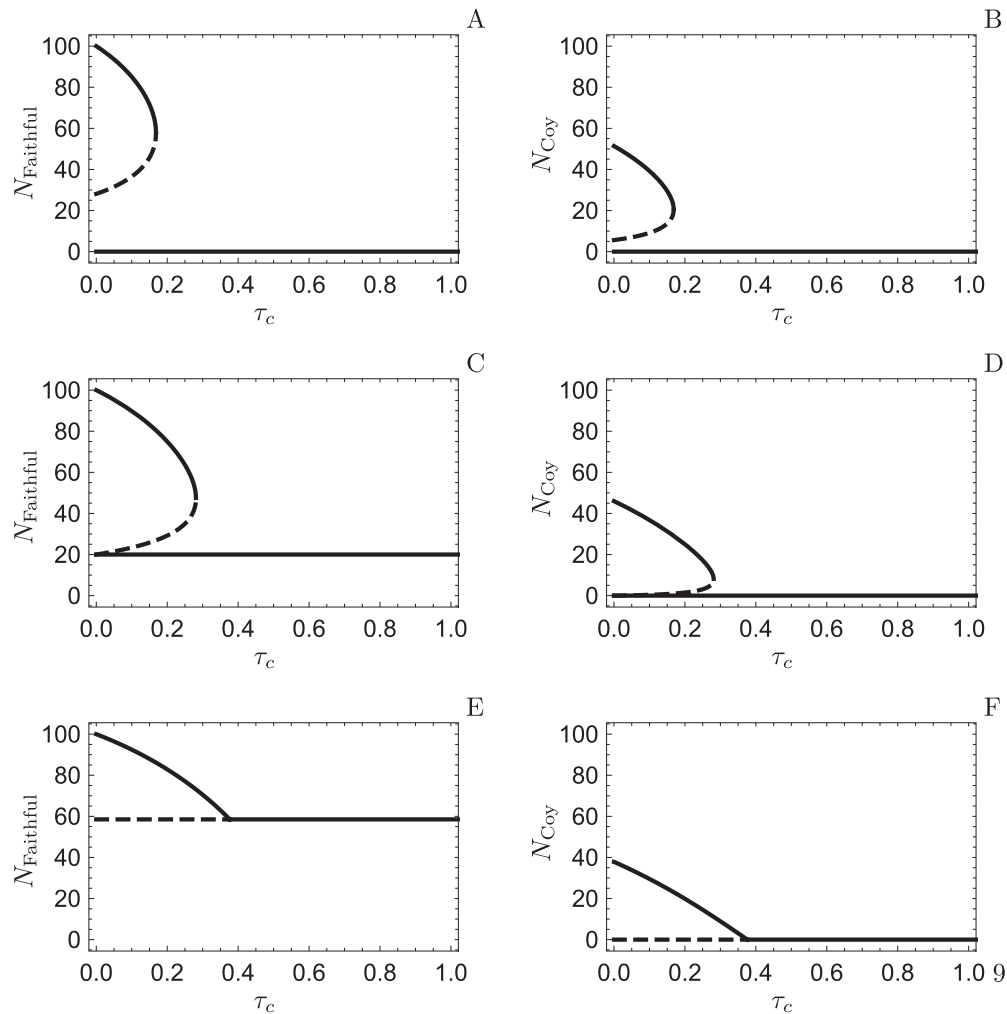


Fig. 4. The dependence of evolutionary outcomes and other rest points of the replicator equation/evolutionary dynamics on τ_c displayed in terms of $N_{\text{Faithful}} \equiv N_{m_1}$ (panel A, C, E) and $N_{\text{Coy}} \equiv N_{f_1}$ (panel B, D, F), for the time-constrained BoS game with payoff bimatrix (18) and time-bimatrix (19). Evolutionary outcomes correspond to stable (with respect to replicator dynamics) NE and are indicated by solid curves. Other rest points are unstable (indicated by dashed curves) and may be NE (e.g., those in the interior) or not (e.g., those on the boundary)^a. Panels A, B assume $B_2 = 1.8$, panels C, D consider the threshold case where $B_2 = 2$, and panels E, F assume $B_2 = 2.3$. Other parameters used in simulations: $N_m = N_f = 100$, $B_1 = 1$, $\tau_r = 1$, $\lambda = 0.1$ ^a Unstable rest points at the vertices are not included in the figure.

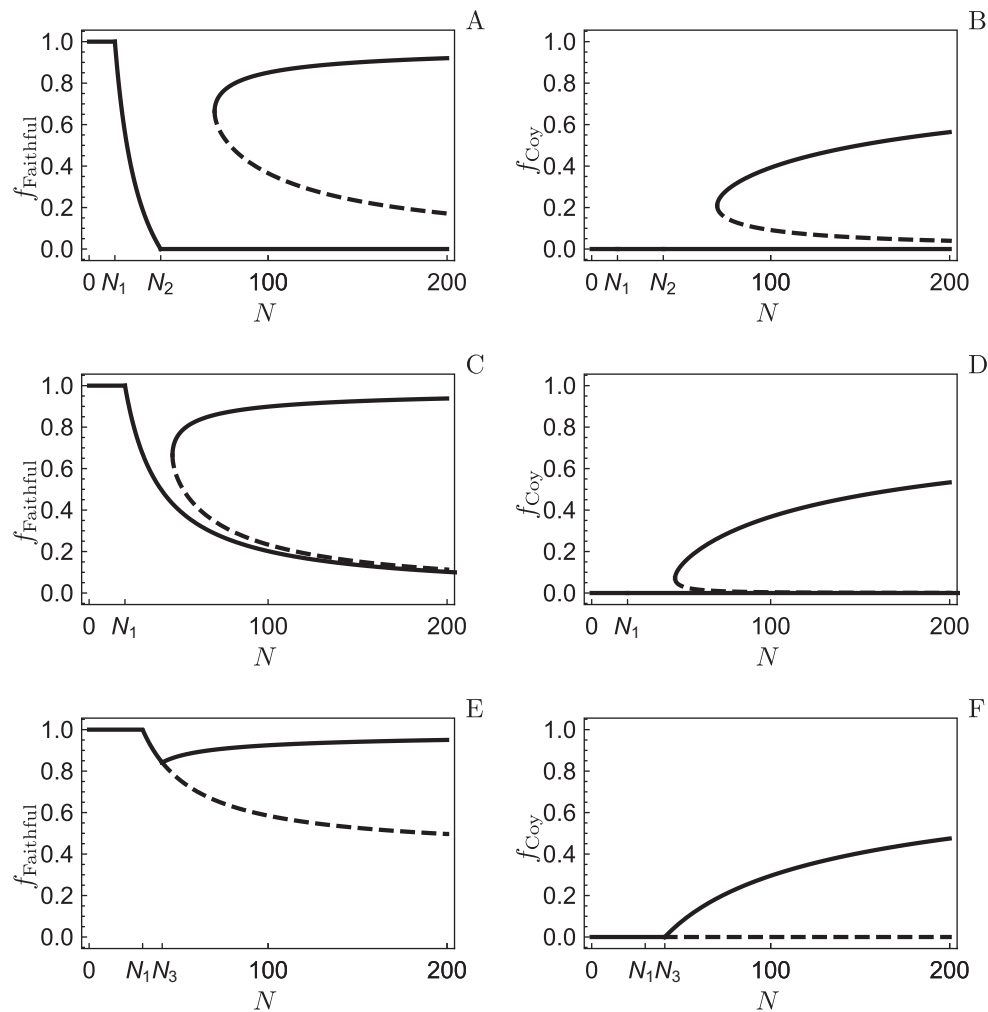


Fig. 5. The dependence of evolutionary outcomes and other rest points of the replicator equation/evolutionary dynamics on population size N displayed in terms of frequencies $f_{\text{Faithful}} \equiv N_{m_1}/N$ (panel A, C, E) and $f_{\text{Coy}} \equiv N_{f_1}/N$ (panel B, D, F), for the time-constrained BoS game with payoff bimatrix (18) and time-bimatrix (19). Solid and dashed curves have the same meaning as in Fig. 4 and panel parameter values correspond as well except now $\tau_c = 0.1$ is fixed and $N_m = N_f = N$ is variable.

evolutionary outcomes similar to those in Section 4.2. This is apparent from the analytic results of Appendix D (which are based on these two assumptions) as well as simulations (not shown) to determine interior evolutionary outcomes numerically.

5. Discussion

We develop a new approach to the Battle of the Sexes game where benefits are measured by offspring produced and costs are measured by time lost. In the classic Battle of the Sexes model (Section 2) introduced by Dawkins (1976), where it is unclear how to measure costs and benefits since they are evaluated in a single currency (namely, payoff), there are three possible evolutionary outcomes depending on payoff parameters as summarized in the first three rows of Table 1. When the benefit is small compared to costs, all males philander and all females are coy (i.e., strategy (Philanderer, Coy) is the evolutionary outcome) and, since coy females do not mate with philanderer males, the population goes extinct. When the benefit is large, the evolutionary outcome is (Philanderer, Fast). For intermediate benefits, the male population includes both Faithful and Philanderer individuals and the females both Coy and Fast under some payoff choices, including the payoffs considered by Dawkins (1976).

In our time-constrained model (Section 4), we use a different currency for benefits (measured by number of offspring) than for

costs (measured by time lost). Then (Philanderer, Coy) is never an evolutionary outcome, i.e., offspring are always produced at all evolutionary outcomes and so the population never goes extinct.¹⁵ In fact, if courtship time is long enough (cf., inequality (11)), then females will decide against courtship and the only evolutionary outcome will be a population where all females are Fast and all males adopt one of their two behaviors or else the male population exhibits a mixture of them. In particular, the (Faithful, Coy) state of marital bliss mentioned by Dawkins (1976) is never the evolutionary outcome in this case.

In order to encourage male–female behavior that is closer to marital bliss, courtship time must be short.¹⁶ In this case, marital bliss behavior becomes more prevalent by reducing courtship time further. The short courtship time reduces the time cost for courtship, leading to more males and females who are willing to spend this short time as a means to better ensure they obtain the advantage of higher benefits (Section 4.2) or lower rearing cost (Section 4.1). A similar phenomenon of increased marital bliss arises by increasing the underlying population size N of the model (Fig. 5). When the

¹⁵ This assumes the birth rate of pairs that produce offspring is at least as high as the death rate in the population.

¹⁶ We again emphasize that our model is based solely on the Dawkins BoS game with costs measured in time lost. We do not claim that it reflects all the behavioral complexities inherent in conflicts between the sexes over parental care (e.g., Trivers, 1972; Maynard Smith, 1977; Webb, 1999; Fromhage et al., 2007).

fixed courtship time is short, the proportion of males (respectively, females) who are Faithful (respectively, Coy) increases at the interior evolutionary outcome as N increases. In fact, as N becomes arbitrarily large (not shown in Fig. 5), the evolutionary dynamics approaches the marital bliss state (Faithful, Coy) from almost all initial population configurations.

The analysis in this article shows clearly that including time constraints changes the evolutionary outcome of the BoS game. It is then a combination of the payoffs for producing offspring together with the activity times that results in the game's evolutionary outcome. Qualitatively similar results emerge (Mylius, 1999) when these activity times are incorporated into the BoS model as time delays, producing a system of delayed differential equations. Both approaches show the assumption often made in game-theoretical models, that costs and benefits can be expressed in a single currency, is questionable.

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Appendix A. The replicator equation for two-strategy bimatrix games with and without time constraints

In Fig. 1, we use the standard replicator equation for bimatrix games to investigate the evolutionary outcome of the classic BoS game. For the general two-strategy bimatrix game with payoff bimatrix (3), the replicator equation is of the form (Hofbauer and Sigmund, 1998)

$$\begin{aligned} \frac{dp_{m_1}}{dt} &= p_{m_1}(1 - p_{m_1})(\Pi_{m_1} - \Pi_{m_2}) \\ \frac{dp_{f_1}}{dt} &= p_{f_1}(1 - p_{f_1})(\Pi_{f_1} - \Pi_{f_2}) \end{aligned} \quad (\text{A.1})$$

where p_{m_1} (respectively, p_{f_1}) is the frequency of strategy m_1 (respectively, f_1) in the first (respectively, second) population and Π_{m_i} (respectively Π_{f_j}) is the expected payoff of an individual using strategy m_i (respectively, f_j) in a random interaction with the other population (e.g., $\Pi_{m_1} = \pi_{11}^m p_{f_1} + \pi_{12}^m p_{f_2}$ where $p_{f_2} = 1 - p_{f_1}$). The replicator Eq. (A.1) for these games without time constraints is a dynamics on the unit square. In order to generalize the dynamics to the time-constrained games in this article, it is better to rewrite (A.1) in terms of strategy numbers rather than frequencies. That is, for fixed N_m and N_f ,

$$\begin{aligned} \frac{dN_{m_1}}{dt} &= \frac{N_{m_1}(N_m - N_{m_1})}{N_m} (\Pi_{m_1} - \Pi_{m_2}) \\ \frac{dN_{f_1}}{dt} &= \frac{N_{f_1}(N_f - N_{f_1})}{N_f} (\Pi_{f_1} - \Pi_{f_2}) \end{aligned} \quad (\text{A.2})$$

where, for example, $N_{m_1} = N_m p_{m_1}$ and $\Pi_{m_1} = \frac{N_{f_1}}{N_f} \pi_{11}^m + \frac{N_{f_2}}{N_f} \pi_{12}^m$. When $N_m = N_f$ the trajectories of (A.2) are identical to those of (A.1) with the unit square scaled by a factor of N_m .

Figs. 2E, F and 3 use (A.2) where Π_{m_i} and Π_{f_j} are now (nonlinear) functions of N_{m_i} and N_{f_j} as in (15).

Appendix B. Uniqueness of distributional equilibrium of (5)

Fix $N_{m_1}, N_{m_2}, N_{f_1}$ and N_{f_2} and define $q_{m_i} \equiv \frac{n_{m_i}}{N_{m_i}}, q_{f_j} \equiv \frac{n_{f_j}}{N_{f_j}}$ as the proportion of searchers among those individuals in the population using a particular strategy. Then, at a distributional equilibrium of (5), from (16) we get

$$\begin{aligned} q_{m_i} &= \frac{1}{1 + \lambda q_{f_1} N_{f_1} (\tau_{i1} + \tau_{m_1}^{f_1}) + \lambda q_{f_2} N_{f_2} (\tau_{i2} + \tau_{m_1}^{f_2})}, \quad i = 1, 2 \\ q_{f_j} &= \frac{1}{1 + \lambda q_{m_1} N_{m_1} (\tau_{j1} + \tau_{f_j}^{m_1}) + \lambda q_{m_2} N_{m_2} (\tau_{j2} + \tau_{f_j}^{m_2})}, \quad j = 1, 2. \end{aligned} \quad (\text{B.1})$$

By Lemma 2 in Garay et al. (2017), there is a unique solution of (B.1) with $q_{m_i}, q_{m_2}, q_{f_1}$ and q_{f_2} between 0 and 1. The equilibrium solution of (5) is then obtained from (16).

Appendix C. Fitnesses at the distributional equilibrium

Appendix B shows that the distributional equilibrium given in (5) is unique as a function of the total numbers (N_{m_i} and N_{f_j}) of individuals playing the different strategies. At the equilibrium distribution (5), we can express these total numbers in terms of n_{m_i} and n_{f_j} as given in (16).

Now we determine fitnesses (i.e., payoffs per unit time) for individuals using one of the four strategies. These fitnesses assume that payoffs are obtained through interaction only, i.e., searchers and disbanded individuals do not gain any additional payoff. When all four strategies are in use (i.e., $N_{m_i} \neq 0 \neq N_{f_j}$ for $i, j = 1, 2$) and all interaction times are positive, the fitness functions are then

$$\begin{aligned} \Pi_{m_1} &= \frac{n_{m_1 f_1} + n_{m_1}^{f_1}}{N_{m_1}} \frac{\pi_{11}^m}{\tau_{11} + \tau_{m_1}^{f_1}} + \frac{n_{m_1 f_2} + n_{m_1}^{f_2}}{N_{m_1}} \frac{\pi_{12}^m}{\tau_{12} + \tau_{m_1}^{f_2}} \\ \Pi_{m_2} &= \frac{n_{m_2 f_1} + n_{m_2}^{f_1}}{N_{m_2}} \frac{\pi_{21}^m}{\tau_{21} + \tau_{m_2}^{f_1}} + \frac{n_{m_2 f_2} + n_{m_2}^{f_2}}{N_{m_2}} \frac{\pi_{22}^m}{\tau_{22} + \tau_{m_2}^{f_2}} \\ \Pi_{f_1} &= \frac{n_{m_1 f_1} + n_{f_1}^{m_1}}{N_{f_1}} \frac{\pi_{11}^f}{\tau_{11} + \tau_{f_1}^{m_1}} + \frac{n_{m_2 f_1} + n_{f_1}^{m_2}}{N_{f_1}} \frac{\pi_{21}^f}{\tau_{21} + \tau_{f_1}^{m_2}} \\ \Pi_{f_2} &= \frac{n_{m_1 f_2} + n_{f_2}^{m_1}}{N_{f_2}} \frac{\pi_{12}^f}{\tau_{12} + \tau_{f_2}^{m_1}} + \frac{n_{m_2 f_2} + n_{f_2}^{m_2}}{N_{f_2}} \frac{\pi_{22}^f}{\tau_{22} + \tau_{f_2}^{m_2}}. \end{aligned} \quad (\text{C.1})$$

For instance, the fitness of a faithful male, Π_{m_1} , is the probability $\frac{n_{m_1 f_1} + n_{m_1}^{f_1}}{N_{m_1}}$ that this male disbands from a pair with a coy female times the payoff per unit time $\frac{\pi_{11}^m}{\tau_{11} + \tau_{m_1}^{f_1}}$ it receives from this interaction plus a similar product $\frac{n_{m_1 f_2} + n_{m_1}^{f_2}}{N_{m_1}} \frac{\pi_{12}^m}{\tau_{12} + \tau_{m_1}^{f_2}}$ from pairs it forms with fast females.

These fitnesses, evaluated at the distributional equilibrium, are then well-defined functions of N_{m_i} and N_{f_j} ($i, j = 1, 2$) when all denominators are different from zero and so completely specify the time-constrained game when the sizes of the two populations are fixed at $N_m \equiv N_{m_1} + N_{m_2}$ and $N_f \equiv N_{f_1} + N_{f_2}$, respectively, and individual fitness is interpreted as its payoff in the time-constrained game.

From (5) and (16), fitness functions (C.1) simplify to

$$\begin{aligned} \Pi_{m_1} &= \frac{\lambda(n_{f_1} \pi_{11}^m + n_{f_2} \pi_{12}^m)}{1 + \lambda n_{f_1} (\tau_{11} + \tau_{m_1}^{f_1}) + \lambda n_{f_2} (\tau_{12} + \tau_{m_1}^{f_2})} \\ \Pi_{m_2} &= \frac{\lambda(n_{f_1} \pi_{21}^m + n_{f_2} \pi_{22}^m)}{1 + \lambda n_{f_1} (\tau_{21} + \tau_{m_2}^{f_1}) + \lambda n_{f_2} (\tau_{22} + \tau_{m_2}^{f_2})} \\ \Pi_{f_1} &= \frac{\lambda(n_{m_1} \pi_{11}^f + n_{m_2} \pi_{21}^f)}{1 + \lambda n_{m_1} (\tau_{11} + \tau_{f_1}^{m_1}) + \lambda n_{m_2} (\tau_{21} + \tau_{f_1}^{m_2})} \\ \Pi_{f_2} &= \frac{\lambda(n_{m_1} \pi_{12}^f + n_{m_2} \pi_{22}^f)}{1 + \lambda n_{m_1} (\tau_{12} + \tau_{f_2}^{m_1}) + \lambda n_{m_2} (\tau_{22} + \tau_{f_2}^{m_2})}. \end{aligned} \quad (\text{C.2})$$

In this form, individual fitness is defined when the formulas in (C.1) are indeterminate due to division by 0. For instance, if $N_{m_1} = 0$, Π_{m_1} is well-defined in (C.2) and equals the invasion fitness of strategy m_1 in a system where all individuals in population one use strategy m_2 . Moreover, fitnesses are defined as well when some of the entries (i.e., τ_{ij} , $\tau_{m_i}^f$, $\tau_{f_j}^m$) in the time-bimatrix (4) are zero. As we will see in the following section, this last observation is quite important for us since our primary interest is to apply these methods to the time-constrained BoS game where some entries of the time-bimatrix are assumed to be zero. In particular, payoffs may then accrue when they are in a searching or disbanded state to individuals that have encountered each other. For a different method based on renewal theory to calculate fitness that avoids the issue of division by zero, see, e.g., Houston and McNamara (1999) or Broom et al. (2019).

Appendix D. Analysis of evolutionary outcomes for Section 4.2

Here, we assume $B_1 < B_2$ in payoff bimatrix (18) and $\tau_{1r} \geq \tau_{2r}$ in time-bimatrix (7). In Section 4.2, we then apply the results with $\tau_{1r} = \tau_{2r} \equiv \tau_r$ (as in time-bimatrix (19)) and $N_m = N_f = N$.

From the main text, we know that all boundary evolutionary outcomes for this time-constrained BoS game must occur on the edge where all females are Fast. We will first examine when the vertices (Philanderer, Fast) and (Faithful, Fast) are strict NE and so evolutionary outcomes.¹⁷ In fact, we initially consider the time-constrained game with general time-bimatrix (4) since the equilibrium distribution of (5) can be solved analytically as a function of N_m and N_f (see (D.2) and (D.3) below) when individuals in each population all use the same strategy. We then use this result to determine exact conditions when a vertex is a strict NE for the time-constrained BoS game with payoff bimatrix (8) and time-bimatrix (7). In particular, D.1 (respectively D.2) determines when (Faithful, Fast) (respectively, (Philanderer, Fast)) is a strict NE. In each of these two situations, we study the general case that does not assume even sex ratio (or that $\tau_{1r} = \tau_{2r}$) as well as strict NE conditions when the sex ratio is even.

Suppose all individuals in populations one and two use strategy m_i and f_j ($i, j = 1, 2$) respectively. Then $N_{m_i} = N_m$, $N_{f_j} = N_f$ and, from (5) and (16),

$$\begin{aligned} N_m &= n_{m_i} + \lambda n_{f_j} n_{m_i} \tau_{ij}^m \\ N_f &= n_{f_j} + \lambda n_{f_j} n_{m_i} \tau_{ij}^f. \end{aligned} \quad (\text{D.1})$$

Eliminating n_{f_j} yields

$$\lambda \tau_{ij}^f n_{m_i}^2 + n_{m_i} \left(1 + \lambda (N_f \tau_{ij}^m - N_m \tau_{ij}^f) \right) - N_m = 0,$$

a polynomial in n_{m_i} of degree at most 2. Solving for $n_{m_i} > 0$,¹⁸

$$n_{m_i} = \begin{cases} \frac{\lambda (N_m \tau_{ij}^f - N_f \tau_{ij}^m) - 1 + \sqrt{(\lambda (N_m \tau_{ij}^f - N_f \tau_{ij}^m) - 1)^2 + 4 \lambda N_m \tau_{ij}^f}}{2 \lambda \tau_{ij}^f} & \text{if } \tau_{ij}^f \neq 0 \\ \frac{N_m}{1 + \lambda N_f \tau_{ij}^m} & \text{if } \tau_{ij}^f = 0. \end{cases} \quad (\text{D.2})$$

Similarly,

$$n_{f_j} = \begin{cases} \frac{\lambda (N_f \tau_{ij}^m - N_m \tau_{ij}^f) - 1 + \sqrt{(\lambda (N_f \tau_{ij}^m - N_m \tau_{ij}^f) - 1)^2 + 4 \lambda N_f \tau_{ij}^m}}{2 \lambda \tau_{ij}^m} & \text{if } \tau_{ij}^m \neq 0 \\ \frac{N_f}{1 + \lambda N_m \tau_{ij}^f} & \text{if } \tau_{ij}^m = 0. \end{cases} \quad (\text{D.3})$$

¹⁷ See Section D.3 for analyzing non-vertex evolutionary outcomes on this edge where all females are Fast.

¹⁸ It should be noted that $n_{m_i} = N_m$ if $\tau_{ij}^m = 0$ from (D.2) as is also clear from (D.1).

The monomorphic system (m_i, f_j) corresponds to a strict NE if $\Pi_{m_i} > \Pi_{m_i}^{19}$ and $\Pi_{f_j} > \Pi_{f_j}$ when n_{m_i} and n_{f_j} in (D.2) and (D.3) (along with $n_{m_i} = 0$ and $n_{f_j} = 0$) are substituted into (6). Since this involves many cases depending on whether τ_{ij}^m and τ_{ij}^f are positive, we will restrict attention to the time-constrained BoS game of Section 4.2 for the remainder of Appendix D where individual fitnesses (6) are given by (9).

D.1. When is strategy (Faithful, Fast) a strict NE?

Here we analyze when strategy (Faithful, Fast), denoted as (m_1, f_2) where all males are Faithful and all females are Fast (i.e., $N_{m_1} = N_m$ and $N_{f_2} = N_f$), is a strict NE. From (D.2) and (D.3) applied to (m_1, f_2) , the distributional equilibrium of searchers is

$$\begin{aligned} n_{m_1} &= \frac{\lambda \tau_r (N_m - N_f) - 1 + \sqrt{4 \lambda N_m \tau_{2r} + (\lambda \tau_{2r} (N_f - N_m) + 1)^2}}{2 \lambda \tau_{2r}}, \\ n_{m_2} &= 0, \\ n_{f_1} &= 0, \\ n_{f_2} &= \frac{\lambda \tau_r (N_f - N_m) - 1 + \sqrt{4 \lambda N_m \tau_{2r} + (\lambda \tau_{2r} (N_f - N_m) + 1)^2}}{2 \lambda \tau_r} \end{aligned} \quad (\text{D.4})$$

and individual fitnesses (9) evaluated at this equilibrium simplify to

$$\begin{aligned} \Pi_{m_1} &= \frac{\lambda B_2 n_{f_2}}{1 + \lambda n_{f_2} \tau_{2r}} \\ \Pi_{m_2} &= \lambda B_1 n_{f_2} \\ \Pi_{f_1} &= \frac{\lambda B_2 n_{m_1}}{1 + \lambda n_{m_1} (\tau_c + \tau_{2r})} \\ \Pi_{f_2} &= \frac{\lambda B_2 n_{m_1}}{1 + \lambda n_{m_1} \tau_{2r}}. \end{aligned}$$

Since $\tau_c > 0$, $\Pi_{f_2} > \Pi_{f_1}$, and so strategy (Faithful, Fast) is a strict NE if and only if $\Pi_{m_1} > \Pi_{m_2}$, i.e.,

$$N_f < \frac{(B_2 - B_1)(B_1 + \lambda B_2 N_m \tau_{2r})}{\lambda B_1 B_2 \tau_{2r}}. \quad (\text{D.5})$$

We observe that strategy (Faithful, Fast) is a strict NE only if the female population is not too large when compared to the male population. This makes sense because when females are rare, it is better for males to be Faithful, while females can easily find a mate so it is better to be Fast.

Under even sex ratio ($N_m = N_f = N$), the distributional equilibrium (D.4) simplifies to

$$n_{m_1} = n_{f_2} = \frac{\sqrt{4 \lambda N \tau_{2r} + 1} - 1}{2 \lambda \tau_{2r}}, \quad n_{m_2} = n_{f_1} = 0$$

and inequality (D.5) for the strict NE becomes

$$N < \frac{B_2(B_2 - B_1)}{\lambda B_1^2 \tau_{2r}}.$$

We observe that strategy (Faithful, Fast) is a strict NE only if the population size is not too large.

D.2. When is strategy (Philanderer, Fast) a strict NE?

Next, we analyze when strategy (Philanderer, Fast), denoted as (m_2, f_2) where all males are Philanderer and all females are Fast, i.e., $N_{m_2} = N_m$ and $N_{f_2} = N_f$, is a strict NE. The distributional equilibrium of searchers is

¹⁹ Here $\bar{i} = 1(2)$ when $i = 2(1)$ and similar notation is used for \bar{j} .

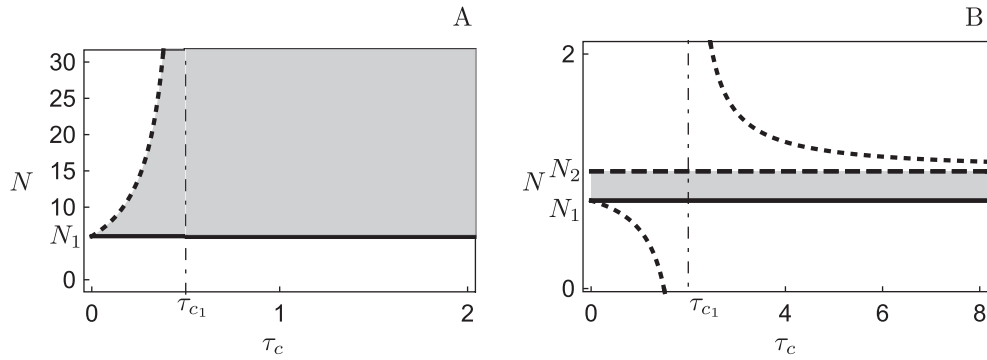


Fig. D.1. Thresholds N_1 (solid line), N_2 (dashed line), and N_3 (dotted curve) as functions of τ_c . Panel A assumes $B_1 = 1$ and $B_2 = 3$ so that inequality $1 + \frac{\tau_{2r}}{\tau_{1r}} < \frac{B_2}{B_1}$ holds. Panel B assumes $B_1 = 1$ and $B_2 = 1.5$ so that the opposite inequality holds. The shaded area shows the range of parameters in τ_c - N parameter space where the boundary equilibrium (D.11) with all females Fast is a NE. Other parameters: $\tau_{1r} = 1$, $\tau_{2r} = 1$, $\lambda = 1$.

$$(n_{m_1}, n_{f_1}, n_{m_2}, n_{f_2}) = \left(0, 0, N_m, \frac{N_f}{1 + \lambda N_m \tau_{1r}}\right) \quad (D.6)$$

from (D.2) and (D.3) applied to (m_2, f_2) . Individual fitnesses (9) evaluated at this equilibrium are

$$\begin{aligned} \Pi_{m_1} &= \frac{\lambda B_2 n_{f_2}}{1 + \lambda n_{f_2} \tau_{2r}} \\ \Pi_{m_2} &= \lambda B_1 n_{f_2} \\ \Pi_{f_1} &= 0 \\ \Pi_{f_2} &= \frac{\lambda B_1 n_{m_2}}{1 + \lambda n_{m_2} \tau_{1r}}. \end{aligned} \quad (D.7)$$

Since $\Pi_{f_2} > \Pi_{f_1}$, (Philanderer, Fast) is a strict NE if and only if $\Pi_{m_2} > \Pi_{m_1}$, i.e., if and only if $n_{f_2} > \frac{B_2 - B_1}{\lambda B_1 \tau_{2r}}$. That is, the number of female searchers must be sufficiently high. Substituting distribution of searcher (D.6)–(D.7) yields the following condition for the NE

$$N_f > \frac{(B_2 - B_1)(\lambda N_m \tau_{1r} + 1)}{\lambda B_1 \tau_{2r}}.$$

It is then straightforward to confirm that (Philanderer, Fast) is a strict NE for even sex ratio ($N_m = N_f = N$) if and only if

$$\frac{B_2}{B_1} < 1 + \frac{\tau_{2r}}{\tau_{1r}} \quad \text{and} \quad N > \frac{B_2 - B_1}{\lambda(B_1(\tau_{1r} + \tau_{2r}) - B_2 \tau_{1r})}.$$

As we assume that $\tau_{1r} > \tau_{2r}$, inequality $\frac{B_2}{B_1} < 1 + \frac{\tau_{2r}}{\tau_{1r}}$ implies that $B_2 < 2B_1$.

D.3. When is there an evolutionary outcome with all females Fast and the male population exhibits a mixture of behaviors

Suppose (N_{m_1}, N_{f_1}) is such an evolutionary outcome. Then it is a NE for which $N_{f_1} = n_{f_1} = 0$ and $N_{f_2} = N_f$. Since the male population exhibits a mixture of its two behaviors at this NE, it is a rest point of the replicator equation on the bottom edge of the square. That is, it satisfies

$$\Pi_{m_1} = \frac{B_2 \lambda n_{f_2}}{1 + \lambda n_{f_2} \tau_{2r}} = \lambda B_1 n_{f_2} = \Pi_{m_2}. \quad (D.8)$$

At the distributional equilibrium (5), we also have (cf., (16))

$$\begin{aligned} N_{m_1} &= n_{m_1} (1 + \lambda n_{f_2} \tau_{2r}) \\ N_m - N_{m_1} &= n_{m_2} \\ N_f &= n_{f_2} (1 + \lambda n_{m_1} \tau_{2r} + \lambda n_{m_2} \tau_{1r}). \end{aligned} \quad (D.9)$$

Under our assumptions that $B_2 > B_1$ and $\tau_{1r} \geq \tau_{2r} > 0$, there exists a unique solution of (D.8) and (D.9); namely,

$$\begin{aligned} n_{m_1} &= \frac{B_1(B_2(1 + \lambda N_m \tau_{1r}) - B_1(1 + \lambda N_m \tau_{1r} + \lambda N_f \tau_{2r}))}{\lambda(B_2 - B_1)(B_2 \tau_{1r} - B_1 \tau_{2r})} \\ n_{m_2} &= \frac{\lambda B_1 \tau_{2r}(B_1 N_m + B_2(N_f - N_m)) + B_2(B_1 - B_2)}{\lambda(B_2 - B_1)(B_2 \tau_{1r} - B_1 \tau_{2r})} \\ n_{f_2} &= \frac{B_2 - B_1}{\lambda B_1 \tau_{2r}} \\ N_{m_1} &= \frac{B_2(B_2(\lambda N_m \tau_{1r} + 1) - B_1(\lambda N_m \tau_{1r} + \lambda N_f \tau_{2r} + 1))}{\lambda(B_2 - B_1)(B_2 \tau_{1r} - B_1 \tau_{2r})}. \end{aligned} \quad (D.10)$$

In what follows, we assume that the sex-ratio is even, i.e., $N_m = N_f = N$ in (D.10), which leads to a simpler analysis. In particular, the rest point of the replicator Eq. (D.10) simplifies to

$$\begin{aligned} n_{m_1} &= \frac{B_1 \lambda N (B_2 \tau_{1r} - B_1(\tau_{1r} + \tau_{2r})) + B_1(B_2 - B_1)}{\lambda(B_2 - B_1)(B_2 \tau_{1r} - B_1 \tau_{2r})} \\ n_{m_2} &= \frac{\lambda B_1^2 N \tau_{2r} - B_2(B_2 - B_1)}{\lambda(B_2 - B_1)(B_2 \tau_{1r} - B_1 \tau_{2r})} \\ n_{f_2} &= \frac{B_2 - B_1}{\lambda B_1 \tau_{2r}} \\ N_{m_1} &= \frac{\lambda B_2 N (B_2 \tau_{1r} - B_1(\tau_{1r} + \tau_{2r})) + B_2(B_2 - B_1)}{\lambda(B_2 - B_1)(B_2 \tau_{1r} - B_1 \tau_{2r})}. \end{aligned} \quad (D.11)$$

Further analysis shows that the rest point (D.11) exists (i.e., $n_{m_1} > 0, n_{m_2} > 0, n_{f_2} > 0, N_m > N_{m_1} > 0$) under either of the following two conditions.

$$1. \quad 1 + \frac{\tau_{2r}}{\tau_{1r}} \leq \frac{B_2}{B_1} \quad \text{and} \quad N > N_1 \quad (D.12)$$

$$2. \quad \frac{B_2}{B_1} < 1 + \frac{\tau_{2r}}{\tau_{1r}} \quad \text{and} \quad N_1 < N < N_2 \quad (D.13)$$

where the threshold population sizes are

$$N_1 = \frac{B_2(B_2 - B_1)}{\lambda B_1^2 \tau_{2r}}, \quad N_2 = \frac{B_2 - B_1}{\lambda(B_1(\tau_{1r} + \tau_{2r}) - B_2 \tau_{1r})}. \quad (D.14)$$

Note that $N_1 < N_2$ (Fig. D.1B) since $B_2 > B_1$ and $\tau_{1r} \geq \tau_{2r}$.²⁰

For (D.11) to be a NE, Coy females cannot invade at this rest point (i.e., $\Pi_{f_2} > \Pi_{f_1}$). At (D.11),

²⁰ These thresholds are also important in D.1 and D.2 respectively where strict NE are determined.

$$\Pi_{f_2} - \Pi_{f_1} = \frac{(B_2 - B_1) \left(B_1^2 \tau_c + B_1 B_2 (\tau_{1r} + \tau_{2r} - \tau_c) - B_2^2 \tau_{1r} \right) + \lambda B_1 N (B_1 (\tau_{1r} + \tau_{2r}) - B_2 \tau_{1r}) (B_2 \tau_c - B_1 (\tau_{2r} + \tau_c))}{B_1 \lambda N \tau_{2r} (\tau_{2r} + \tau_c) (B_1 (\tau_{1r} + \tau_{2r}) - B_2 \tau_{1r}) + \tau_{2r} (B_1 - B_2) (B_1 \tau_c + B_2 \tau_{1r})} \quad (\text{D.15})$$

and there is a unique critical population density

$$N_3 = \frac{(B_2 - B_1) \left(B_1^2 \tau_c + B_1 B_2 (\tau_{1r} + \tau_{2r} - \tau_c) - B_2^2 \tau_{1r} \right)}{\lambda B_1 (B_1 (\tau_{1r} + \tau_{2r}) - B_2 \tau_{1r}) (B_1 (\tau_{2r} + \tau_c) - B_2 \tau_c)} \quad (\text{D.16})$$

at which $\Pi_{f_2} = \Pi_{f_1}$. We note that N_3 has a vertical asymptote at

$$\tau_{c_1} = \frac{B_1 \tau_{2r}}{B_2 - B_1}$$

(the vertical line in Fig. D.1) and at $1 + \frac{\tau_{2r}}{\tau_{1r}} = \frac{B_2}{B_1}$.

By combining conditions for existence of the boundary rest point in (D.12) and (D.13) with the condition for its non-invasibility based on (D.15)²¹ we find that the boundary rest point (D.11) is a NE under each of the following cases:

1. $1 + \frac{\tau_{2r}}{\tau_{1r}} < \frac{B_2}{B_1}$, $\tau_c < \tau_{c_1}$, $N_1 < N < N_3$, see Fig. D.1A.
2. $1 + \frac{\tau_{2r}}{\tau_{1r}} < \frac{B_2}{B_1}$, $\tau_c > \tau_{c_1}$, $N_1 < N$, see Fig. D.1A.
3. $1 + \frac{\tau_{2r}}{\tau_{1r}} > \frac{B_2}{B_1}$, $N_1 < N < N_2$, see Fig. D.1B.

We observe that when $\tau_{1r} = \tau_{2r}$ then condition $1 + \frac{\tau_{2r}}{\tau_{1r}} < \frac{B_2}{B_1}$ ($1 + \frac{\tau_{2r}}{\tau_{1r}} > \frac{B_2}{B_1}$) simplifies to $B_1 < 2B_2$ ($B_1 > 2B_2$). Conditions 1-3. are listed in the corresponding entries of Table 1.

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²¹ This can be efficiently done using command `Reduce` in Mathematica.