

Evolutionary games with sequential decisions and dollar auctions

Mark Broom · Jan Rychtář

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Abstract Conflict occurs throughout the animal world. Such conflicts are often modelled by evolutionary games, where individual animals make a single decision each within the game. These decisions can be sequential, in either order, or simultaneous, and the outcome of the game can depend strongly upon which case is assumed to occur. Real conflicts are generally more complex, however. A fight over a territory, for instance, can involve a succession of different stages, and therefore choices, to be made by the protagonists. In this paper we thus introduce a method of modelling a more complex class of interactions, where each individual can make a sequence of decisions. We show that despite the inherent complexity, under certain assumptions, the resulting game often leads to the case where both animals fight to the fullest extent or where one concedes immediately, thus mirroring the outcomes of simpler single decision games. However, for other cases we see that the outcome is not so simple, and intermediate level contests can occur. This occurs principally in cases where the duration of contests is uncertain, and partially governed by external factors which can bring the contest to a sudden end, such as the weather or the appearance of a predator. We thus develop a theory grounded in simple evolutionary models, but extending them in various important ways.

Keywords Game theory · Nash equilibrium · animal conflict · Hawk-Dove game · extensive form games

Mark Broom
Department of Mathematics, City University London, Northampton Square, London,
EC1V 0HB, UK
E-mail: mark.broom@city.ac.uk

Jan Rychtář
Department of Mathematics and Statistics, The University of North Carolina at Greens-
boro, Greensboro, NC 27412, USA
E-mail: rychtar@uncg.edu

1 Introduction

Conflict is ubiquitous throughout the animal world, taking many different forms (see e.g. Huntingford, 2013). Such conflicts can be modelled using evolutionary game theory, where different behaviours within the conflict, for example be aggressive or passive, are represented by the game strategies (Maynard Smith and Parker, 1976; Maynard Smith, 1982; Hofbauer and Sigmund, 1998; Broom and Rychtář, 2013). A common feature of evolutionary game theoretical models is that contests are often assumed to involve only a single decision by each participant. These decisions can be taken simultaneously, without knowledge of the other player's choice, or in sequence, so that the second player observes the choice of the first before making its own decision. It is well known that whether the decisions are simultaneous or sequential, and if sequential which order the decisions are made, can fundamentally change the outcome of the game (Houston and McNamara, 1999).

A classic example of the type of behaviour that we are interested in involves stags, which compete for territories and the associated mating opportunities with females. These contests can be complex, involving observation of the size of opponents, parallel walking, pushing and potentially lethal fighting. The contests are thus not just single events, but go through stages, where the protagonists can make decisions at different points. Such a situation was first modelled by Maynard Smith and Price (1973); Maynard Smith (1982) using the Hawk-Dove game, one of the most important games in biology. In the classical game, two individuals compete over a resource of value V , with two available strategies, the aggressive Hawk strategy and the passive Dove strategy. If one player plays Hawk and the other Dove, the Hawk-player gains V and the Dove player 0. If both play Dove, the winner is selected at random, so each receives an average reward of $V/2$. If both play Hawk, they fight until one receives an injury of cost C , the other then receiving the reward; the winner is decided at random, so the average reward is $(V - C)/2$. Assuming that $C > V$, if each simultaneously chooses a strategy, for indistinguishable individuals, the unique evolutionarily stable strategy (ESS) is a mixed strategy, where Hawk is played with probability V/C (and Dove with probability $1 - V/C$). For a sequential game, the unique ESS is that the first player plays Hawk and the second Dove, so that the first to play always gains the reward. Here the initial choice by the first player of Hawk commits that player to fight if the other also chooses Hawk, so that the second player knows that a choice of Hawk commits it to obtain the negative reward $(V - C)/2$, forcing it to choose Dove. The Hawk-Dove game was extended to involve asymmetries with the Owner-Intruder game (Maynard Smith and Parker, 1976) and this has been elaborated more recently in a number of ways (see e.g. Sherratt and Mesterton-Gibbons, 2015, for a review).

Real animal conflicts are often more complex than just involving a single decision by each combatant, and animals may make a sequence of decisions affected by the decisions made by themselves and their opponent, and the outcomes of those decisions, earlier in the contest. This is the case in the example

of stags competing for a territory considered above. Games with a single decision are often a useful simplification for the more complex case, with the significant advantage of analytical simplicity, but the potential disadvantage of a lack of realism. Thus in the sequential Hawk-Dove game, the first player gains from the unrealistic assumption that its initial aggressive act commits it to fight with full aggression for the whole contest. The models of Mesterton-Gibbons et al (2014, 2016) consider a contest for a resource which can feature many stages of challenge and rechallenge. The model is based upon an iterated Hawk-Dove game, which has similar features to the iterated Prisoner's Dilemma (Axelrod, 1981), in that optimal behaviour is heavily influenced by both the expectation of an opponent's future strategy and also the likelihood of further contests.

An alternative situation that can lead to complex contests is animal foraging. Whilst foraging, animals may discover patches of resources, the value of which can vary considerably, and they must balance out the benefit of staying in the patch and continuing to feed, or to leave and seek a potentially richer patch elsewhere. If there is a single individual only and the patch becomes increasingly depleted through time, the individual does not have to consider the choices of an opponent (though the value of patches elsewhere may depend upon some population strategy of others), and it must simply pick the best time to leave (Charnov, 1976). However, if there is more than one individual, the choices of others are important. For a non-depleting patch with no movement costs, this relates to the Ideal free distribution (Fretwell and Lucas, 1969; Cressman et al, 2004). When resources become depleted, then individuals play a game where costs and benefits change through time, and this becomes a generalized war of attrition (Bishop and Cannings, 1978). This is a development of the classical war of attrition (Bishop and Cannings, 1976) where two individuals compete for a reward by trying to outwait the other individual, see also Maynard Smith and Parker (1976); Hammerstein and Parker (1982). A specific example with parasitoid wasps visiting a patch of host larvae is given in Haccou et al (2003).

In this paper we introduce a method of analysing an animal conflict over an indivisible valuable resource, as in the Hawk-Dove game, involving a potentially long sequence of decisions. These are binary in form, where individuals choose to persist in the contest (at some additional cost) or concede, concession allowing the opponent to take the resource. The costs may vary, depending upon the stage of the contest, for example if the nature of the contest changes (as in the case of the mentioned stags above). Each possess a level of resources which may prevent them from competing indefinitely. Similarly the contest may eventually stop due to some external influence, for example the arrival of night or a predator, and at that point the resource will be allocated to one of the individuals at random (generally not uniformly at random, however). We analyse our game under a number of scenarios, and also connect it to the dollar auction, a game from Economics with some similar features.

2 The model

Two individuals I_1 and I_2 compete for a valuable resource, which is worth V_i to individual i for $i = 1, 2$. The contests follows a sequence of alternating decisions, one at each time step, starting with I_1 , where the individual can remain in the game at a cost, or concede the resource to its opponent. As individuals have to pay a cost any time they decide to remain in the contest, we will also refer to the decision to stay in the contest as an *investment* and we will denote the cost of the j th investment of individual I_i by $c_{i,j}$. We assume that $c_{i,j} \geq \varepsilon$, for some $0 < \varepsilon < \min(a_1 V_1, a_2 V_2)$ and all i, j . We assume that the game may continue for up to $T \in \mathbb{N} \cup \{\infty\}$ time steps.

If $T < \infty$, then the game ends no later than after step T by either (a) an individual giving up at any step $T' \leq T$, or (b) the contest reaching the *stopping point* just after step T . If T is odd, the stopping point happens after I_1 's investment; if T is even, the stopping point happen after I_2 's investment. In any case, an individual I_i can invest up to a maximum of J_i times where

$$J_1 = \text{int} \frac{T+1}{2}, \quad (1)$$

$$J_2 = \text{int} \frac{T}{2}. \quad (2)$$

At the stopping point, I_i gains the reward with probability a_i , so that $a_2 = 1 - a_1$. See Figure 1 for an illustration of the game. After their j th investment, I_i has paid a total cost $C_{i,j} = \sum_{k=1}^j c_{i,k}$. Each individual has a maximum level of resources R_i that they can invest, so that $C_{i,j}$ can never exceed R_i . When $R_i < \infty$, this condition together with the minimum investment level $\varepsilon > 0$ guarantees that individuals have to eventually concede at some point. There are three distinct cases for the payoffs in this game.

1. If I_1 concedes at its j th decision, then I_1 receives payoff $-C_{1,j-1}$ and I_2 receives $V_2 - C_{2,j-1}$.
2. If I_2 concedes at its j th decision, then I_1 receives payoff $V_1 - C_{1,j}$ and I_2 receives $-C_{2,j-1}$.
3. If neither concedes and the game reaches the stopping point after step T , I_1 receives payoff $a_1 V_1 - C_{1,J_1}$ and I_2 receives $a_2 V_2 - C_{2,J_2}$.

We are interested in finding the optimal strategy for each player. Assuming that an individual can find itself in the I_1 or I_2 role, a strategy is then a combination of what to do as I_1 , and what to do as I_2 . Each player only has the chance to play if all previous investments of both players have been made, so that a pure strategy is simply the round in each case that an individual would concede, assuming that it were reached, as I_1 or I_2 . This can be reduced to a pair of integers (including infinity as an allowable choice), so that S_{j_1, j_2} represents invest in the first $j_i - 1$ rounds and then concede as I_i .

We shall consider a number of cases. In Section 3 we consider the case where all parameters $V_i, c_{i,j}, a_i, R_i$ and T are a priori fixed and known to both players. In Section 4 we will consider parameters $V_i, c_{i,j}, a_i, R_i$ fixed and known

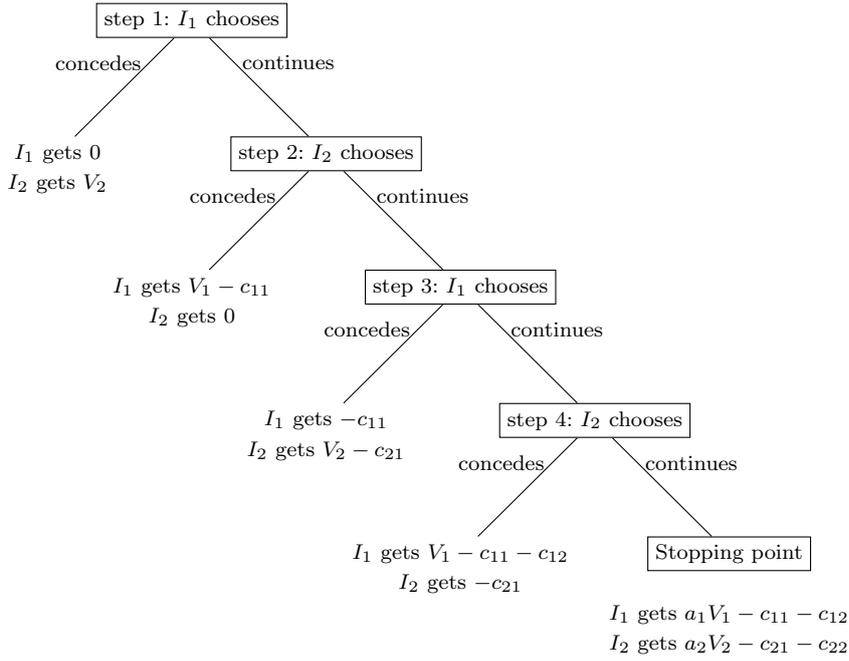


Fig. 1: An example of the game for $T = 4$ where each individual can make (up to) two choices.

but will assume that T follows a random distribution, i.e. the stopping time is not a priori fixed, and so unknown to either of the players. In Section 5 we will consider the parameters V_i, a_i, R_i and T known and fixed, but we will allow individuals to choose the cost of staying in the game themselves (under the condition that if the game reaches step T , their total investment must reach an a priori known and fixed value C_i). Finally, in Section 6, we will consider the *dollar auction* game (Shubik, 1971), as a special case of our game and in particular we will solve a variant of the dollar auction game where individuals are assumed to have no memory.

3 Fixed and known parameter values

In this section consider the game $\Gamma = \langle T, V_i, R_i, a_i, c_{i,j} \rangle$ described above where the values of $V_i, c_{i,j}, a_i, R_i$ and $T < \infty$ are a priori fixed and known to both players. Since the $c_{i,j}$ and T are fixed and known, I_i knows how much it will have to invest to reach the end of the contest, which we denote by $C_1 = C_{1,J_1}$ and $C_2 = C_{2,J_2}$, for I_1 and I_2 respectively; here J_1 and J_2 are given by (1) and (2).

We can work from the end of the contests, using the standard backwards induction method (see e.g. Broom and Rychtář, 2013), to solve the game. We

shall take this approach throughout the paper; when applying this method we shall use the shorthand “working backwards”. Note that, less often, we shall need to work from the start of the game, denoted as “working forwards”.

Let $B_{i,j}$ denote the *expected future payoff* to I_i before its j th choice and let $A_{i,j}$ denote the expected future payoff after its j th choice (assuming that it has not conceded). At any step j , the individual I_i chooses the better of the following two options

1. to concede, get no reward (and pay the cost $C_{i,j-1}$ after already investing $j - 1$ times), or
2. to continue, pay the cost $c_{i,j}$ (plus the cost $C_{i,j-1}$ of already investing $j - 1$ times), and expect to get payoff $B_{i,j}$.

However, the individual can continue only if it has sufficient resources to do so. Consequently,

$$B_{i,j} = \begin{cases} 0, & \text{if } R_i < C_{i,j}, \\ -c_{i,j} + A_{i,j}, & \text{if } R_i \geq C_{i,j} \text{ and } A_{i,j} > c_{i,j}, \\ 0, & \text{otherwise,} \end{cases} \quad (3)$$

where

$$A_{1,j} = \begin{cases} V_1 & \text{if } B_{2,j} = 0, \text{ and} \\ B_{1,j+1} & \text{otherwise;} \end{cases} \quad (4)$$

$$A_{2,j} = \begin{cases} V_2 & \text{if } B_{1,j+1} = 0, \text{ and} \\ B_{2,j+1} & \text{otherwise.} \end{cases} \quad (5)$$

In (3) the cases appropriately correspond to (a) inability to continue due to not having sufficient resources, (b) ability to continue and a profitability of doing so, and (c) ability to continue but not a profitability of doing so. If (a) happens, we say that I_i reached a *point of concession by inability*. If (c) happens, we say that I_i reached a *point of concession by unprofitability*. A *block* is a point of concession by unprofitability where $c_{i,j} \geq V_i$ (note that $A_{i,j}$ is never more than V_i).

We note that in equations (4) and (5) we have assumed that if the expected future reward for the two choices of continuing and conceding are identical, then the individual concedes. If ties were (sometimes) resolved the other way, then our equations would be slightly different. Often in evolutionary games, we make the *generic payoff assumption* (Samuelson, 1997; Broom and Rychtář, 2013), assuming that as payoffs occur from nature, following some natural variation, such ties never occur. This assumption is reasonable for games where there is a clear end point, which we consider in the rest of this section, Section 5 and the first part of Section 6.1. There are complications when there is not such an end-point, as then the selection of mixed strategies (allowing concession at a given position with a probability between 0 and 1) can generate equalities. In cases with clear roles, such mixtures are unstable (Selten, 1980), so that the assumption is valid for the rest of the paper too, with the exception of

Section 6.3, where extremely limited memory but infinite resources allows a game without roles and which carries on indefinitely (and where we see that such mixed strategies feature).

3.1 Blocks and unblocking

Here, we present the main four results for games without blocks. The games in this section are all examples of truly asymmetric finite extensive form games and thus, following Theorem 4.5.3 of Cressman (2003), there is a one-to-one correspondence between ESSs and strict Nash equilibria (NE). If we assume generic games and no equalities, then the solutions for each of our main results yields a unique strict NE, which is thus the unique ESS. Without this assumption, they are (perhaps non-strict) Nash equilibria only. The results are summarised in Table 1.

Theorem 1 *The first individual that would reach a concession point must concede immediately, i.e. before making its first investment.*

Proof Suppose without loss of generality that I_2 reaches the concession point first and that it happened at its j th investment, $j > 1$. In this case, we have:

1. $B_{2,j} = 0$ (I_2 reached a concession point),
2. $B_{2,j-1} > 0$ (it was the first concession point for I_2),
3. $B_{1,j} > 0$ (I_1 has not reached a concession point yet).

Hence I_1 invests at the previous step and thus $A_{2,j-1} = B_{2,j} = 0$ which leads to

$$B_{2,j-1} = \max(-c_{2,j-1}, 0) = 0, \quad (6)$$

and so I_2 should concede at its $j - 1$ th step, which is a contradiction. Thus if I_2 would reach a concession point first, it should concede at $j = 1$. \square

In general, a game may contain a number of blocks, say at time steps T_{b_1}, T_{b_2}, \dots . However, the game must stop at $T_b = \min_j \{T_{b_j}\}$. Any game can be *unblocked* by considering a game with identical parameters except that T_b replaces T and $(0, 1)$ (or $(1, 0)$) replaces (a_1, a_2) if T_b is odd (or even). Here the outcome (i.e. the optimal strategies and eventual payoffs) of the unblocked game is the same as the original one.

3.2 Solving games with no blocks or unblocked games

The solution of the unblocked game depends upon two types of conditions:

$$\text{Condition R1:} \quad R_1 \geq C_1; \quad (7)$$

$$\text{Condition R2:} \quad R_2 \geq C_2; \quad (8)$$

$$\text{Condition P1:} \quad a_1 V_1 > C_1; \quad (9)$$

$$\text{Condition P2:} \quad a_2 V_2 > C_2; \quad (10)$$

Note that condition R holds if the individual has enough resources to continue to the end and condition P holds if it is profitable for the individual to do so.

Theorem 2 *In the unblocked game, if either condition R1 or condition R2 (or both) does not hold, then at least one individual would run out of resources before T is reached and the first individual who would run out of resources must concede immediately. Specifically, if, for some j*

$$R_1 - \sum_{k=1}^j c_{1,k} < 0 \text{ while } R_2 - \sum_{k=1}^{j-1} c_{2,k} \geq 0 \quad (11)$$

then I_1 should concede immediately. If, for some j ,

$$R_2 - \sum_{k=1}^j c_{2,k} < 0 \text{ while } R_1 - \sum_{k=1}^j c_{1,k} \geq 0 \quad (12)$$

then I_2 should concede immediately.

Note that it is clear that at most one of (11) and (12) can hold.

Proof The first individual to run out of resources has reached a concession point. Assume that it is individual I_2 . As the game is an unblocked game, individual I_1 has not yet reach a block or a point of concession by inability. Working backwards, there is no earlier point of concession by unprofitability. Indeed, once $B_{2,j} = 0$, then $A_{1,j} = V_1 > 0$. Since there is no block, $V_1 > c_{1,j}$ and so $B_{1,j} = V_1 - c_{1,j} > 0$, i.e. it is not a point of concession by unprofitability for I_1 . Also, $A_{2,j-1} = B_{2,j} = 0$ and thus $B_{2,j-1} = 0$ and so on. Thus, I_2 reaches a first concession point, and must thus concede before making the first investment by Theorem 1. \square

Theorem 3 *In the unblocked game, if conditions R1 and R2 hold, but at least one of condition P1 and P2 does not, then at the start of the contest, the expected reward of remaining in the contest is non-positive, conditional on the other player not conceding, for at least one player. Moreover, the player for which this expected payoff becomes positive last should concede immediately.*

Proof Suppose that T is even, and thus $J_1 = J_2 = T/2$. We let $J = J_1$. Then we have

$$B_{2,J} = \max(0, a_2 V_2 - c_{2,J}). \quad (13)$$

Assuming that $A_{2,J} > 0$ we then obtain

$$B_{1,J} = \max(0, a_1 V_1 - c_{1,J}). \quad (14)$$

Supposing that, working backwards, the first time that the expected future reward to either individual becomes negative is for I_1 at the point where it

would make its j th investment. Sequential application of (3)-(5) yields

$$B_{2,j} = \max \left(0, a_2 V_2 - \sum_{k=j}^J c_{2,k} \right) > 0, \quad (15)$$

$$B_{1,j} = \max \left(0, a_1 V_1 - \sum_{k=j}^J c_{1,k} \right) = 0. \quad (16)$$

This means that I_1 should concede at stage j , which then yields $A_{2,j-1} = V_2 - c_{2,j-1} > 0$ because there are no blocks. Working then follows that for Theorem 1, and so I_1 should concede at the very start of the game. Working is similar whether T is odd, or if I_2 's future expected reward becomes negative first. \square

We note that here the individual which would make large investments towards the end of the contest is the one that has to concede. Thus an individual that would make large investments at the beginning of the contest might never have to make them, as its opponent concedes immediately. We revisit this idea in Section 5.

Theorem 4 *If conditions R1, R2 and P1, P2 hold, then each player has positive expected future reward at the start of the contest no matter what the other player does, so both should continue to the end of the contest.*

Proof Suppose again that T is even. and thus $J_1 = J_2 = T/2$. We let $J = J_1$. Then we have

$$B_{2,J} = a_2 V_2 - c_{2,J} > 0, \quad (17)$$

$$B_{1,J} = a_1 V_1 - c_{1,J} > 0. \quad (18)$$

Sequential application of (3)-(5) yields

$$B_{2,j} = a_2 V_2 - \sum_{k=j}^J c_{2,k} > 0, \quad (19)$$

$$B_{1,j} = a_1 V_1 - \sum_{k=j}^J c_{1,k} > 0. \quad (20)$$

Since $a_i V_i \geq C_i = \sum_{k=1}^J c_{i,k}$, both individuals should clearly invest at every stage. A similar argument holds for odd T . \square

Conditions	Outcomes
R1, R2, P1, P2	I_1, I_2 invest at every step
R1, R2, P1, \neg P2	I_2 concedes immediately
R1, R2, \neg P1, P2	I_1 concedes immediately
R1, R2, \neg P1, \neg P2 and (15) and (16) hold for some j	I_1 concedes immediately
R1, R2, \neg P1, \neg P2 and neither (15) nor (16) hold for any j	I_2 concedes immediately
R1, \neg R2	I_2 concedes immediately
\neg R1, R2	I_1 concedes immediately
\neg R1, \neg R2 and (11) holds for some j	I_1 concedes immediately
\neg R1, \neg R2 and (12) holds for some j	I_2 concedes immediately

Table 1: Result summary for the case of fixed and known parameter values. For strict inequality of parameter conditions these are strict NEs and so ESSs, otherwise they are NEs.

4 A variable stopping time

Now suppose that T follows a random distribution. In particular, we shall assume that, conditional upon not having stopped prior to this point, the probability that the game stops after the j th investment of I_i is $\gamma_{i,j}$.

This leads to a modification of the equations (3)-(5) into

$$B_{i,j} = \begin{cases} 0, & \text{if } R_i < C_{i,j}, \\ -c_{i,j} + \gamma_{i,j}a_iV_i + (1 - \gamma_{i,j})A_{i,j}, & \text{if } R_i \geq C_{i,j} \text{ and } \gamma_{i,j}a_iV_i + (1 - \gamma_{i,j})A_{i,j} > c_{i,j}, \\ 0, & \text{otherwise,} \end{cases} \quad (21)$$

$$A_{1,j} = \begin{cases} V_1 & \text{if } B_{2,j} = 0 \text{ and} \\ (1 - \gamma_{2,j})B_{1,j+1} + \gamma_{2,j}a_1V_1 & \text{otherwise;} \end{cases} \quad (22)$$

$$A_{2,j} = \begin{cases} V_2 & \text{if } B_{1,j+1} = 0 \text{ and} \\ (1 - \gamma_{1,j+1})B_{2,j+1} + \gamma_{1,j+1}a_2V_2 & \text{otherwise.} \end{cases} \quad (23)$$

4.1 Bounded games

There are a number of ways in which a contest can have a clear endpoint, and we describe each of these below. In these cases, we can work backwards, as usual.

1. If there is a first block at time T_b (i.e. no block at time $T < T_b$), then, as we have seen in Section 3.1, this is equivalent to a game with a fixed endpoint $T = T_b$ and $(a_1, a_2) = (0, 1)$ or $(1, 0)$, and we analyse the game following the method from Section 3. We note that in this case theoretically the game could continue indefinitely, if a player mistakenly invests at a block, but optimal play leads to termination of the game.
2. If there is at least one $\gamma_{i,j}$ which takes value 1, then T is bounded above. If $\gamma_{I,J}$ is the earliest such γ , then we have a fixed endpoint at $T = 2J + I - 2$.

3. If R_i is finite for $i = 1, 2$, then there will be a point when one player must concede (assuming that the contest reaches this point), so the future values at the point of concession will either be $(V_1, 0)$ or $(0, V_2)$.

If there are both finite resources and T is bounded above, the earliest such occurrence determines which of the cases 2) and 3) occurs.

We thus have the following procedure for determining the optimal strategy. Working backwards, as identified by 1-3) above, we find the expected future reward following equation (21) and equations (22), (23). If this is ever 0, then an individual would concede, and so the expected future values when concession occurs will be either $(V_1, 0)$ or $(0, V_2)$. We can thus find the expected future rewards for all positions in the game. Now, working forwards, individuals should play until they reach the first value of $A_{i,j}$ which takes value 0, at which point the individual in question should concede.

We note that Theorems 2, 3 and 4 follow from a special case of the above procedure, since as $\gamma_{i,j} = 0$ for all positions in the game, if ever $A_{1,j} = 0$, then this leads to $A_{2,k} > 0$ and $A_{1,k}$ for $k < j$, and a similar result for $A_{2,j}$.

The results in this section thus follow a similar pattern to those in Section 3, and are strict NE/ESSs or NEs under the same conditions (the former if equalities of conditions can be ruled out, the latter otherwise). The bound on the game means that there is a fixed end point which we can work back from, and games will be divided into the same three categories; those where I_1 concedes, those where I_2 concedes, and those where both players invest until the end of the contest. In Section 3, however, the fact that games could only end by the concession of one of the players led to a deterministic process that meant that if I_i would concede, it would do so at the start of the contest. Here this is not so, because individuals doomed to eventually concede can hope that chance intervenes and ends the contest before that concession is necessary. We can see this in the example in Figure 2.

4.2 Unbounded contests with infinite resources

Now we shall assume that $\gamma_{i,j} < 1$ for all i, j , so that T has no upper bound, and that resources are infinite. This case with unbounded contests is more complicated, as the game could potentially carry on indefinitely. Thus our game becomes an infinite extensive form game and the results from Cressman (2003) do not extend to this case. In particular we shall make no claim about ESSs here (or in later sections where there are an infinite number of available strategies), and we claim only that solutions are Nash equilibria.

We shall only consider the case where:

1. $\gamma_{i,j}$ is constant, so that $\gamma_{i,j} = \gamma$ for all i, j (this corresponds to T having a geometric distribution with parameter γ) and
2. costs of investments are constant for each individual, so that $c_{i,j} = c_i$ for all j .

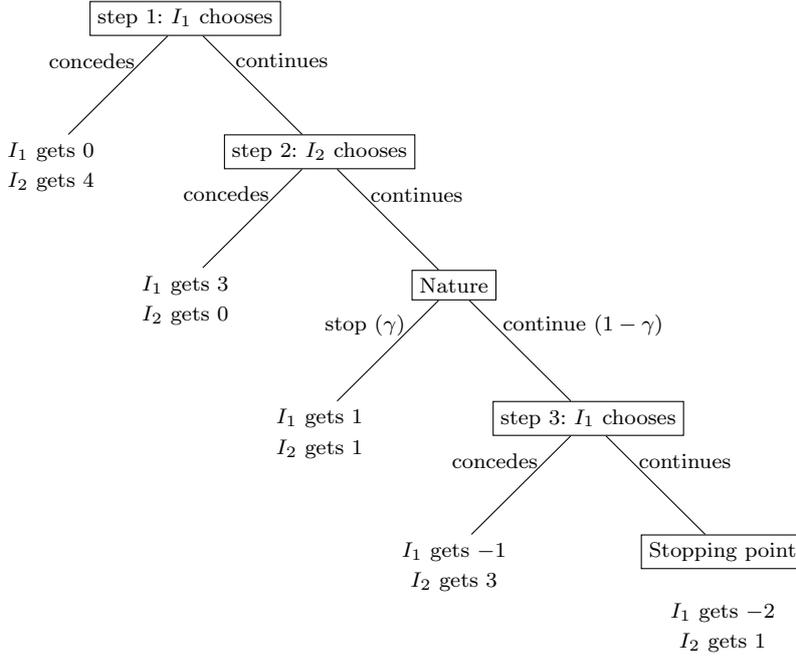


Fig. 2: A scheme of the game with $T = 3$, $V_1 = V_2 = 4$, $a_1 (= a_2) = 1/2$, $c_{1,1} = c_{2,1} = 1$, $c_{1,2} = 3$, $\gamma_{1,1} = 0$, $\gamma_{2,1} = \gamma$. Note that at step 3 I_1 would gain -2 by investing, and -1 by conceding, so it should concede. This means that the expected rewards after I_2 invests at step 2 are $2\gamma - 1$ and $3 - 2\gamma$ respectively. The latter is clearly greater than 0, so that I_2 should invest at step 2. Thus I_1 should invest at step 1 if and only if $2\gamma - 1 > 0$ i.e. $\gamma > 1/2$. Thus I_1 should initially invest if the chance of the contest stopping at this intermediate point is sufficiently large, and if the subsequent decision is reached, it should concede.

As we shall see this can present us with significant complications, and without such assumptions it is hard to make progress in any generality.

In this case, equations (21) - (23) become

$$B_{i,j} = \max\left(0, -c_i + \gamma a_i V_i + (1 - \gamma) A_{i,j}\right) \quad (24)$$

$$A_{1,j} = \begin{cases} V_1 & \text{if } B_{2,j} = 0 \text{ and} \\ (1 - \gamma) B_{1,j+1} + \gamma a_1 V_1 & \text{otherwise;} \end{cases} \quad (25)$$

$$A_{2,j} = \begin{cases} V_2 & \text{if } B_{1,j+1} = 0 \text{ and} \\ (1 - \gamma) B_{2,j+1} + \gamma a_2 V_2 & \text{otherwise.} \end{cases} \quad (26)$$

At any given step $2j - 1$, I_1 should concede whenever

$$c_1 > \gamma a_1 V_1 + (1 - \gamma) A_{1,j}. \quad (27)$$

Similarly, I_2 should concede whenever

$$c_2 > (1 - \gamma)a_2V_2 + (1 - \gamma)A_{2,j}. \quad (28)$$

If (27) holds, and I_1 concedes at step $2j - 1$, this means that $A_{2,j} = V_2$, and thus assuming $V_2 > c_2$ as above, I_2 should invest at time $2j - 2$. This in turn means that $A_{1,j-1} = 0$. Hence (28) holds at step $2j - 3$ and consequently I_1 should never invest.

Alternatively, if (27) does not hold, and (28) holds, I_2 does not invest (while I_1 would invest if given a chance). This means that $A_{1,j} = V_1$ and thus I_1 should invest at time $2j - 1$. This yields $A_{2,j-1} = 0$ and hence, that I_2 should never invest.

If (27) and (28) do not hold, then $I_1(I_2)$ should invest at step $2j - 1(2j)$. Expressing the reward for T_i at its j th step in terms of that at its $j + 1$ st step yields

$$B_{i,j} = -c_i + (\gamma + (1 - \gamma)\gamma)a_iV_i + (1 - \gamma)^2B_{i,j+1}. \quad (29)$$

We shall now use the above equations to find the solution to our game under four distinct cases. We note that Case 4 has close links to the classical *dollar auction* of Shubik (1971), and we discuss this in Section 6.

4.2.1 Case 1

Firstly let us assume that

$$c_1 < (2 - \gamma)\gamma a_1V_1, \quad (30)$$

$$c_2 < (2 - \gamma)\gamma a_2V_2. \quad (31)$$

Then, (27) and (28) never hold and thus individuals always invest. Here, the inclusion of the uncertainty of ending makes the individuals continue rather than concede. The formula (29) is a recurrence relation of the type

$$x_j = \alpha x_{j+1} + \beta \quad (32)$$

with $0 < \alpha < 1$ and $\beta > 0$. Denoting $x^* = \beta/(1 - \alpha)$ we obtain

$$x_{j+1} - x^* = \frac{1}{\alpha}(x_j - x^*) = \left(\frac{1}{\alpha}\right)^{(j+1)}(x_0 - x^*). \quad (33)$$

As $1/\alpha > 1$, then it is clear that unless $x_j = x^*$ for all j , then $|x_j| \rightarrow \infty$ as $j \rightarrow \infty$. But the latter clearly cannot occur, as from (24) x_j is bounded, so we must have that $x_j = x^*$ for all j . Consequently, the expected payoffs for I_i are given by

$$B_{i,j} = \left(a_iV_i - \frac{c_i}{1 - (1 - \gamma)^2} \right). \quad (34)$$

4.2.2 Case 2

Now, assume that

$$c_1 \geq (2 - \gamma)\gamma a_1 V_1, \quad (35)$$

$$c_2 < (2 - \gamma)\gamma a_2 V_2. \quad (36)$$

Thus, I_2 should always invest, but perhaps I_1 should not invest. If that is the case, then I_1 should not invest at the beginning; whereas if I_1 invests at the beginning it should always invest. If I_1 always invests, it obtains the expected reward

$$\left(a_1 V_1 - \frac{c_1}{1 - (1 - \gamma)^2} \right) = \frac{(2 - \gamma)\gamma a_1 V_1 - c_1}{(2 - \gamma)\gamma} \leq 0. \quad (37)$$

Consequently, I_1 should concede at the beginning.

4.2.3 Case 3

Similarly, if we assume that

$$c_1 < (2 - \gamma)\gamma a_1 V_1, \quad (38)$$

$$c_2 \geq (2 - \gamma)\gamma a_2 V_2. \quad (39)$$

then I_2 will have to concede at the beginning.

4.2.4 Case 4

It remains to investigate the case of

$$c_1 \geq (2 - \gamma)\gamma a_1 V_1, \quad (40)$$

$$c_2 \geq (2 - \gamma)\gamma a_2 V_2. \quad (41)$$

Suppose that I_2 does not concede. Then since inequality (40) holds, following Case 2 we obtain the same expected reward as in inequality (37). Thus I_1 should concede. Moreover, if I_1 concedes, it will clearly be best for I_2 not to concede. Now suppose that I_1 does not concede. Then since inequality (41) holds, following Case 3 we obtain the expected reward as in the equivalent inequality to (37). Thus I_2 should concede. Similarly, if I_2 concedes, it will clearly be best for I_1 not to concede.

So it is clear that one of the individuals must concede, but which should be the first to do so? In the biological case that underlies this paper, this can be solved using the idea of roles as previously discussed. If I_1 chooses to (always) invest and I_2 to concede immediately, the strategy $S_{\infty,1}$, then this is a strict NE. Similarly $S_{1,\infty}$, I_1 conceding immediately with I_2 investing conditional upon I_1 investing, is also a strict NE.

5 Individuals can choose how to allocate their investments

In this game we again consider fixed total costs C_i , but further develop the model by allowing individuals to choose how to split their investment, i.e. to choose $c_{i,j}$ so that $\sum c_{i,j} = C_i$. Here we set no maximum number of moves T , though there will be an effective maximum as we see below. Should the players pay a little or a large amount initially?

At first sight it would appear that any individual should simply either concede, or pay the smallest cost possible to be able to remain in the contest. What benefit is there in paying more? As we shall see below (see Theorem 6), however, there are situations where an individual should pay more than this minimum value.

We again assume that individuals have to invest at least some minimal $\varepsilon > 0$, unless they have already invested more than $C_i - \varepsilon$, in which case they have to simply complete their investment up to C_i . Specifically, $c_{i,j}$ have to satisfy

$$c_{i,j} \geq \min\{\varepsilon, C_i - C_{i,j-1}\}, \quad (42)$$

for some $\varepsilon > 0$ and all i, j . Here the length of the game tree is finite, but as any investment can be chosen, there are an infinite number of choices at most vertices, and so we again make no claim about evolutionary stability.

For a moment, assume $R_i < C_i$, for some $i = 1, 2$, i.e. at least one individual, namely I_i , does not have resources to invest to the end of the game. So the end of the game will not be reached and thus both individuals should invest as little as possible, i.e. at any point they should either give up or will have to invest ε . This turns the game into the game from Section 3 and we can solve it through the methods presented there.

If $R_i < C_i$, then I_i cannot make more than $j_i = \text{int}(R_i/\varepsilon)$ investments. Firstly assume that $R_i < C_i$ for $i = 1, 2$. If $j_1 \leq j_2$ then I_1 must concede immediately, otherwise I_2 must concede immediately. If $R_i < C_i$ for precisely one of $i = 1, 2$, following arguments analogous to those of Theorem 2, the individual with insufficient resources must concede immediately.

So, for the rest of the section, we will assume that

$$R_i \geq C_i, \quad i = 1, 2, \quad (43)$$

and we will also consider only strategies for which $c_{i,j} < V_i$. This way, we have a game without blocks.

Theorem 5 *a) If $a_i V_i \leq C_i$ holds for exactly one individual, then that individual must concede at the start of the contest. If I_2 will be giving up, I_1 will invest $c_{1,1} = \varepsilon$.*
b) If (9) and (10) both hold, then both individuals invest until the end of the contest.

Proof a) follows from Theorem 3, and b) follows from Theorem 4. □

Theorem 6 *Assume $a_i V_i \leq C_i$ for both i . Let j_i be such that*

$$C_i - j_i V_i < a_i V_i \leq C_i - (j_i - 1)V_i \quad i = 1, 2. \quad (44)$$

Then, I_1 should concede immediately if and only if $j_1 > j_2$. Otherwise I_2 should concede immediately. More specifically, if $j_1 < j_2$, then I_1 should invest $c_{1,1} = \varepsilon$ and I_2 should concede immediately. If $j_1 = j_2$, then I_1 invests (slightly more than) $C_1 - (j_1 - 1)V_1 - a_1 V_1$ which may be close to V_1 , and then I_2 will concede immediately.

Proof Assume that, during its first j moves, an individual I_i has already invested $C_{i,j} = \sum_{k=1}^j c_{i,j}$ such that

$$C_{i,j} > C_i - a_i V_i. \quad (45)$$

Then, no matter what the other individual does, I_i now has to invest $C_i - C_{i,j} < a_i V_i$ in order to get to the end of the contest and at the end it expects to win either $a_i V_i$ (when the other individual continues to the end of the contest) or V_i (if the other individual gives up before the end of the contest). In other words, when the condition (45) is satisfied for an individual I_i after j moves, then the individual I_i will continue to the end of the contest since the expected future reward is positive.

Also, note that if (45) is not satisfied for an individual I_i , then it has to invest at least $a_i V_i$ to get to the end of the contest.

Now, assume that for some j ,

$$C_{1,j} > C_1 - a_1 V_1, \quad (46)$$

$$C_{2,j-1} \leq C_2 - a_2 V_2, \quad (47)$$

and I_2 is currently deciding whether and how much to invest. It follows that (a) I_1 will stay in the contest to its end, (b) I_2 would have to invest at least $a_2 V_2$ in order to stay to the end of the contest, and (c) I_2 's expected reward at the end of the contest is $a_2 V_2$, i.e. I_2 's future reward at the j th decision is not positive. Consequently, I_2 has to give up. Similarly, if

$$C_{1,j} \leq C_1 - a_1 V_1, \quad (48)$$

$$C_{2,j} > C_2 - a_2 V_2, \quad (49)$$

and I_1 is currently deciding whether and how much to invest, then I_1 should give up.

Note that (44) means that I_i can achieve (45) in j_i but not in $j_i - 1$ investments (each investment would have to be almost V_i). So, if $j_1 > j_2$, then I_2 can get to (45) faster than I_1 and at that point I_1 will be forced to concede, following an inductive argument analogous to that from the proof of Theorem 3. It follows that I_1 should concede at the beginning. Consequently, I_2 will never have to invest over V_2 unless I_1 invests over V_1 first. Since I_1 is not going to do that, I_1 should concede at the beginning of the game.

By a similar argument, if $j_1 \leq j_2$, then I_1 can get to (45) faster than I_2 and at that point I_2 should concede. Thus, I_2 should concede at the beginning. It

remains to identify how much I_1 should invest before I_2 gives up. Note that after an investment of $c_{1,1}$ by I_1 , the game can be seen as the game with changed roles, I_2 starts first and has to invest C_2 , I_1 plays second and has to invest $C_1 - c_{1,1}$. Consequently, if $j_1 < j_2$, I_1 just needs to invest ε (because even after I_2 invests V_2 in the first round, I_1 can get to (45) faster than I_2). However, when $j_1 = j_2$, then I_1 needs to invest just over $C_1 - (j_1 - 1)V_1 - a_1 V_1$, to make sure that when I_2 invests close to V_2 , I_1 still gets to (45) faster than I_2 . \square

Remark 1 If, within the setting of Theorem 6, $j_1 = j_2$, the exact amount of how much I_1 should invest at the beginning may vary. If $a_i = 1/2, C_i \approx V_i$, then I_1 need to invest a bit over $V_1/2$. When $a_i = 1/2$ and $C_i = 3/2 * V_i - \delta$ (for some small $\delta > 0$), then I_1 needs to invest almost V_1 , but when $C_i = 3/2 * V_i + \delta$, then I_1 just needs to invest “a little bit” over δ .

Remark 2 Consider the case when $a_i V_i \leq C_i$ for $i = 1, 2$, $C_1 = C_2, a_1 = a_2 = 1/2$ and $V_1 > V_2$. Then the resource is more valuable to individual I_1 and according to Theorem 6, I_2 should concede immediately. Similarly, if $a_i V_i \leq C_i$ for $i = 1, 2$, $C_1 = C_2, V_1 = V_2$ and $a_1 > a_2$, then I_1 is more likely to win the resource at the end of the game than I_2 and according to Theorem 6, I_2 should concede immediately.

Remark 3 The advantage of a significant early investment can be clearly seen from the following example. Suppose that $a_1 = a_2 = 1/2, C_1 = 0.7V, C_2 = 0.6V, \varepsilon = 0.11V$.

The expected reward for reaching the end of the contest is $V/2$. Thus any individual whose remaining investment falls below $V/2$ should continue to invest rather than concede. Further, if an individual to choose has a remaining investment of greater than $V/2$ whilst its opponent has less than this, it knows its opponent will continue to the end, and so must concede.

Thus how should our first playing individual above proceed?

- If it concedes, it of course receives 0.
- If it invests less than $0.2V$ it will still have more than $0.5V$ to invest. Thus player 2 should keep investing, its minimum investment would take it within $0.5V$ so the first player would then have to concede. Thus this choice yields player 1 a negative return.
- If it invests more than $0.2V$, it will then have remaining investment under $0.5V$, so that player 2 will then have to concede, thus the expected return for player 1 will be V minus this initial investment.

Thus the best investment level is “just over” $0.2V$, i.e. almost twice the minimal required level ε .

6 The dollar auction

The classical dollar auction was introduced by Shubik (1971). In this game a number of players are invited by an auctioneer to bid for a dollar. In Shubik’s

game there were potentially many players, and any bids were allowed (although these had to be in a multiple of 5 cents). The person who won the auction got the dollar minus the value of their winning bid, but crucially the second highest bidder also had to pay the value of that bid. If bids jump in small amounts, at any stage a player has the potential of winning the “large” prize of a dollar for a small extra outlay. If a player was convinced that their next bid would be the last, then any bid up to (but not including) a dollar is worthwhile. An initial dollar bid is clearly a bad idea, as 0 is obtained if the other player does not bid, and less than 0 otherwise (this would be a non-optimal further bid, but we can assume this will happen with a very small probability, using the classical idea of the “trembling hand” Selten (1975); Myerson (1978)). If any player is convinced that their next bid would be the last, then any bid up to (but not including) a dollar is worthwhile; however, for a player that is currently second highest bidder, any bid, including a bid of up to (but not including) a dollar *above their previous bid* is worthwhile (if their bid will be the last one). If a player was convinced that the other player will keep bidding then it is not worth bidding themselves. There seems no sensible solution to such a game, at first sight.

We shall consider a variant of the dollar auction, where there are only two players, who bid alternately (with one nominated to start), and are only allowed to raise the previous bid by one cent (or bid one cent if it is the start of the auction). We thus have the game as described in Section 4 with $c_{11} = 1$, $c_{i,j} = 2$ otherwise, $\gamma_{i,j} = 0$, $V_1 = V_2 = 100$. We shall first consider two cases a) with infinite resources, $R_i = \infty$ for $i = 1, 2$, and b) with finite resources. Then, we will consider the dollar auction with no memory.

6.1 A dollar auction with full memory and infinite resource

We start with the infinite resources case; this corresponds to the original idea from Shubik (1971). As we have discussed previously, for a biological population, we can consider this as a game with two distinct roles, where a strategy is a combination of what to do as the first player, and what to do as the second. The strategy S_{j_1, j_2} represents invest in the first $j_1 - 1$ ($j_2 - 1$) rounds and then concede as player I_1 (I_2). It is clear that S_{1, j_2} is a Nash equilibrium for any strategy j_2 where $j_2 > 50$ and $S_{j_1, 1}$ is a Nash equilibrium for any j_1 where $j_1 > 51$, since in each case one player concedes immediately, but would need to invest over a dollar to “win” if it changed its strategy. Within a population comprised of individuals of this type, in Shubik’s terminology we would have a (credible) threat, which is enough to force an opponent to concede. This is very similar to the situation from Theorem 4, Section 4.2.4. See also Dekel et al (2007) for a generalisation of this scenario.

6.2 A dollar auction with full memory and finite resource

Now consider the case with finite resources, $R_i < \infty$ for $i = 1, 2$.

Clearly here the game cannot carry on indefinitely, and must be terminated by the concession of one of the players. We can reformulate this game in the form of a game with a fixed contest end from Section 3, but where the end time is such that $R_i < C_i$ for $i = 1, 2$, which can never be reached. Thus, following Theorem 2, the first player to run out of resources must concede immediately (and since we have applied Theorem 2, this is a strict NE/ESS). Unless both players have identical wealth, this will be the poorer of the two players. In the unlikely case that the players are equally rich, the first to play must concede immediately if they possess an even number of cents, otherwise the second to play must concede immediately. Note that for any two players with given wealth, swapping their positions in the game does not affect the result, unless their wealth is the same; this thus emphasises the symmetry of the game. As in the previous section, see Dekel et al (2007) for a generalisation of this scenario.

6.3 A dollar auction with no memory

The idea of the original dollar auction was that the players kept returning to the identical situation but with positions reversed. We interpret this as a game with no memory, where a player sees only the choice ahead of them. Thus the roles I_1 and I_2 can no longer be distinguished, and we obtain a different kind of solution. Here we do not have a truly symmetric game, and so the result of Cressman (2003) cannot be applied, and so again we seek Nash equilibria only. In this case there are effectively three positions, two of which require the player to make a decision:

1. S: A player (either I_1 or I_2 selected at random) is about to start the game by potentially investing a cent, or conceding;
2. D: A player (either I_1 or I_2) is about to make an investment after the game has started, which must be of two cents, given it must go from one down to one up, or to concede;
3. U: A player (either I_1 or I_2) is a cent up, and waiting to see if its opponent keeps investing.

We denote the expected future rewards for a player I_i in the three positions as $B_{i,S}$, $B_{i,D}$ and $B_{i,U}$ respectively, measured in cents.

We need to consider the best choice for a player in either of the two possible situations that it can make a choice, namely in the initial position S or in the D position, when considering the possible choices of the other player from the same positions. An individual's optimal choices depend only upon the choices that will be made subsequently, and so clearly they cannot depend upon what the other player might do in the initial position. Thus they depend only upon the choice of the other player in position D . Without loss of generality, we can thus restrict ourselves to considering the two choices of I_1 against the possible choice of I_2 .

Now, assume that player I_2 employs a strategy $p_{2,D}$, i.e. concedes at position D with probability $p_{2,D}$. We are looking for an optimal response of player

I_1 , i.e. we are looking for optimal values of probabilities to concede at stage S , $p_{1,S}$, and at stage D , $p_{1,D}$.

Assume that at S a player I_1 concedes with probability $p_{1,S}$. If it invests, it is in the U position, so that

$$B_{1,S} = p_{1,S}0 + (1 - p_{1,S})(B_{1,U} - 1). \quad (50)$$

Similarly at D a player I_i concedes with probability $p_{i,D}$. If they invest they are again in the U position, so that

$$B_{1,D} = p_{1,D}0 + (1 - p_{1,D})(B_{1,U} - 2). \quad (51)$$

At U players wait upon the decision of the other player, and it either receives 100 if the other one concedes, or it moves to D if the other player continues. Thus,

$$B_{1,U} = p_{2,D}100 + (1 - p_{2,D})B_{1,D}. \quad (52)$$

First, observe that if we assume $B_{1,U} \leq 2$, we get, by (51), $B_{1,D} = 0$. Thus, by (52), $B_{1,U} = 100p_{2,D}$. Consequently $p_{2,D} \leq \frac{1}{50}$.

Similarly, if we assume that $B_{1,U} \geq 2$, we get, by (51), $B_{1,D} = B_{1,U} - 2$ and thus, by (52), $B_{1,U} = 102 - \frac{2}{p_{2,D}}$. Consequently $p_{2,D} \geq \frac{1}{50}$.

Also, it follows from (51) that whenever $B_{1,U} < 2$, it is optimal to pick $p_{1,D} = 1$ (i.e. always concede), (b) whenever $B_{1,U} > 2$, it is optimal to pick $p_{1,D} = 0$ (i.e. always invest), and (c) if $B_{1,U} = 2$, then any value of $p_{1,D}$ yields $B_{1,D} = 0$ (and, from (50), it is optimal to have $p_{1,S} = 0$).

Putting the above observations together, we find that

- if $p_{2,D} < \frac{1}{50}$, then the optimal response is $p_{1,D} = 1$,
- if $p_{2,D} > \frac{1}{50}$, then the optimal response is $p_{1,D} = 0$,
- if $p_{2,D} = \frac{1}{50}$, then the optimal response is any value for $p_{1,D}$.

Consequently, $p_D (= p_{1,D} = p_{2,D}) = \frac{1}{50}$ is the unique Nash equilibrium value. This then gives $B_{1,U} = 2$ and from 50 it follows that $p_S = 1$.

Thus an individual should invest at the first step, and then invest at each subsequent step with probability $49/50$. Thus after the first step, each individual concedes following a geometric distribution with parameter $p = 1/50$. Note that this solution is similar to that of the war of attrition (Bishop and Cannings, 1976, 1978; Maynard Smith, 1982) where the solution follows an exponential distribution (in each case the stopping time follows a distribution with the lack of memory property, discrete in our case, continuous for the war of attrition, with a mean that yields an expected reward of zero).

7 Discussion

7.1 Our model and its conclusions

In this paper we have considered an extension to the modelling of evolutionary contests where contests follow a sequence of decisions, rather than a single

instantaneous decision made by each protagonist. This is a natural extension of previous models such as the Hawk-Dove game or the Owner-Intruder game, which can be regarded as overly simplistic, and not allowing for dynamic interaction between the contestants.

An important conclusion of our work is that, under many circumstances, individuals should fight to the end of the contest, or one should concede immediately. These are thus no more complex than the solutions of the original simple games from e.g. Maynard Smith (1982), and provides in our view a strong justification for employing these simple models as approximations of more complex situations.

The exception to the above in our model is when the contest lasts a variable time, governed by random events as well as by strategic decisions of the players, and so an individual may continue to invest in the hope of a short contest, but when it becomes clear that the contest will not be stopped by some early random occurrence and be protracted, it may then concede. We note that in the model of Mesterton-Gibbons et al (2016) there was also a similar possibility of random events terminating the contest. In their model, if termination probability was low, then the classical Bourgeois solution to the owner-intruder model where the intruder always concedes was stable, but other solutions were possible for higher termination probabilities.

An interesting prediction is that if individuals have a choice of how much they invest at a given stage, they should often choose to invest heavily early on, even if this does not immediately help them gain the reward, but means that their remaining investment is sufficiently small that it demonstrates to their opponent that they will fight to the end of the contest, thus forcing that opponent to concede. This at first sight appears to fall foul of the *concorde fallacy* (Weatherhead, 1979); namely the error of making decisions based upon past already lost investments, when only future returns should matter. However, it works in this case precisely because there is a direct correlation between past investments and required future investments, and choices are made by both players based upon the future values rather than the past ones.

The one example in our paper where there was a stochastic solution, was in a special case of the classical dollar auction game discussed in Shubik (1971), see also Greenberg (1990) Colman (2014), O'Neill (1986), O'Neill (1986), Leininger (1989) and for an overview see Stark and Rothkopf (1979). This is a game in economics with sequential investment which occurs in a similar way to our model, and we obtain the stochastic solution by making the individuals have no memories of past events, introduced as being in the spirit of the original problem. As soon as individuals remember the sequence of bids, with a fixed starting point, then the familiar solution of one individual conceding immediately appears.

7.2 Related models

The main differences between our model and previous works can be summarised as follows. Firstly we introduce sequential games to a repeated evolutionary game scenario. This is different to standard time-based evolutionary contests such as the war of attrition in either continuous or discrete time Bishop and Cannings (1976, 1978); Cannings and Whittaker (1995) (also see Axelrod (1981) and the vast related literature for discrete simultaneous games more generally). Sequential evolutionary games with repeated stages have been relatively underexplored (but see Cressman (2003) for important general theoretical work), although they are more common when each player has just a single decision (Houston and McNamara, 1999). These models have been extended to consider a whole population where there are many decisions, carried out simultaneously, but where only a subset of the individuals get to make a decision at any given time point, whether any given individual gets to make the choice depends upon its previous play (see e.g. McNamara et al, 2000). Such sequential games are more common in classical game theory, for example with the dollar auction Shubik (1971), which is the closest example to the type of game that we have considered. Below we explore some of the models most similar to ours.

The extended contests considered in our model are of a particular kind; namely contests where each individual has a set of potential exit points, and at each point it decides whether to continue, making a suitable investment, or concede the resource to its opponent. This is thus reminiscent of the classical war of attrition (Bishop and Cannings, 1976, 1978), but with discrete stages which are sequential, and so our game does not have this aspect of symmetry of the war of attrition. This leads to a completely different character of solution, where the war of attrition has a probability density function over the stopping times, our individuals either concede with probability 1 or do not concede (although in the contests with an uncertain finish time, the time of the contest follows a probability distribution due to a natural random contest duration). We note that when other asymmetries e.g. of reward values or costs, or even of simple of perceived role (Maynard Smith and Parker, 1976; Hammerstein and Parker, 1982) are considered, mixed strategies similarly disappear (they are only maintained through, for example, uncertainty of role).

Whilst simultaneous choices are perhaps natural for the passive waiting game that is assumed in the war of attrition, more active contests might be better modelled using a sequential game as we consider here. We would contend that in many circumstances, such contests would indeed involve a sequence of moves and counter moves, and so often this asymmetry will be more representative of the real situation. This could happen in the fast timescale of actual fights, such as those involved in food stealing (Broom et al, 2004; Iyengar, 2008; Broom et al, 2015), but can also be seen in contests over a longer timescale, for example in the classical owner intruder type games, where the dispossessed animal may subsequently rechallenge the resident; in these cases it is the previous loser that has the first move (Mesterton-Gibbons et al, 2016).

An alternative type of contest where sequential moves would also be appropriate is the modelling of brood care and desertion, as modelled in Houston and McNamara (1999). Maynard Smith and Harper (2003) argued that the standard constant cost situation of the war of attrition is rarely satisfied in biology, and more complex strategies than the simple memoryless “sit and wait” type as in the war of attrition would be more appropriate. This provides some justification for our type of model, where a sequence of distinct choices are made. Note that such complex animals interactions are demonstrated in Hack (1997), who considers many tactics of crickets in an “active” war of attrition type fight. Even the classical real example of the war of attrition, between dung flies Parker and Thompson (1980), involved an active contest between the participants, rather than mere waiting.

In the economic literature, the concept of an all pay auction is discussed, which is equivalent to the war of attrition (the dollar auction with two players is an all pay auction). Dekel et al (2007) considered an all pay auction with alternating moves, which featured a minimum investment level of ϵ , as in our game. They considered different values of the reward V_1 and V_2 , including version with finite and infinite budgets. This paper is actually a generalization of our game in Sections 6.1 and 6.2 (our simplified versions was actually relatively straightforward, so we only discussed these briefly). Their work includes results which have similarities to our Theorem 6 for this different case. An alternative model of an all pay auction/ war of attrition is given in Hörner and Sahuguet (2011), who consider a game with incomplete information where individuals can choose effort levels, and need to match efforts in sequence. Incomplete information. Their model yields similar results to some of ours; one player immediately concedes, so that the stronger player wins at no cost. Note that this is also similar to the standard asymmetric war of attrition which this can be considered a version of, as we have alluded to above (e.g. see Hammerstein and Parker, 1982). The original modelling work on choosing resource levels to invest in a contest was carried out by Tullock (1980) (see Broom et al (2015) for a biological model of this type).

Maskin and Tirole (1988) consider an alternating move scenario, again of dollar auction type; in particular related to dollar auction with no memory. They consider a specific competition game, where payoffs are similar to as in a Cournot competition game (see also Fudenberg and Tirole, 1991). The alternating move system of the above games (and ours) are a special case of that in Libich and Stehlík (2008), who considers a specific game (the “time inconsistency game”) but in a general move setting with a series of move points, not necessary alternating between the players (see also Leininger, 1991; Libich and Stehlík, 2010).

7.3 Future work

We note, finally, that a number of other generalisations of the single stage game are possible, not just a sequence of choices of “continue to invest or concede”.

It may be that individuals can adjust their level of aggression at any time in a contest, and this may directly affect the time of the end of the contest, and also the costs of both players to remain in the contest in terms of energy usage or risk of injury. More generally individuals might have a range of strategies and they might employ any given sequence of them, as in iterated games such as the iterated prisoner's dilemma Axelrod (1981) or in the ownership games of Mesterton-Gibbons et al (2014, 2016), with some reward received at every potential decision point. The game we have considered here is thus just one example (albeit, we would argue, an important one) of a game of this type, and there are a number of other interesting cases which can and should be considered as the subject of future research.

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References

- Axelrod R (1981) The emergence of cooperation among egoists. *American Political Science Review* 75(02):306–318
- Bishop D, Cannings C (1976) Models of animal conflict. *Advances in Applied Probability* 8:616–621
- Bishop D, Cannings C (1978) A generalized war of attrition. *Journal of Theoretical Biology* 70(1):85–124
- Broom M, Rychtář J (2013) *Game-theoretical models in biology*. CRC Press
- Broom M, Luther R, Ruxton G (2004) Resistance is useless? - Extensions to the game theory of kleptoparasitism. *Bulletin of Mathematical Biology* 66(6):1645–1658
- Broom M, Johannis M, Rychtář J (2015) The effect of fight cost structure on fighting behaviour. *Journal of Mathematical Biology* 71(4):979–996
- Cannings C, Whittaker J (1995) The finite horizon war of attrition. *Games and Economic Behavior* 11(2):193–236
- Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9(2):129–136
- Colman AM (2014) *Game theory and experimental games: The study of strategic interaction*. Elsevier
- Cressman R (2003) *Evolutionary dynamics and extensive form games*, vol 5. MIT Press
- Cressman R, Křivan V, Garay J (2004) Ideal free distributions, evolutionary games, and population dynamics in multiple-species environments. *The American Naturalist* 164(4):473–489
- Dekel E, Jackson M, Wolinsky A (2007) Jump bidding and budget constraints in all-pay auctions and wars of attrition. Discussion Paper: Center for Mathematical Studies in Economics and Management Science, Northwestern University

- Fretwell SD, Lucas H (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19(1):16–36
- Fudenberg D, Tirole J (1991) *Game theory*. MIT Press Cambridge, MA
- Greenberg J (1990) *The theory of social situations: an alternative game-theoretic approach*. Cambridge University Press
- Haccou P, Glaizot O, Cannings C (2003) Patch leaving strategies and superparasitism: an asymmetric generalized war of attrition. *Journal of Theoretical Biology* 225(1):77–89
- Hack MA (1997) The energetic costs of fighting in the house cricket, *acheta domesticus* l. *Behavioral Ecology* 8(1):28–36
- Hammerstein P, Parker G (1982) The asymmetric war of attrition. *Journal of Theoretical Biology* 96:647–682
- Hofbauer J, Sigmund K (1998) *Evolutionary games and population dynamics*. Cambridge University Press
- Hörner J, Sahuguet N (2011) A war of attrition with endogenous effort levels. *Economic Theory* 47(1):1–27
- Houston AI, McNamara JM (1999) *Models of adaptive behaviour: an approach based on state*. Cambridge University Press
- Huntingford FA (2013) *Animal conflict*. Springer Science & Business Media
- Iyengar E (2008) Kleptoparasitic interactions throughout the animal kingdom and a re-evaluation, based on participant mobility, of the conditions promoting the evolution of kleptoparasitism. *Biological Journal of the Linnean Society* 93(4):745–762
- Leininger W (1989) Escalation and cooperation in conflict situations the dollar auction revisited. *Journal of Conflict Resolution* 33(2):231–254
- Leininger W (1991) Patent competition, rent dissipation, and the persistence of monopoly: the role of research budgets. *Journal of Economic Theory* 53(1):146–172
- Libich J, Stehlík P (2008) Macroeconomic games on time scales. *Dynamic Systems and Applications* 5:274–278
- Libich J, Stehlík P (2010) Incorporating rigidity and commitment in the timing structure of macroeconomic games. *Economic Modelling* 27(3):767–781
- Maskin E, Tirole J (1988) A theory of dynamic oligopoly, I: Overview and quantity competition with large fixed costs. *Econometrica: Journal of the Econometric Society* pp 549–569
- Maynard Smith J (1982) *Evolution and the theory of games*. Cambridge University Press
- Maynard Smith J, Harper D (2003) *Animal signals*. Oxford University Press
- Maynard Smith J, Parker G (1976) The logic of asymmetric contests. *Animal Behaviour* 24:159–175
- Maynard Smith J, Price G (1973) The logic of animal conflict. *Nature* 246:15–18
- McNamara JM, Szekely T, Webb JN, Houston AI (2000) A dynamic game-theoretic model of parental care. *Journal of Theoretical Biology* 205(4):605–623

- Mesterton-Gibbons M, Karabiyik T, Sherratt TN (2014) The iterated hawk-dove game revisited: The effect of ownership uncertainty on bourgeois as a pure convention. *Dynamic Games and Applications* 4(4):407–431
- Mesterton-Gibbons M, Karabiyik T, Sherratt TN (2016) On the evolution of partial respect for ownership. *Dynamic Games and Applications* 6(3):359–395
- Myerson RB (1978) Refinements of the nash equilibrium concept. *International Journal of Game Theory* 7(2):73–80
- O’Neill B (1986) International escalation and the dollar auction. *Journal of Conflict Resolution* 30(1):33–50
- Parker G, Thompson EA (1980) Dung fly struggles: a test of the war of attrition. *Behavioral ecology and sociobiology* 7(1):37–44
- Samuelson L (1997) *Evolutionary Games and Equilibrium Selection*. MIT Press, Cambridge, Mass.
- Selten R (1975) Reexamination of the perfectness concept for equilibrium points in extensive games. *International Journal of Game Theory* 4(1):25–55
- Selten R (1980) A note on evolutionarily stable strategies in asymmetric animal conflicts. *Journal of Theoretical Biology* 84(1):93–101
- Sherratt T, Mesterton-Gibbons M (2015) The evolution of respect for property. *Journal of evolutionary biology* 28(6):1185–1202
- Shubik M (1971) The dollar auction game: A paradox in noncooperative behavior and escalation. *Journal of Conflict Resolution* 15(1):109–111
- Stark RM, Rothkopf MH (1979) Competitive bidding: A comprehensive bibliography. *Operations Research* 27(2):364–390
- Tullock G (1980) Efficient rent-seeking. In: Buchanan J, Tollison R, Tullock G (eds) *Toward a theory of the rent-seeking society*, Texas A&M Press, pp 269–282
- Weatherhead PJ (1979) Do savannah sparrows commit the concorde fallacy? *Behavioral Ecology and Sociobiology* 5(4):373–381