



Research

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Partner choice creates fairness in humans

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Many studies demonstrate that partner choice has played an important role in the evolution of human cooperation, but little work has tested its impact on the evolution of human fairness. In experiments involving divisions of money, people become either over-generous or over-selfish when they are in competition to be chosen as cooperative partners. Hence, it is difficult to see how partner choice could result in the evolution of fair, equal divisions. Here, we show that this puzzle can be solved if we consider the outside options on which partner choice operates. We conduct a behavioural experiment, run agent-based simulations and analyse a game-theoretic model to understand how outside options affect partner choice and fairness. All support the conclusion that partner choice leads to fairness only when individuals have equal outside options. We discuss how this condition has been met in our evolutionary history, and the implications of these findings for our understanding of other aspects of fairness less specific than preferences for equal divisions of resources.

1. Introduction

Partner choice is a major force that has driven the evolution of cooperation in humans [1]. Experimental studies show that in situations where people choose others as cooperative partners, individuals try to outbid competitors by increasing their investment in cooperation [2–4]. Investing more in cooperation is costly but also leads to a good reputation: if partner choice is possible, the benefits of being a good cooperator can outweigh its costs [5,6]. Theoretical models point in the same direction: incorporating partner choice in models of cooperation selects for cooperative behaviours [7–9]. All of these studies support the theory of 'competitive altruism' (CA) [2,10]: when people monitor and choose others on the basis of their cooperative behaviours, costly cooperative behaviours can pay off.

Although the importance of partner choice for the evolution of human cooperation is clear, very little is known about its importance for the evolution of fairness. Most studies on partner choice are primarily concerned with how much people invest in cooperation and not how people *divide* the common goods produced through cooperation. The most famous experimental evidence of fairness in the division of goods comes from the ultimatum game [11,12]. In this two-player laboratory experiment, one of the players (the 'proposer') makes an offer to the other (the 'responder') on how to divide a sum of money. If the offer is accepted then both players receive the money, otherwise neither of the players receives any money. Traditional game theory, which assumes players to be super-rational, predicts that responders will accept any offer, however small, because getting something is always better than getting nothing. Anticipating this, proposers should only offer the smallest possible amount. But experimental tests have not confirmed these theoretical predictions: proposers' modal offer usually falls between 40 and 50%, and responders are prepared to reject very low offers just for the sake of 'fairness' [13,14].

To our knowledge, the only evolutionarily minded paper studying the impact of partner choice on the fairness of money divisions is a study by Chiang [15]. Using a repeated ultimatum game, Chiang [15] shows that partner choice increases offers from 42.20 to 46.28%, getting closer to the 'fair' expected offer

of 50% after 15 repetitions. Chiang [15] concludes that his findings are 'consistent with the predictions of CA theory', which is interesting because the predictions of CA theory in this case have not always been thoroughly discussed. Indeed, an interesting evolutionary question is to know up to what point people should attempt to appear generous when partner choice is possible. Some authors have argued that people will increase their generosity until the marginal costs of doing so exceed the marginal benefits, but what costs and benefits should be taken into account remains unclear.

Outside the evolutionary field, the consequences of partner choice for the evolution of fairness are studied in behavioural economics. In a seminal paper by Roth & Prasnikar [16], nine proposers are in competition to make offers to a single responder. The responder then chooses an offer—and thus a single proposer. In this experimental set-up, offers rose very rapidly to 99.5%. The same pattern of highly generous offers was replicated in Fischbacher *et al.* [17], and a similar 'runaway' effect of partner competition has been found in laboratory market experiments [18].

Interestingly, a few studies have showed that partner choice can also lead to the opposite pattern of offers—extremely self-ish offers [17,19,20]. In Fischbacher *et al.* [17] for instance, two responders were in competition to access the offers made by a single proposer. After 20 repetitions of the game, the average offer decreased to 18.8%. The effect was even more dramatic when five responders were in competition to access the offer of a single proposer: proposers became increasingly selfish and offered an average of 13.8% in the last repetition.

In summary, a cross-disciplinary review reveals that partner choice leads to very unbalanced divisions of benefits in two opposite directions: the proposer either makes highly generous offers or highly selfish ones. In this paper, we aim to understand the origin of these opposite findings. We hypothesize that it is not partner choice in itself that is responsible for such unbalanced divisions, but rather unequal 'outside options'. Outside options are the individual's expected payoff in the same timespan if she had refused the current interaction. It is perfectly possible to be able to choose partners but only have bad options to choose from: in this case, it will be difficult to know whether unbalanced divisions are the result of the mere possibility to choose partners or of the existence of those bad outside options. We predict that when partner choice is possible, players should be 'rewarded' according to their outside options: if proposers have better outside options than responders, runaway selfishness (RS) should be the result. If responders have better outside options than proposers, runaway generosity should be the result. Finally, and more importantly, we hypothesize that when proposers and responders have the same outside options, partner choice leads to a fair, 50/50 division.

We tested this hypothesis empirically and theoretically. In the behavioural experiment, groups of four participants played a modified version of the dictator game that allows for partner choice. We contrasted a condition in which proposers had better outside options than responders to a condition in which responders had better outside options than proposers. We predicted that offers would be over-selfish in the first case and over-generous in the second. In a third condition, we equalized the outside options of proposers and responders and predicted that fair offers would evolve. In the agent-based simulations and the game-theoretic model, we considered larger populations of agents and introduced

a continuum of partner choice to demonstrate the robustness of the evolution of fairness when outside options are equal.

2. Behavioural experiment

(a) Methods

The experiments were conducted in March and May 2014 at the Nuffield Centre for Experimental Social Sciences (CESS). The experiment was programmed and conducted with the software z-Tree [21].

(i) Participants

A total of 120 participants were recruited from the University of Oxford using a web-based recruitment system. Participants were told that they would earn £4 for showing up and would earn additional money during the course of the experiment. The average earnings per subject were calculated to be at least £10 per hour.

(ii) General procedure

Participants were seated at computer terminals separated by partitions so that they could not see one another. We also ensured anonymity: the subjects did not have access to identifying information about the other players at any point during (or after) the experiment. Once seated, participants read instructions that explained the procedure. The instructions were then read aloud by the experimenter while participants read along. Participants then had time to ask questions. The participants first performed a practice round, followed by 30 experimental rounds. After the experiment, subjects answered a questionnaire about their behaviour and thought process during the experiment.

The experiment included three conditions: CA, RS and equal options (EO). Each participant played in only one condition. Forty subjects took part in the CA condition, 44 in the RS condition and 36 in the EO condition (differences are owing to unequal show-up rates between conditions). Conditions CA and RS present asymmetries of outside options between proposers and responders and should allow us to replicate the results of previous studies. They also serve as a baseline against which to compare results from the EO condition, in which outside options are equalized.

We start by describing the procedure common to all conditions before detailing procedures specific to each condition. In all conditions, subjects played 30 rounds of a four-player game. Groups of four were stable across rounds. At the beginning of each condition, subjects were randomly assigned to one of two roles ('proposer' or 'responder') and were informed of their role. In each round, proposers and responders could form partnerships to split a pool of money: proposers made offers and responders could accept them. Subjects were informed that they would gain their average payoff across all rounds. Subjects did not know how many people were in their group, nor the number of proposers and responders in each round. The only information they had was whether or not one of their offers was accepted (proposers) or what offers remained available to them in the current round (responders). This enhanced the probability that the money divisions we observed in our experiment would result mechanically from each individual's outside options, and not from strategic thinking.

(iii) Conditions

CA. In the CA condition, there were three proposers and only one responder in each group of four subjects: proposers were thus in competition to be chosen by responders. Proposers and responders kept the same role for the entire 30 rounds. Each round proceeded in the following steps:

- each proposer in a group decides what division of £10 with a responder from the group to propose;
- the one responder in the group chooses among the proposers' offers (with the obligation to choose one offer—she cannot refuse them all) and
- participants are informed of their own earnings for the round. The responder and the selected proposer receive the portions of the £10 corresponding to the chosen offer. The two proposers who were not chosen by a responder earn £0.

Because in this condition proposers are in competition to be chosen by responders, their outside options are worse than those of responders. We thus predicted that this asymmetry would lead to biased money divisions in favour of responders.

RS. The RS condition is similar to the CA condition, except that the numbers of proposers and responders in each group were reversed: three responders were in competition to access the offers made by a single proposer. Each round proceeded in the following order:

- the only proposer in the group makes an offer;
- one responder in each group is randomly selected to accept this offer (as in a dictator game, the responder cannot refuse it) and
- earnings are reported to each participant. The two responders who were not selected for the offer in this round earn £0 in this round.

In this condition, responders had worse outside options than proposers, because they were in competition to gain access to proposers' offers. We thus predicted that partner competition would lead to biased money divisions in favour of proposers and ever-decreasing offers—RS.

Note that subjects who participated in the CA and RS conditions received the exact same sheet of instructions. The only difference between the two conditions was the number of proposers and responders in each group, a parameter that was not communicated to subjects. Hence, any difference in behaviour observed between these two conditions can only be attributed to the change in this parameter, and the resulting difference in the asymmetry of outside options between the conditions. Note also that if subjects knew their number of rivals, we would make the same predictions. We decided to give subjects as little information as possible to increase the probability that the effects we could observe would be the result of a 'mechanical' effect of outside options, and not the result of strategic thinking (although we cannot entirely rule out this possibility).

EO. In the EO condition, all subjects had the same outside options. Although the condition began with two randomly selected proposers and responders in each group, subjects could decide to switch roles at the end of each round after having been informed of their payoff. Hence, proposers and responders who were not satisfied with their payoff could decide to play the opposite role in the next round. As before, subjects were not informed of the current numbers

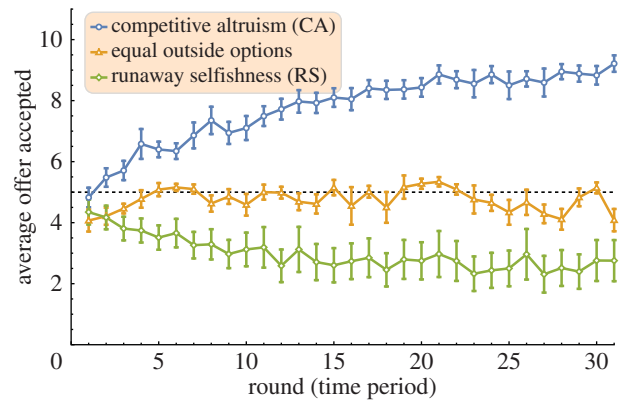


Figure 1. Evolution of the average offer accepted by responders in each of the three conditions. In the CA condition, responders have better outside options than proposers. In the RS condition, proposers have better outside options than responders. In the equal outside options condition, proposers and responders can choose partners and have the same outside options. Round 1 is a practice round. Error bars represent standard errors. (Online version in colour.)

of proposers and responders in their group, nor were they informed of how many people were willing to change their role in the current round. In case all four subjects decided to play the same role, no partnership was concluded in the next round and all subjects received a null payoff.

We predicted that because outside options were equal in this condition, partner choice would lead to a stable 'fair' equilibrium and the evolution of equal divisions. Note that having the same number of proposers and responders in each group but with *fixed* roles would not be enough to make this condition different from the RS condition: with an equal number of proposers and responders, proposers see their offers being accepted in each round and should decrease their offers as in the RS condition.

(b) Results

Figure 1 plots the evolution of the average offer accepted in each condition. We include the first round in this graph for informative purposes, but this round was a practice round and was not included in statistical analyses. Figure 1 confirms our predictions: each condition influenced the offers in the expected direction. In all rounds except the first (practice) round, mean accepted offers \bar{o} followed the inequality $\bar{o}_{CA} > \bar{o}_{EO} > \bar{o}_{RS}$. Figure 1 also suggests an increasing trend over time in the CA condition and a decreasing trend over time in the RS condition.

We tested the significance of the differences between conditions using Mann–Whitney tests. We analyse each group as an N of 1 as a way of dealing with non-interdependence of decisions within a group. Significant differences were found between all conditions in pairwise comparisons: CA and EO ($n_1 = 9$, $n_2 = 10$, $U = 90$, $p < 0.001$), EO and RS ($n_1 = 9$, $n_2 = 11$, $U = 17$, $p = 0.012$), and RS and CA ($n_1 = 10$, $n_2 = 11$, $U = 110$, $p < 0.001$). An nptrend test [22] rejected the null hypothesis that there was no trend across conditions ($z = 4.65$, $p < 0.001$). Using data from the last 10 rounds only, the differences between pairs of conditions CA and EO, EO and RS, RS and CA remained significant ($p < 0.001$ and $U = 90$, $p = 0.028$ and $U = 21$, $p < 0.001$ and $U = 110$ respectively), and the nptrend test was still significant ($z = 4.55$, $p < 0.001$). Differences were still significant at least at

Table 1. Pooled regression predicting the average accepted offer. Reported numbers are ordinary least-squares coefficients. Numbers between parentheses are standard errors. The left column gives a regression using data from all rounds. In the right column, only data from the last 10 rounds were used. RS, runaway selfishness; CA, competitive altruism. Statistical significance in probability tests is indicated by asterisks.

	all rounds	last 10 rounds
constant	4.669** (0.171)	4.375** (0.299)
RS	-2.366** (0.228)	-1.741** (0.398)
CA	4.779** (0.233)	4.622** (0.407)
time	-0.006 (0.0102867)	-0.046 (0.055)
time × RS	-0.036* (0.013)	0.060 (0.074)
time × CA	0.115** (0.013)	0.095 (0.075)
<i>N</i>	878	295
<i>R</i> ²	0.71	0.76
<i>F</i>	429.054	188.731
<i>Prob</i> > <i>F</i>	0.000	0.000

* $p = 0.01$, ** $p = 0.001$.

the 5% level when the last eight or twelve rounds were analysed instead of the last ten.

Table 1 shows the results of a regression analysis of the average offer accepted in the round, pooling the three conditions CA, RS and EO, and setting EO as the omitted category. In column 1, all rounds are considered and numbered from -29 to 0 so that the reported coefficients in the table represent effects in the last round of the experiment. In column 2, only data from the last 10 rounds are used, and rounds are numbered from -9 to 0. The data were checked for linearity, normality, homoscedasticity and autocorrelation.

The estimated accepted offer in the last round of the EO condition was 4.67 (column 1, line 1), very close to the 50% fair division. The negative coefficient in the RS condition and the positive coefficient in the CA condition, both significant, show that the predicted offers in these conditions differed in the expected direction. Offers in the CA condition are expected to be 4.8 units higher than in the EO condition, and offers in the RS condition are expected to be 2.4 units lower than in the EO condition. A comparison of column 1 with column 2 shows that there is no substantial difference of average offers accepted in the last 10 rounds compared to all rounds, controlling for time trends.

Time did not have a significant effect on the offers accepted in the EO condition (columns 1 and 2): offers remained stable across all rounds in this condition. Conversely, significant interactions were found between time and RS and time and CA. The effect of time was especially large in the CA condition: offers increased by 0.12 units at each round. However, these interactions were no longer significant in the last 10 rounds (column 2), suggesting that offers ended up reaching a stable level in all conditions, as is already suggested by figure 1.

3. Theoretical model

(a) Methods

We model a population of agents who have the same outside options and play ultimatum games repeatedly throughout

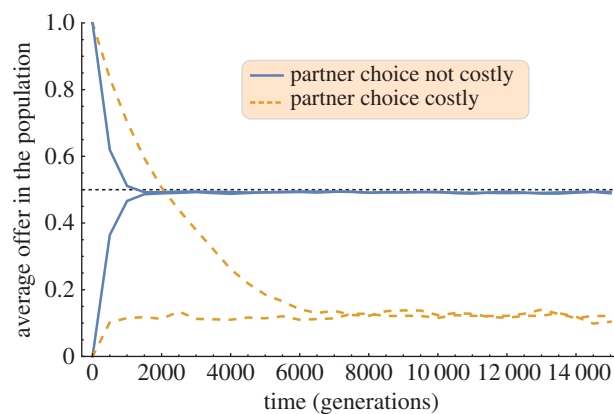


Figure 2. Evolution of the average offer in the ultimatum game when individuals have the same outside options and for two different costs of partner choice (simulation results). Two starting points (0 and 1) are used for each cost of partner choice. Each curve represents an average over 20 simulation runs. Parameter values used for these simulations can be found in the electronic supplementary material, §2.2. (Online version in colour.)

their lifespan. Individuals meet each other in pairs at a constant rate β . When they meet, one individual is randomly selected to play the role of proposer, while the other plays the role of responder. The proposer makes a genetically encoded offer to the partner. If the offer is accepted, the two partners enter a cooperative interaction, which is assumed to take time. During this cooperative interaction, they divide a resource of size 1 according to the accepted offer until the end of the interaction, which occurs at a constant rate τ . If the proposer's offer is rejected, the two partners are separated without interacting and return to the population to find an unpaired partner.

At the end of their life, all individuals reproduce according to the amount of resource they have accumulated. Individuals pass on their offers and requests (the minimum offer they are ready to accept when they play the role of responder) to their offspring, with a small probability of mutation on these traits. The model is fully explained in the electronic supplementary material, §§1 and 2.

When the encounter rate β is high, it is easy to find a new partner in the population. When the split rate τ is low, interactions last a long time. Hence, when the β/τ ratio is high, partner choice is not costly, as rejecting an unfair offer does not mean that time will be wasted looking for a new partner. Moreover, because the roles of proposer and responder are assigned randomly in each new encounter, all individuals have the same outside options. In this environment where all individuals have the same outside options and can choose their cooperative partners, we observe what offers are made at the evolutionary equilibrium, which represent the fitness-maximizing offers. We also produce a resident-mutant analysis of the model, allowing us to pinpoint the offers that cannot be invaded by mutants once they have spread in the population. This analysis is detailed in the electronic supplementary material, §1.

(b) Results

Our simulations show that the average offer accepted in the population tends towards 50% at the evolutionary equilibrium when partner choice is not costly (figure 2, plain lines). The resident-mutant analysis shows that a resident

population cannot be invaded by mutants as long as the offer p characterizing the population lies in the interval

$$p \in \left[\frac{\beta/2}{\beta + \tau}, 1 - \frac{\beta/2}{\beta + \tau} \right]. \quad (3.1)$$

Hence, when partner choice is not costly ($\beta \gg \tau$), the range of evolutionary stable offers is restricted to $p \in [1/2, 1/2]$. Analytical results are thus in perfect agreement with simulation results and confirm that partner choice in a context of equal outside options leads to the evolution of fairness.

On the other hand, simulations show that when partner choice is costly ($\beta \ll \tau$), the average offer accepted at the evolutionary equilibrium is very low (figure 2, dashed lines): proposers can afford to be selfish. This result holds whether we consider an initial population of ‘over-selfish’ individuals offering 0% or an initial population of ‘over-generous’ individuals offering 100% of the resource to their partner, showing that our results are not limited by the initial conditions of our model (figure 2, dashed lines).

4. Discussion

Our study shows that partner choice creates fairness, but only in a context of equal outside options. Partner choice is the mechanism that allows individuals to receive offers corresponding to their outside options; whether or not the offers will be fair depends ultimately on the equality of those outside options. This emphasis on outside options also helps to explain why previous studies reported opposite effects of partner choice. Although the subjects in our CA and RS conditions received the exact same instructions, the inequality of outside options between the two conditions led to the evolution of offers in two opposite directions. Specifically, an asymmetry of outside options in favour of responders leads to runaway generosity, whereas an asymmetry in favour of proposers leads to RS.

Although the importance of outside options may have been overlooked in evolutionary studies, it has already been investigated in behavioural economics [18,23]. A parallel could even be drawn between our results and the classical idea that an excess of supply or demand affects the price at which a commodity is exchanged (for a discussion of this parallel, see [24]). Nonetheless, in behavioural economics, most studies fix outside options *a priori* and observe, once they are fixed, how they affect prices or bargaining outcomes. Here, on the contrary, we provide a condition in which equal outside options emerge endogenously from a partner choice-based environment. Hence, our work contains two main contributions to the literature. For scholars with a biological background, we draw attention to the prime importance of outside options when studying human partner choice and the evolution of fairness. And for scholars with an economics background, we show how the well-known effects of outside options are not limited to economic markets, but also have an impact over longer, evolutionary timescales, in ‘biological markets’ [25–27]. In a nutshell, what we suggest is that the human sense of fairness is the result of natural selection optimizing human behaviour in a market environment (without neglecting potential cultural or contextual effects, see [28]).

Our work represents a number of methodological advances on previous related work. First, it uses a modified

version of a dictator game, rather than an ultimatum game, to measure the fairness of money divisions: when only one offer is left, responders have no choice but to accept it. As divisions in the dictator game are known to be more asymmetric than those in the ultimatum game [13,14], the dictator game offers a more conservative way to observe the evolution of fairness. Second, we modified the dictator game so that it can be played not only between two players but in groups of four players, to introduce a first level of partner choice. A second level of partner choice is implemented by allowing subjects not only to choose their partner but also to change role between rounds. Finally, we observed behaviours on a longer timescale and with more independent observations than in previous studies.

The mechanism leading to fairness in our EO condition is easy to understand. When there are more proposers than responders in a group, offers start to increase following the predictions of CA. But as offers rise, proposers start to receive decreasing payoffs, which leads some of them to decide to play responder in the next round. This incentive to switch roles in turn leads to an excess of responders over proposers. At some point, the asymmetry of outside options is reversed, and responders want to change role and become proposers. These two forces working in opposite directions lead to the evolution of fair, balanced divisions that oscillate around 50%. The mechanism at play is similar in our theoretical study: proposers cannot make offers lower than 50%, as responders would reject them and prefer to play proposer. Conversely, proposers have no incentive to make offers higher than 50%, as they would be better off playing responder themselves to benefit from those generous offers.

Although the mechanism in our study is clear, it is interesting to ask what its biological equivalent in the real world might be. The roles of proposer and responder are a convenient way to model asymmetries of bargaining power in the laboratory: the proposer is in a strategically advantageous position, because the responder has no choice but to accept her offer. Allowing subjects to change roles means removing this asymmetry from the game. Although it is hard to imagine a strict equivalent of the roles of proposer and responder in nature, asymmetries of bargaining power are plentiful. For example, a physically stronger individual could benefit from a local competitive advantage at the moment of sharing the benefits of cooperation. Weaker individuals cannot ‘choose’ to become stronger in this situation, so what could be the ecological equivalent of being able to change role from proposer to responder and vice versa? We suggest it is a way to implement the variety of roles humans play across all their lifelong cooperative interactions, including interactions in which they are not the weakest anymore. This assumption is well justified by the empirical literature on human cooperation: humans cooperate frequently and in diverse contexts, both with kin and non-kin [29,30]. In a review of the human social organization, Kaplan *et al.* [31] insist on the ‘high-quality, difficult to acquire resources’ hunter–gatherers consume, which require ‘high levels of knowledge, skill, coordination’. Because knowledge, skill or coordination are not necessarily correlated with physical strength, weak individuals can be good cooperators and have access to good outside options even if they are locally in a poor bargaining position. In a sense, we think it is interesting to reverse the question: what could be the ecological equivalent of playing a repeated

dictator game when the roles of proposers and responders are fixed? Whereas it can probably adequately represent some situations in economics where the roles of sellers and buyers never change, it does not seem realistic for a hunter–gatherer to always be stuck in the same social role in all his lifelong interactions. Hence, without saying our paradigm is a perfect representation of humans' social life, we think it captures some interesting aspects of it, and is thus worth exploring.

Our study has a few important limitations. First, the small number of subjects in our groups means that the offers in each round may have been sensitive to noise. It would also be interesting to introduce asymmetries of outside options in a more natural way than by artificially fixing the number of proposers and responders in each group. In our theoretical study, we do not consider variations between individuals in outside options in the form of strong and weak individuals, for example. We also do not model the formation of reputation, as we suppose individuals have perfect information on the past behaviour of other individuals. Examining if and how less-than-perfect information could prevent the evolution of partner choice-based fairness would thus be another way to extend our results.

Nonetheless, our study has interesting implications for our understanding of the evolution of human fairness as a whole. Whereas almost all theoretical studies of the evolution of human fairness have examined the evolution of equal divisions in the ultimatum game [32–34], fairness in real life is not only characterized by equal divisions. People also consider unequal divisions as fair when they reflect inequalities of skills or talent, or an unequal investment of time, resources and energy [35–37]. Our study offers hints as to why this would be the case. If the reason why humans evolved a sense of fairness is linked to the best way to reward social partners in a biological market (at the ultimate level), each

social partner having to be rewarded according to her outside options, then maybe the reason why humans consider that the best contributors should get a bigger part of the benefits is that the best contributors have better outside options in a biological market. An interesting follow-up to our study would thus be to consider the fact that outside options can vary not only because of strength, but also because of skills, talents, effort, etc. Testing this prediction theoretically and empirically would also provide a good entry point to study fairness outside the ultimatum game and its associated always-equal divisions.

Data accessibility. Source code for the simulations and data for the simulations and behavioral experiment are archived online on the first author's website: <http://stephandedobove.net/?p=176> and on data-dryad.org <http://datadryad.org/resource/doi:10.5061/dryad.6v4c0>.

Ethics statement. All conditions were approved by the CESS Ethics Review Committee.

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Authors' contributions. S.D. designed the behavioural experiment, collected data, carried out the statistical analysis, developed the agent-based simulations, and wrote the manuscript. J.-B.A. designed the behavioural experiment, built the analytical model and coordinated the study. N.B. designed the behavioural experiment and coordinated the study. All authors gave final approval for publication.

Competing interests. We declare no competing interests.

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