**Title**
# Bordered tug-of-war models are neither general nor predictive of reproductive skew



**Journal**
Journal of Theoretical Biology, 266(4)

**ISSN**
0022-5193

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**Publication Date**
2010-10-01

**DOI**
10.1016/j.jtbi.2010.07.029

Peer reviewed


Volume 266
Issue 4
21 October 2010
ISSN 0022-5193
ELSEVIER
Journal of Theoretical Biology

Journal of Theoretical Biology 266 (2010) 739–741

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Letter to Editor

# Bordered tug-of-war models are neither general nor predictive of reproductive skew

ARTICLE INFO

*Keywords:*
Cooperative breeding
ESS
Reproductive skew

ABSTRACT

Models of reproductive skew assume reproductive shares are either conceded, competed over, or both. Previous mathematical evaluations found that simultaneous concessions and contests are evolutionarily unstable. Recently, Shen and Reeve (2010) challenged these conclusions and developed a series of sub-models they argued to be a unified approach to reproductive skew: the general bordered tug-of-war (BTOW). However, BTOW fails as a general model for two reasons: (1) the BTOW strategy cannot invade populations where individuals either only compete for or only concede reproductive shares and (2) contrary to Shen and Reeve's assertion, BTOW populations are easily invaded by strategies with fewer or no concessions, but competing at lower levels. The failure of BTOW as a general model has major implications for interpreting experiments on reproductive skew. A large number of studies have measured the effects of genetic relatedness and competitive ability on reproductive skew, with a great majority finding no significant correlation between variation in within-group relatedness or competitive ability and across-group differences in skew. No model of reproductive skew except one variant of the BTOW predicts such results. With the rejection of BTOW as a valid general model, it is clear that these results are contradictory to reproductive skew theory rather than supportive of it.



Reproductive skew theory has generated numerous models of how offspring parentage ought to be divided among group members (Nonacs and Hager, in press). There have been several attempts to unify the disparate approaches into a single model, with the most recent being the general bordered tug-of-war model (BTOW) of Shen and Reeve (2010). The first iteration of this model (Reeve and Shen, 2006) was strongly criticized by Nonacs (2007) for its constrained optimization methodology that allowed solutions only where both the dominant and subordinate group members have fitness identical to what they expect from a solitary, non-cooperative life. Nonacs further showed through numerical simulations that 'bordered' solutions in which group members simultaneously contest and concede parentage are unstable and would always be invaded by a pure tug-of-war strategy (PTOW) that contests all reproduction (without any concessions). Nonacs (2007), unlike Reeve and Shen (2006), concluded that competition could lead to destabilization and break-up of groups where cooperation did not have the potential to produce great benefits. In a subsequent paper, Cant and Johnstone (2009) derived a proof demonstrating that a mixed strategy of conceding some portion of reproduction while at the same time competing for another portion could not be an evolutionarily stable strategy (ESS).

Nevertheless, Shen and Reeve (2010) have expanded their original model using the same constrained optimization methods to a broader set of environmental conditions. Along with their elaboration to four sub-models, they present a set of verbal and graphical arguments that claim to show Nonacs' erred in his conclusions and that the Cant and Johnstone proof applies to only non-iterated games. In summary, the basis of the Shen and Reeve argument rests on rules of behavior they give as follows: "we assume that the BTOW strategist behaves according to the following rule: (1) initially, choose the selfish effort and incentive of the general BTOW solutions. (2) At the next time–step, compare the inclusive fitness that resulted to that for the non-cooperative option; if the latter is greater than the former, take the non-cooperative option at the current time step. If not, continue cooperating. (3) If cooperation continues, repeat the decisions unless the incentive given by the partner on the previous step fell below that described by the BTOW solution, in which case lower the incentive given to the partner to zero on the current time step. Optimize the selfish effort. (pg. 4)". Rules (2) and (3) add a threat of punishment in terms of withdrawing cooperation and without them, the PTOW strategy is the global ESS and will invade any other population of strategies (Nonacs, 2007; Fig. 1). I will show, however, that even adding these restrictive rules fails to validate the general bordered tug-of-war model in two substantive ways.

First, Shen and Reeve (2010) assume an initial population where all individuals play the BTOW strategy. Any mutant playing a pure-tug-of-war would have higher within-pair fitness (because it takes advantage of the first move concession by the BTOW player), but as posited by Shen and Reeve, the PTOW strategy would have a lower global fitness to the BTOW strategy because most groups are composed of BTOW players with stable, long-term cooperation. Unfortunately, Shen and Reeve fail to recognize that the opposite condition is true: a mutant BTOW strategy could not invade a population of all-PTOW. The mutant would be exploited by all other members of the population. Thus, a mutant strategy that concedes any amount of reproduction cannot invade a population where no other players offer concessions. This follows from PTOW being a global ESS where no player can increase their fitness within a group by changing their effort devoted to competition or offering a concession (Nonacs, 2007).

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doi:10.1016/j.jtbi.2010.07.029

Furthermore, if a population is composed of individuals that exhibit purely transactional cooperation (all shared reproduction is conceded and none is contested), this population also cannot be invaded by BTOW if this population follows Shen and Reeve's three rules (i.e., substitute "transactional" for "BTOW" in the above statements). In this case, the transactional player would immediately withdraw cooperation from the BTOW mutant. Therefore, the same set of rules Shen and Reeve hypothesize would make BTOW resistant to invasion by PTOW, would also make pure transactional strategies immune to invasion by BTOW. Thus it is difficult to imagine how BTOW populations could arise since the strategy appears unable to invade either non-cooperative populations or non-contesting ones.

Second, even if we assume the population is composed of BTOW players and apply Shen and Reeve's three rules, BTOW is not an ESS. A simple numerical example will suffice to demonstrate this. I use the following values: potential group productivity ($G=2.5$); relatedness ($r=0.25$); relative competitive efficiency of subordinate ($b=0.6$); lone dominant success ($L=1$); and lone subordinate success ($S=0.8$). With these values if both individuals

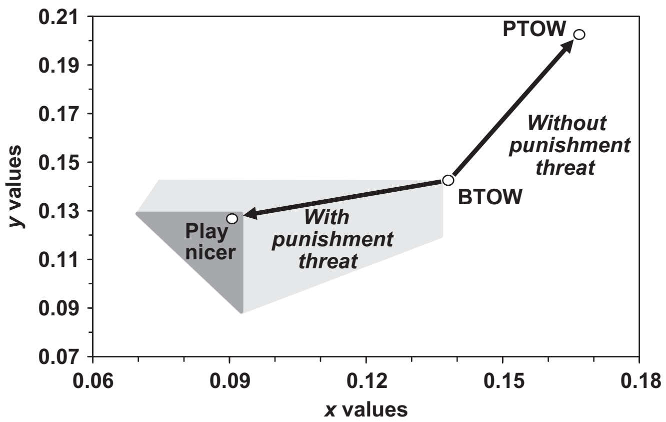


**Fig. 1.** Predicted levels of competition. Predicted values of $x*$ and $y*$ are shown for the mutual-pay bordered tug-of-war (BTOW) and the pure tug-of-war (PTOW) for the set of conditions given in Table 1. The BTOW solution is unstable without the threat of punishment (i.e., the immediate withdrawal of cooperation). Here each group member can change its strategy from the BTOW solution to increase its fitness, and a series of such moves lead the players to the PTOW solution which has no reproductive concessions ($p*=q*=0$; $x*=0.167$; $y*=0.203$). This PTOW solution is an ESS as neither player can change its behavior to gain fitness. With the threat of punishment, the BTOW solution becomes unstable relative to "play nicer" strategies that both compete and concede less. The light gray zone defines the range of higher-fitness strategies that offer lower, but positive concessions ($p$ or $q>0$). In dark gray zone are the highest fitness strategies that do not offer any concessions ($p$ and $q=0$). The point in the dark gray zone represents the $x$ and $y$ values for the "play nicer" strategy described in Table 1.

are non-cooperative, the inclusive fitness of a solitary dominant ($Is_d$)=1.144, and the inclusive fitness of a solitary subordinate ($Is_s$)=1.106. I use the equations from Shen and Reeve (2010) to calculate the optimal concessions ($p*$ and $q*$) and level of contest effort ($x*$ and $y*$) for the BTOW solution (Table 1; note the BTOW predicted inclusive fitness values are the same as those for being non-cooperative, as per the constraining assumption). Inserted into this population is a mutant strategy that "plays nicer" by conceding nothing but competing less (interested readers can check the numbers in an Excel® spreadsheet given in supplementary materials). In doing so, both players in a mixed pair would have higher fitness relative to pairs of two BTOW players (independent of whether "play nicer" is dominant or subordinate in a mixed group). The average "play nicer" player would have an expected fitness of 1.215, assuming it is equally likely to be a dominant or subordinate player. This is considerably greater than average fitness across the population of BTOW players, which would approximate 1.125. Nor would a mutant BTOW strategy have higher mean fitness in a pure "play nicer" population. As predicted by Cant and Johnstone (2009), the BTOW mutant has lower mean fitness than "play nicer" within mixed pairs (1.136 vs. 1.215), and it considerably lags the mean fitness of "play nicer" across the entire population (1.227). Overall, there are many strategies in terms of simultaneously reduced competition and concession that have higher fitness than the BTOW strategy (Fig. 1). Determining where conflict resolves to specific solutions within this zone of higher fitness will likely depend on the non-cooperative (outside the group) options that each group member has (see Buston and Zink, 2009; Cant and Johnstone, 2009).

The existence of multiple "play nicer" strategies capable of replacing the BTOW strategy reveals a critical flaw in the logic of Shen and Reeve's Rule (3). Strict adherence to Rule (3) would require a BTOW player to withdraw cooperation in reaction to no concession by "play nicer" even though the BTOW player's overall fitness has increased! Therefore, Shen and Reeve's Rule (3) violates the basic principles of natural selection by having one kind of direct reproductive 'fitness' be intrinsically more valuable than another.

Withdrawing cooperation in response to a lower than expected concession could result if the concession must precede the contest and therefore a BTOW player reacts before it receives the second increased payoff. However, Reeve and Shen are explicit in positing that the order of concession and contest is not important in a bordered tug-of-war, and that their solutions are based on both factors being considered simultaneously (Reeve and Shen, 2006; Shen and Reeve, 2010). The general model of Johnstone (2000), which is mathematically identical to the bordered tug-of-war, does assume such a proscribed order of interactions (note that the author later questioned the generality of this assumption: Cant and Johnstone, 2009; Johnstone and Cant, 2009). Indeed, dropping this assumption was the basis for Reeve and Shen's (2006)

**Table 1**
The expected fitnesses of dominant ($Ig_d$) and subordinate ($Ig_s$) players in paired combinations of the "bordered tug-of-war" and "play nicer" strategies (the second number is the change in fitness a player expects relative to doing the BTOW strategy in a BTOW–BTOW pair). The predicted levels of concession ($p*$ and $q*$) and effort devoted to competition ($x*$ and $y*$) for the BTOW strategy are calculated through equations given in Shen and Reeve (2010). (See Excel® spreadsheet in Supplementary materials for equations and all calculations.)

| Dominant | Subordinate | $p$ | $q$ | $x$ | $y$ | $Ig_d$ | $Ig_s$ |
|---|---|---|---|---|---|---|---|
| BTOW | BTOW | 0.224 | 0.091 | 0.138 | 0.142 | 1.144<br>+0 | 1.106<br>+0 |
| BTOW | Play nicer | 0.224 | 0 | 0.138 | 0.125 | 1.156<br>+0.012 | 1.149<br>+0.042 |
| Play nicer | BTOW | 0 | 0.091 | 0.090 | 0.142 | 1.282<br>+0.138 | 1.117<br>+0.011 |
| Play nicer | Play nicer | 0 | 0 | 0.090 | 0.125 | 1.293<br>+0.151 | 1.160<br>+0.053 |

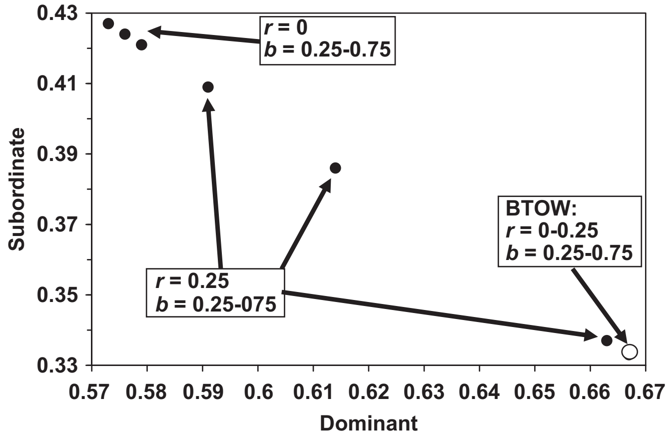


**Fig. 2.** Predicted proportions of reproduction for dominant and subordinate group members. The open circle is the single predicted solution for the mutual-pay BTOW model across two levels of relatedness and three levels of competitiveness (from the cases considered in Shen and Reeve's (2010) Table A1). The solid circles are predicted values from "play nicer" strategies that have the greatest fitness advantage relative to each respective BTOW strategy. All the "play nicer" solutions are affected by both genetic relatedness and differences in competitive ability, and none offer any conceded reproduction ($p$ and $q=0$).

justification for why their predicted outcomes differed from those of Johnstone (2000).

The replacement of BTOW by the "play nicer" strategy is key in that neither player's outcome is on a border of equal fitness for the cooperative or non-cooperative option. This can be seen by allowing a "play nicer" strategy to invade the six mutual-pay outcomes given in Shen and Reeve's (2010) Table A1 (note this table errs in assigning $x$ and $y$ values to $\alpha$-pay, $\beta$-pay and PTOW solutions. The values should be reversed such that $y$ is always greater than $x$). In each of their mutual-pay outcomes, the reproductive skew of the pair is identical, with the dominant individual getting 2/3rds of the reproduction. Neither relatedness nor competitive ability affects skew, but as in the example given in Table 1, a "play nicer" strategy with lowered competition and no concessions has higher fitness and invades. However, for each combination of relatedness and competitive ability, the "play nicer" strategy that has the greatest advantage over BTOW differs. Each case predicts a different level of skew between dominant and subordinate (Fig. 2). Thus unlike for the mutual-pay BTOW, the "play nicer" solutions are sensitive to both relatedness and competitive asymmetry.

The consistent invasion of BTOW populations by "play nicer" strategies shows that Shen and Reeve (2010) erred in claiming that the Cant and Johnstone (2009) proof for concessions being unstable applies only to non-iterated situations. The proof likely holds for iterated outcomes as well. The ESS solutions that lie on the borders in the various Shen and Reeve sub-models do so only because of these sub-models' arbitrary constraints that fitness for one or both group members must exactly equal their fitness apart from the group. Hence, the extensive sets of relationships between skew, conflict and within-group and environmental variables given in Tables 1 and 2 of Shen and Reeve (2010) are special cases and not broadly predictive. Indeed reproductive skew models are "rich in specific predictions (Shen and Reeve, 2010)" only when they include difficult to validate assumptions about how within-group conflict is resolved. There are far fewer robustly testable predictions when such relationships are not known (see Nonacs and Hager, in press).

In conclusion, the argument over the generality of the bordered tug-of-war approach is important. Nonacs and Hager (in press) recently reviewed 45 different cases that examined the relationships between variables such as observed skew, genetic relatedness, competitive ability, aggression, ecological constraints and group size (see also Port and Kappeler, 2010). The studied taxa ranged from insects to primates. Concurrently, they also developed a set of predictions that are consistent across all variants of skew models. Foremost among these is that skew should vary significantly across groups if the groups vary in either the genetic relatedness of the individual group members, or vary in within-group competitive abilities. The major pattern, however, is that neither relatedness nor competitive ability affects skew within a cooperatively breeding group: in 21 of 27 measured relationships there was no significant correlation between within-group genetic relatedness and reproductive skew across groups; and in 13 of 18 cases there was no significant correlation between measures of within-group competitive advantage or aggression and skew across groups. The only variant of any skew model that would consistently predict no effect of these variables on reproductive skew is the mutual-pay sub-model of the bordered tug-of-war (Shen and Reeve, 2010). Thus without realizing that the premise of the general model itself is flawed, one might view such results as strong 'support' for this variant of reproductive skew theory (although ecological constraints having a significant correlation with skew in only 3 of 18 measured relationships would argue otherwise). Therefore, the most parsimonious conclusion to be drawn from the ubiquity of non-significant results is that reproductive skew theory is not a good general predictor of the within-group dynamics responsible for patterns of reproductive sharing.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jtbi.2010.07.029.

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Received 3 March 2010

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