# Simulating the Evolution of Contest Escalation

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# Abstract

Empirical studies of animal contests have shown that escalation to costly fights is usually initiated by their likely winners; in some species however, it is the likely losers who tend to initiate escalation; see (Morris et al., 1995) for a particularly striking example. Game-theoretic models developed in (Just and Morris, in review) and (Just et al., in review) show a possible explanation for the latter phenomenon. Here we test one of these models with simulated evolution.

## 1 THE MODEL

We model animal contests that have up to two stages: a display stage, during which no physical contact occurs, followed in some cases by a fight stage during which physical contact occurs. Note that this structure implies that passage from the display stage to the fight stage requires escalation by only one of the contestants. The objective of a contest is to gain access to a resource that has a value V for each of the contestants. The payoff for each individual is determined by the outcomes of contests, and an individual may be involved in one or more contests during its lifetime. Displaying carries a small cost to each of the contestants that is assumed proportional to the duration of the display stage. The cost of a fight has two components: a cost born only by the loser (denoted by K) and a cost that is incurred by both the winner and the loser (denoted by L).

We assume that during the display stage contestants try to assess the probability of winning a fight. It is assumed that from the point of view of a given contestant, this probability is partitioned into four classes; it is either  $very\ low\ (<\frac{K+L}{V+K};\ escalation\ to\ fighting$ 

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would be disadvantageous), low (< 0.5 so that the opponent is more likely to win, but >  $\frac{K+L}{V+K}$  so that that escalation to the fighting stage would be advantageous), high (the opponent is more likely to lose, but still should prefer escalation to the fighting stage over unilateral retreat), or  $very\ high$  (opponent should retreat). We are only interested in parameter settings where the classes low and high can actually occur. A contestant may somewhat misperceive the class of the probability of winning; for example, if this probability is low, then a contestant may misperceive it as  $very\ low$  (with probability q) or high (also with probability q), but not as  $very\ high$ . The probability q of misperception is a crucial parameter of the model.

At the beginning of the display stage, the players have no information about the probability of winning, and during the process of displaying they may gain partial and eventually full information about the winning probability. We assume that partial information is obtained in two bits: one bit designates the role of a given player ( $P^{\ell}$  if the given player is more likely to win,  $P^H$  if the opponent is more likely to win); the other bit tells whether the probability of winning for the weaker player is below or above the threshold for escalation. We say that the absolute value of the difference in fighting ability is large in the former case and small in the latter. While the model of Just and Morris (in review) and the simulations of Just et al. (2000) assume that information about the role is known at the beginning of an encounter, and while the model of Just et al. (in review) does not allow for partial information, we assume here that the two bits of information can be obtained in any order. Thus at any given time of the display stage, a player will be in one of eight perception states: (no info, no info),  $(P^{\ell}, no info), (P^{H}, no info)$ no info), (no info, small),  $(P^{\ell}, small)$ ,  $(P^{H}, small)$ ,  $(P^{\ell}, large), (P^{H}, large).$  For example, a player in perception state (no info, small) will assume that the probability of winning is either low or high; a player in perception state  $(P^{\ell}, large)$  will have determined that the probability of winning is  $very \ low$ . Note that a perception state  $(no \ info, \ large)$  is implausible and should never be reached.

In each of the perception states, a player has a choice between three actions: R (retreat), D (continue displaying), and F (escalate to the fighting stage). Thus a strategy can be conceptualized as a function that specifies one of the three actions for each of the eight possible perception states, and we can code strategies as strings of eight letters from the alphabet  $\{D, F, R\}$ . Note that there are altogether  $3^8 = 6,561$  different strategies in this game. This number makes it difficult to study the game analytically and calls for an approach using simulated evolution.

## 2 OUR SIMULATIONS

We simulated the evolution of strategies in populations of 3,000 players over 100,000 mating seasons. Each player was characterized for life by its innate fighting ability and its strategy. In each mating season, each player had on average 6 encounters per mating season, and lived for 10 mating seasons. The outcomes of individual encounters were simulated taking into account the participant's innate fighting abilities and strategies. The times at which the player's perception states changed to more informative ones as well as the actual outcomes of the fights were randomized ( $P^{\ell}$  won with probability a if the difference in fighting ability was large and with probability b if this difference was small, where 0 < a < b < 0.5were user-definable parameters). The fitness of each individual was set to an initial fitness at the beginning of each mating season and was then decreased or increased according to the outcomes of this player's encounters. At the end of a mating season, the fitness was used to determine the probability that males will mate (all individuals had an equal probability of being treated as male or female). After each mating season the 300 oldest players were removed and replaced by new players. The new players inherited the actions in their strategy from their parents with mutations and either uniform crossover or a crossover operator that favored inheritance of certain actions in blocks. A detailed description of the program as well as the source code can be found at the following URL: http://www.math.ohiou.edu/~just/Escalate/.

### 3 RESULTS

The model of Just et al. (in review) suggests that if the probability of misperception q is positive, then for

a wide range of parameter settings a mix of the strategies DDDDFDRD and DDDFFFRD should emerge as an evolutionarily stable strategy (abbreviated ESS). The first of these strategies calls for a player to escalate to fighting precisely when the probability of winning is perceived as low, to retreat when the probability of winning is perceived as very low, and to continue displaying in all other perception states. The second of these strategies calls for a player to escalate to fighting when the probability of winning is perceived as low or high, to retreat when the probability of winning is perceived as very low, and to continue displaying in all other perception states. Any nontrivial mix of these two strategies will lead to a situation where most fights are initiated by their eventual losers. In contrast, the same model suggests that if the probability of misperception q is zero, then no ESS should emerge and about half of all fights should be initiated by their eventual losers.

For two of the parameter settings where the model of Just et al. (in review) makes the above predictions we run 120 simulations each with q > 0, and 30 simulations each with q = 0. Some of these simulations started from random initial populations; other simulations started from initial populations where all players followed a fixed strategy that was different from the predicted ESS. The program monitored the proportion of selected strategies between mating seasons 10,000 and 100,000 as well as the proportion of fights that were initiated by the likely loser. Output files of all our simulations as well as more detailed summaries of our results than can be given here can be found at the following URL: http://www.math.ohiou.edu/~just/Escalate/.

The results of these simulations confirm that for the particular parameter settings studied, the results of Just et al. (in review) that were obtained without modeling the process of information acquisition carry over to our model where the process of information acquisition is considered: In the simulations with q>0, over 75% of all fights were initiated by their likely loser, and most of the time, a mix of strategies in which DDDDFDRD dominated was observed. In the simulations with q=0, the percentage of fights initiated by the weaker contestant was not significantly different from 50%, and no (mixed or pure) ESS appeared to evolve.

However, exploratory runs for several other parameter settings did show patterns that differed from the predictions in Just et al. (in review). Characterizing the region of the parameter space where the results of the latter model remain valid if the process of informa-

tion acquisition is explicitly modeled remains an open problem.

## Acknowledgment

This work was partially supported by NSF grant DBI-9904799 to W.J.

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