

# War of attrition with implicit time cost

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Many animals have a formidable arsenal of teeth, hooves or horns, and violent fights among these animals often result in death or serious injury. It is thus perhaps not surprising that there is a wide variety of ways in which animals settle disputes over food, mates or territory without resorting to violence. A common theme in such contests, is that the animals display until one of them gives up, leaving the prize to the animal that endured. It is then safe to assume that a cost can be associated with the length of the display, since otherwise animals would wait indefinitely.

Maynard Smith and Price (1974, *J. Theor. Biol.*, 47, p. 209) pioneered the waiting-game as a model of wars of attrition. In this game, there is a prize worth one unit of fitness, that goes to the winner of the contest. For instance, the prize could be a desirable territory, and the fitness is then the expected number of offspring in the territory. The loser has to settle for a less attractive territory, which entails  $k < 1$  fitness units. It is assumed that the contest costs  $c$  fitness units per unit of time, and both contestants pay the cost until one of them gives up, losing the contest. Making standard assumptions of the mating structure of the population, e.g. abundance of waiting-times in the population obey the replicator dynamics, this model has been thoroughly investigated in the literature.

The standard waiting-game assumes that all individuals in the population play the same number of games per unit of time. We investigate the co-evolutionary dynamics of a population where players engage in wars of attrition, where the time cost is not explicitly given, but instead depends implicitly on the strategies of the whole population (Eriksson *et al.* 2004, *J. Theor. Biol.*, 230, p. 319). Each player participates in a series of games, where those prepared to wait longer win with higher certainty but play less frequently. The players in the population can be in one of two states: either they are involved in a contest with another player, or they are available for entering a new contest. The activity of the players in the population, during a generation, is modelled as a process that randomly selects pairs of available players to engage in contests. This leads to an implicit time cost, which is higher for players involved in longer games.

The model is characterised by the ratio of the winner's score to the loser's score, in a single game. The fitness of a player is determined by the accumulated score from the games played during a generation. We derive the stationary distribution of strategies under the replicator dynamics. When the score ratio is high, we find that the stationary distribution is unstable, with respect to both evolutionary and dynamical stability, and the dynamics converge to a limit cycle. When the ratio is low, the dynamics converge to the stationary distribution. For an intermediate interval of the ratio, the distribution is dynamically but not evolutionarily stable.

We find that our model has immediate implications for two earlier models that takes implicit costs into account. Hines (1977, *J. Theor. Biol.*, 67, p. 141) proposed a model in which animals forage for food. When an animal finds a piece of food, with a given probability it may consume the food undisturbed, otherwise it enters a war of attrition for the food parcel. Here, it is assumed that engaging in competitions prevents foraging, so that there is a trade-off between the probability of winning a contest and the time spent foraging. It turns out that we can capture the evolutionary dynamics of this model within our model (assuming replicator dynamics), although the original model has four parameters and our model only has one. Cannings and Whittaker (1994, *J. Theor. Biol.*, 167, p. 397) studied a modification of the model by Maynard Smith, similar to the one we present. They suggest a mechanism that implies more games for players that finish faster, but keep the explicit time cost. Unlike our model, their approach is restricted to positive integer waiting-times. Here, we are able to apply our results in the limit of long games and to calculate the stationary distribution analytically.

Finally, we note that the dynamics of the population during a generation modelled here can be useful for studies of game-theoretic problems in general; one example could be the study of the Prisoner's Dilemma game with refusal in which a player may quit a repeated game when encountering a deviation from cooperation. Here, the threat to abandon is equivalent to an outside option, where the value of the option is again implicit: it depends on the composition of the population.