

# Is the Predicted ESS in the Sequential Assessment Game Evolvable?

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**Abstract.** The Sequential Assessment Game model of animal contests predicts an evolutionarily stable strategy (ESS) that is a sequence of thresholds for giving up. Simulated evolution experiments reveal that the selection pressure on higher-numbered thresholds is most likely too low to allow for the theoretically predicted ESS to evolve in nature.

## 1 Simulating the Sequential Assessment Game

In game-theoretic models of animal contests, contestants are treated as players whose objective is to maximize their expected number of offspring. A strategy is a prescription of how a player should behave in every possible situation. A strategy  $S$  is evolutionarily stable, or an ESS, if a population of players that all follow  $S$  cannot be invaded by a mutant strategy  $S'$  [2]. Being an ESS is only a necessary condition for a strategy to actually evolve. Simulated evolution can be used to investigate whether theoretically predicted ESS's are indeed evolvable.

The objective in the classical Sequential Assessment Game of Enquist and Leimar [1] is to gain access to a resource. The game proceeds in successive bouts. After each bout, each player makes a decision to either give up or continue. The decision is based on the player's current estimate of relative fighting ability. These estimates are made by statistical sampling and become more reliable after each bout. The resource is obtained by the player who persists longer in the game. Both players incur fitness costs for each bout of the game.

A strategy in this game can be conceptualized as a sequence of thresholds  $S = \{S_1, S_2, \dots, S_k, \dots\}$  for giving up: Let  $X_i$  denotes a player's estimate of relative fighting ability after the  $i$ -th bout. A player who follows Strategy  $S$  gives up after  $k$  bouts if, and only if,  $X_1 > S_1, \dots, X_{k-1} > S_{k-1}, X_k \leq S_k$ , unless his opponent gives up earlier. In [1], an apparent ESS for the Sequential Assessment Game was found that corresponds to an increasing sequence of thresholds.

We tested the model by simulated evolution of finite populations of competing strategies. The original model does not put an upper limit on the number of bouts in this game. In order to represent strategies in the computer, we limited fights to  $T$  bouts, and each strategy was coded as the sequence of thresholds for giving up after each one of these  $T$  bouts. If none of the players gave up after  $T$  or fewer bouts, then the program randomly picked a winner and subtracted an extra punishment (equivalent, on average, to continuing for  $E$  additional bouts) from the fitness of both the winner and the loser. For more details see [3].

In a number of trial runs with this setup and for a variety of parameter settings we did not observe a pattern of evolution towards a strategy that would resemble the predicted ESS. While means for the first two thresholds were usually highly consistent between different runs of the simulation, the means for the higher-numbered thresholds evolved towards very different numbers, depending on the seed. In order to understand this phenomenon, we ran simulations that monitored the number of fights in the last season that were terminated after any given bout. Table 1 gives some representative numbers for the last season in simulations with  $T = E = 5$ , out of 30,000 total encounters.

**Table 1.** Total number of encounters that were terminated after bout  $t$

Seed	$t = 1$	$t = 2$	$t = 3$	$t = 4$	$t = 5$
1	28,405	743	118	734	0
2	27,582	68	2,350	0	0
3	27,920	1,563	309	208	0

## 2 Discussion

Our results strongly suggest that the reason for the observed lack of a clear pattern in the evolution of higher-numbered thresholds is the absence of a sufficiently strong selection pressure on them. We obtained three independent pieces of evidence for this: The absence of clear patterns of evolution in our simulations, the low occurrence of higher-numbered bouts, and the fact that a simple change in the rules that created artificial selection pressure on higher-numbered bouts lead to fairly consistent outcomes that fit the predictions of [1] remarkably well. The latter results were reported in [3].

We believe that our results show a serious weakness of the classical Sequential Assessment model. It is not clear how the predicted ESS could evolve in nature. We suggest that the problem of selection pressure on individual thresholds needs to be investigated by researchers in mathematical biology.

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## References

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