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The evolution of aggressive losers

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Abstract

We examine the question of when aggressive behavior of likely losers should be part of an evolutionarily stable strategy. We modified an earlier model by the authors that found situations where likely losers initiate aggressive interactions more often than likely winners. The modifications allowed us to examine the robustness of the previous study by including an unusually high number of possible strategies ($n = 81$) and to examine a wide range of parameter settings. First, we show that restricting attention to only a few most plausible strategies may change the overall results. Second, within the space where escalation is predicted, for a large percentage of the parameter settings (85%), an ESS exists that leads to a somewhat counterintuitive situation where escalation is more often initiated by the likely loser than by the likely winner of the contest. In contrast, an ESS that favors escalation by likely winners was found only for about 3% of parameter settings. Furthermore, we use simulations of evolution in a finite population to verify for certain parameter settings that the analytically predicted ESS's could in fact evolve. Our results suggest that ESSs in which the likely loser rather than the likely winner is expected to initiate escalation are generic and ESSs in which the opposite is true need to be explained by incorporating specific features of the biology of a given species into more detailed models.

Keywords: Animal contests; Assessment of RHP; Escalation; Game theory; Simulated evolution

Game-theoretic models are widely used to examine the conditions under which animal contests are expected to escalate to costly and potentially dangerous fights. When two contestants differ greatly in their fighting ability, i.e., if there is a large asymmetry in resource holding power (RHP) as defined in (Parker, 1974), the probable loser should retreat without escalation (Archer, 1988). However, in those contests that do escalate to the use of costly fighting behaviors, which individual attacks first (i.e. *initiates* escalation)? Evidence that individuals with the relatively higher RHP (likely winners) initiate escalated contests has been reported for several different organisms (e.g. gorillas, Watts, 1994; fishes, Figler and Einhorn, 1983; Turner and Huntingford, 1986; Keeley and Grant, 1993; Barlow et al., 1986; hermit crabs, Dowds and Elwood, 1983; sea anemones, Brace and Pavey, 1978; and mollusks, Zack, 1975). However, other empirical studies have detected cases where likely losers are more aggressive than expected (Lorentz, 1966; Morris et al., 1995; Third contest, Keeley and Grant, 1993; Smith et al., 1994; Ribowski and Franck, 1993; Enquist and Jakobsson, 1986; Dow et al., 1976). In particular, in a study by Morris et al. (1995), 78% of the observed fights between male swordtails were initiated by the smaller animal, and in 70% of the fights, the fish that delivered the first bite lost the contest.

The aggressive behaviors of likely losers have been explained in several ways. Likely losers might be expected to be more aggressive if the value of the resource is greater for the likely loser than the likely winner, in other words, if there is an asymmetry in the value of the resource to the two contestants (Parker, 1974; Dugatkin and Ohlsen, 1990; Dugatkin and Biederman, 1991). Another possible mechanism for the aggressive behavior of smaller males is that likely losers may misperceive themselves as likely winners (Bradbury and Vehrencamp, 1998). The mechanism behind these behaviors could also be similar to the Desperado Effect in which losers are aggressive because they have no other options (Grafen, 1987). Note that this situation creates in effect a hidden payoff asymmetry. Morrell et al. (2005) showed that if initiating a fight increases the winning probability by a fixed amount, then likely losers would be expected to initiate contests. However, it remains unclear whether their findings generalize to cases where an increase in the probability of

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winning due to attacking first is not fixed, but depends on the difference in fighting abilities.

While the above explanations may apply to some systems, none of these assumptions appears generic to all animal contests. In contrast, we have been interested in a possible reason for the aggressiveness of likely losers that does not rely on assumptions other than a possible error in perception of fighting ability, which we believe to be realistic whenever actual animals are considered. The Napoleon Complex model (Just and Morris, 2003) suggested that in some cases, even without a payoff asymmetry and allowing for only a small error in perception, likely losers are expected to attack first. If the value of the resource exceeds the cost of losing a fight, the cost of displaying is sufficiently small, and assessment of resource holding power is reasonably accurate but not perfect, the evolutionarily stable strategy (ESS) prompts those contestants who perceive themselves as the likely losers to initiate fights, while it prompts those contestants who perceive themselves as the likely winners to wait for the adversary to attack or retreat. While it is true that in our previous model likely losers sometimes initiate fights by mistake, this does not occur because they misperceive themselves as likely winners, as was erroneously claimed in (Morrell et al., 2005), but because they misperceive their winning probability as above the threshold for escalation. The previous model (Just and Morris, 2003) however, would have been too complicated to solve analytically, which forced us to rely on a simulation that monitored the percentages of a few most plausible strategies in an evolving population for a few parameter settings. Thus the question arises whether the findings of Just and Morris (2003) might have been artifacts due to the restriction to a few strategies or due to untypical parameter settings used in the simulations. The main purpose of this paper is to determine if the findings of Just and Morris (2003) are fairly generic for the most basic model that incorporates differences in fighting ability and perception error, across a wide range of parameter settings and potential strategies.

In constructing game-theoretic models of animal contests, one usually faces a tradeoff between constructing analytically tractable models that postulate a very limited scope of possible behaviors, or models that allow for a wider range of behaviors, but are no longer analytically tractable. The risk in limiting the range of behaviors is that strategies which can invade the postulated ESS may be overlooked. For example, in the classical Hawk–Dove game (Maynard Smith and Price, 1973), if only the strategies Hawk and Dove are considered, a fixed-percentage mix of Hawk and Dove is often an ESS. However, this putative ESS can be invaded by a strategy called Assessor.

The Assessor is a contestant that displays first, evaluates whether it is the larger or smaller contestant (likely winner or loser), and then retreats if it assesses itself to be the likely loser or escalates if it assesses itself to be the likely winner (Maynard Smith, 1982). Even though players assess their probability of winning before escalating in the assessor strategy of the Hawk–Dove game, due to the constraint inherent in this strategy of retreating if one is the likely loser, it is not possible to examine the potential benefits of escalating as a likely loser with this model. The acquisition of information during a contest was modeled more explicitly in the sequential-assessment game (Enquist and Leimar, 1983), in which strategic decisions about giving up or continuing the contest are based on repeated estimates of relative fighting ability. The sequential-assessment model predicts that once an animal is fairly certain that engaging in additional bouts of the contest is too costly, it will end the contest by retreating. While in this case the strategy set is continuous rather than discrete, only a single behavior pattern is considered, and therefore only the decision to keep going or retreat, not of switching from displaying to a more costly fighting stage, can be addressed. Moreover, decisions to engage in one more bout of the contest are made simultaneously by both players in this model, and so the question of who *initiates* a subsequent bout cannot be addressed. Therefore, neither the Assessor strategy in the Hawk–Dove game nor the sequential-assessment game provide a suitable framework for examining the question of aggression by likely losers. The model presented here, like the Napoleon Complex model, permits us to do so.

To test the robustness of our earlier findings, we present here a modification of the Napoleon Complex model that allows us to address three additional questions. First, how will an analysis of the complete set of possible strategies influence the finding that likely losers escalate as part of the ESS? Second, how typical are parameter settings where we find ESSs that call for escalation by likely losers rather than likely winners? And finally, are the predicted ESS's *evolvable* in the sense that a simulated population of initially randomly behaving individuals would eventually evolve into a population that exhibits the predicted ESS?

To address these questions, we proceed in two ways. First, we use an analytical approach (Analysis I) to detect ESS's. As our model allows for 81 different strategies, this is done with the help of a computer program that identifies, for any given parameter setting, all ESS's that are either pure-strategy ESS's or consist of a mix of no more than two pure strategies out of the 81. We used the same program to sample the parameter space and investigate the frequency of those parameter settings for which an ESS that favors escalation by likely losers is predicted. This sampling approach has certain parallels with the study of large biomolecular networks as random Boolean networks that was pioneered by Kauffman (1993). In this approach, one assumes, in the absence of empirical data about most of the network connectivity and interactions, that the network will have properties close to those of a typical network with certain global parameters, which can be found by studying random networks. Here we do not know the actual parameters for the contests of a particular species, but we sample over a wide range of possible parameter settings. While we will report our findings in terms of percentages, it should be emphasized that our goal is only a qualitative assessment of whether parameter settings for which an ESS prompts the likely loser instead of the likely winner to escalate a contest appear to be rare, common, or a majority of possible parameter settings.

Second, we use simulations of evolution in a finite population to test the predictions of the first analysis for some parameter settings (Analysis II). The simulations also allow us to investigate the stability of the ESS's when payoffs are not just expected values but are determined by outcomes of individual fights and reproductive success is influenced by random drift. In addition,