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Does cheating pay? Re-examining the evolution of deception in a conventional signalling game

Ian M. Helgesen [a], Steven Hamblin [b,*], Peter L. Hurd [a]

[a] Department of Psychology, University of Alberta, Edmonton, AB, Canada
[b] School of Biotechnology and Biomolecular Sciences, University of New South Wales, Sydney, NSW, Australia

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The study of reliability, or 'honesty', in communication between individuals with conflicting interests has been a major focus of game theoretical modelling in evolutionary biology. It has been proposed that mixed populations of honest and deceptive signallers can be evolutionarily stable in a model of conventional, or 'minimal cost', signals of competitive ability, and evolutionary simulations have been presented to support this hypothesis. However, we find that these results are questionable on both theoretical and methodological grounds. Here, we examine the theoretical issues raised by this model and examine the proposed 'cheating' strategy through the use of a genetic algorithm. Our evolutionary simulations do not support the hypothesis that deception can be evolutionarily stable in this game. Intuition and common sense have it that animals communicate using ambiguous threat displays that have an underlying probabilistic mixed strategy type of mechanism, but there remains no working game theoretical model of such a communication system.

The application of game theory to biological questions (Maynard Smith & Price 1973; Maynard Smith 1982) has played a major role in reshaping our view of animal communication, transforming it from a mutualistic sharing of information into a self-serving contest between 'mind-readers' and 'manipulators' (Caryl 1979; Krebs & Dawkins 1984). This change has highlighted the issue of honesty in communication when individuals have conflicting interests, such as in threat displays. A display carries none of the risk of injury found in a physical confrontation, but if a threatening display alone was sufficient to displace an opponent, there would seem to be little reason to refrain from using the most threatening signals available regardless of one's ability or motivation to back the signal with action. Were this the case, the signals would rapidly become useless as any correlation with underlying traits was destroyed. However, the widespread presence of threat displays, and the repertoire available to many species (Hurd & Enquist 2001) indicates that threat displays do, on average, carry reliable information.

What keeps these signals 'honest' in the face of selective pressures to cheat? The best known of the proposed solutions to this problem comes from Zahavi (1975, 1977), who argued that honesty could be maintained by an artificial cost, or handicap, associated with the most desirable signals. In principle, only those individuals who were truly fit enough to back the signal with some costly investment or action could afford to pay this cost. While Zahavi's handicap principle may effectively explain some excessive and cumbersome traits, such as the peacock's tail, there are many other signals that cannot be explained by this argument. Aggressive postures that do not put the signaller in a vulnerable position cannot be seen as handicaps, nor can 'song matching' displays, where aggression is signalled by matching the opponent's song rather than singing any particularly threatening song (Wilson et al. 2000; Vehrencamp 2001; Hurd & Enquist 2005). Many of these signals fall into the class of 'conventional signals', where meaning is unconnected to the form of the signal (Guilford & Dawkins 1995). In a simple model, Enquist (1985) showed that conventional signals could be evolutionarily stable as threat displays, with reliability being enforced by the social consequences of sending the signal associated with the more desirable state. In other words, weak individuals will avoid signalling that they are strong, even though this would allow them to defeat other weak individuals without contest, because by doing so they give up the chance to escape from confrontation with strong individuals.

Determining conditions that may allow for stable deceptive signalling has long been a question of interest both theoretically and empirically (Dawkins & Krebs 1978; Caryl 1979; Hinde 1981; Grafen 1990; Bradbury & Vehrencamp 1998; Johnstone 1998; Maynard Smith & Harper 2003; Enquist et al. 2010). More recently Szalai & Számadó (Számadó 2000; Szalai & Számadó 2009)

* Correspondence: S. Hamblin, Department of Psychology, University of Alberta, Edmonton, AB T6G 2R3, Canada.
E-mail address: s.hamblin@unsw.edu.au (S. Hamblin).

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have argued that conventional signalling systems can remain stable even when bluffing is common; they supported this argument with an evolutionary simulation, which they claim demonstrates the evolutionary stability of a mixture of honesty and dishonesty in Enquist's (1985) conventional signalling game. Is bluffing a stable strategy for some players in a conventional signalling game? If so, this would represent a significant modification to our understanding of these games.

To evaluate these claims we must further examine Szalai & Számadó's treatment of Enquist's (1985) model (hereafter referred to as the 'E85' game). The E85 game describes a contest between two players over an indivisible resource of value *V*. Individuals are assigned a state (Strong or Weak), choose between two signals (X or Y), and then respond to their opponent's signal with one of three behaviours: an Attack, a Pause-Attack (allowing a Fleeing opponent opportunity to escape unmolested), or Flee. The two signals have no inherent cost, and as such the meanings of the signals are arbitrary and unconnected to the form of the signal (Hurd & Enquist 2005). This stands in contrast to 'handicap signals', where the costlier signal generally represents the more desirable state (Zahavi 1975, 1977; but see Hurd 1997). While Szalai & Számadó claim their results demonstrate bluffing within the E85 game, the models used to generate these results differ significantly from Enquist's in terms of conceptualization, model structure and payoffs (differences detailed in Figs 1, 2).

The original model was presented by Enquist (1985) as tersely as possible, to formally demonstrate the central thesis in the context of a larger work, and did not include a full payoff matrix for the model. Subsequent work on this model has used the full payoff matrix presented in Hurd (1997) as a starting point, but other payoff variations exist, for example, a version with the minimum number of payoff variables (four) in Appendix C of Hurd & Enquist (1998). Generally, these variations either act to simplify the model (as in the minimum payoff parameter version) or attempt to incorporate more biologically realistic assumptions (as in the variation to allow *N* strength states in the Appendix to Hurd (1997)). A third rationale for exploring alternative payoffs is to investigate what modifications would be required to produce outcomes of interest, in this case bluffing, so that their biological plausibility, or modelling elegance, can be assessed.

The largest change made to the E85 game in Szalai & Számadó's (2009) version is in the treatment of state. In Enquist's original model, state represented an individual's ability to win in an escalated fight, often referred to as resource holding potential (RHP; Hurd 2006). This state is determined with a random 'move by nature' beyond the control of the player, and Strong individuals both win fights against Weak individuals as well as suffer a reduced cost of fighting against Weak opponents. By contrast Szalai & Számadó define state in a way consistent with aggressiveness willingness to persist or escalate in a fight (Maynard Smith et al. 1988; Kim 1995; Hurd 2006). This can be seen in the model developed by Számadó (2000), and extended by Szalai & Számadó (2009), which allows players to choose their state (Fig. 1). Players in Enquist's original model are either of high RHP (Strong) or low RHP (Weak). Szalai & Számadó also call the individual's states 'Strong' and 'Weak', but we shall refer to these states as 'Savage' and 'Wimp' to reflect the difference in interpretation, and to disambiguate the concepts (we retain the use of S to represent Strong or Savage and W to represent Weak or Wimp). We refer to this new version of the model, in which players choose their state, as the 'strategic-choice-of-state' model. Note the potential for confusion, as Szalai and Számadó's work uses the Strong/Weak terminology throughout and does not make clear which version of the model (original with move-by-nature, or modified strategic-choice-of-state) is being discussed.

Even if aggressiveness signalling is theoretically sensible (see Hurd 2006, for an analysis), making this change creates a problem: if state represents RHP and being stronger than the opponent improves the probability of winning (as it does in the E85 model), no animal would adopt a strategy that involved choosing to be Weak. Without this variation in state, signal variation becomes meaningless and so the signalling system collapses. To maintain a polymorphism in signal usage under Szalai & Számadó's formulation of the model, the authors were required to add a penalizing cost to Savage versus Savage encounters in a way (see Methods, Fig. 2) that follows the logic of a Hawk–Dove game. This penalty maintains the usage of the Wimp state and thus allows for signalling, but despite the authors' claims that they are using the E85 model, this is no longer the same game; players are now signalling about their aggressiveness and not their RHP (which is implicitly assumed to be equal, just as in the Hawk–Dove game; Maynard Smith & Price

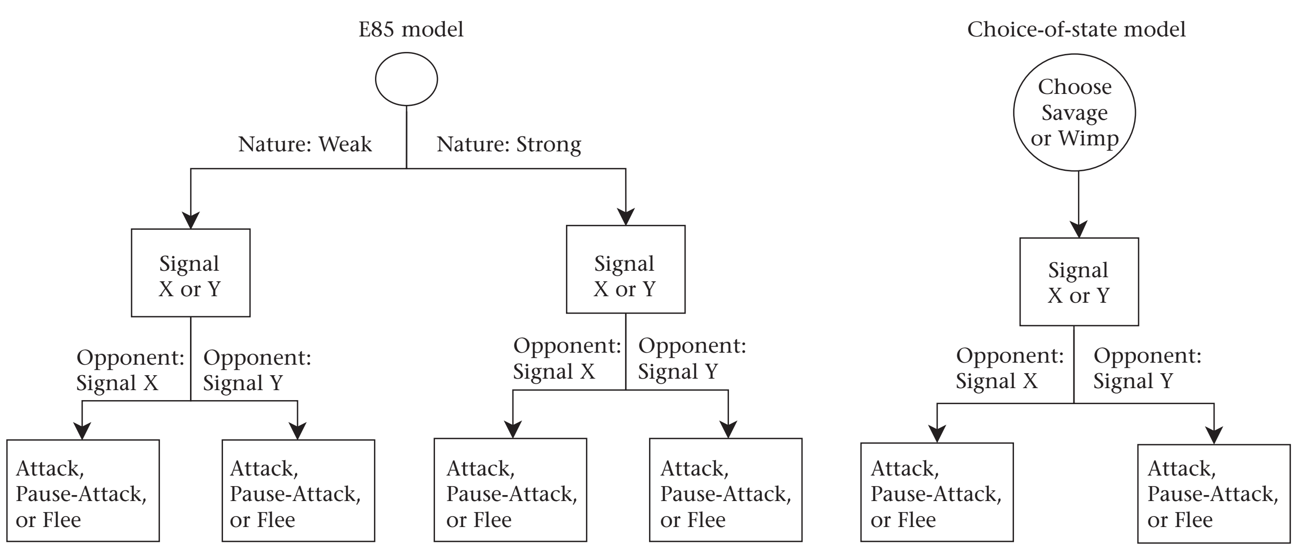

Figure 1. Decision trees for a single player in each model. The circle indicates the start of the tree, and text inside the circle and squares indicates the player's potential moves. Branching lines indicate moves by nature or the opponent. The extensive forms of the games are identical except that the two initial moves by nature, which determine player states, are made by players in the strategic-choice-of-state model, and an information set joins the second player's choice of state, so that it does not know the first player's state.