



# Genetic algorithms and non-ESS solutions to game theory models

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Game theory is not only the primary method for the formal modelling of interactions between individuals, but it also underlies how biologists think about social interactions on an intuitive level. Most biologists equate game theory with the notion of an evolutionary stable strategy (ESS). Maynard Smith's definition of an ESS formalized an intuitive concept of stable population equilibria in game theory models. This has proven extremely useful, both to formal modelling efforts, and to a much wider range of biologists in general. The formal definition of an ESS often cannot be met for an entire class of games, extensive form games with nodes off the supported path. Games of this form are the most reasonable models for a great many animal behaviours. This means that formal ESSs will not exist for these games, even though evolutionary stable strategies, in the intuitive sense, do exist. More powerful analytical solution concepts, such as evolutionarily stable sets (ES sets), are required to describe stable endpoints formally, but finding such solutions can be extremely difficult. In this paper we use genetic algorithms as an alternative method of searching for such solutions in a well-studied game of biological communication. Using this technique, we show a previously unknown solution to this game. We discuss the properties of biological communication that make it a particularly difficult subject to model using ESSs as the solution concept, and suggest that these issues also apply to a larger class of social models.

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Game theory is one of the most well-established tools for modelling of social interactions, the application of which has led to notable advances in biological topics as diverse as sex ratio theory, cooperative behaviour, sexual selection, sperm competition, parent–offspring conflict, social foraging and agonistic behaviour (Hamilton 1967; Maynard Smith 1982; Axelrod 1984; Andersson 1994; Giraldeau & Livoreil 1998; Riechert 1998). The topic of biological communication has been particularly influenced by game theoretical thinking (Johnstone 1997, 1998; Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2003; Searcy & Nowicki 2005). The question of whether or not animals with conflicting interests should be expected to communicate reliably (or 'honestly') has been strongly shaped by either intuitive (e.g. Zahavi 1975, 1977; Dawkins & Krebs 1978; Caryl 1979; Hinde 1981; Krebs & Dawkins 1984) or formal (e.g. Enquist 1985; Enquist et al. 1985; Grafen 1990; Maynard Smith 1991; Owens & Hartley 1991; Johnstone & Grafen 1993; Johnstone & Norris 1993; Hurd 1995; Kim 1995; Hurd & Enquist 1998) game theoretical models.

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In this paper we draw attention to properties of communication that make it a particularly difficult subject to model using formal game theory. In particular, we argue that the highly influential concept of an evolutionary stable strategy (ESS) is a poorly suited solution concept for models of communication, and we discuss the need for the use of more powerful analytical solution concepts on such models. To aid in this task, we explore genetic algorithms as an alternative method of finding analytical outcomes to a relatively complicated model of communication. Communication requires a more complex model structure than many other biological game theoretical problems; while we focus on models of biological communication to provide a concrete setting for our discussion, the general lessons and caveats apply to any game theoretical model of comparable structure. Any game theoretical model in which players have underlying states, or make more than one move per game, will have the level of complexity required for these ESS-preventing effects to exist (Selten 1975, 1983, 1988; Cressman 2003).

Most behavioural biologists are familiar with game theoretical models presented in their normal form, as payoff matrices. This form is appropriate in games where all players choose and play their strategies simultaneously (Gibbons

1992). Such interactions, with a single simultaneous behaviour, fail to capture the essence of communication and most other social interactions. Communication requires that individuals not only react to each other in a temporal sequence, but that they are also likely to vary in some underlying states such as differing RHP states, varying resource valuations, or territorial ownership status that may be hidden from each other (Johnstone 1998; Maynard Smith & Harper 2003). Extensive form games are the appropriate game theoretical formulation of such interactions as they allow strategies to be explicitly composed of several different possible moves made under different contingencies (Selten 1983, 1988; Cressman 2003; Hurd & Enquist 2005). Any game theoretical model that incorporates individual variation in ability or need, or variable moves made in response to the choices of the other players, cannot properly be expressed in payoff matrix form alone.

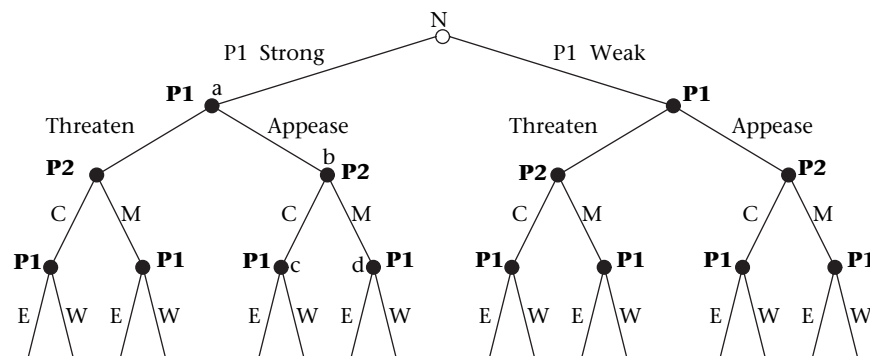
The extra clarity inherent in the extensive form is especially obvious when the game is one of imperfect information, where one or more choices may be made by a player who is unaware of the outcome of decisions made by other players. Card games such as poker are the classic examples of games of this type. Each player knows the cards in their hand, but not those of other players (except in a probabilistic sense), while actions such as bets are common knowledge and provide information (even if ambiguous) to receivers about the signallers' hand. The parallels to biological communication are clear, but the discussion is not limited to communication games. For instance, a forager in a social foraging game who makes use of one conditional strategy when hungry and another when relatively satiated, or a sequence of life-history decisions in which the payoffs are not only frequency dependent but a function of the earlier and subsequent decisions, will have the same structural consequences as the communication game studied here.

Whether in their normal or extensive forms, game theoretical models in biology are typically solved by identifying evolutionary stable strategies (ESSs; Parker 1984; Houston & McNamara 1999). ESSs are single strategies (or a single specific mixture of strategies; see Appendix 1) which,

if adopted by all members of a population, cannot be invaded by any other strategy (Maynard Smith 1982). The ESS concept has the virtue of intuitive clarity that allows for a greater understanding of social behaviour, but it is a mathematical formalism that is strongest when applied to simple models. Attempts to increase the biological realism of these models, by adding variables such as strength states or signalling stages, can easily create a model that has no ESS (Kim 1995). This problem is especially pressing in extensive form games (Selten 1975, 1980, 1983, 1988), because of two inter-related problems: nonpervasive strategies and large strategy spaces.

The first, and most serious, problem in solving extensive form games stems from the formal conditions required to be an ESS (Appendix 1), which can only be met if the strategy is 'pervasive' (Selten 1983). Pervasiveness is a property of strategies in which all possible decision points (information sets) in the game are reached with a nonzero probability. For example, consider the game presented in Fig. 1. Player 2's node 'b' is never reached when the players are playing optimally, and therefore neither are Player 1's nodes 'c' and 'd'. It does not matter which moves the players would make at these nodes, but the formal definition of an ESS requires not only that the moves to be made be specified under such moot conditions, but that the strategy be stable against invasion by strategies that differ only in the moves at these nodes. This requires that the 'ESS' be stable against invasion by the moves at these nodes. This requirement that the 'ESS' be stable against invasion by silent mutations is obviously impossible to meet.

To cope with the problem of nonpervasive strategies, more powerful analytical solution concepts, such as evolutionarily stable sets (ES sets), must be used. In intuitive terms, an ES set is a set of strategies that, individually, would be ESSs were it not for the fact that each member of the set scores equally well against all other members of the set, making the set's members neutral to each other (Thomas 1985a, b; Cressman 1992; Balkenborg & Schlag 2001; see also Appendix 1). Thus, any strategy that would be invaded by a silent mutation will be part of the ES set. Note that this is different from



**Figure 1.** An example of a simple non-ESS extensive form game solution. The game has two players. Player 1 (P1) is either Strong or Weak, and chooses an initial move, either 'Threaten' or 'Appease'. Player 2 (P2) responds with either 'Challenge' or 'Mitigate', then Player 1 moves again choosing one of 'Engage' or 'Withdraw'. Assume that evolution converges upon an optimal strategy in which Player 1 always chooses 'Threaten' when Strong, so that the population evolves to a point at which, whenever the node marked 'a' is reached, play never proceeds to the node marked 'b'. Since 'b' is never reached, Player 2's behaviour at this node is never under any selective pressure, and neither is Player 1's at nodes 'c' and 'd'. Strategies that differ only in their choice of behaviour at these nodes are functionally equivalent, but no single strategy can possibly meet the definition of an ESS.

a mixed ESS in that a mixed ESS requires a precise mixture of pure strategies to be present, while for an ES set, any of the members may be present in any ratio. If we view the players as being chosen from a polymorphic population where each member plays a pure strategy, then at equilibrium, a mixed ESS would be in the form of a specific ratio of each pure strategy in support of the ESS. An ES set would differ in that the equilibrium population could be equivalently composed of any conceivable mixture of the ES set strategies, to the point where the entire population could play only one member of the set. ES sets are not the only way to circumvent the pervasiveness issue (e.g. limit ESSs: Selten 1983, 1988; Leimar 1997; McNamara et al. 1997), but they are the most amenable to an intuitive definition and fit naturally with the results of our genetic algorithm explorations (see below).

The second problem to solving realistic communication games is that of large strategy spaces. Simple communication models are constrained to produce a single type of signal, and more complicated models are required to produce phenomena such as conventional signals, which arguably have good empirical support (Hurd & Enquist 2001, 2005; Hurd 2004). For example, in the simplest signalling game (Hurd 1995) each player has four pure strategies to choose from. The original Sir Philip Sidney game (Maynard Smith 1991) has four pure strategies per player, the version presented by Johnstone & Grafen (1993) has four for the donor and 16 for the beneficiary, while Maynard Smith's (1994) mutual signalling version has four beneficiary strategies and 64 donor strategies. In Kim's (1995) aggressiveness signalling game, each player has 32 pure strategies, while in the conventional signalling game (hereafter called the E85 game; Enquist 1985), each player has 324 pure strategies. Increasing the number of player states in the E85 game from two states to two states with three levels each, while retaining the dichotomous signals and three end moves, results in over 10 million pure strategies per player. Even if an ESS exists in such a large game, other forms of solutions, such as ES sets, or limit cycles in strategy space, will be more likely as the strategy space expands. The existence of any single form of solution does not preclude other, potentially more biologically relevant forms. This suggests that analytical demonstrations of stable outcomes ought to be supplemented by searches for other regular patterns of strategy change.

A commonly used alternative for identifying solutions to games is an approach known as 'evolutionary game theory' (Hammerstein 1998), or 'replicator dynamics', in which a reasonable method of strategy replication and population dynamics is posited and the space of all possible population compositions is mapped analytically (Taylor & Jonker 1978; Hofbauer & Sigmund 1988; Cressman 2003). Evolutionary game theory analysis may be tractable when there are few pure strategies, but as each new strategy adds another dimension to the strategy space, analysing dynamics in a dozen, or more, dimensions is not.

Furthermore, in terms of population evolution, equilibria such as ESSs and ES sets are strategies that are presupposed to have reached fixation in a population. There is nothing in the definition of an ESS that requires

that selection takes the strategy to fixation from even a small proportion of the phenotypic strategy space. In other words, while ESSs are stable points, they are not necessarily attracting states (Nowak 1990). Games may also have more than one equilibrium solution, and the question of which solution has more attractive power in the strategy space may be analytically intractable. Games with large strategy spaces may even have nonequilibrium solutions, such as strategies with large attractive basins that are none the less beaten by an otherwise poor strategy, or quasistable outcomes such as limit cycles through strategy space. Although evolutionary game theory can provide a picture of the population dynamics, we have already noted the problems of analysing these dynamics in a large strategy space.

ES sets and other solution concepts provide a remedy to the shortcomings of the ESS formalism, but as noted in the introduction, a final problem remains. Analytical solutions are a way of describing what an evolutionarily stable population equilibrium will look like, in terms of what strategy or strategies will be used by the population when it is at that equilibrium. Yet for all but the most simplistic models, finding these solutions to begin with can prove to be a vexing exercise. For games as large as E85 or the Kim game, considerable effort is required to find and show these solutions, and for games that are much larger than E85, the task may prove difficult or even impossible.

To help deal with the computational challenge of finding the required solutions to more complex game theory models, we suggest a possible alternative. Genetic algorithms (GAs; Holland 1975; Goldberg 1989; Sumida et al. 1990), computer simulations of strategy change by natural selection, hold great promise as a method for solving games. By tapping their heuristic optimization capabilities, the use of a GA can clarify attractive points in the strategy space that correspond to analytical solutions of game theory models, and by examining the evolution of the population over time and across runs, we can gain insight into the population dynamics. Despite the apparent promise, this approach remains relatively unexplored. To show the advantages of adopting this technique, we have applied a genetic algorithm to a well-studied game of communication, the conventional signalling game (Enquist 1985; Hurd 1997; Enquist et al. 1998; Hurd & Enquist 1998; Számadó 2000, 2003) to compare the simulation results to prior analytical work.

## METHODS

### The Conventional Signalling Game

In the E85 game, two players of varying discrete strength states compete over an indivisible resource, communicating with conventional signals before choosing behaviours with which to respond. The structure of the game is as follows.

- (1) Each player is randomly assigned a strength state, either 'Strong' or 'Weak' in a 'move by nature'.
- (2) Knowing their own state, but not that of their opponent, each player then chooses a signal ('A' or 'B') and sends it simultaneously.

(3) Knowing their own state and the opponent's signal, each player chooses and executes a behavioural response, one of 'Full Attack', 'Pause-Attack', or 'Flee' (hereafter A, P or F) at the same time.

(4) Payoffs are then calculated based on the players' strength states and their behavioural responses.

Note that the choice of signal has no direct effect on payoff; any cost to making a particular signal will come from the response of the other player, which makes the signals 'conventional' (Hurd & Enquist 2005). The E85 game, with its 324 pure strategies, is the simplest example of a conventional signalling game that we are aware of (Hurd & Enquist 2005).

The E85 model has more than one payoff parameterization. We used two different payoff quantifications for the genetic algorithm's fitness function. The first, which we will refer to as TCNP, is the minimum variable version of the E85 game (Table A3.1 in Hurd & Enquist 1998), where  $T = 1.0$ ,  $C = 0.7$ ,  $N = 0.4$ , and  $P = 0.1$ . The second payoff scheme, referred to here as VCDF, is from the most biologically plausible version of the model (Table 1 in Hurd 1997); where  $V = 100$ ,  $C_{-1} = 15$ ,  $C_0 = 15$ ,  $C_1 = 70$ ,  $F_A = 5$ ,  $F_P = 5$ .

Both the TCNP and VCDF payoffs used have only one ESS, the communicating strategy described by Enquist (1985) (actually, there are two ESSs, which are identical by symmetry, when the use of the costless signals is reversed; we can safely ignore this for the most part, but we will revisit the mirror ESS briefly in the results). The property of having a single ESS is useful in that it allows us to identify, a priori, a single strategy that should predominate. We can also use this strategy as a test of the genetic algorithm's ability to find the 'correct' solution.

## The Genetic Algorithm

Simulations of the E85 model were done with a population size of 100 for a total of 500 generations. We calculated the fitness of each population member in each generation as the mean from five plays of the game against other randomly chosen individual members of the population. Five per cent of the population was killed in each generation. The probability that a population member was killed was inversely proportional to their share of the total fitness of the population, and each killed member was replaced with a strategy chosen at random from the top 20% of the population, as ranked by fitness. After replacing the killed strategies, each locus was mutated with a probability set by the mutation rate parameter. If a locus was selected to be mutated, the current value was replaced equiprobably with any of the allowable values (including the original value) for that locus.

We tested the genetic algorithm on simpler problems with known solutions; the genetic algorithm performed well in finding the ESS to the hawk-dove game, and readily found the ESS to the E85 game when the opponent population was fixed to that strategy (Appendix 2). Preliminary work with alternative genetic algorithm methods, such as other methods of selecting strategies to die or reproduce, or implementation of crossover matings showed

no discernible sensitivity to the details of the simulation methodology (Appendix 3).

Representation of a strategy from the E85 game in the GA was done using a six character chromosome in string form. Each locus specified the pure local strategy (sensu Selten 1983) for a different information set. All information sets in the game except for the move by nature, which assigns strength states to each player, corresponded to a chromosome locus, so that the entire chromosome codes for a pure behaviour strategy (sensu Selten 1983) with the noted exceptions. The first two loci represented the signalling portion of the chromosome, and the final four loci represented the end-game behaviours when: ego state is strong and the opponent uses signal 'B', state is weak and opponent uses signal 'A', state is strong and opponent signals 'B', and state is weak and opponent signals 'A', respectively. A strong strength state or signal that the player is strong is rendered as 'A', and a weak state or signal is rendered as 'B'. Thus, the representation of the E85 ESS under this scheme is 'ABAFPA': signal strong when strong, signal weak when weak, and end-game behaviours of Attack, Pause-Attack, Flee, and Pause-Attack under the combinations given above. Another example: a nonsignalling strategy that displays strong when strong and strong when weak and then attacks at all end-move combinations would be represented as 'AAAAAA'. Further example strategies are presented in Table 1.

We carried out two sets of simulations, the first varied mutation rate from 0.001 to 0.005 at levels of initial 'seed' (percentage of the population initialized to the ESS strategy) from 0% to 75%; 10 runs were done at each combination of mutation rate and initial seed, for a total of 750 distinct simulations. This set was used to explore the probability of the ESS achieving fixation at different levels of the parameters (experiment 1). The second set was used to investigate non-ESS endpoints found by the GA (experiment 2). These runs varied mutation rate from 0.001 to 0.005 at three levels of initial seed: 0%, 5%, and 10%. One hundred runs at each combination of mutation rate and seed were done for this set, giving a total of 1500 distinct simulations. This set was used to enumerate the various outcomes of the GA and determine the formal solutions that arose from the runs.

## Characterizing Outcomes

For each simulation we plotted the change in strategy composition of the population over the course of the 500 generations. To plot the strategies, we first divided each into two components, those loci used when weak, and those used when strong. Each of these two components had 18 possible permutations and can be represented as a point in a three dimensional array. One dimension indicated which signal the player uses (A or B), the other two dimensions indicated which behaviour to use (A, P or F) in response to opponent signal A, and which behaviour to use (again, A, P or F) in response to opponent signal B. Nine colours were chosen to represent the possible allelic combinations of the two behaviour loci (Table A1) with dark or light shades indicating whether the players signal

**Table 1.** Encoding strategies onto chromosomes

Locus number	End-game behaviour choice loci						Chromosome
	Signal choice loci		Opp. signal is 'A'		Opp. signal is 'B'		
	When ego is strong	When ego is weak	Ego strong	Ego weak	Ego strong	Ego weak	
	1	2	3	4	5	6	
Example strategies							
ESS	A	B	A	F	P	A	ABAFPA
Anti-ESS	B	A	P	A	A	F	BAPAAF
Nonsignalling (A), All-Attack	A	A	A	A	A	A	AAAAAA
Signalling, All-Attack	B	A	A	A	A	A	BAAAAA
Nonsignalling (B), Attack if strong, Flee if weak	B	B	A	F	A	F	BBAFAF

Five examples of strategies are presented here as encoded into chromosome form for the genetic algorithm. The first two loci code for signal choice, either signal 'A' or 'B' when strong and weak, respectively. If the signals used in these two strength states are the same (i.e. the alleles at loci number 1 and 2 are identical), then we say that the strategy is nonsignalling. Loci 3–6 code for end-game moves as a function of the opponents signal choice and ego's strength state.

move was A or B, respectively. We used the red–green colour dimension for the 'Always Attack' to 'Always Flee' dimension, and the yellow–blue colour dimension for the orthogonal dimension (running from Flee from A signallers and Attack B signallers, yellow, to Attack A signallers and Flee B signallers, blue).

This colour coding was used to graph the evolution of strategies over the 500 generations (Fig. 2). The strategy each run fixated on was recorded, or if no strategy predominated, this was also recorded. A strategy was considered to have gone to fixation if it had achieved 80% representation in the population in the last 50 generations (10% of the simulation). Dominance of 80% was chosen to serve as a criterion for those runs with higher mutation rates, where mutation pressure could create a large amount of noisy variation from the clearly dominant strategy. Only a small number of cases required this liberal threshold. For example, in the simulations done for experiment 2, only 87 (7%) of the 1263 runs that were labelled as having achieved fixation did so at less than 95% representation.

**RESULTS**

We tested the performance of the GA in a number of runs in which the opponent population was held fixed at the ESS. Instead of playing the game against other random members of the population, strategies played against only the ESS. In every single run, the GA evolved from a random starting population to fixation on the ESS in under 100 generations.

**Experiment 1: ESS Fixation as a Function of Mutation Rate and Seed Level**

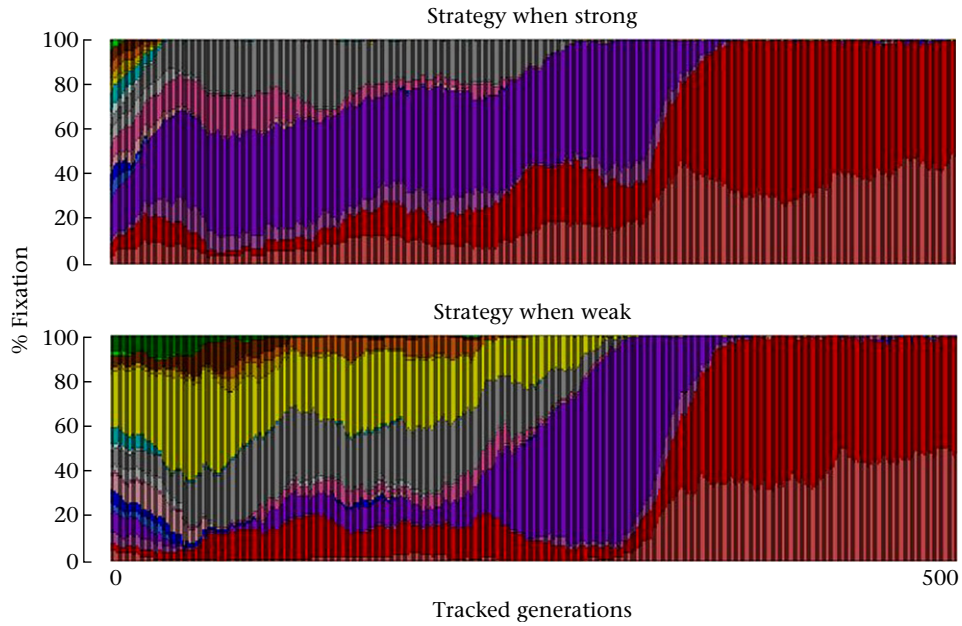
The genetic algorithm only converged on the ESS when the initial population was seeded with a high proportion

of ESS players (Fig. 3). Both payoff parameters and mutation rate influenced the probability that the ESS would go to fixation. Fixation on the ESS was more likely in the TCNP payoff version of the model. At least 10–15% of the initial ESS players were required to ensure a reliable fixation on the ESS in this case. Mutation rate had a larger effect on probability of ESS fixation in the VCDF payoff version. Higher rates made it more and more difficult for the GA to fixate on the ESS. Even at low mutation rates, 20–30% of the initial population had to be playing the ESS before fixation was likely. In both cases, the ESS is clearly a very weak attractor and the probability that a randomly generated population will evolve to the ESS is virtually nil, particularly at high mutation rates.

**Experiment 2: Characterization of Non-ESS Outcomes**

While the ESS appears to have a very small basin of attraction (only 11% of the runs converged on the ESS; Figs 4 and 5), there is another outcome that the GA converges upon with high probability for most parameter combinations (73% of the runs). This outcome corresponds to the strategy set \*\*AAAA, where \* is any choice of allele at the loci responsible for choice of signal. None of these strategies is an ESS because they are invaded by their fellow set members, but the set as a whole meets the definition of an ES set (Thomas 1985a, b; Appendix 2). This solution has not been identified in previous analytical work on the model (e.g. Enquist 1985; Hurd 1997; Hurd & Enquist 1998; Számadó 2000, 2003), and will be referred to hereafter as the All-Attack ES set.

We can easily verify that the ESS is a global optimum and the ES set is a local optimum by examining the payoffs to ESS and ES set players in populations of either ESS or ES set players. From the stability table (see Appendix 2 in Hurd & Enquist 1998), we can show that the expected payoff in a population of ESS players



**Figure 2.** A representative graph of strategy change over 500 discrete generations of time. The run depicted was conducted at mutation rate 0.003 and initial ESS (light purple–dark yellow) seed of 10%. The ES set (light red–red) reaches fixation by approximately the 300th generation.

(summed over all four possible ego and opponent state combinations) is:

$$\left(\frac{1}{2}V - C_0\right) + V + 0 + \left(\frac{1}{2}V - C_0\right) = 2V - 2C_0 \quad (1)$$

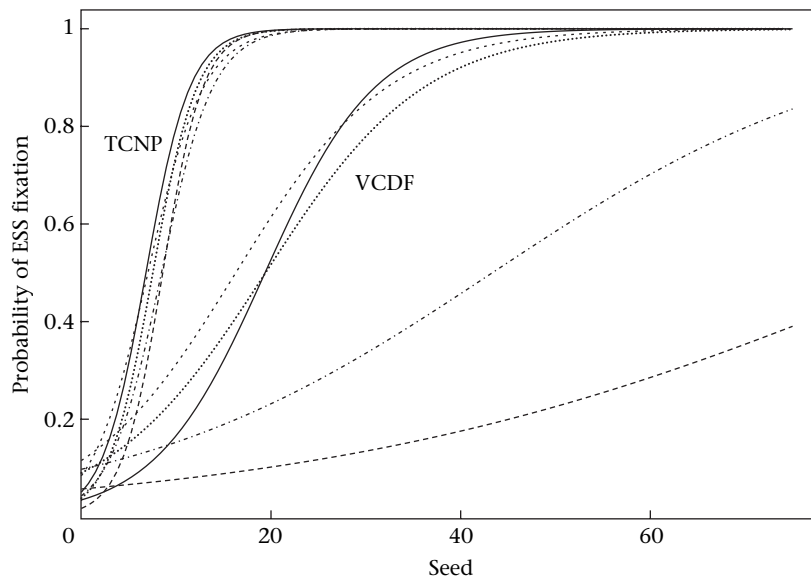
or, the value of winning twice minus the cost of fighting an opponent of equal strength twice.

The expected payoff to any member of the ES set playing in a population of ES set players (from Table A3 in Appendix 4) is:

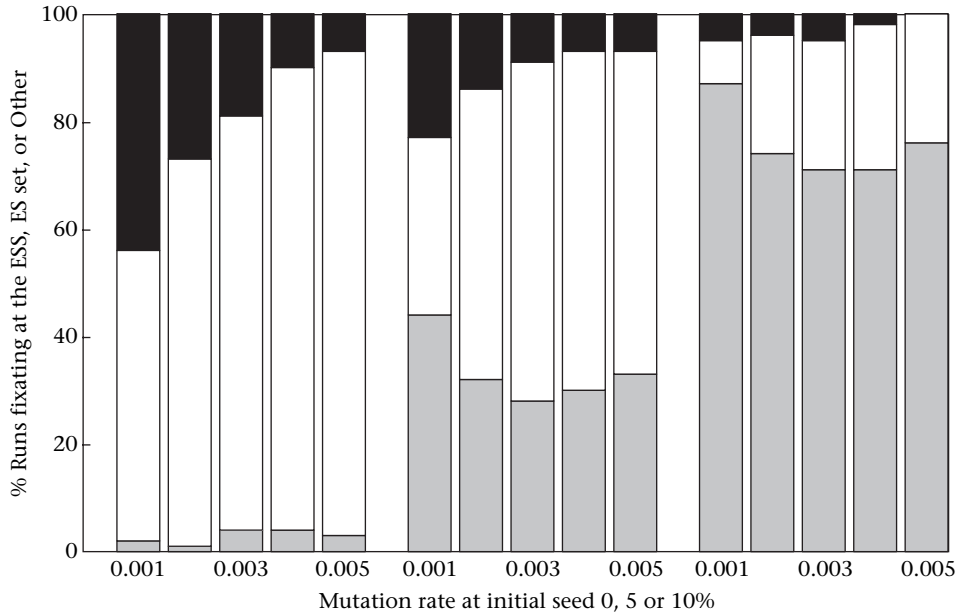
$$\begin{aligned} &\left(\frac{1}{2}V - C_0\right) + (V - C_{-1}) + (-C_{-1}) + \left(\frac{1}{2}V - C_0\right) \\ &= 2V - 2C_0 - C_{-1} - C_1 \end{aligned} \quad (2)$$

or, the value of winning twice minus the cost of fighting twice against an opponent of equal strength and once each against a stronger and a weaker opponent.

The ESS equilibrium payoff is greater, on average, than the All-Attack ES set equilibrium payoff by  $C_{-1} + C_1$ , or the



**Figure 3.** The probability that the ESS goes to fixation as a function of initial seed from 0% to 75%, increasing by 5% each time, and mutation rate from 0.001 to 0.005 (—: 0.001; - - : 0.002; ···: 0.003; ····: 0.004; — · — ·: 0.005), increasing by 0.001 each time. Logistic curves were fitted to data from 10 simulations per mutation rate and initial seed combination, for a total of 750 individual runs used.

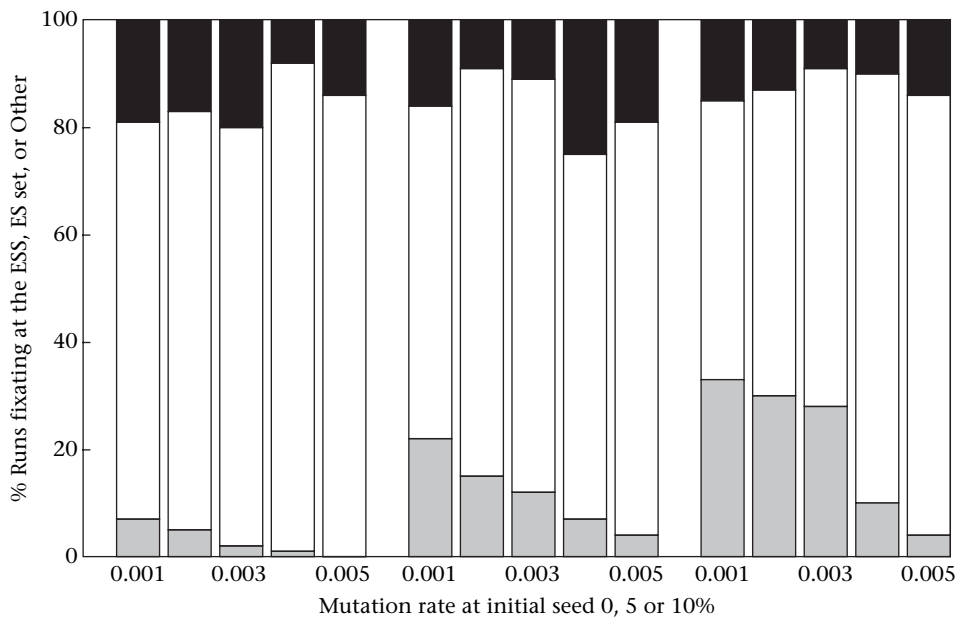


**Figure 4.** Stacked bar graph showing the percentage of runs for the TCNP model in which the ESS (■) ES set (□), or Other (■) strategies fixated at each level of mutation rate (0.001–0.005) and initial seed (0, 5, or 10%). Each combination of mutation rate and initial seed was simulated 100 times, for a total of 1500 individual runs.

cost of two fights, one against a stronger opponent, the other against a weaker opponent, for every four encounters. From this, it is clear that a population composed of ESS players will be globally maximizing their fitness, making the ES set a local optimum.

The ESS and ‘Light red/Red’ All-Attack ES set are not the only outcomes from the GA simulations (Figs 4 and 5).

Two hundred and thirty-six of the 1500 runs (16%) resulted in outcomes that were neither of the two stable outcomes identified above. These are grouped into several different classes summarized in Table A2. In the first case, the GA did not fixate on a single strategy or set of strategies and the population was still in flux at the end of the run. The second case is where the GA was clearly



**Figure 5.** Stacked bar graph showing the percentage of runs for the VCDF model in which the ESS (■) ES set (□), or Other (■) strategies fixated at each level of mutation rate (0.001–0.005) and initial seed (0, 5, or 10%). Each combination of mutation rate and initial seed was simulated 100 times, for a total of 1500 individual runs.

trending towards either the ESS or Light red/Red but simply did not reach the fixation criteria in time. In some runs at higher mutation rates, this occurred when mutation pressure kept enough other players in the population to forestall any strategy from reaching the cutoff for fixation no matter how dominant it was. Between them, the strategies in the first two categories accounted for 12% of the 1500 runs of the VCDF model (see the first entry in Table A2). The third case is composed of outcomes where the GA found the reversed signal convention version of the E85 ESS, the strategy BAPAAF. The small number of outcomes in which this occurred is not surprising given that when a run was seeded with ESS players, it was done solely with the ABAFPA version of the ESS.

The fourth case includes all of those runs wherein the GA fixated on a strategy or strategy set not yet mentioned. The single strategy outcomes (rows 2–8 in Table A2) are composed of nonsignalling strategies that appear to be indifferent at two loci and play Pause-Attack at loci 3 (strategies that always signal A) or 4 (strategies that always signal B) as well as similarly playing Flee at loci 5 or 6. Analytical investigation has confirmed that these strategies are indifferent at some loci, similar to the All-Attack ES set, but they do not meet the formal criteria of an ES set and should not be stable. Their ability to invade each other probably gives them a slightly greater attractive power in the strategy space, but they still amount to a relatively small basin of attraction that the GA was stranded on by the end of the simulation. The sporadic appearance of these strategies, their rapidly declining representation as the mutation rate increases, and their lack of analytically demonstrated stability suggests that runs in which they appeared to be dominant were simply not continued long enough for them to be displaced. These cases do, however, highlight that the GA will find outcomes that might be attracting (if only temporarily) even if they do not show analytical stability. They also highlight the continued need for analytical investigation to distinguish between and describe outcomes that are stable and outcomes that merely appear stable.

In the fifth case are outcomes where the GA appeared to be stable on a mixture of three or more strategies. These were not analysed extensively, but their low rate of occurrence (1.3%) suggests that these are unstable local attractors, although a more detailed analytical examination would be required to prove that conclusively.

## DISCUSSION

In our genetic algorithm investigation of the E85 conventional signalling game, we discovered a previously unknown ES set solution to the game. The ES set, always attack, is a noncommunicating strategy that does not respond to signals and that has a very large basin of attraction in the fitness landscape. This equilibrium is a local optima, it scores less at fixation than does the ESS.

What these results mean for the E85 game as a model of the evolution of conventional signalling is not clear. The simulations show the importance of assumptions about the evolutionary starting points of strategic signalling systems. The process of display ritualization (Tinbergen

1952) may mean that the strategic evolution of signal use starts so close to the eventual ESS that arguments based on the relative sizes of the attractive basins are moot. However, the difficulty in reaching the global optimum, the ESS, in this case is quite remarkable.

Since its formal introduction by Maynard Smith & Price (1973), the notion of an evolutionary stable strategy has had a profound impact not merely on formal models of social behaviour, but more informally in verbal models and discussions. Among nontheoreticians the term 'ESS' has become nearly synonymous with frequency dependence and game theoretical thinking in general. This term communicates an important and intuitive biological concept. While undoubtedly useful, this wider nontechnical use risks theoretical work by focusing formal attention on this one single equilibrium definition. There are several reasons why it is necessary to widen the definition of evolutionary stability when solving communication models and other games of similar complexity.

First, as in the E85 game studied here, ESSs may not be strong attractors. As Nowak (1990, page 237) noted of ESSs some time ago 'it is a common but misleading conclusion that evolution will tend towards such a strategy'. Although other investigations have examined the dynamic stability of a population that is already at or in the neighbourhood of an evolutionarily stable solution (Selten 1975, 1983, 1988; Taylor & Jonker 1978; Thomas 1984, 1985a, b; Hofbauer & Sigmund 1988; Nowak 1990; Takada & Kigami 1991; Leimar 1997), little attention has been paid to the process by which a population might come to approach an ESS in the first place. We have shown that a local optimum in the form of an ES set with a large basin of attraction is most probably the evolutionary endpoint from most starting populations of this game.

Second, and possibly more importantly, is the likelihood that games will not have an ESS at all. Any game of realistic complexity will probably have problems with nonpervasive strategies, and may therefore have no ESS. The number of strategies per player increases geometrically with increases in the complexity of extensive form games. While the condition of pervasiveness is met by the ESS solutions of communication games such as E85 and Kim's aggressiveness signalling game (Enquist 1985; Kim 1995), it becomes less and less likely as variables are added. Games any more complicated than E85, especially games with both variable RHP and subjective resource valuation states, are virtually guaranteed not to have ESSs for this reason. Methods using other solution definitions must be developed to allow for the complexity of biological models. Given that these models are exceptionally difficult to solve by hand, genetic algorithms provide one tractable alternative to analytical investigation. Genetic algorithms can never replace analytical work completely, even for complicated game theoretical problems. Ideally, once potential solutions are identified by the genetic algorithm, analytical methods may be brought to bear to investigate the strategy properties. This is the process that we followed in proving analytically that the solution the genetic algorithm converged on is an ES set (Appendix 4).



A potential caveat to the use of genetic algorithms on game theory models lies in the nature of the search space. A genetic algorithm is a powerful optimization tool with which we can quickly and reliably simulate the process of evolution as it applies to the E85 game, to determine what solution a random starting population playing the game will come to find. However, despite the widespread use of genetic algorithms to solve optimization problems in a variety of fields (Mitchell 1998), GAs work best on a solution space that is static and unchanging (e.g. a system of equations); less is known about the performance of GAs in a dynamic solution space, such as a constantly evolving population. The magnitude of this effect can be seen in the difference in fixation times when the target population is set at the ESS (<100 generations) versus the time to fixation when the target population evolves ( $\approx$ 300 generations).

Previous investigations using genetic algorithms have either usually investigated the effect of stochastic events on very simple  $2 \times 2$  matrix games (e.g. Maynard Smith 1988; Bergstrom & Godfrey-Smith 1998; Orzack & Hines 2005), or explored interactions far too complicated to be solved analytically (Barta et al. 1997; Hoffmeister & Roitberg 1998; Just & Morris 2003). More work needs to be done on games of intermediate complexity if genetic algorithms are to be applied to game theory with the intention of finding the solutions that would be found using analytical techniques. The results of the two techniques must be compared before their results are considered interchangeable. This caveat does not apply to the use of genetic algorithms in evolving neural networks to address the same issues (e.g. Enquist & Arak 1993, 1994; Johnstone 1994; Ezoë & Iwasa 1997; Huse et al. 1999; Blumstein et al. 2006). Neural network models seek to avoid assumptions made by game theoretical models about signal space divisions, and whose purpose is to produce results at odds with game theory. When stochastic simulations disagree with analytical results (e.g. McNamara et al. 2004), it may be argued that the simulations are more biologically important than the analytical results. In the present case, however, the simulations identify an overlooked class of analytical solutions, ES sets. These non-ESS evolutionarily stable outcomes may or may not be more biologically plausible outcomes than the ESS depending upon the assumptions made about the evolutionary starting point of the population.

Taken together, the questions raised by our application of evolutionary algorithms to the conventional signalling model present an interesting avenue for exploration in game theoretical approaches to evolutionary questions, as well as casting healthy scepticism on the biological relevance of ESSs. Not all evolutionarily stable outcomes are ESSs. ESSs are not the best, or only, solutions to biological game theory questions.

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## Appendix 1: Stability Concepts

The following are definitions of the solution concepts used in this paper.

### Nash equilibrium

A Nash equilibrium (Nash 1951) is a set of strategies, one for each player, such that no player can increase their payoff by unilaterally switching to another strategy. In a symmetrical game such as E85, if a player choosing strategy  $J$  in a population where all other players play strategy  $I$  receives a payoff of  $E(J,I)$ , then strategy  $I$  is a Nash equilibrium if

$$E(I,I) \geq E(J,I) \quad \forall J \neq I \quad (\text{A1})$$

The Nash equilibrium definition allows for the possibility that strategy  $J$  is a neutral alternative to  $I$ . It may score equally well, but not better. A Nash equilibrium is presumed to be stable even if  $J$  scores equally well, on the assumption that players do not play  $J$  because of the application of rational foresight. Strict Nash equilibria are stable without such biologically implausible foresight.

### Strict Nash equilibrium

At a strict Nash equilibrium (Harsanyi 1973) no player can unilaterally switch to another strategy without decreasing their payoff.

$$E(I,I) > E(J,I) \quad \forall J \neq I \quad (\text{A2})$$

An ESS is a less restrictive subset of Nash equilibria than strict Nash but still requires no rational foresight to maintain stability.

### Evolutionary stable strategy

Maynard Smith (1982) defined an ESS as either

$$E(I,I) > E(J,I) \quad \forall I \neq J \quad (\text{A3})$$

or

$$E(I,I) = E(J,I) \quad (\text{A4})$$

and

$$E(I,I) > E(J,J) \quad \forall I \neq J \quad (\text{A5})$$

Condition (A3) is that  $I$  is a strict Nash or, failing that, an ESS may be a Nash equilibrium (equation (A4)) that meets the additional condition (equation (A5)) that the strategy is a better alternative against a potential neutral invader than that neutral invader is against itself. This 'second condition' means that a strategy may invade by drift, but that it must be selected against by the original strategy if the invader becomes appreciably common in the population.

ES sets relax the 'second condition' (equation (A5)) and allow for equilibria composed of a set of mutually interinvading strategies whose proportions are free to drift.

### Evolutionarily stable sets

A set of Nash equilibrium strategies  $L$  is an ES set (Thomas 1985b) if

$$E(I,J) > E(J,J) \quad \forall I \in J, J \notin L \quad (\text{A6})$$

and

$$E(I,J) = E(J,J) \quad \forall I, J \in L \quad (\text{A7})$$

### ES sets versus mixed equilibria

An ES set is only superficially similar to the concept of a mixed Nash equilibrium or a mixed ESS. Mixed equilibria, either Nash or ESS, are compositions of two or more pure strategies at precise proportions. Any deviation of the population away from this optimal mixture, either in terms of population composition in the case of a polymorphic population of pure strategists, or a uniform population of probabilistic mixers, will be returned to the optimal mixture in the case of an ESS, or lead to non-equilibrium strategies in the case of a mixed Nash. Either way, these mixed equilibria form a single equilibrium point in the strategy space. On the other hand, an ES set produces a line, area, or volume in the strategy space that contains an infinite number of different pure strategy mixtures that are all co-equilibria.

## Appendix 2: Performance of the GA on Other Tasks

To test the ability of the genetic algorithm to find the ESS to a simpler game we ran a minimally modified version on several versions of the hawk–dove game (Maynard Smith 1982) without role asymmetry (Hurd 2006). This game has a simple mixed ESS when  $V < C$ , to play hawk with probability  $P = V/C$ , and a pure hawk ESS when  $V > C$ . We ran three versions in which  $V$  and  $C$  were varied so that the ESS was to play hawk with 16%, 83% or 100% probability.

We ran 10 replications for each of the three variable combinations, the GA parameters were kept as close as possible to those used in the E85 simulations: population size of 100, simulation length of 500 generations, five encounters per individual per generation, and mutation rate of 0.005. Initial seed of ESS players was not used (all initial populations were randomly generated). No cross-over operator was used (since the chromosome consisted of a single locus (hawk or dove allele) none could be implemented anyway). The percentage of the population playing hawk was averaged over the last 200 generations of each run.

When the ESS was to play hawk with 16%, the GA resulted in a mean of  $17.4 \pm 0.6\%$ , when the ESS was 83%, the GA produced a mean of  $80.0 \pm 0.7\%$ , and when the ESS was 100%, the GA produced a mean of  $97.9 \pm 0.3\%$ . The bias towards 50% evident in these results can be explained by the fact that mutation will increase the percentage of the least common strategy. Indeed, when we did a further set of 10 simulations for the 83% hawk ESS

with mutation set to zero, the mean outcome was 82.9% hawk.

We also ran a number of simulations of the E85 GA in which we held the opponent strategy constant at the ESS. From a 0% ESS seed starting point, the population evolved to the ESS in about 100 generations. These results show that the genetic algorithm is capable of finding ESSs when they exist and have large basins of attraction and other non-ESS optima do not exist.

**Appendix 3: Sensitivity of the Results to Methods and Parameters**

To test for sensitivity of the major results to the simulation parameter values, we ran a set of simulations in which we varied the following model parameters: length of simulation (i.e. number of generations), population size, number of fights per individual per generation, and the use of a crossover operator to make reproduction sexual. Each manipulation was simulated 50 times at each of two levels of initial ESS seed, 0% and 25%. Mutation rate was held constant at 0.002 (a value favourable to the ESS), and all other parameters were held constant at the values used in the main simulations.

These simulations are compared to two similar sets with no manipulations (one at each of 0% and 25% ESS seed) with respect to the number of ESS, ES set, or Other outcomes obtained. The parameter manipulations comprised six sets of simulations in which we increased the number of fights per individual per generation from 5 to 25, 50, and 100 fights, two sets in which we increased population size to 1000, and four sets in which we increased the generations simulated from 500 to 1000 and 5000. Finally, we added a uniform crossover operator that formed an offspring chromosome by swapping between parental chromosomes with a fixed percentage (the crossover ‘weight’) at each locus. For example, if the first parent was AAAAAA and the second was BBFFFF, with a crossover weight of 20%, each locus would be evaluated individually and swapped with a 20% change. Thus, if the second and sixth loci were selected to be swapped, the returned offspring would be ABAAAF and BAFFFA. We ran four sets of simulations, with crossover weights of 20% and 50% (and ESS seed at 0% and 25%).

None of the manipulations showed an improvement in convergence on the ESS (Table A3) with the exception of the population size increasing at 25% initial seed. Significant improvement in convergence on the ESS was found at both the 1000 ( $G_2 = 10.5$ ,  $P = 0.005$ ) and 2500 ( $G_2 = 10.3$ ,  $P = 0.006$ ) population sizes. The number of Other outcomes did not decrease, but the ES set outcomes were less likely at these larger population sizes. Note, however, that no such effect was seen when the population was started from a random point in strategy space. When the ESS seed was 0% the population never evolved to the ESS at these population sizes.

In conclusion, above and beyond the demonstrated analytical stability of the evolutionarily stable set (see Appendix 4), the present results suggest that our discovery

**Table A1.** Colours used to map strategy evolution

		Behaviour when		
		Opponent signal is A		
Opponent signal is B	A	P	F	
	A	Red	Pink	Yellow
P	Purple	Grey	Brown	
F	Blue	Cyan	Green	

Each of the nine possible behaviour strategies (given the player’s own strength) was assigned a different colour. The red–green dimension was used to map the always Attack to always Flee dimension, and the blue–yellow dimension was used to map the Other dimension. A lighter shade denoted use of signal ‘A’ and a darker shade the use of signal ‘B’. This scheme allowed for 18 colours to represent behaviour in a given strength state, and therefore each of the 324 possible strategies could be denoted by a colour pair. The ESS is light purple–dark yellow.

**Table A2.** Breakdown of every unclassified outcome in 1500 runs of the VCDF model by mutation rate and outcome type

Outcome	0.001	0.002	0.003	0.004	0.005	Total
Unstable mixture	21	25	27	40	36	149
Did not fixate in time	3	1	3	10	14	31
BAPAAF (alternative ESS)	8	8	6	0	0	22
BBAPAF	5	0	0	0	0	5
BBAPPF	2	0	0	0	0	2
AAPAAF	1	0	0	0	0	1
AAPPF	1	2	0	0	0	3
AAPAFF	0	1	0	0	0	1
BBAPPF	0	1	1	0	0	2
Stable mix of three or more strategies	11	3	6	0	0	20

Note that stable non-ESS and non-ES set runs are increasingly uncommon as the mutation rate increases, with most nonoptimal outcomes at mutation rates of 0.004 and 0.005 composed of unstable mixtures or runs that did not reach the fixation criteria by the end of 500 generations. With the exception of the symmetric version of the ESS (BAPAAF), none of the alternative outcomes was analytically stable.

of the new solution to the E85 game using the genetic algorithm was not simply because of our specific choice of implementation or parameter values.

**Appendix 4: Proof that \*\*AAAA is an ES Set**

Following Enquist (1985) and Hurd (1997) we can confirm the stability of the Light red/Red All-Attack ES set analytically using what we have termed ‘stability tables’. A stability table for a particular strategy lists the payoffs to a player playing against a population of the target strategy (e.g. the ESS or the ES set) and is logically equivalent to performing a dynamic programming optimization (Houston & McNamara 1999) against the target

**Table A3.** Effect of varying genetic algorithm parameters on the simulation outcomes

Parameter	Value	ESS	ES set	Other
<b>0% ESS seed</b>				
Baseline	Defaults	1	41	8
No. of fights	25	4	38	8
	50	3	46	1
	100	1	41	8
Population size	1000	0	44	6
	2500	0	49	1
	5000	1	40	9
Simulation length	1000	3	41	7
	5000	1	40	9
Crossover	Weight: 20%	0	46	4
	Weight: 50%	1	46	3
<b>25% ESS seed</b>				
Baseline	Defaults	40	7	3
No. of fights	25	28	19	3
	50	38	11	1
	100	36	11	3
Population size	1000	45	0	5
	2500	46	0	4
	5000	39	9	2
Simulation length	1000	34	14	2
	5000	39	9	2
Crossover	Weight: 20%	28	15	7
	Weight: 50%	23	24	3

The parameters varied (and their default values) were: No. of fights: the number of fights used to calculate each individual's fitness each generation (5); Population size (500); Simulation length: the number of generations simulated (500); Crossover weight: the likelihood of recombination (0). The only parameter to increase the probability that the ESS would go to fixation in the population was the population size but only when the initial population was heavily loaded with ESS players. Increasing the population size did not favour the ESS when starting from a random population.

strategy. From the table, we can determine what the best reply to the target strategy is; if the best reply is the target strategy alone, then it is a strict Nash. Here, we present stability tables for two strategies in the Light red/Red set, ABAAAA and AAAAAA (Tables A4, A6). The other strategies of the set, BAAAAA and BBAAAA, are identical by symmetry to the two presented, and so we have omitted their stability tables.

From the tables, it is clear that the following conditions will make ABAAAA stable (Table A4; numbers in square brackets below refer to the numbered cells in the table):

$$\frac{1}{2}V > C_0 \text{ and } V > C_{-1} \quad [1, 2]$$

and

$$F_p > 0 \quad [3, 4, 5, 6, 7]$$

Since cells [3] and [5] are equal, the best reply to ABAAAA is \*\*A[A/F]AA, where \* is any allele at the signalling loci. To show that a strategy choosing F at the fourth locus is not a member of the ES set, we present its stability table (Table A5). The best reply to ABFAAA, one of the potential set members, is not itself but a different strategy AAA[A/F]PP. This strategy is therefore not a member of the ES set. Similar analysis (data not shown) showed that the other three strategies with F at the fourth locus (AAAFAA, BAAF AA, BBFAAA) were not ES set members either.

The situation for AAAAAA is slightly more complicated, as the strategy violates pervasiveness such that the best response to AAAAAA is \*\*AA\*\* (Table A6). As in the previous case, the two alleles at the signalling loci all achieve the same payoff. The last two loci, which code for responses to the 'B' signal are silent, since the target population never uses the 'B' signal. The stability table is constructed with the labels strong

**Table A4.** Stability table for ABAAAA

Display	Opponent display	Opponent behaviour	Behaviour		
			Attack	Pause-Attack	Flee
Strong	A	Attack	$\frac{1}{2}V - C_0$ [1]	$\frac{1}{2}V - C_0 - F_p$	$-C_0$
		Attack	$V - C_{-1}$ [2]	$V - C_{-1} - F_p$	$-C_{-1}$
	B	Attack	$\frac{1}{2}V - C_0$ [1]	$\frac{1}{2}V - C_0 - F_p$	$-C_0$
		Attack	$V - C_{-1}$ [2]	$V - C_{-1} - F_p$	$-C_{-1}$
Weak	A	Attack	$-C_1$ [3]	$-C_1 - F_p$ [4]	$-C_1$ [5]
		Attack	$\frac{1}{2}V - C_0$ [6]	$\frac{1}{2}V - C_0 - F_p$ [7]	$-C_0$
	B	Attack	$-C_1$ [3]	$-C_1 - F_p$ [4]	$-C_1$ [5]
		Attack	$\frac{1}{2}V - C_0$ [6]	$\frac{1}{2}V - C_0 - F_p$ [7]	$-C_0$

Payoffs for all possible outcomes while playing against the communicating All-Attack strategy ABAAAA. The variables used as in Hurd (1997): V: value of the resource;  $C_x$ : cost of an escalated fight against an opponent x of higher ( $C_1$ ), lower ( $C_{-1}$ ) or equal ( $C_0$ ) strength;  $F_p$ : cost of pausing before attacking an opponent that is simply attacking. ABAAAA is stable when  $\frac{1}{2} V > C_0$  and  $V > C_{-1}$  [1,2] and  $F_p > 0$  [3,4,5,6,7].

**Table A5.** Stability table for ABAFAA

Display	Opponent display	Opponent behaviour	Behaviour		
			Attack	Pause-Attack	Flee
Strong A	A	Attack	$\frac{1}{2}V - C_0$	$\frac{1}{2}V - C_0 - F_P$	$-C_0$
	B	Flee	$V - F_A$	$V$	$\frac{1}{2}V$
B	A	Attack	$\frac{1}{2}V - C_0$	$\frac{1}{2}V - C_0 - F_P$	$-C_0$
	B	Attack	$V - C_{-1}$	$V - C_{-1} - F_P$	$-C_{-1}$
Weak A	A	Attack	$-C_{-1}$	$-C_{-1} - F_P$	$-C_{-1}$
	B	Flee	$V - F_A$	$V$	$\frac{1}{2}V$
A	A	Attack	$-C_{-1}$	$-C_{-1} - F_P$	$-C_{-1}$
	B	Attack	$V - F_A$	$V$	$\frac{1}{2}V$

Payoffs for all possible outcomes while playing against the communicating strategy ABAFAA. The variables used are as in Table A4;  $F_A$  is the cost of attacking an opponent who is fleeing.

(‘s’) or weak (‘w’) in place of the signals ‘A’ or ‘B’. Both these rows happen equiprobably following an ‘A’ signal, and so the expected payoff is the mean of their values. The **\*\*AA\*\*** silent mutations produces 36

potential invaders (18 by symmetry). The method for separating the ES set members from the nonmembers proceeds exactly as in the last case. In the interest of space, the details are omitted.

**Table A6.** Stability table for AAAAAA

Display	Opponent display	Opponent behaviour	Behaviour		
			Attack	Pause-Attack	Flee
Strong A	A (s)	Attack	$\frac{1}{2}V - C_0$	$\frac{1}{2}V - C_0 - F_P$	$-C_0$
	A (w)	Attack	$V - C_{-1}$	$V - C_{-1} - F_P$	$-C_{-1}$
B	A (s)	Attack	$\frac{1}{2}V - C_0$	$\frac{1}{2}V - C_0 - F_P$	$-C_0$
	A (w)	Attack	$V - C_{-1}$	$V - C_{-1} - F_P$	$-C_{-1}$
Weak A	A (s)	Attack	$-C_1$	$-C_{-1} - F_P$	$-C_1$
	A (w)	Attack	$\frac{1}{2}V - C_0$	$\frac{1}{2}V - C_0 - F_P$	$-C_0$
B	A (s)	Attack	$-C_1$	$-C_{-1} - F_P$	$-C_1$
	A (w)	Attack	$\frac{1}{2}V - C_0$	$\frac{1}{2}V - C_0 - F_P$	$-C_0$

Payoffs for all possible outcomes while playing against the noncommunicating All-Attack strategy AAAAAA. The variables used are as in Table A4.