An exploration of signalling behaviour by both analytic and simulation means for both discrete and continuous models

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Abstract

Hurd's (1995) model of a discrete action-response game, in which the interests of signallers and receivers conflict, is extended to address games in which, as well as signal cost varying with signaller quality, the value of an observer's response to a signal is also dependent on signaller quality. It is shown analytically that non-handicap signalling equilibria exist for such a model.

Using a distributed Genetic Algorithm (GA) to simulate the evolution of the model over time, the model's sensitivity to initial conditions is explored, and an investigation into the attainability of the analytically derived Evolutionarily Stable Strategies (ESSs) is undertaken. It is discovered that the system is capable of attaining signalling equilibria in addition to those derived via analytic techniques, and that these additional equilibria are consistent with the definition of conventional signalling.

Grafen's (1990) proof of Zahavi's handicap principle is generalised in an analogous manner, and it is demonstrated analytically that non-handicap signalling equilibria also exist for this continuous model of honest signalling.

1 Introduction

In the wake of the fall of group selectionist thought during the mid-sixties, theoretical biologists were left with many problems which had previously been comfortably dealt with through some appeal to the worth of behaviours at a group level. The existence of stable signalling systems was one such problem. Although it was feared that the selfish actions of individuals might compromise the stability of natural signalling systems, such systems appeared to be the frequent products of evolution. In the mid-seventies Zahavi (1975, 1977) proposed that the stability of such signalling systems may be maintained by a 'handicap principle' i.e., that the differential costs paid by signallers of differing quality ensure that honest advertisement is an Evolutionarily Stable Strategy (ESS). The reasoning runs something like this...

> "If signallers differ in some variable of interest to an observer (let's call it quality), observers will be selected to take advantage of any honest indicator of this quality. A signal made as an advertisement of quality will necessarily incur some cost. If, for any signal, high quality signallers suffer less production costs than low quality signallers, then signallers are able to demonstrate their true quality through advertising more strongly than their poorer competitors. Once this strategy is adopted by the signalling population, the signal is an honest indicator of underlying quality. It cannot be invaded by cheats because to signal more strongly than your quality dictates results in a production cost which is not compensated for by the observer response."

However, a parallel argument runs something like this...

> "If signallers differ in some variable of interest to an observer (let's call it need), observers will be selected to take advantage of any honest indicator of this need. A positive response made to an advertisement of need will necessarily induce some benefit. If, for any observer response, high need signallers gain more benefit than low need signallers, then signallers are able to demonstrate their true need through advertising more strongly than their less needy competitors. Once this strategy is adopted by the signalling population, the signal is an honest indicator of underlying need. It cannot be invaded by cheats because to signal more strongly than your need dictates can only result in a response which is not worth enough to compensate the increased production cost."

Notice that whilst the former argument (e.g., Enquist, 1985; Grafen, 1990; Hurd, 1995) assumes differential costs (i.e., that signaller quality might, to some extent, affect the cost of signal production), the latter does not, and that whilst the latter argument (e.g., Godfray, 1991) assumes differential benefits (i.e., that signaller quality might, to some extent, affect the worth of an observer's response), the former does not.

The former argument might be used to support claims that stotting gazelles are honestly informing predators of their ability to outrun a potential pursuer (e.g., Grafen, 1990). Similarly, the latter argument might be used to support claims that begging nestlings are honestly informing their parents of their need for food items.

Godfray (1991) has provided just such an argument for offspring begging calls. He demonstrates that honest signals of offspring need may be ensured by the facts that (i) signals are costly (he assumes that signal costs are constant across offspring irrespective of their need), and that (ii) the worth of parental resources increases with offspring need (i.e., differential benefits but no differential costs). In Godfray's model, parents are selected for responding positively to offspring with high need.

Grafen (1990) considers a similar situation, but with differing assumptions. He suggests that honest signals of offspring quality might be ensured by the facts that (i) parental resources are valuable (he assumes that either resource value is constant across offspring irrespective of their quality, or that resource value increases with offspring quality), and that (ii) the cost of signalling decreases with offspring quality (i.e., differential costs and constrained differential benefits). In Grafen's model, parents are selected for responding positively to offspring with high quality.

In the following sections a simple discrete game, originally due to Hurd (1995), is extended to explore the effects upon signalling equilibria of including, within a signalling model, the impact of both differential costs and differential benefits upon signaller fitness. Section 2 will detail the basic game and the simple extension to it. Section 3 will describe an implementation of the model as an iterative genetic algorithm simulation. Section 4 will consider Grafen's (1990) model, and the relation between its results and those of Hurd's (1995) model. It will be concluded that ensuring Zahavi's two handicap conditions is neither necessary nor sufficient for the existence of an honest communication ESS.

2 A Discrete Signalling Game

Hurd (1995) described a game in which a Signaller (S) is privy to some secret (either High or Low) which is of interest to an Observer (O). S makes a signal (East or West) to O. O, in return, makes a response (Up or Down) of interest to S. The game is schematised in Figure 1.

A signalling strategy determines which signal to make in each of the two states. There are exactly four such strategies. Similarly a response strategy determines which response to give to each signal. There are four such response strategies (see Table 1). Under Enquist's (1985) definition of communication, only four of the 16 possible signal-strategy/response-strategy pairs constitute communication, as only these four prescribe different signals in response to different Signaller states, and different Observer responses to these different signals. This is represented schematically in Table 2.

The fitness consequences of moves in this discrete action-response game will follow those defined by Hurd (1995). In addition, and in contrast, to Hurd's model, we will assume that the value, to a Signaller, of an Observer's response to a signal is *not* independent of the Signaller's initial state.

Signaller fitness, w_S, is calculated as the cost of signalling subtracted from the benefit derived from the Observer response. The former term is defined as a function, c, of the Signaller's initial state, I (either High or Low), and the signalling action, A (either East or West), whilst the latter is defined as a function, v, of the Signaller's initial state, and the Observer's response, R (either Up or Down),

$$w_S = v(I, R) - c(I, A).$$

Similarly, Observer fitness, w_O, is calculated as a function, f, of the state of the Signaller, and the Observer response,

$$w_O = f(I, R).$$

The fitness consequences of each of the eight possible signalling scenarios are depicted in Figure 1.

Hurd defined the payoffs in order that the interests of S and O conflicted. Observers benefit from responding Up to High-state Signallers, and Down to Low-state Signallers,

$$w_O(H, U) > w_O(H, D),$$

$$w_O(L, U) < w_O(L, D),$$

whilst Signallers benefit from eliciting an Up, rather than a Down, response from Observers,

$$v(H, U) > v(H, D),$$

$$v(L, U) > v(L, D).$$

After Hurd, we define the relative value of an Up response for each class of Signaller as

$$V_H = v(H, U) - v(H, D) > 0,$$

$$V_L = v(L, U) - v(L, D) > 0.$$

Similarly, we define the relative cost of signalling West for both classes of Signaller,

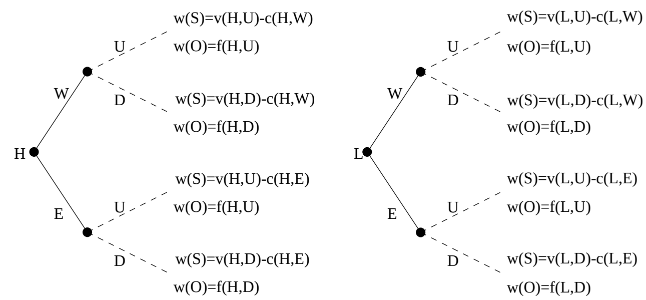

Figure 1: Decision trees and fitness consequences for a discrete action-response game. Initially, a Signaller (S) finds itself in one of two possible states (H or L) depicted by the two leftmost nodes of the decision trees. S makes one of two possible signals (E or W) depicted by a labelled solid line. Subsequently an Observer (O), naive as to the state of S, but informed by S's signal, makes one of two possible responses (U or D) depicted by a labelled dashed line. The fitness consequences of each of the eight possible interactions are depicted at the terminal node of each branch of the two decision trees. See text for further clarification.

Signalling Strategies and Response Strategies				
Bit Pattern	Signalling Strategy		Response Strategy	
(0,0)	S(East,East)	Cynic	O(Down,Down)	Mean
(0,1)	S(East,West)	Honest	O(Down,Up)	Believer
(1,0)	S(West,East)	Liar	O(Up,Down)	Non-Believer
(1,1)	S(West,West)	Bluffer	O(Up,Up)	Generous

Table 1: Each of the four possible Signalling Strategies, depicted in the form S(what to do if state is Low, what to do if state is High), and four possible Response Strategies, depicted as O(what to do if S plays East, what to do if S plays West), with their associated bit-pattern and descriptive. See Section 3 for the rationale underlying the allocation of descriptive terms to strategies.

Signalling Strategy-Response Strategy Pairs				
	Response Strategy			
Signalling Strategy	O(Up,Up)	O(Up,Down)	O(Down,Up)	O(Down,Down)
S(East,East)	.	.	.	.
S(East,West)	.	x	x	.
S(West,East)	.	x	x	.
S(West,West)	.	.	.	.

Table 2: Each of the four possible Signalling Strategies and Response Strategies are shown. The four Signalling-Strategy/Response-Strategy pairs which constitute communication (*sensu* Enquist, 1985) are denoted 'x' whilst non-communicative pairings are denoted with a period.

$$C_H = c(H,W) - c(H,E),$$

$$C_L = c(L,W) - c(L,E).$$

In order that S(E,W) be the unique, best response to O(D,U) (the communication Signalling-Strategy/Response-Strategy pair arbitrarily chosen by Hurd as a candidate ESS), it must be the case that,

$$v(H,U) - c(H,W) > v(H,D) - c(H,E),$$

$$v(L,D) - c(L,E) > v(L,U) - c(L,W).$$

By substitution, it follows that,

$$V_H > C_H,$$

$$V_L < C_L.$$

It is plain that Hurd's result, $C_L > V > C_H$, is the special case inequality resulting from the substitution of $V = V_H = V_L$, i.e., the assumption that "V is equal for all signallers"(Hurd, 1995, p.219). Hurd depicts his special case graphically (see Figure 2a). He points out that signalling equilibria exist in part of the region of the graph defined by $C_H \leq 0$, which he interprets as indicating that 'handicap' signals need not be costly for High-state Signallers at equilibria, and indeed may be chosen preferentially by High-state Signallers. He also points out that despite the fact that all signalling equilibria satisfy the inequality $C_L > C_H$, signalling equilibria do not exist in certain areas of the graph satisfying this inequality, i.e., that $C_L > C_H$ is necessary but not sufficient for communication to be stable.

However, under conditions, modelled here, in which $V_L \neq V_H$, it can be shown that Zahavi's handicap principle is neither necessary nor sufficient for the existence of signalling equilibria (see Figure 2b and c). When the value of a beneficial response is greater for Low-state Signallers than High-state Signallers (i.e., $V_L > V_H$, see Figure 2b) signalling equilibria lie above the line $C_L = C_H$, but when the value of a beneficial response is higher for High-state Signallers (i.e., $V_L < V_H$, see Figure 2c) signalling equilibria may lie below the line defined by this inequality.

3 An Iterative Simulation of a Discrete Signalling Game

Simulations are sometimes presented as 'artificial worlds' worthy of investigation for their own sake; "Communication evolved within this world", "Different classes of parasite evolved within this world", "Mean fitness increased within this population when tools were introduced". However, this practice is theoretically bankrupt, and thus such statements have no scientific currency.

The 'creator' of artificial worlds is confused if she feels that she mimics the naturalist in simply observing her subject matter under various conditions. True naturalism takes place within an overarching theoretical framework, marshalling observations in order to support, or challenge, current biological theory. In contrast, the observations made of an artificial world constructed within no such framework can neither challenge, nor support, any theory with application wider than the artificial world itself. Such observations can serve no theoretician whose interests reach further than a full understanding of a specific artificial world. The extent to which the facts revealed by such observations constitute new knowledge is simply the extent to which the creator of an artificial world initially failed to understand it.

In baldly comparing and contrasting an artificial world with the real thing, the creators of such artificial worlds are attempting to both have their cake and eat it. However, there is no cake to be had in any appeal to 'interesting' similarities between the artificial world and the natural world, nor is there any cake to be eaten in drawing attention to 'interesting' contrasts between them. Unless such parallels were previously hypothesised to exist, they are either merely accidental (and thus not interesting), or merely purposed (and thus not interesting).

Within experimental scientific paradigms, no project is validly undertaken without an explicit hypothesis in mind; an explicit hypothesis requiring a theoretical framework, a reasonably rigorous vocabulary, etc., etc. Under such a paradigm, theory precedes experiment, informing and validating experimental design. The simulation becomes a means of testing hypotheses, of exploring the consequences of theories, of revealing the implications of a scientific position. The gathering of observations ceases to be an aimless whim, becoming a process with a goal wider than merely understanding a specific simulation. For an experimental scientist, the collection of observations is not valuable in and of itself, as certain simulation designers would seem to have us believe, but is only valuable with respect to hypotheses within a theoretical framework. It is in this light that the simulation presented within this section is intended to be viewed.

Whilst the analysis presented in the previous section reveals which areas of the parameter space admit of honest evolutionarily stable strategies (ESSs), it makes no claims concerning admissible trajectories in the state space occupied by a population of signallers and receivers playing a particular version of this discrete action-response game. In addition, the analysis above makes no attempt to describe the behaviour of systems which fail to attain an honest signalling ESS. Simulation-based paradigms seem perfectly placed to step into this breach, and indeed seem ill-prepared for any other scientific enterprise (de Bourcier & Wheeler, 1994; Miller, 1995; Noble, 1997).

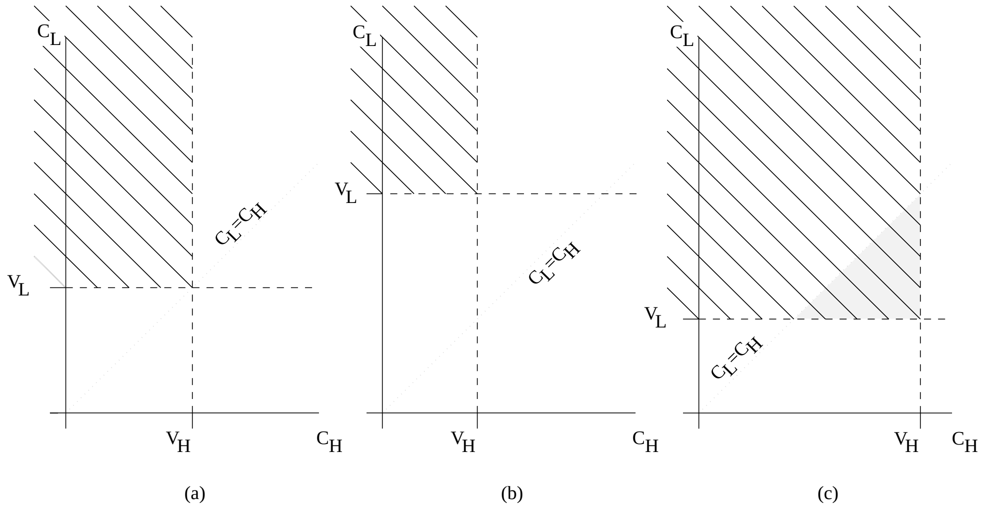

Figure 2: In each graph a pair of cost parameters (C_H, C_L) specifies a point in the plane of all possible versions of the discrete action-response game for a particular pair of value parameters (V_H, V_L) which divide the space into four quadrants. Graphs depict *(a)* Hurd's (1995) result in which $V_H = V_L$, *(b)* a scenario in which $V_H < V_L$, and *(c)* a scenario in which $V_H > V_L$. In each graph the diagonal hatching corresponds to (C_H, C_L) parameter values which afford stable communication equilibria, the line $C_L = C_H$ divides the space into two areas, the upper of which is predicted, under Zahavi's model, to contain handicap equilibria, whilst the lower is predicted to offer no communication equilibria. The shaded area in *(c)* highlights non-handicap parameter values in which (*contra* Zahavi) stable signalling may occur.

Therefore, in order to discover empirically whether signalling equilibria are attainable by a population initially behaving 'randomly', and to explore the behaviour of the system prior to (potentially) achieving an honest signalling ESS, an iterative simulation approach was undertaken[1].

A population of signallers/receivers was distributed across a 25-by-25 grid world. Each cell in the grid contained one signaller and one receiver. Each signaller was allocated a discrete internal state (either High or Low) at random[2]. In addition, each signaller inherited one of the four possible signalling strategies (represented as a two-bit binary number) from its parent. Similarly each receiver inherited one of the four possible response strategies (again represented as a two-bit binary number) from its parent (see Table 1). The fitnesses of signallers and receivers were calculated as shown in Figure 1, each signaller interacting once with the receiver sharing its cell.

Once each signaller and receiver had been assessed the whole population was updated synchronously. The location of a parent was chosen using a normal probability distribution with standard deviation 0.75 centred on the location of the offspring's cell. Six potential parents were chosen for each offspring signaller. An offspring signaller inherited its signalling strategy from the fittest of these six. Similarly, an offspring receiver inherited its response strategy from the fittest of six receivers chosen from the previous generation in the same manner. A mutation rate of one bit in one hundred ensured that offspring sometimes inherited a strategy which differed from that of their parents. Populations were simulated for 500 generations in this manner, during which time the proportions of signallers playing each of the four possible signalling strategies, and the proportions of receivers playing each of the four possible response strategies, were recorded.

In order to fully specify a simulation run, several parameter values must be decided upon. The costs of signalling each of the two possible signals (East or West) must be specified for each of the two possible signaller

[1] Copies of the code, and a version of this paper with colour figures, are available from the W^3 URL: `http://www.cogs.susx.ac.uk/users/sethb/ecal97.html`

[2] i.e., the internal trait was non-heritable. This is in accordance with many models of signalling evolution (e.g., Hurd, 1995; Grafen, 1990). Models in which the advertised trait, in addition to the advertising strategy, is itself heritable encounter a problem known within evolutionary theory as the lek paradox. A full account of this problem is beyond the scope of this paper (interested readers are directed to Kirkpatrick & Ryan, 1991; Pomiankowski & Møller, 1995). Briefly, in simple models of signal evolution involving a heritable advertised trait, the variability of the trait across the population tends to decrease over evolutionary time. As the variation in the trait falls observers find any signal which distinguishes between signallers with differing traits less and less informative. As a consequence signalling (which involves some cost to the signaller and, possibly, the observer) tends to die out.

states (High or Low). Similarly, the benefit of obtaining each of the two possible responses (Up or Down) must be specified for each of the two possible signaller states. Finally the value to the receiver of making each of the two possible responses must be specified for each of the two possible signaller states.

The fitness consequences of receiver responses *for the receiver* were fixed at 40 for responding Up to a High-state signaller, or Down to a Low-state signaller, and zero otherwise.

The cost of signalling East for both Low-state signallers and High-state signallers was fixed at zero. All 576 possible pairs drawn from the set {10.0, 12.5, 15.0, ..., 70.0} were explored as costs of signalling West for High-state signallers, and signalling West for Low-state signallers.

The value *to a signaller* of a Down response was fixed at zero for both High- and Low-state signallers. The value *to a signaller* of a receiver response Up was drawn from the set {(40,40), (50,30), (30,50)} where the figures in parentheses denote (value to Low-state signaller, value to High-state signaller). These three pairs can be represented by Figures 2a, 2b, and 2c respectively.

These parameter values allow the exploration of cost parameters lying in each of the four quadrants for each of the three classes of scenario depicted in Figure 2.

The rationale underlying the choice of labels used throughout the results section to describe the possible strategies (see Table 1) reflects the costs and benefits descried above. Signalling East is a costless action and is thus the default signalling behaviour, whereas signalling West is costly and will be regarded as a positive action in comparison. Thus a signaller which always signals West will be dubbed a 'Bluffer', and one which signals West only when High state will be described as 'Honest' in that a positive signal is being used to advertise a positive (High) trait. Similarly, as obtaining a Down response is not beneficial to signallers, receivers which always respond Down will be termed 'Mean' in comparison to 'Generous' strategists which always respond Up.

The initial conditions imposed upon the populations were also varied. Populations initially with random behaviour (strategies drawn at random from the strategy set), were compared to populations initially converged at an Honest signalling strategy and Believing response strategy, and populations initially converged at a Cynical signalling strategy and Mean response strategy. These three classes of initial conditions will hence forward be referred to as 'Random', 'Honest', and 'Cynical' initial conditions, respectively.

3.1 Results

For each setting of the value parameters, a pair of cost parameters was taken to specify a system lying within one of four quadrants defined by the two inequalities

$$V_H > C_H,$$

$$V_L < C_L.$$

From the analysis carried out in Section 2, systems residing in the top-left quadrant of parameter space (hereafter Quadrant 1) satisfy the conditions for the existence of an honest signalling ESS. Systems residing in the top-right quadrant (hereafter Quadrant 2) cannot support honest communication as the costs of signalling are too great for both High- and Low-state signallers. Systems residing in the bottom-left quadrant (hereafter Quadrant 3) cannot support honest communication as the costs of signalling are bearable for signallers of Low state allowing them to mimic High-state signallers. Systems residing in the bottom-right quadrant (hereafter Quadrant 4) cannot support honest signalling as High-state signallers cannot afford to signal, whilst Low-state signallers can.

Five classes of behaviour were exhibited by the system. Stereotypical examples of trajectories through strategy space for four of these classes are presented in Figure 3, whilst their distribution across parameter space is represented by Figure 4. Trajectory (a): *Honesty* is produced only by systems with Quadrant 1 parameters; populations converge on Honesty and Belief. This class of behaviour corresponds to the honest signalling ESS predicted in Section 2. Although this ESS existed for all games within Quadrant 1 (i.e. from Honest initial conditions, no simulation ever deviated from Honesty), simulations from Random initial conditions, with parameters for which the inequality $V_H > V_L$ held, often failed to reach it.

Trajectory (b): *Conventional Cheating* is found only for games in which $V_H > V_L$. For such games, this class of trajectory accounts for all behaviour within Quadrants 2, and 4, some of the behaviour within Quadrant 3, and (for simulations from Random initial conditions) some of the behaviour within Quadrant 1; signalling populations converge on Cynic with a fluctuating proportion of Liars, whilst receiver populations converge on Non-Believers with a fluctuating proportion of Generous strategists. This class of behaviour is a non-signalling scenario suffering a low level of Liars which exploit Generous strategists (by signalling West when Low state). As the frequency of Lying rises the fitness of Generous strategists falls and they are replaced by Non-Believers, but as the frequency of Liars falls the fitness of Generous strategists rises and they replace Non-Believers. This pair of processes ensures that the populations never settle, and continually cycle due to the intransitive dominance hierarchy instantiated by the signalling and receiving strategies. I term this class of behaviour *conventional* due to the fact that the behaviour is maintained by negative feedback interactions typical of conventional signalling scenarios.

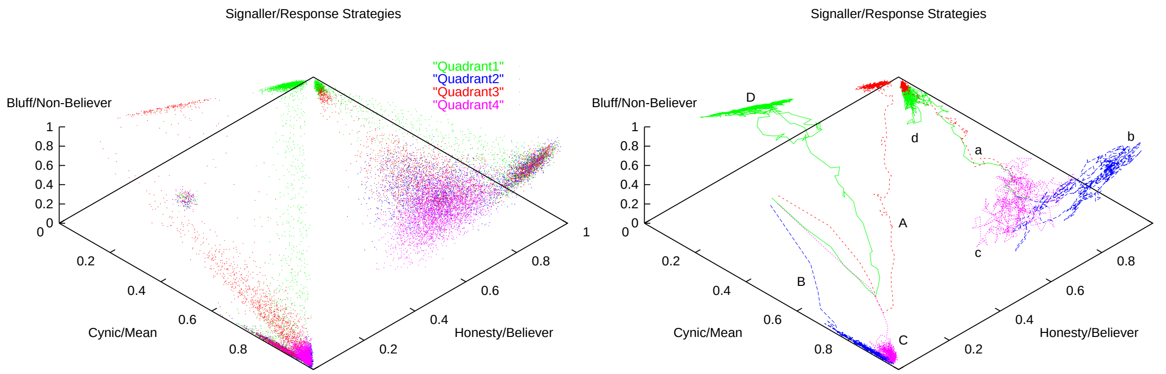

Figure 3: *Left plot:* Population evolution from Random initial conditions. The left and right sides of the plot contain four data sets. The left-side data set pertains to 20 populations of signallers, whilst the right-side data set pertains to 20 populations of receivers. Each data set represents points on state-space trajectories followed by evolving populations under parameters which fall into one of the four possible parameter quadrants. The co-ordinates of each point represent the proportion of signallers/receivers using each of the strategies denoted by the axis labels at instants sampled every 10 generations over 500 generations of evolution. The remaining fourth strategy is implicit in the graph (decreasing with distance from origin) as each strategy space has only three degrees of freedom, i.e., each population state-space is wedge shaped rather than cubic. Thus the density of points indicates the amount of evolutionary time populations spend in an area of strategy space. *Right plot:* Stereotypical trajectories through strategy-space for four of the five classes of system behaviour. Populations were evolved from Random initial conditions. Associated pairs of signaller and receiver trajectories are denoted by the same letter (upper case denotes signaller trajectories, lower case denotes receiver trajectories).

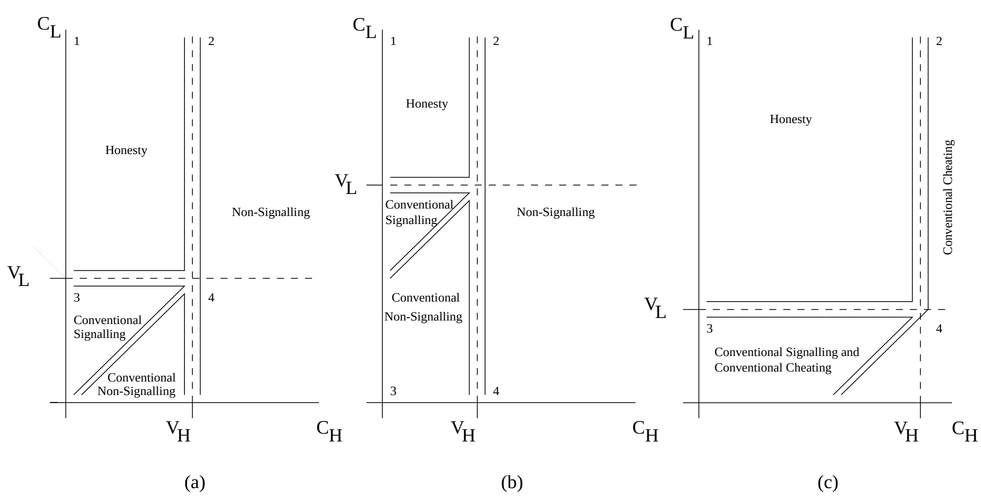

Figure 4: Graphs as per Figure 2 showing the classes of behaviour observed across the parameter space of the extended discrete action-response model. Honest behaviour is confined to the predicted quadrant of parameter space for all three graphs (although from Random initial conditions Conventional Cheating trajectories were observed within Quadrant 1 for simulations in which $V_H > V_L$). Non-Signalling trajectories account for the behaviour within Quadrants 2 and 4 (although Conventional Cheating trajectories are observed within Quadrants 2 and 4 for simulations in which $V_H > V_L$). Within Quadrant 3 two regions were observed separated by the line $V_L - C_L = V_H - C_H$. Conventional Signalling trajectories accounted for the region above this line, whilst Conventional Non-Signalling accounted for the region below it (although, for simulations in which $V_H > V_L$, Conventional Cheating trajectories were observed across the whole of Quadrant 3, whilst no Conventional Non-Signalling was observed).

Trajectory (c): *Non-Signalling* is found in Quadrants 2 and 4 for parameter values satisfying the inequality $V_H \leq V_L$; signalling populations converge on Cynic, whilst receiver populations wander in the centre of strategy space. Within this class of behaviour any strategy adopted by the receiver population can be exploited by the Low-state signallers, thus no clear response strategy emerges, and signallers cut their losses by refusing to signal.

Trajectory (d): *Conventional Signalling* is found only for parameter values lying within Quadrant 3, and satisfying the inequality $V_H - C_H > V_L - C_L$; signalling populations converge on a fluctuating mixture of Honesty and Bluffing, whilst receiver populations converge on Belief but maintain a significant, but very low (and fluctuating) frequency of both Mean and Generous strategists. This class of behaviour is a conventional signalling scenario suffering a degree of Bluffing strategists who exploit Believing receivers. In a manner similar to (b) above, the stability of this scenario is maintained through weak negative feedback interactions which induce cyclic trajectories typical of conventional signalling scenarios.

The fifth class of behaviour: *Conventional Non-Signalling* is also found only in Quadrant 3, under parameter values satisfying the inequalities $V_H - C_H < V_L - C_L$, and $V_H \leq V_L$; signalling populations converge on Cynic with regular insurgences of Bluffing strategists whilst receiver populations wander in the centre of strategy space with a slight over-representation of Believers. The invading Bluff strategy exploits the over-representation of Believing receivers, but is prevented from dominating the signaller population by negative feedback from the receiver population.

To summarise, several interesting, robust phenomena, which were opaque to the analysis carried out in Section 2 have been detailed. The behaviour of this very simple system varies from non-signalling equilibria, through scenarios in which stability is maintained through reciprocal fitness interactions which constitute the negative feedback indicative of conventional signalling(Maynard Smith & Harper, 1988, 1995), to honest signalling equilibria in which honesty is maintained though the interaction of differential costs and benefits. Further exploration of the system's behaviour will be necessary before the factors governing which mode of behaviour will evolve in a particular case are made explicit.

However, the discrete nature of the action-response game considered here, although attractively tractable, also risks lacking application to natural signalling through its very simplicity. Do the classes of behaviour exhibited in a discrete game such as the one considered above exist for more complex models? As a first step towards answering this question, an analysis of Grafen's (1990) model is undertaken in an effort to demonstrate that at least the results derived analytically in Section 2 will generalise to a continuous model.

4 A Continuous Signalling Model

Alan Grafen's (1990) model of Zahavi's handicap principle upheld Zahavi's contentions that in order for communication to be stable certain relationships between signal cost and signaller quality had to hold. Specifically, the criteria which Zahavi (1975, 1977) specifies are that (i) signals must be costly, and that (ii) for any given level of advertisement, signallers of low quality must suffer higher production costs than signallers of higher quality.

After defining signaller (male) fitness (w) as a function of three variables, the signaller's level of advertisement (a), the strength of observer (female) preference for advertising (p), and signaller quality (q), Grafen asserted that Zahavi's criteria could be formalised as conditions placed on various partial derivatives of the fitness function. First order derivatives were represented as w subscripted with a digit denoting the variable (a, p, or q) with respect to which the rate of change of fitness was being derived. Second order derivatives were similarly denoted by w subscripted with a pair of digits.

For example, the condition that signals must be costly (i.e., that, as advertising levels increase, fitness decreases) is maintained by the inequality, $w_1 < 0$,

$$\frac{\partial w}{\partial a} < 0.$$

That female preference is beneficial is similarly maintained by the inequality, $w_2 > 0$,

$$\frac{\partial w}{\partial p} > 0.$$

A further condition ensured that "better males do better by advertising more"(Grafen, 1990, p.520),

$$\frac{\partial w / \partial a}{\partial w / \partial p} \text{ is strictly increasing in q.} \qquad (1)$$

Grafen demonstrated that if the beneficial fitness consequence of female preference was independent of signaller quality ($w_{23} = 0$, which Hurd's (1995) model also assumes), or if the beneficial fitness consequences of the strength of female preference were greater for signallers of higher quality ($w_{23} > 0$), then that equation (1) holds can be ensured by the maintenance of the following inequality: $w_{13} > 0$ (i.e., that higher quality signallers pay lower advertising costs – Zahavi's second handicap criterion). Grafen proceeds to show that communication equilibria exist under these conditions.

Grafen then attempts to reverse this proof in order to show that *any* stable communication equilibria require that Zahavi's criteria hold, and thus that handicap equilibria are not merely "quirky possibilities"(Grafen, 1990, p.521).

4.1 General Solution

Condition (1) can be presented as

$$\frac{\partial(\frac{w_1}{w_2})}{\partial q} > 0$$

which, after application of the quotient rule, can be re-written as

$$\frac{w_{13}w_2 - w_1 w_{23}}{(w_2)^2} > 0.$$

The denominator is necessarily positive, and by assumption, w_1 is negative, whilst w_2 is positive. Thus, discarding the denominator, and dividing through by w_2 casts the general solution to equation (1) as

$$w_{13} + w_{23} * |\frac{w_1}{w_2}| > 0. \quad (2)$$

We will now explore the form that this inequality takes under each of the three classes of condition governing the manner in which the beneficial effects of signalling for the signaller are moderated by the signaller's quality; an analysis analogous to that carried out in Section 2 for the extension of Hurd's (1995) model.

First, under the condition in which the beneficial fitness consequence of female preference is independent of signaller quality (i.e., $w_{23} = 0$, analogous to Hurd's $V = V_H = V_L$), equation (2) reduces to $w_{13} > 0$. This is Grafen's result (i.e., Zahavi's second handicap criterion).

Under the condition in which the beneficial fitness consequences of female preference are higher for poorer quality signallers (i.e. $w_{23} < 0$), equation (2) reduces to,

$$w_{13} > |w_{23}| * |\frac{w_1}{w_2}|.$$

It is plain that, whilst this inequality *requires* that $w_{13} > 0$, it remains the case that the satisfaction of $w_{13} > 0$ is not *sufficient* for signalling to be stable. Lower quality signallers must not merely suffer higher advertising costs than their higher quality competitors, but must suffer advertising costs that are higher *by some amount large enough to balance any fitness benefits accrued through signalling.*

Conversely, under the condition explored by Grafen, in which the beneficial fitness consequences of female preference are higher for higher quality signallers (i.e., $w_{23} > 0$), equation (2) reduces to,

$$w_{13} > -w_{23} * |\frac{w_1}{w_2}|.$$

It is equally plain that whilst, as Grafen maintains, ensuring that $w_{13} > 0$ is *sufficient* to ensure a solution to this inequality, it is not *necessary*. This inequality admits of solutions in which $w_{13} < 0$, i.e. non-handicap equilibria exist.

4.2 Discussion

The partial differential equation denoted by w_{23} can be interpreted as governing the manner in which signaller quality might mediate the contribution to signaller fitness of observer responses. Grafen (1990) asserts that it is reasonable to assume that $w_{23} > 0$ in certain natural signalling scenarios (aggressive displays by harem defenders, begging nestlings, and stotting gazelles) which are paradigmatic of many (if not most) stable signalling systems.

However, consider a line of reasoning which might support the claim that Zahavi's second handicap criterion (that poor quality signallers must pay more for a certain signal than their higher quality competitors) is true of natural signallers. "Poor quality signallers", the reasoning runs, "pay higher signalling costs because, in proportion to their reserves, the energy expenditure, time expenditure etc., required for any signal is higher for poor quality signallers than for those of higher quality".

This line of reasoning has a corollary in the claim that "Poor quality individuals gain more from a particular observer response than their higher quality competitors because any resource gain would be greater proportionally for poor quality signallers than for those of higher quality". If this argument holds then typically (*contra* Grafen) $w_{23} < 0$.

This argument relies on what I shall call a 'relative' reading of Zahavi's second handicap criterion. Under this reading, although two signallers of differing quality use identical amounts of energy to produce a signal, the fitness consequences of making that signal differ as a result of the relative cost of signal production. From the perspective of a low quality signaller, the signal is *relatively* expensive, whereas from the perspective of a high quality signaller, it is *relatively* cheap. By relative I am referring to the energetic demands of signal production when compared to the signallers' energy resources. Such a reading allows one to construct the corollary above.

However, Zahavi's (1977) exposition of the second handicap criterion seems to promote a more 'absolute' account of signal costs. He claims that "it is reasonable to assume that high quality phenotypes and experienced individuals pay less for the cost of the same sized handicaps than low quality phenotypes" (p. 604). The thought here perhaps, is that the superior skills, metabolism, morphology, etc., of high quality phenotypes might just make signalling easier. This would result in a situation in which the absolute energetic expenditure required to make the same signal differs between signallers of differing quality. This absolute reading does not licence a corollary of the kind outlined above. In contrast, the benefit of an observer response might be considered to be best utilised by the same high quality individuals which find it easier to produce signals. For example, a particular worm might have a particular calorific value which could be best exploited by the metabolism of a large, fit, chick.

Such reasoning would support Grafen's (1990) contention that "the fitness gained by a marginal improvement in the parent's assessment of a chick is at least as great for big as for small chicks" (p. 527). However, a more 'relative' reading of signalling costs/benefits seems to motivate Godfray's (1991) model of offspring begging signals. He (directly reversing Grafen's assumption) assumes that "the benefits of [solicited parental] resources increase with [offspring] need". Yet, despite this contrast, Godfray reached the conclusion suggested by Grafen, that honest advertisement could be an ESS, and could be ensured by costly signalling.

The reason for this agreement is due to a second contrast between Grafen's appraisal of the begging scenario and that of Godfray's. Whereas Grafen assumes that the costs of signalling vary with need (with weaker signallers incurring higher production costs than their stronger competitors), Godfray assumes that they are constant. For Grafen differential signalling *costs* impose honesty, the associated signal benefits are either neutral with respect to need ($w_{23} = 0$), or favour the strong ($w_{23} > 0$). For Godfray, differential signalling *benefits* impose honesty through favouring the weak; the associated signalling costs are neutral with respect to need.

However, as was demonstrated in previous sections, once both costs *and* benefits are allowed to vary with signaller need, honesty can be seen to be maintained by a simple cost-benefit relationship. In the general case under consideration here, one cannot maintain that ensuring Zahavi's two handicap conditions is either necessary or sufficient for the existence of an honest communication ESS.

5 Conclusion

In summary, signalling equilibria were shown to exist under three conditions defined by Grafen (1990) using the inequalities, $w_{23} < 0$, $w_{23} = 0$, and $w_{23} > 0$, and also defined for the extension of Hurd's (1995) discrete action-response game explored here using the inequalities, $V_L < V_H$, $V_L = V_H$, and $V_L > V_H$. In concert these three classes of scenario were used to explore the effects of the benefits to signallers of their signalling behaviours, not merely the costs of such behaviours. Non-handicap signalling equilibria were shown to obtain under certain conditions. It was demonstrated that in order to show that a signalling system is stable, a relationship between signalling costs, signaller quality, *and* (*contra* Zahavi) signalling *benefits* must be shown to hold, *not* merely a relationship between signalling costs and signaller quality.

In addition to these analytically derived results, further exploration of Hurd's (1995) discrete action-response game was carried out utilising a simulation-based paradigm which allowed a qualitative account of the system's dynamics to be formulated. As a result of this exploration, several interesting, robust phenomena, which were opaque to the analysis carried out in Section 2 were detailed. Amongst the phenomena described were classes of conventional signalling scenario. These stable signalling scenarios cannot be characterised as fixed points in the system's dynamics. They exist as higher dimensional attractors (e.g., limit cycles) in strategy space, and as such are not amenable to a simple ESS approach.

Further work, both analytic and simulation-based, must be undertaken before a full characterisation of the dynamics of these systems (both discrete and continuous) can be constructed, and the extent of their applicability to the evolution of natural signalling systems can be assessed.

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