*J. theor. Biol.* (1998) **192,** 197–211

# Conventional Signalling in Aggressive Interactions: the Importance of Temporal Structure

Peter L. Hurd* and Magnus Enquist

*Division of Ethology, Department of Zoology, University of Stockholm, S-106 91 Stockholdm Sweden*

(*Received on* 6 *October* 1997, *Accepted on* 10 *December* 1997)

Animals often communicate using signals which seem to be completely arbitrary. These postures and ritualised acts give the impression that they have no other effect than to simply appear as they do to the receiver. Such signals, whose meanings are associated to their form through arbitrary convention, are called conventional signals. Theoreticians have directed much less attention to the topic of conventional signalling than to alternative signal types, such as handicapping signals. This lack of attention has lead to a poor understanding of threat displays and other communication contexts in which signals do not appear costly. We present what we believe to be the simplest possible model of conventional signalling between individuals with conflicting interests. This model requires a more complicated, and realistic, time structure than the action–response games widely used to model handicapped signalling. We demonstrate that this need for extended time structure is due to the exchange of information that conventional signalling requires. Signallers must be in a state of ignorance when choosing a signal, they must later receive information before choosing a subsequent action. The order in which these events happen is critical to conventional signalling. These results demonstrate the necessity of investigating communication with more complicated games than action–response games.


## 1. Introduction

Game theoretical approaches have led to dramatic changes in the understanding of biological communication. The full realisation that receivers should use signalled information to their fullest advantage, quite likely to the ultimate disadvantage of the sender, had particularly profound impact. (Maynard Smith, 1974; Dawkins & Krebs, 1978). It became clear that such information ought not necessarily to be given away as had been assumed by classical ethology (see Dawkins & Krebs, 1978; Hinde, 1981; Krebs & Dawkins, 1984), and references therein). In no situation is this clearer than in aggressive communication, where a successful threat or bluff will yield an immediate gain. Receivers should ignore claims of desperation, or boasts of extreme strength, from signallers as they are expected to produce nothing else. These arguments assumed implicitly that signallers could escape highly escalated bluffs without costly ramifications. This assumption was largely imposed by assuming a simplified interaction such as action–response game, or some other game with minimal time structure. Enquist (1985) demonstrated that conventional signalling could occur in aggressive interaction if one considered games with more complicated sequences of events.

Conventional signals are those for which the meaning and form of the signals are associated by arbitrary convention, it is communication in its most pure sense. What makes conventional signalling so interesting is that many signals, particularly those used in aggressive communication, do not seem to be particularly wasteful, signallers do not appear to be put into positions of remarkable vulnerability by their signals. Subsequent models of biological communication (Grafen, 1990) concentrated on signals with

*Author to whom correspondence should be addressed at: 4145, Fisher Road NE, apt. no. 59, Salem, Oregon 97305, U.S.A.

0022–5193/98/100197 + 15 $25.00/0/jt970611

such inherent costs. These models have properties quite unlike those of conventional signalling systems (Hurd, 1997).

Formally, a conventional signal is one in which there is no difference in cost for the use of alternative signals.

$$U^S(z,s_iF) = U^S(z,s_j,F) \,\forall\, z,F$$
$$U^R(z,s_iF) = U^R(z,s_j,F) \,\forall\, z,F \qquad (1)$$

where $U^S$ is the pay-off to the signaller, $U^R$ to the receiver, $z$ is the current state of the game (or history, Fudenberg & Tirole, 1992), $s$ is the signal used, and $F$ is the sequence of future moves made by the players to the end of the game.

This means that the signaller pay-off depends only on the states and subsequent actions of the players, not on the particular signal used. The sole effect of the signal is to influence the receiver's subsequent actions, and variation in signal use is maintained through this effect. [We may also require that the same properties apply to the receiver pay-offs with respect to the same signal, this is the case for biological "displays" (Moynihan, 1960)].

The first biological model of conventional signalling was Enquist's 1985 model, which demonstrated that conventional signalling can be used both to communicate fighting ability (Model I) and motivation (Model II) (the work we present here is based on Model I, and we shall not be discussing Model II further). Model I describes two contestants who meet and compete over some non-divisible resource. These contestants are either strong or weak [for a treatment of more than two strength states see Hurd (1997)] and have three possible fighting behaviours. The game can be divided into two distinct phases, the first, "signalling phase" in which the contestants learn of their own strength and choose a signal to use, and the second "fighting phase" in which they observe their opponent's signal and choose a fighting behaviour. Each contestant has three possible behaviours at his disposal, Attack, Pause–attack, and Give-up.

Attacking always entails a cost, the magnitude of which depends on the relative strength of the two contestants. This cost can be avoided by Pause–attacking as long as the opponent Gives-up. Pause–attacking an opponent who does not Give-up, but who Attacks, is more costly than if the choice had been to Attack instead of Pause–attacking. Stronger contestants always win against weaker ones, and the probability of winning is equal for contestants of equal strength. Players who Give-up always lose, if both players give-up the resource is randomly awarded to one of them.

The ESS strategy is to accurately signal strength in the signalling phase, then Attack if states are equal, to Give-up when weaker than the opponent, and to Pause–attack a weaker player.

The stability of this conventional signalling system is dependent upon two conditions:

(1) the value of the resource being contested is approximately equal to the costs incurred during an escalated contest;
(2) that these costs are inescapable.

The first condition reflects the sort of conditions under which threats are seen in biological systems. Uncommunicative, all-out, fights are seen in contests over very valuable resources. The second condition also receives empirical support from ethological work: threat displays which are effective not only deter some opponents, but invoke more costly escalated responses from those who are undeterred (Enquist *et al.*, 1985; Popp, 1987). The main restriction of this model, however, is its reliance upon the use of a simultaneous signal by the two contestants.

Our objectives in this paper are to identify the conditions under which conventional signalling is evolutionarily stable, and identify the conditions necessary for a non-simultaneous conventional signalling system. Typically games of this nature are solved backwards, we will proceed in a number of steps beginning with solving the fighting phase, and then apply various assumptions about the information available to the contestants in this phase. In this way we hopefully gain some insight into the role of information in the process.

### 1.1. THE BASIC MODEL AND ASSUMPTIONS

The game we present here is inspired by Enquist's (1985) Model 1, but has been simplified somewhat.

We want to model fights between two individuals, Ego ($E$) and Opponent ($O$), who compete over some indivisible resource of value $V$. A player is equally likely to be weak, $Z = 1$, or strong, $Z = 2$. Based on available information players use one of three possible behaviours, Attack ($A$), Pause–attack ($P$), and Give-up ($G$).

Players who give-up will lose the contest (unless the opponent also gives-up in which case they receive $\frac{1}{2}V$ each). But avoid the cost of fighting. Alternatively, players may choose to attack, $A$, and win $V$ if they are stronger, or $\frac{1}{2}V$ if they are equally strong, and pay a cost of fighting, $C(a)$. This cost of fighting depends on the asymmetry in strength, $a =$ (Ego strength − Opponent strength), and includes the cost of launching an attack. For instance, a player who is weak and fights a player who is strong will incur a cost $C(-1)$. Fights against stronger opponents are more costly, so that

$$C(-1) > C(0) > C(1) > 0 \quad (2)$$

Players who attack opponents who give-up do not pay the full cost of fighting, but instead pay a smaller cost of attacking, $F$. Players who give-up and are attacked cannot escape all costs but pay a cost, $E(a)$. This cost is less than the cost of fighting, and also depends on the relative fighting ability.

$$C(a) > E(a)\forall a \quad (3)$$

$$E(-1) > E(0) > E(1) > 0 \quad (4)$$

In addition to attacking or giving-up, a player may choose to pause–attack, ($P$). This is the same as an attack but a pause is assumed to allow an opponent who is giving-up to escape. If the opponent attacks this pause will impose a disadvantage cost, $-D$, conversely the attacking player gains an advantage of $+D$ (the assumption that the magnitude of these opposite effects are equal is made for convenience, none of the results depend upon this assumption. The assumption that a pause, *per se* is costly is not crucial. It is demonstrated in Appendix C that the critical assumption is merely that players benefit at the ESS by choosing a different attack behaviour against an opponent who will not contest the resource than against an equally strong opponent who intends to fight). If both players pause–attack then there is no disadvantage, and the pay-offs are as they would have been if they had both chosen to attack. Both $F$ and $D$ are assumed to be small.

$$F,D < E(a),C(a),V\forall a \quad (5)$$

Given these assumptions the pay-offs given in Table 1 emerge.

The resource being contested is assumed to be worth fighting over, at least between individuals of equal strength, so that

$$\frac{1}{2}V > C(0) \quad (6)$$

and it is also assumed that all the parameters are positive,

$$V,C(a),E(a),D,F > 0 \quad (7)$$

### 1.2. EVOLUTIONARY STABILITY

Ego's strategy, $S^E$ is a function that specifies a signal for each Ego state, and a behaviour for each possible combination of Ego and Opponent states. An ESS solution exists when there is a pair of $S^{E*}$ and $S^{O*}$ which are strict best replies to each other Maynard Smith (1982). Each sub-game has a single ESS solution.

## 2. Fighting

Which solutions emerge will depend upon what information the players have about their own strength and that of their opponent. To get some background information we will first examine how players will fight when certain types of information are available. In the first case we assume that players are perfectly informed about both their own and their opponent's strength, in the second we make the biologically realistic assumption that players know only their own strength.

### 2.1. FIGHTING WITH PERFECT INFORMATION

How should a contestant play when he is fully informed of both his own, and his opponent's strength? This is the game presented in Section 1.1

TABLE 1
*The fighting game*

| | | A | P | G |
|---|---|---|---|---|
| | | *States equal*: opponent | | |
| | A | $\underline{\frac{1}{2}V - C(0) / \frac{1}{2}V - C(0)}$ | $\frac{1}{2}V - C(0) + D/\frac{1}{2}V - C(0) - D$ | $V - F/-E(0)$ |
| Ego | P | $\frac{1}{2}V - C(0) - D/\frac{1}{2}V - C(0) + D$ | $\frac{1}{2}V - C(0)/\frac{1}{2}V - C(0)$ | $V/0$ |
| | G | $-E(0)/V - F$ | $0/V$ | $\frac{1}{2}V/\frac{1}{2}V$ |
| | | *States unequal*: weak | | |
| | A | $V - C(1)/-C(-1)$ | $V - C(1) + D/-C(-1) - D$ | $V - F/-E(-1)$ |
| Strong | P | $V - C(1) - D/-C(-1) + D$ | $V - C(1)/-C(-1)$ | $\underline{V/0}$ |
| | G | $-E(1)/V - F$ | $0/V$ | $\frac{1}{2}V/\frac{1}{2}V$ |

Pay-offs in each cell are to Ego/Opponent; underlined cell are the ESS solutions to the game of perfect information.

without signalling. We can divide the game into two sub-games which can be analysed separately (we avoid a third sub-game by specifying the game such that matches between players of equal strength are identical, regardless of whether they are both weak or both strong). In one subgame Ego and Opponent are equally strong, in the other one player is strong and the other weak. These subgames are presented in the normal (matrix) form in Table 1.

A strategy is a complete description of which behaviours to use in all possible circumstances. In this case a prescribed behaviour is required for each of the four possible combinations of state (Ego weak & Opponent weak, Ego weak & Opponent strong, Ego strong & Opponent weak, Ego strong & Opponent strong). The ESS is $(A, G, P, A)$. The ESS behaviours for each sub-game are to attack when both players have equal states, to give-up when weaker than the Opponent, and to pause–attack when stronger. The cells corresponding to the equilibrium profiles are underlined in Table 1. The result is that players fight over the resource only when they are of equal strength. Players of differing strength have a mutual interest in avoiding a physical fight, the weaker player gives-up and the stronger player wins without having to resort to attacking in a contest that it would have won anyway.

### 2.2. FIGHTING WITH LIMITED INFORMATION

There is another relevant form of this game in which there is no communication. This is the case in which each contestant knows his own strength, but not that of his opponent. A player in this game finds himself in one of two states (in which he is strong or weak) and behaviour must be contingent upon these two possibilities. Strategies are of the form (behaviour when weak, behaviour when strong). There are several possible solutions to this game depending on the relative values of the parameters. They are: $(A, A)$ always attack; $(G, A)$ give-up if weak, and attack if strong; $(G, P)$ give-up if weak, pause–attack if strong. The derivation of these ESSs and the conditions for their stability are presented in Appendix A.

## 3. Communication

We have now solved the basic fighting game when there is either perfect information, or no information about opponent strength. We now model communication by allowing Ego to signal his strength to the opponent with one of two signals, $s_1$ or $s_2$, before the players choose fighting behaviours. Opponent does not signal, but we may allow Ego to perceive Opponent strength at some point in the game. This simplification allows us to avoid unnecessary complexity with no loss of illustrative value. We will study three different versions of this game, each of which is one of the three possible variations on the timing of the signal.

### 3.1. INFORMATION REVEALED AFTER EGO SIGNAL

In this version of the game the Opponent's strength is revealed to Ego after he has used his signal, but before the players choose their pay-off determining behaviours (this is essentially Enquist, 1985, Model I). Ego uses one signal or the other depending on his strength. There are then four possible signalling strategies, $(s_1, s_1)$, $(s_1, s_2)$, $(s_2, s_1)$, and $(s_2, s_2)$, the first value in the pair specifies which signal to use when weak, and the second specifies which to use when strong. Note that only $(s_1, s_2)$ and $(s_2, s_1)$ impart information, the pooling strategies $(s_1, s_1)$ and $(s_2, s_2)$ are in effect, "don't signal" strategies which convey no information.

To solve this game we first identify four so-called continuation games (Gibbons, 1992), one for each Opponent state and Ego signal (two of which are drawn in the extensive form in Fig. 1). The benefit of identifying continuation games is that we can then solve each one independently. On first inspection it seems that Ego is in a situation very similar to the perfect information game (Section 2.1), the difference is that a costless signal is introduced before his information becomes perfect, but Ego's pay-off determining moves (attack, pause–attack, or give-up) are still made with perfect knowledge of Opponent strength. On the other hand, the Opponent is playing a different game, since the availability of information depends on Ego's signalling strategy. Unlike in the previous information games the Opponent's "beliefs" become critical. The two continuation games in Fig. 1 illustrate the problem.

If Ego does not signal his strength, then the Opponent must choose some compromise behaviour against strong and weak Ego players as he did in Section 2.2. If, however, Ego signals his strength the Opponent can then choose a behaviour that is optimal for each Ego strength. If Opponent believes that Ego uses $s_1$ when weak and $s_2$ when strong, then he will assume he is in the left half of the tree when Ego uses $s_1$ and the right hand side of the tree if Ego uses $s_2$. The continuation games when the different signals are used are identical, the difference is entirely in the Opponent's beliefs. An ESS will require that such Opponent's beliefs match Ego's strategy.

Strategies for this version of the game will be specified in three parts; first Ego's signalling strategy in the form (Signal when weak, Signal when strong),

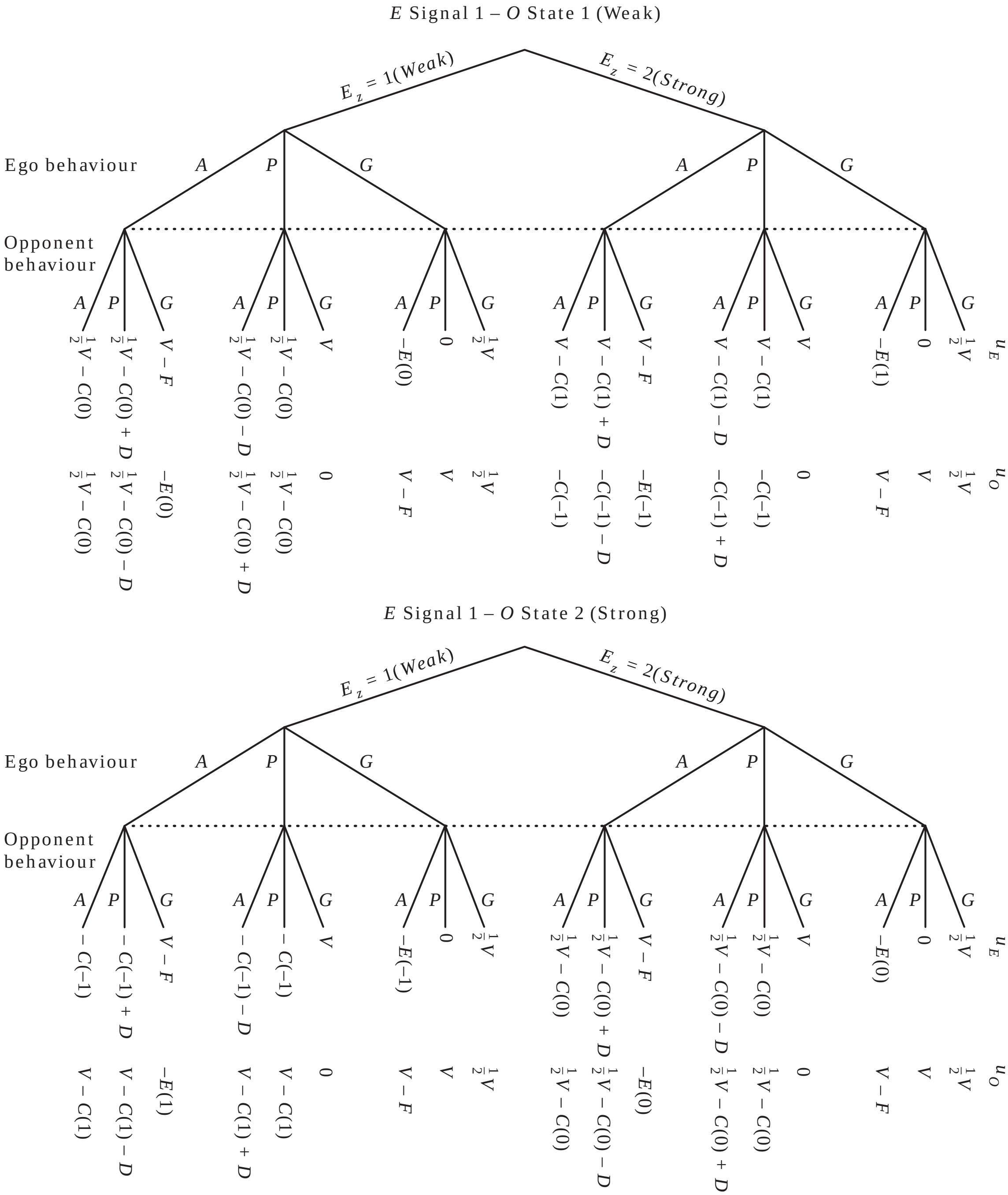


FIG. 1. Continuation games in the conventional signalling game, when information is received after the signal. The two other games, which follow the condition in which $E$ signals 2, have the same structure and pay-offs as the two games above. They differ, however, in the beliefs that $O$ has about the probabilities that $E$ is either in state 1 or 2.

second Ego's behaviour strategy $E$ (behaviour when both weak, behaviour when weaker than Opponent, behaviour when stronger than Opponent, behaviour when both strong), and third Opponent's behaviour strategy $O$ (behaviour when weak and Ego uses $S_1$, behaviour when weak and Ego uses $s_2$ behaviour when strong and Ego uses $s_1$, behaviour strong and Ego uses $s_2$).

There are two functionally identical ESSs in which Ego signals his strength [either $(s_1, s_2)$, or $(s_2, s_1)$], then Ego and Opponent follow the same behaviour as they did in the perfect information game (Section 2.1) and their strategies are $E(A, G, P, A)$ and $O(A, G, P, A)$ if Ego is playing $(s_1, s_2)$, and $O(G, A, A, P)$ if ego is playing $(s_2, s_1)$. Since these two strategies differ only in Ego's use of reversed signals to indicate his strength, we can ignore one of these ($s_2$, $s_1$) and assume that if strength is signalled that $s_1$ is used when weak, and $s_2$ when strong. If Ego signals his strength, then the rest of the game is identical to the perfect information game as both players enter the fighting game with the correct knowledge of both their strengths. The question is whether it actually pays Ego to do this rather than defecting by signalling strength when in fact weak? Given that the Opponent is playing in this way [i.e. $O(A, G, P, A)$], then the pay-offs for all Ego strategies can be determined from Table 2.

At ESS both players must be receiving the highest possible pay-off, given each others' strategy. The highest pay-off for each combination of Ego strength, Opponent strength and Ego signal is numbered in square brackets. Ego's choice of rows is constrainted by Ego and Opponent strengths. Rows *a–d* are played when Ego is weak, and *e–h* when strong. Rows are paired by Opponent strength, Ego is unable to choose between *a & b*, *c & d*, *e & f* or *g & h*, these rows must be played in pairs as Ego does not know the Opponent strength before choosing a signal. This timing requires that Ego choose whether to play rows *a & b* with $s_1$ or *c & d* with $s_2$ when weak, and *e & f* with $s_1$ or *g & h* with $s_2$ when strong. If signalling is to be an ESS it must pay Ego to use $s_1$ when weak, and $s_2$ when strong. This is the case when

$$[1] + [2] > [3] + [4]$$

$$\tfrac{1}{2}V - C(0) > V - E(-1)$$

$$E(-1) > \tfrac{1}{2}V + C(0) \qquad (8)$$

$$[7] + [8] > [5] + [6]$$

$$1\tfrac{1}{2}V - C(0) > 1\tfrac{1}{2}V - C(0) - C(1) + D$$

$$0 > -C(1) + D \qquad (9)$$

Condition (8) determines behaviour when weak, if it is met then cheating by signalling strength when weak does not pay (this equilibrium also requires that $D$ & $F > 0$). This condition specifies that the cost of being attacked by a stronger opponent must be large compared to the cost of fighting an opponent of equal strength and the value of the resource. A weak player who bluffs strength gains an extra $\frac{1}{2}V$ by causing weak opponents to quit, and avoids the cost $C(0)$ of fighting those opponents, but pays an extra cost, $E(-1)$, for escalated fights against stronger opponents who would have allowed escape if strength had not been bluffed.

Condition (9) determines behaviour when strong, if this condition is met then it pays strong players to advertise their state. This means that the cost of fighting a weaker opponent must be greater than the cost of pausing before attacking when being attacked. The benefit of communication to strong players is that they avoid contests which they would otherwise have won anyway, if this benefit [$C(1)$ the cost of fighting a weaker opponent] is very small, and the benefit of attacking a player who is pause–attacking ($D$) is large, then strong signallers will signal weakness and attack directly, gaining the advantage of first attack at the cost of unnecessary fights against weaker opponents). Condition (9) is quite plausible, and was assumed in Section 1.1. Note also the assumption in row *e* that $V - C(1) > -E(1)$, this is a less restrictive form of (6), this assumption is also applied in line *f*.

Signalling will be an ESS when (8) and (9) are met. The most biologically relevant assumption is that the value of the resource be approximately the same as the costs of fighting (8).

TABLE 2
*The conventional signalling pay-offs*

| | Ego | | Opponent | | Ego last move | | |
|---|---|---|---|---|---|---|---|
| Row | Strength | Signal | Strength | Move | *A* | *P* | *G* |
| *a* | 1 | 1 | 1 | *A* | $\frac{1}{2}V - C(0)$ [1] | $\frac{1}{2}V - C(0) - D$ | $-E(0)$ |
| *b* | 1 | 1 | 2 | *P* | $-C(-1) + D$ | $-C(-1)$ | 0 [2] |
| *c* | 1 | 2 | 1 | *G* | $V - F$ | $V$ [3] | $\frac{1}{2}V$ |
| *d* | 1 | 2 | 2 | *A* | $-C(-1)$ | $-C(-1) - D$ | $-E(-1)$ [4] |
| *e* | 2 | 1 | 1 | *A* | $V - C(1)$ [5] | $V - C(1) - \mathrm{D}$ | $-E(1)$ |
| *f* | 2 | 1 | 2 | *P* | $\frac{1}{2}V - C(0) + D$ [6] | $\frac{1}{2}V - C(0)$ | 0 |
| *g* | 2 | 2 | 1 | *G* | $V - F$ | $V$ [7] | $\frac{1}{2}V$ |
| *h* | 2 | 2 | 2 | *A* | $\frac{1}{2}V - C(0)$ [8] | $\frac{1}{2}V - C(0) - D$ | $-E(0)$ |

Pay-offs to Ego for the conventional signalling game. Information about Opponent state is made available to Ego after Ego has chosen a signal. It is assumed that Ego uses signal 1 when weak and 2 when strong and that the Opponent than plays ($O(A,G,P,A)$ (i.e. Attacks Ego has signalled an equal strength, Gives-up if Ego has signalled a stronger state and Pause–attacks if Ego has signalled a weaker state).

TABLE 3
*Conventional signalling with perfect information*

| Row | States: Ego | States: Opponent | Ego Signal | Opponent Move | Ego last move: A | Ego last move: P | Ego last move: G |
|---|---|---|---|---|---|---|---|
| *a* | 1 | 1 | 1 | *A* | $\frac{1}{2}V - C(0)$ | $V - C(0) - D$ | $-E(0)$ |
| *b* | 1 | 1 | 2 | *G* | $V - F$ | $V$ | $\frac{1}{2}V$ |
| *c* | 1 | 2 | 1 | *P* | $-C(-1) + D$ | $-C(-1)$ | 0 |
| *d* | 1 | 2 | 2 | *A* | $-C(-1)$ | $-C(-1) - D$ | $-E(-1)$ |
| *e* | 2 | 1 | 1 | *A* | $V - C(1)$ | $V - C(1) - D$ | $-E(1)$ |
| *f* | 2 | 1 | 2 | *G* | $V - F$ | $V$ | $\frac{1}{2}V$ |
| *g* | 2 | 2 | 1 | *P* | $\frac{1}{2}V - C(0) + D$ | $\frac{1}{2}V - C(0)$ | 0 |
| *h* | 2 | 2 | 2 | *A* | $\frac{1}{2}V - C(0)$ | $\frac{1}{2}V - C(0) - D$ | $-E(0)$ |

Pay-offs to an omniscient Ego for the conventional signalling game. Information about Opponent state is made available to Ego before a signal is chosen. It is assumed that the Opponent believes that Ego uses signal 1 when weak and 2 when strong, Opponent then plays $O(A,G,P,A)$ (i.e. Attacks Ego has signalled an equal strength, Gives-up if Ego has signalled a stronger state and Pause–attacks if Ego has signalled a weaker state).

### 3.2. THE OMNISCIENCE GAME—INFORMATION REVEALED BEFORE SIGNAL

In the previous game Ego was able to signal strength only before receiving information about the Opponent's strength. We demonstrated that conventional signalling could be an ESS in this case. Next we investigate the effect of allowing Ego to signal after he perceives the Opponent's strength, rather than before. It would seem that this would have no effect on the ESS, since Ego's signal is merely providing the Opponent with information. The results show, however, that this is not the case.

Table 3 shows Ego's pay-off if the Opponent is following the same strategy as in the previous section—assuming that Ego is reliably signalling strength, the difference is that Ego knows the Opponent's strength before signalling. Ego is now free to choose from rows *a* or *b* when both Ego and Opponent are weak, *c* or *d* when Ego is weak and Opponent is strong, *e* or *f* when weak and the Opponent is strong, and *g* or *h* when both are strong. Communication will not be stable wheneer any Ego pay-off in row *b* is higher than the highest in *a* which is most likely, but the communication will also not persist if the highest in *d* is higher than the highest in row *c*, or $\max(e) > \max(f)$, or $\max(g) > \max(h)$]. There is no need for Ego to trade-off amongst the costs and benefits of signals against different strengths of Opponent (pairs of rows) as was necessary in Section 3.1. Ego may now "cheat" and indicate strength when weak against only those Opponents who will not retaliate, those who are weak. When this happens Ego will indicate a high strength whenever Ego is weak and gain the maximum pay-off. Ego will signal a low strength when both players are strong to gain an additional benefit by causing the opponent to pause, and when Ego is weak and the Opponent is strong to gain a costless escape. So, Ego will always signal the opposite of the Opponent strength, and so no information about Ego's strength will be transmitted. The Opponent will then stop responding to signals of strength and a non-signalling ESS will emerge. The solution from the no-information game (Section 2.2) does not apply here because the signaller knows the opponent strengths.

There are four possible non-communication ESSs; $(E(A, A, G, A), O(A, A))$, $(E(A, A, G, A), O(A, P))$, $(E(P, P, G, A), O(G, A))$, $(E(P, P, G, A), O(G, P))$, which are derived in Appendix B.

### 3.3. NO INFORMATION REVEALED

The last case to consider is that in which Ego receives no information. We will allow Ego to signal but never learn what the Opponent's strength is. The signaller will choose a signal while in the same information state as he was in Section 3.1 when signalling was an ESS, but no further information will be made available upon which to base a fighting decision, and so behaviour will be something like it was in the limited information game (Section 2.2). In this case, however, if Ego signals his strength the Opponent will know Ego strength, but the reverse will not be true. This situation is the same as in Section 3.2, but the roles are reversed, with Ego in the dark and the Opponent in the know. The ESS is for Ego not to signal, and the solution is the same as in Section 3.2 with reversed roles. The non-signalling ESS strategy profile is one of $(E(A, A)\ O(A, A, G, A))$, $(E(A, P)\ O(A, A, G, A))$, $(E(Q, A)\ O(P, P, G, A))$, $(E(Q, P)\ O(P, P, G, A))$ depending on the status of conditions (B.1) and (B.2) (see Appendix B).

## 4. Discussion

Theorists working to explain signalling during the 1970s (e.g. Parker, 1974; Maynard Smith, 1974, 1982) understood that some sort of cost had to balance, and exceed, the gains possible through "bluffing". An animal must have some expectation of cost when entering a conflict. Enquist (1985, Model I) demonstrated that inescapable costs, even if they are due entirely to the receiver's response, are a necessary condition for the stability of conventional signalling. Our present results demonstrate the existence of additional conditions related to uncertainty and the timing of information exchange.

The three models we have just investigated suggest some critical properties of conventional signalling. In the first model (Section 3.1) the signaller was not informed about his opponent's fighting ability when choosing a signal, but received this information before playing the fighting game. In this situation signalling could be an ESS. In the second case (Section 3.2) signallers were given information about opponent fighting ability before choosing a signal and, somewhat surprisingly, communication was no longer an ESS. This suggests that the signaller must be in a state of uncertainty when the signal is chosen. In the third case (Section 3.3) the signaller was in a state of uncertainty when choosing a signal, and remained uninformed throughout the fighting game. Surprisingly, communication is not an ESS in this situation either. This suggests that in addition to the need for uncertainty, there must be some information received which resolves the ambiguity, and that the timing of these events are critical. Signalling was only an ESS when the signaller was forced to trade-off the costs and benefits of a single signal across different types of receiver, but was able to mitigate the outcome using subsequently acquired information.

How can this rather counter-intuitive result be understood? If the signaller has perfect knowledge then the response to any signal is known without any ambiguity. Such a signaller may then choose a signal for each type of opponent knowing what the response will be. The signaller can use this control over the receiver by signalling strength to a weak receiver, and weakness to a strong one. The signaller will choose a signal based on the strength of his opponent, rather than his own. If, however, the signaller is uncertain about receiver strength when signalling, then the only information which he can signal is his own strength. By signalling this he can avoid being attacked by stronger opponents and avoid unnecessary attacks against weaker ones.

Our second finding was that, not only does conventional signalling require the existence of some ambiguity, but that the ambiguity must be resolved after the signal has been chosen. The signaller must be able to later make use of newly received information in a second move—the fighting game—to "fine-tune" the trade-off of the consequences of the signal against receivers of different types. It is not enough that a single signal is used against more than one type of receiver, but there must be a second stage in which more behaviours can be chosen based on the receivers' type. If the signaller does not receive additional information for use in the fighting-game, then that subsequent move must be based only on the signallers' state, just as the signal was. If all of the signallers actions are based on a single decision criterion, as it must if he receives no additional information, then the game becomes an action–response game (in which there cannot be conventional signalling without perfect common interest, Appendix D). This need to avoid the structure of an action–response game highlights the role of timing in the exchange of information that conventional signalling requires.

### 4.1. NON-SIMULTANEOUS SIGNALLING

In nature, however, we usually see aggressive signals used in sequences, with the two contestants alternating signals to some degree. Enquist (1985) modelled an exchange of simultaneous signals. This fulfils the timing of information requirements, but longer sequences of conventional signals have never been successfully modelled. The current results should shed some light on how to proceed in order to create a true model of sequential threat displays.

It is necessary that each signal be chosen while in a state of some uncertainty, and the expectation must exist that information will be gained before the next signal is chosen. This presents quite a task for the modeller, how to successively inform the players without extinguishing the supply of ambiguity? Current models of biological communication reveal most, or all, information with the first signal and there does not remain enough ambiguity to support a second signal, this same problem hinders models of asynchronous signalling by two players. If the first signal reveals all, there is no need for its receiver to signal anything (with a conventional signal).

Clearly, some insight into the nature of the information transferred between animals would be extremely useful. One possibility is that players are poorly informed and receive additional information about the value of the resource, the risks of predation, or about their opponent, independently of the opponent's signals. A series of signals may indicate a range of strengths, and subsequent signals may narrow the range of communicated state. What we now know is that if a signaller provides too much information with a given signal, it will not benefit his opponent to reply in an informative way (Section 3.3). The requirement that information be received by the signaller during the course of an interaction is not met by the vast majority of threat models.

It is possible that the results of this particular model do not generalise over all conventional signalling systems. A more general version of the fighting game is presented in Appendix C. These pay-offs preserve all the communication properties of the basic fighting game, but simplify the pay-off parameters to four variables. It is our belief that no simpler conventional signalling game can exist (unless there is no conflict between the players).

## 5. Conclusion

We have presented what we believe to be the simplest possible model of conventional signalling between individuals with conflicting interests. There is clearly no theoretical reason to believe that signals between individuals must be costly to be reliable. The most important lessons to be learned from this model, however, are not about costs, but about time and information. The requirement for an extended time structure is due to the need for information exchange between signaller and receiver. The signaller must receive, and use, information during the course of the interaction. The order in which events happen is critical to conventional signalling.

These results demonstrate the necessity of investigating communication with more complicated games than action–response games, and with games more complicated than the simple extensive form games we have used here.

We wish to thank Olle Leimar, Bo Sundborg, and Bertil Borg for thoughtful input.

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## APPENDIX A

### The Limited Information Game

Here we change the game so that each contestant knows only their own strength, and not that of their opponent. Compared to the perfect information game, a player finds himself in one of two states (in which he is strong or weak) and behaviour must be contingent upon these two possibilities (behaviour when weak, behaviour when strong). There are possible several solutions to this game depending on the relative values of the parameters. They are: $(A, A)$ always attack; $(G, A)$ give-up if weak, and attack if strong; $(G, P)$ give-up if weak, pause–attack if strong. We shall examine each one of the possible ESSs in turn, and determine the conditions for it's stability.

#### STRUCTURE

The game is presented in normal form in Table A1.

#### *Always attack*—$(A, A)$

The strategy to attack regardless of strength, $(A, A)$, is an ESS unless weak players gain more by giving-up [some strategies other than $(G, A)$ can invade a population of $(A, A)$ players they all require more extreme conditions than $(G, A)$, and so we need only consider this one alternative strategy]. Weak $(A, A)$ players score $\frac{1}{2}V - C(0)$ when playing

TABLE A1

*Limited information, no communication*

| Ego | Opponent AA | PA | GA | AP |
|---|---|---|---|---|
| $AA$ | $2V - C(-1) - 2C(0) - C(1)$ | $2V - C(-1) - 2C(0) - C(1) + 2D$ | $2.5V - C(-1) - C(0) - 2F$ | $2V - C(-1) - 2C(0) - C(1) + 2D$ |
| $PA$ | $2V - C(-1) - 2C(0) - C(1) - 2D$ | $2V - C(-1) - 2C(0) - C(1)$ | $2.5V - C(-1) - C(0) - F - D$ | $2V - C(-1) - 2C(0) - C(1)$ |
| $GA$ | $1.5V - C(0) - C(1) - E(-1) - E(0)$ | $1.5V - C(0) - C(1) - E(-1) + D$ | $2V - C(0) - E(-1) - F$ | $1.5V - C(0) - C(1) - E(0) + D$ |
| $AP$ | $2V - C(-1) - 2C(0) - C(1) - 2D$ | $2V - C(0) - C(-1) - C(1) - C(0)$ | $2.5V - C(-1) - C(0) - F - D$ | $2V - C(-1) - 2C(0) - C(1)$ |
| $PP$ | $2V - C(-1) - 2C(0) - C(1) - 4D$ | $2V - C(-1) - 2C(0) - C(1) - 2D$ | $2.5V - C(-1) - C(0) - 2D$ | $2V - C(-1) - 2C(0) - C(1) - 2D$ |
| $GP$ | $1.5V - C(0) - C(1) - E(-1) - E(0) - 2D$ | $1.5V - C(0) - C(1) - E(-1) - D$ | $2V - C(0) - E(-1) - D$ | $1.5V - C(0) - C(1) - E(0) - D$ |
| $AG$ | $0.5V - C(-1) - C(0) - E(0) - E(1)$ | $0.5V - C(-1) - C(0) - E(0) + D$ | $1.5V - C(-1) - E(0) - F$ | $0.5V - C(-1) - C(0) - E(1) + D$ |
| $PG$ | $0.5V - C(-1) - C(0) - E(1) - E(0) - 2D$ | $0.5V - C(-1) - C(0) - E(0) - D$ | $1.5V - C(-1) - E(0) - D$ | $0.5V - C(-1) - C(0) - E(1) - D$ |
| $GG$ | $-E(-1) - 2E(0) - E(1)$ | $-E(-1) - E(0)$ | $V - E(-1) - E(0)$ | $-E(0) - E(1)$ |

| Ego | Opponent PP | GP | AG | PG | GG |
|---|---|---|---|---|---|
| $AA$ | $2V - C(-1) - 2C(0) - C(1) + 4D$ | $2.5V - C(-1) - C(0) - 2F + 2D$ | $3.5V - C(0) - C(1) - 2F$ | $3.5V - C(0) - C(1) + 2D + 2F$ | $4V - 4F$ |
| $PA$ | $2V - C(-1) - 2C(0) - C(1) + 2D$ | $2.5V - C(-1) - C(0) - F + D$ | $3.5V - C(0) - C(1) - F - D$ | $3.5V - C(0) - C(1) - F + D$ | $4V - 2F$ |
| $GA$ | $1.5V - C(0) - C(1) + 2D$ | $2V - C(0) - F + D$ | $2.5V - C(1) - E(0) - F$ | $2.5V - C(1) - F + D$ | $3V - 2F$ |
| $AP$ | $2V - C(-1) - 2C(0) - C(1) + 2D$ | $2.5V - C(-1) - C(0) - F + D$ | $3.5V - C(0) - C(1) - F - D$ | $3.5V - C(0) - C(1) - F + D$ | $4V - 2F$ |
| $PP$ | $2V - C(-1) - 2C(0) - C(1)$ | $2.5V - C(-1) - C(0)$ | $3.5V - C(0) - C(1) - 2D$ | $3.5V - C(0) - C(1)$ | $4V$ |
| $GP$ | $1.5V - C(0) - C(1)$ | $2V - C(0)$ | $2.5V - C(1) - E(0) - D$ | $2.5V - C(1)$ | $3V$ |
| $AG$ | $0.5V - C(-1) - C(0) + 2D$ | $1.5V - C(-1) - F + D$ | $2V - C(0) - E(1) - F$ | $2V - C(0) - F + D$ | $3V - 2F$ |
| $PG$ | $0.5V - C(-1) - C(0)$ | $1.5V - C(-1)$ | $2V - C(0) - E(1) - D$ | $2V - C(0)$ | $3V$ |
| $GG$ | $0$ | $V$ | $V - E(0) - E(1)$ | $V$ | $2V$ |

Stategies given in the form Move When Weak, Move When Strong. Pay-offs are to the row player.

weak Opponents, and $-C(-1)$ against strong Opponents, whereas $(G, A)$ players score $-E(0)$ and $-E(1)$. Thus $(A, A)$ is a best reply to itself when,

$$\tfrac{1}{2}V - C(0) - C(1) > -E(-1) - E(0) \quad (A.1)$$

*Give-up if weak, attack if strong*—$(G, A)$

To give-up when you are weak and to attack when you are strong can also be an ESS if,

$$E(-1) > \tfrac{1}{2}V - C(-1) - F \quad (A.2)$$

$$V - C(0) - F > -E(0) \quad (A.3)$$

$$D > F \quad (A.4)$$

$$\tfrac{1}{2}V - C(0) - E(-1) > -C(-1) - E(0) \quad (A.5)$$

These four conditions make $(G, A)$ a better reply against itself than some possible invading strategy (more strategies are capable of invasion than the ones we will discuss, but they all require conditions more extreme than these four).

This potential ESS may be invaded by players who attack when weak as well as when strong. The pay-off to weak $(G, A)$ strategists is $\frac{1}{2}V$ when meeting weak opponents plus $-E(-1)$ when meeting strong opponents, whereas an invading weak $(A, A)$ player receives $V - F$ when encountering weak opponents plus $-C(-1)$ when encountering strong opponents, attacking when weak will not invade while (A.2) is true.

Another strategy capable of invading is to always give-up, $(G, G)$. Here strong individuals give-up rather than fight, fighting when strong vs. a population of $(G, A)$ strategists pays $V - F$ when the opponent is weak plus $\frac{1}{2}V - C(0)$ when the opponent is strong, in contrast an invader who plays $G$ when strong scores $\frac{1}{2}V$ when encountering weak opponents plus $-E(-1)$ when encountering strong ones. Always give-up will not invade while (12) is true.

The third possibility is that a strategy in which strong players pause before attacking rather than attacking directly, $(G, P)$, will invade. These players will gain an advantage because they will not have to pay the cost $F$ when attacking a weak opponent who is giving up, but will pay an extra cost $D$ for pausing before attacking a strong opponent who is attacking directly. This strategy cannot invade while (A.4) is true.

The last possibility is a little less credible, a strategy in which strong players give-up and weak ones attack, $(A, G)$. The pay-off of the $(G, A)$ strategy against itself is $\frac{1}{4}(2V - C(0) - E(-1) - F)$, the somewhat paradoxical $(G, A)$ strategy scores $\frac{1}{4}(1\frac{1}{2}V - C(-1) - E(0) - F)$ against a population of $(G, A)$ strategists. The paradoxical strategy loses $\frac{1}{2}V$ but may gain this lost reward back. The paradoxical strategy chooses to fight a stronger opponent and be attacked by an opponent of equal strength, while $(G, A)$ chooses to be attacked by a stronger opponent while giving-up, and fights an opponent of equal strength. If the difference between being attacked while giving up by a stronger and equal strength opponent is $\frac{1}{2}V$ greater than the difference between fighting a stronger and an equal opponent, then the paradoxical strategy can invade. When (A.5) is true, $((A, G))$ cannot invade.

*Give-up if weak, pause–attack if strong*—$(G, P)$

The strategy in which weak players give-up and strong ones pause–attack is also a potential ESS. Not surprisingly, it is vulnerable to invasion by the previous potential ESS, $(G, A)$, in which strong players attack without pausing. When (A.6) is true, this strategy cannot invade.

Another potential invader is the strategy $(P, A)$ in which weak players pause–attack, gaining $V$ rather than $\frac{1}{2}V$ when the opponent is weak, but losing $-C(-1) + D$ rather than 0 when the opponent is strong. This strategy cannot invade while (A.7) is true.

$(G, P)$ is an ESS if

$$F > D \quad (A.6)$$

$$0 > \frac{1}{2}V - C(-1) + D \quad (A.7)$$

## APPENDIX B

### The "Omniscience" Game

In Section 3.2. we presented a version of the signalling game in which Ego learns the Opponent strength before signalling, and demonstrated that communication was not an ESS. To solve for the non-signalling ESSs for this game we identify two sub-games based on the common knowledge of the Opponent strength. In one sub-game the Opponent is weak and in the other he is strong.

Strategies will be specified for Ego as $E$ (behaviour when both weak, behaviour when opponent stronger, behaviour when opponent weaker, behaviour when both strong), and for Opponent as $O$ (behaviour when weak, behaviour when strong). Since this game has sub-games, there will be circumstances in which some portion of the strategy is irrelevent, we shall denote this with a "wildcard-dot".

The ESS for this game can be determined from the values in (normal-like form) Table B1.

TABLE B1

| | | $A$ | $P$ | $G$ |
|---|---|---|---|---|
| | | Opponent weak | | |
| Ego | $A$ | $*\frac{1}{2}V - C(0)/\frac{1}{2}V - C(0)$ [1] | $*\frac{1}{2}V - C(0) + D/\frac{1}{2}V - C(0) - D$ [3] | $V - F/-E(0)$ |
| weak | $P$ | $\frac{1}{2}V - C(0) - D/\frac{1}{2}V - C(0) + D$ | $\frac{1}{2}V - C(0)/\frac{1}{2}V - C(0)$ | $*V/0$ [5] |
| | $G$ | $-E(0)/V - F$ | $0/V$ | $\frac{1}{2}V/\frac{1}{2}V$ |
| + | $A$ | $*V - C(1)/-C(-1)$ [2] | $*V - C(1) + D/-C(-1) - D$ [4] | $V - F/-E(-1)$ |
| Ego | $P$ | $V - C(1) - D/-C(-1) + D$ | $V - C(1)/-C(-1)$ | $*V/0$ [6] |
| strong | $G$ | $-E(1)/V - F$ | $0/V$ | $\frac{1}{2}V/\frac{1}{2}V$ |
| | | Opponent strong | | |
| Ego | $A$ | $-C(-1)/V - C(1)$ | $-C(-1) + D/V - C(1) - D$ | $V - F/-E(1)$ |
| weak | $P$ | $-C(-1) - D/V - C(1) + D$ | $-C(-1)/V - C(1)$ | $*V/0$ [11] |
| | $G$ | $*-E(-1)/V - F$ [7] | $*0/V$ [9] | $\frac{1}{2}V/\frac{1}{2}V$ |
| + | $A$ | $*\frac{1}{2}V - C(0)/V - C(0)$ [8] | $*\frac{1}{2}V - C(0) + D/\frac{1}{2}V - C(0) - D$ [10] | $V - F/-E(0)$ |
| Ego | $P$ | $\frac{1}{2}V - C(0) - D/\frac{1}{2}V - C(0) + D$ | $\frac{1}{2}V - C(0)/\frac{1}{2}V - C(0)$ | $*V/0$ [12] |
| strong | $G$ | $-E(0)/V - F$ | $0/V$ | $\frac{1}{2}V/\frac{1}{2}V$ |

Optimal Ego behaviour at each Ego information set for each possible Opponent behaviour is marked with a "*". Opponent pay-off for each of these optimal Ego replies are numbered in square brackets. Assumption (6) means that $\frac{1}{2}V - C(0) > -E(1)$.

The ESS solution when Opponent is weak is both players always attack, $E(A, \cdot, A, \cdot)\ O(A, \cdot)$, as long as $[1] + [2] > [5] + [6]$ (note that $[1] + [2]$ are always greater than $[3] + [4]$, so we can discount the possibility that $P$ is ever optimal behaviour for a weak Opponent), if the reverse is true (i.e. $[1] + [2] < [5] + [6]$) Ego will always pause–attack while Opponent gives-up, $E(P, \cdot, P, \cdot)\ O(G, \cdot)$.

When the Opponent is strong the ESS solution is $E(\cdot, G, \cdot, A)\ O(\cdot, A)$ when $[7]+[8] > [9] + [10]$, and $E(\cdot, G, \cdot, A)\ O(\cdot, P)$ when the reverse is true. Assumptions (5) and (6) mean that $[11] + [12]$ is always less than $[7] + [8]$ and $[9] + [10]$ and thus $O(\cdot, G)$ is never an ESS. Simplifying these conditions a bit: when Opponent is weak and,

$$\tfrac{1}{2}V - C(0) - C(-1) > 0 \qquad \text{(B.1)}$$

the ESS is for Ego to always attack, $E(A, A, \cdot, \cdot)$, and the Opponent to attack also, $O(A, \cdot)$. If (B.1) is not true, then the ESS is for Ego to Pause before attacking $E(P, P, \cdot, \cdot)$, and for the Opponent to give-up $O(G, \cdot)$, when the Opponent is weak

When the Opponent is strong and

$$D > F \qquad \text{(B.2)}$$

The ESS is for Ego to give up when weak and Attack when strong, $E(\cdot, \cdot, G, A)$ and the Opponent to attack, $O(\cdot, A)$. When the Opponent is strong and (B.2) is not true, Ego ESS remains $E(\cdot, \cdot, G, A)$, but the Opponent ESS is to pause before attacking, $O(\cdot, P)$.

So, depending on the relative values of the parameters, conditions (B.1) and (B.2), there may be one of four ESSs to the complete game.

$$\text{(B.1)(B.2)} \Rightarrow E(A, A, G, A),\ O(A, A)$$

$$\text{(B.1)}\neg\text{(B.2)} \Rightarrow E(A, A, G, A),\ O(A, P)$$

$$\neg\text{(B.1)(B.2)} \Rightarrow E(P, P, G, A),\ O(G, A)$$

$$\neg\text{(B.1)}\neg\text{(B.2)} \Rightarrow E(P, P, G, A),\ O(G, P)$$

## APPENDIX C

### The Simplified Conventional Signalling Game

This section presents an attempt to represent all the dynamics and trade-offs of the basic fighting game with as few parameters as possible.

The basic fighting game is essentially a coordination/discoordination game. When states are equal the equilibrium solution is to coordinate on $A$, when states are unequal the equilibrium solution is to discoordinate with the individual with the higher state playing $P$ and the individual with the lower state to play $G$. A conflict exists between the players due to the fact that the highest pay-off is paid to one player while discoordinating, and this pay-off is always available if he can convince his opponent to play $G$. The present task is to simplify the pay-offs leading to this ESS while preserving all the properties of the larger model. We do this to expose the critical properties underlying conventional signalling games.

The relative values of some of the pay-offs are more critical than others, we present them here in decreasing order of relevance:

(1) the highest pay-off, the temptation pay-off $t$, is paid to the player with the higher state when discoordinating on $P/G$. A neutral pay-off, $n$ is paid to the opponent when this discoordination is played;

TABLE C1
*The Minimised Fighting Game*

| | | A | P | G |
|---|---|---|---|---|
| | | *States equal*: opponent | | |
| | A | $\underline{c/c}$ | $n/p$ | $n/p$ |
| Ego | P | $p/n$ | $p/p$ | $t/n$ |
| | G | $p/n$ | $n/t$ | $c/c$ |
| | | *States unequal*: lower | | |
| | A | $c/p$ | $n/p$ | $n/p$ |
| Higher | P | $p/p$ | $p/p$ | $\underline{t/n}$ |
| | G | $p/n$ | $n/t$ | $c/c$ |

(2) the temptation to bluff and make the opponent choose $G$ and gain the temptation pay-off exists for all states (to maintain the conflict we specify that the pay-offs paid when either player chooses $G$ are unaffected by their relative states);

(3) an intermediate, coordination pay-off, $c$, is paid when coordinating at equal states;

(4) when both players choose one of $A$ or $P$, the player with the lower state receives a punishment pay-off, $p$. If both players are of equal strength, then they receive neutral pay-offs if they discoordinate, and coordination pay-offs if they coordinate (actually produces several communication ESSs, in which players coordinate on $A$ if they are both strong, and $P$ if they are both weak, and vice versa. Punishment pay-offs are paid if they coordinate on $P$, to cut down on the number of ESSs. This does not change any of the results with respect to conventional signalling, and simplifies some of the solutions, but at a bit of a loss in simplicity in explaining the initial pay-off values;

(5) we simplify by specifying that pay-offs when playing $A$ or $P$ are the same when the states are equal as they are when state is higher);

(6) the last pay-offs are those paid when $A$ and $G$ are played against each other, in this case the $G$ player is punished, and the $A$ player receives a neutral pay-off.

A set of pay-offs which preserves the conflict is presented in Table C1.

Assume,

$$t > c > n > p \tag{C.1}$$

Given inequality (C.1) it can be demonstrated that always $A$ is the only ESS for the limited information version of this game (both players know own state, and never gain additional information).

The communication properties demonstrated elsewhere in this paper are all met by these simplified pay-offs. In the information revealed after signal version, conventional signalling is an ESS iff

$$c + n > t + p \tag{C.2}$$

Communication is not an ESS in the "omniscient" version of the game (when information is revealed before the signal), neither (by reasons of symmetry) is it an ESS in the version in which no information is gained after the signal.

## APPENDIX D

### Conventional Signals in Action–Response Games

Conventional signalling cannot be stable in Action–Response games unless there is no conflict between the players.

#### PROPERTIES OF ACTION–RESPONSE GAMES

An action–response game has the following properties:

(1) two players, an actor $A$ and a responder $R$;

(2) a move by Nature initially determines a state, $z$ [according to some distribution $Pr(z)$], which is known to the actor but not to the responder;

(3) the actor strategy, $S^A$, is to choose an action, $a$, as a function of state, $a = S^A(z)$;

(4) the responder strategy, $S^R$, is to choose a response (we shall call moves made by the responder, a "response", and a move or strategy to be played against something a "reply" to that something—since, at equilibrium, the opponent's move or strategy is anticipated), $r$, as a function of action, $r = S^R(a)$;

(5) for each play of the game pay-offs to the actor are $w^A(z, a, r)$ and pay-offs to the responder are $w^R(z, r)$. (So the signal may be "costly" to the actor, but has no effect on the responder beyond the transfer of information).

#### PROPERTIES OF PAY-OFFS AND EQUILIBRIA

(1) We define best reply to moves as $a^*$ and $r^*$. Given a responder strategy, $S^R$ and state $z$, the actor's best reply is,

$$\exists a^*(z,S^R))\ w^A(z,a^*,S^R) = \max_a[w^A(z,a,S^R)] \tag{D.1}$$

Given an actor strategy, $S^A$ and action $a$, the responder's best move is,

$$\exists r^*(a,S^A)) \sum_z Pr(z|a,S^A)\ w_R(z,r^*) = \max_r[\sum_z Pr(z|a,S^A)\ w_R(z,r)] \tag{D.2}$$

(2) The expected pay-off to the actor is $W^A(S^A, S^R, Pr(z))$, likewise the expected pay-off to the responder is $W^R(S^R, S^A, Pr(z))$, where

$$W^A(S^A,S^R,Pr(z)) = \sum_z Pr(z)\ w^A(z,S^A(z),S^R(S^A(z))) \quad (D.3)$$

$$W^R(S^R,S^A,Pr(z)) = \sum_a \sum_z Pr(z|a,S^A)\ w^R(z,S^R(S^A(z))) \quad (D.4)$$

(3) We define a best reply to a strategy as $S'$,

$$(\exists S^{A'}(S^R))\ W^A(S^{A'},S^R) = \max_{S^A}[W^A(S^A,S^R)]$$
$$(\exists S^{R'}(S^A))\ W^R(S^{R'},S^A) = \max_{S^R}[W^R(S^R,S^A)] \quad (D.5)$$

(4) A Nash equilibrium requires,

$$(\exists S^{A*})\ S^{A*} = S^{A'}(S^{R'}(S^{A*}))$$
$$(\exists S^{R*})\ S^{R*} = S^{R'}(S^{A'}(S^{R*})) \quad (D.6)$$

## COMMUNICATION IN ACTION–RESPONSE GAMES

We impose two restrictions on the game, such that a communication equilibrium exists.

(1) Optimal response varies with state

$$(\exists z_i,z_j)\ r'(z_i) \neq r'(z_j) \quad (D.7)$$

where:

$$(\exists r'(z))\ w^R(z,r') = \max_r[u^R(z,r)] \quad (D.8)$$

(2) Given such an optimal responder strategy, the optimal actor strategy is to vary the action with state

$$(\exists z_i,z_j)\ a'(z_i,S^{R*}) \neq a'(z_j,S^{R*}) \quad (D.9)$$

where:

$$(\exists a'(z,S^{R*}))\ w^A(z,a',S^{R*}) = \max_a[w^A(z,a,S^{R*})] \quad (D.10)$$

## SEPARATING EQUILIBRIA

It will greatly simplify things to make the assumption that the signalling equilibria is a separating equilibria (Gibbons, 1992). We shall turn later to the alternative, semi-pooling equilibria after examining separating equilibria.

Given the restrictions (D.7) and (D.9) we can then impose an association between $z_i$, $a_i$, $r_i$ such that:

$$a_i = a^*(z_i,S^{R*})$$
$$r_i = r^*(a_i,S^{A*}) \quad (D.11)$$

## PROPERTIES OF COMMUNICATION ESSs

Communication will be an ESS as long as

$$w^A(z_i,a_i,r_i) \geqslant w^A(z_i,a_j,r_j)\ (\forall\, j \neq i) \quad (D.12)$$

It follows from (D.12) that the responder's preference ranking is,

$$w^B(z_i,r_i) > w^B(z_i,r_j)\ (\forall\, j \neq i) \quad (D.13)$$

## COMMUNICATION WITH CONFLICT

To impose conflict between the players we specify that the actors preference ranking be different from that of the responders. It does not matter much how we do this, and so we shall assume a constant actor preference for lower responses across all states. (The proof will rely on this assumption only in so far as it produces a different preference from the responder for the states 1 and 2, so the assumption made here is much stronger than it needs to be).

**Assumption**

Actors have the same preference ranking for responses, across all states and actions, such that,

$$w^A(z,a,r_1) \geqslant w^R(z,a,r_2) \geqslant \ldots \geqslant w^R(z,a,r_n) \quad (D.14)$$

It follows from (D.12), (D.13), and (D.14) that the response which is optimal will differ for the two players for all $z \neq 1$, and so they are said to be in conflict.

## PROPERTIES OF CONFLICTING INTEREST COMMUNICATION ESSs

It can be easily seen that the only way to reconcile (D.12) and (D.14) is for $a$ to have an effect on $w^A$ that is independent of its effect on $r$. For instance,

$$w^A(z_2,a_2,r_1) > w^A(z_2,a_2,r_2) \text{ by (D.14)}$$
$$w^A(z_2,a_2,r_2) > w^A(z_2,a_2,r_1) \text{ by (D.12)}$$
$$\therefore w^A(z_2,a_2,r_1) > w^A(z_2,a_1,r_1) \quad (D.15)$$

This is the handicap result, and demonstrates that a cost free signalling ESS cannot exist in an action–response game when the players are in conflict.

## PARTIAL-POOLING EQUILIBRIA

The result presented above makes a critical assumption in (D.11), which is that it is optimal for the actor to use a different action in each state, this is known as a separating equilibrium (Gibbons, 1992). Alternatively, actors of several states may share a common optimal action, while actors from another set of states use different optimal actions, this is known as a partially-pooling equilibrium (it may also be that receivers pool responses across several actions). Restrictions (D.7) and (D.9) allow for partial-pooling while ruling out uncommunicative pooling equilibria.

Let $\tilde{a}_i$ be the set of all actions to which the responder uses $r_i$ at ESS.

$$\tilde{a}_i \equiv \{S^{R*}(a) = r_i\} \quad \text{(D.16)}$$

this allows responders to pool across actions, though we continue to impose the restriction that at least two responses are used, restrictions (D.7) and (D.9). Let $\tilde{z}_i$ be the set of all $z$ for which the actor uses action $a_i$,

$$\tilde{z}_i \equiv \{S^{A*}(z) = a_i\} \quad \text{(D.17)}$$

For this to be the case, it must be that,

$$(\forall\ \tilde{z}_i) \sum_{z \in \tilde{z}_i} w^R(z, r_i) > \sum_{z \in \tilde{z}_i} w^R(z, r_k) \quad \text{(D.18)}$$

At ESS, the same properties hold as in the separating equilibrium case, except that all members of $\tilde{z}_i$ are effectively averaged into a single class $zi$. So conventional signalling in action–response games need only be "honest on average", to the extent that they have common interest, though "average common interest" can seem quite counter-intuitive.

The extent to which this is a game without conflict is debatable. Consider false alarm-calls of the White-winged Shrike-tanager Munn (1986). These shrike-tanagers stand as sentries for flocks of heterospecific foragers and give alarm calls both when predators are present and when they want to steal prey from their wards. About half of all alarm calls are "false" and are used to steal prey from the receivers (this system demonstrates an interesting information theoretic property; before receiving an alarm call receivers are almost certain that no predator is present, after an alarm call they are totally uncertain. They have gained both information and uncertainty). Averaged across pooled signaller states, Gave Alarm Call ( = intending to steal + detected a predator) vs. Did Not Give Alarm Call, the optimal reply is to flee. The fraction of signallers in the state which uses the misleading signal is set by non-strategic factors external to the game. This is also true of action–response games with "dishonest" subsets within the signaller population (Johnstone & Grafen, 1993; Adams & Mesterton-Gibbons, 1995).

## THE LITERATURE

Maynard Smith (1991, 1994) has demonstrated these results in a subset of action–response games known as Sir Philip Sidney games. A mutual signalling version of the Sir Philip Sidney game (Maynard Smith, 1994) in which signalling is sequential also conforms to these results since the continuation games decompose into action–response games wherever a separating equilibrium exists.

The only model of conventional signalling in an action–response game of which we are aware in the biological literature is Viljugrein's (1997) mate signalling game. The extensive form is that of the basic action–response game with a third move, Divorce, a conditional acceptance, available to the responder when the actor indicates high quality (the other two responder moves are Stay and Reject, the actor moves are High and Low signals). Three equilibria exist, depending on the relative values of the pay-off parameters, a separating equilibrium, a pooling equilibrium and a semi-pooling mixed equilibrium.

The preference rankings at the separating equilibrium are;

$$\text{actor } (H,D) = (H,S) = (L,S) > (H,R) = (L,R) \quad \text{(D.19)}$$

$$\text{responder } (H,D) > (H,S) = (L,S) > (H,R) = (L,R) \quad \text{(D.20)}$$

when the actor is of high quality, and;

$$\text{actor } (H,S) = (L,S) > (H,R) = (L,R) > (H,D) \quad \text{(D.21)}$$

$$\text{responder } (H,R) = (L,R) > (H,D) > (H,S) = (L,S) \quad \text{(D.22)}$$

and when actor quality is low.

The responder's $S$ move is strictly dominated by $D$: in no actor state is the $S$ response better than $D$, and so $S$ can be removed from the responder's repertoire. When actor quality state is high both players prefer responder move $D$ over $R$, and when the state is low both players prefer the responder move $R$ over $D$; the preference rankings match, there is no conflict between the players.

The players have perfect common interest in the pooling equilibrium. It is not clear that the semi-pooling equilibrium is dynamically stable. A receiver population playing all Divorce seems to push the system into the pooling equilibrium.