

The Evolution of Bluffing in Animal Contests:
an ESS Approach

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Abstract. This paper studies the contest behaviour of territorial animals, where a contest begins with an explicit signalling stage. A resident has a choice of two signals, denoting either strong or weak resource holding power. A signal constitutes a bluff when a weak resident signals strong; bluffing, however, entails a cost. An intruder must then assess the signal before choosing whether to attack or retreat. The equilibrium concept applied is that of evolutionary stable strategy (ESS). For the contests we model, there is a unique ESS. The ESS depends crucially on the asymmetry of information between residents and intruders, as well as on the value of a territory V and cost of losing a contest C . When the ration V/C is low and residents have better information than intruders, all weak residents bluff, but bluffing decreases as V/C rises. The ESS predictions are used to reevaluate agonistic encounters in two species of fiddler crabs, *Uca pugilator* and *U. pugnax*.

There has been much confusion about the role of signalling in encounters between animals in conflict situations. In this paper, we apply the theory of extensive form games to signalling behaviour in conflict situations. In the extensive form, opponents move sequentially which allows for assessment. Assessment is an important aspect in animal contests that has not received much formal attention. To demonstrate the applicability of games in extensive form, we model a territorial contest that addresses the following questions: (1) Do displays contain reliable information? (2) If so, what kind of information? (3) To what extent is this information used by opponents? Throughout the behavioural literature, these questions have been addressed in a number of ways with varying results. From the work on this set of problems comes what might be called the "conventional view" of signalling in agonistic encounters. This view has arisen as a result of theoretical analyses of the evolution of stable behavioural strategies (ESS's) and empirical studies of actual behaviour in natural environments. Three general tenets of this position can be identified, although none are held universally.

(1) Information contained in displays is largely irrelevant to either subsequent behaviour or overall outcome of encounters. The traditional ethological view was that in some instances, displays function to inform animals of each others' intentions. Caryl (1979) cites several authors with this view (e.g. Cullen 1966), only to attack it. Caryl re-analysed data from several previous studies of bird agonistic displays. Correlations between specific ritualized behaviour patterns and

subsequent behaviour were consistently low, leading Caryl to conclude that displays are of only limited use in gaining information about the motivational state of the opponent. Other studies have led to similar conclusions (see, for instance, the classic study of agonistic encounters between Betta splendens males by Simpson, 1968) .

(2) Information contained in displays is not indicative of intention. Obviously, animals display during confrontations, and in the technical sense, displays carry information. However, the information may not be "about" intention or motivational state. Maynard Smith (1974, 1982) has argued on theoretical grounds that the signalling of intention or motivational state could not be stable since "cheaters", utilizing a bluffing strategy could easily invade. Signalling an opponent honestly about one's resource holding power (RHP, Parker 1974) is a stable strategy so long as the cost of bluffing a signal that indicates a greater RHP is large (Maynard Smith 1982). Empirical studies have shown that signals that correlate well with RHP are common (e.g. Davies and Halliday 1979, Clutton-Brock and Albon 1979) .

Recently, in a discussion of signalling capacity, Enquist (1985) pointed out the distinction between the variation in choice of behaviours and variation in quality of behaviours. This is an extremely important distinction inasmuch as information is unavoidably conveyed by the latter, even if this information is disadvantageous, for instance revealing low status or RHP. Although this is an important point in identifying different kinds of signals, information about real status (conveyed by performance) is invariably confounded with information about intent, and vice versa.

(3) To the extent that any information relevant to intentions or motivational state is present in displays, opponents should ignore it. This is the logical extension of Maynard Smith's line of argument on theoretical grounds. The presence of "cheaters" in a population renders any reliable signal suspect, in much the same way that a flush of counterfeit bills would increase skepticism among bank tellers. In other words, if the cost of bluffing is low, soon it pays everyone to bluff and the signal no longer conveys information.

We contend that much of the analysis of agonistic encounters between animals has been handicapped by assumptions that are too simplistic. This is as true of empirical studies as those concerned entirely with theory. An important component of all animal behaviour is assessment (Parker 1974, Parker and Rubenstein 1981), yet the strategic aspects of assessment are rarely incorporated into models. Because the techniques used to analyse the evolution of agonistic behaviour demanded it, the assessment phase of encounters has typically been modeled in such a way that players can not alter their behaviour based on information gained during the contest. In reality, opponents often go through many evident phases of display before any eventual outcome occurs. Studies that have attempted to model sequential features of behaviour have had to do so in a piecemeal fashion (Leimar and Enquist, 1984), and empirical studies have not been designed with this important aspect in mind.

We analyze a simple confrontation by extensive form, and show how and under what conditions a mixed ESS of bluffing and an informative signal might evolve. This result is difficult to obtain using the analysis of normal form games. In general, we

assign a cost to bluffing but keep it low in relation to the cost of losing a fight. We also consider an information index that reflects the knowledge an individual possesses about his own role in relation to his opponent, and allow for information asymmetries. Finally, we re-evaluate a study of agonistic encounters between male fiddler crabs, Uca (Hyatt and Salmon 1978 and 1979) in light of the predictions from the theory.

INFORMATION ASYMMETRY

To begin, several definitions will be helpful. Role refers to a combination of variables describing the players, e.g., relative size and ownership status ("large owner"). Individual variables are referred to as aspects of a role (Hammerstein, 1981). Roles are distinguished from types by the fact that the latter are invariant, whereas roles are defined only within the context of a particular encounter. Resource Holding Power (RHP) is the absolute ability of an individual to win an escalated contest (Parker 1974). Signals are defined here as transmissions that manipulate an opponents behaviour (Krebs & Dawkins 1984). A contest is an encounter between two animals in conflict over the possession of a resource. In our model, contests consist of two stages, a signalling stage and an attack or withdraw stage. Finally, bluffing is the transmission of a signal that indicates a higher RHP or level of motivation than the signaller actually possesses. Conversely, trap-passing is the transmission of a signal that indicates a lower RHP or level of motivation than the signaller actually possesses.

Let A and B be roles in an asymmetric game played by animals

labeled 1 and 2. Information about roles held by each animal at the start of the game is represented by a vector of probabilities \underline{P}^i for each player over all possible role pairs:

$$\underline{P}^i = [P^i(A,A), P^i(A,B), P^i(B,A), P^i(B,B)]. \quad (1)$$

$P^i(A,A)$ is the probability held by player i that player 1 is of role A and player 2 of role A , $P^i(A,B)$ the probability that 1 is in role A and 2 in role B , and so on. We posit such a set of probabilities \underline{P}^i for each player i .

Informational situations can be defined in terms of this framework. Information is symmetric when $\underline{P}^1 = \underline{P}^2$. In this case, the animals start out with the same information about roles. On the other hand, information is asymmetric whenever $\underline{P}^1 \neq \underline{P}^2$. In this case, the animals start out with different information about roles. Let P^* be the actual roles of the players in a particular encounter. When a player i knows his role, then the positive elements of the \underline{P}^i distribution are over his opponents possible roles. For example, if player 1 knows his role is A , and the probability that player 2 is role A is x , then $\underline{P}^1 = (x, 1-x, 0, 0)$. Similarly, if player 2 knows his role is A , and the probability that player 1 is role A is y , then $\underline{P}^2 = (y, 0, 1-y, 0)$. Finally, when each player knows his own role and that of the other player, there is complete information, and each probability vector has one entry equal to one.

In asymmetric games, the state of information about roles has important implications for the kind of ESS that can evolve. In the case of complete information, Hammerstein (1981) shows that an ESS must take the form of a strong Nash equilibrium in pure strategies. At a strong Nash equilibrium, each strategy being played is the unique best response to the other strategy.

This is a special case of a more general result due to Selten (1980). Suppose that every player in a game knows his own role, and also knows that his opponent is in a different role. Then any ESS must involve only pure strategies. In the present model, we relax Selten's assumptions; not every player need know his own role. With this relaxation, mixed strategy ESS's are once again possible (see for example Hammerstein and Parker 1982).

The condition of complete information is stringent. It leaves no logical room for signalling to convey information about roles. We expect incomplete information games to arise in any environment where players are uncertain about roles. Only in incomplete information games is signalling likely to evolve. We will show below how signalling is an integral part of the ESS for a class of incomplete information games.

These concepts can be extended in a straightforward fashion to information about more than a single role asymmetry. For some role asymmetries, such as resource holding power, the potential for informational asymmetry is considerable. For other asymmetries, such as resident/intruder, the role situation is usually much clearer and informational asymmetries are less likely to arise. Thus, one could have symmetric information with respect to one role aspect and asymmetric information with respect to another. In the model below, there is complete information about the resident/intruder asymmetry but incomplete information about RHP.

In a game with an information asymmetry, it is sometimes possible to identify one of the players as having better information than the other. For instance, if $\underline{p}^1 = p^* \neq \underline{p}^2$, it is

clear that player 1 has better information than player 2; indeed, player 1 has the best information possible. Other less clear cut cases can also be singled out. For instance, suppose player 1 is A and player 2 is B, so that $\underline{p}^* = (0, 1, 0, 0)$. Suppose further that $\underline{p}^1 = (\underline{x}, 1-\underline{x}, 0, 0)$. Player 1 knows his own role but not player 2's. While $\underline{p}^2 = (\underline{y}, 1-\underline{y}, 0, 0)$, so that player 2 doesn't know his own role. If $\underline{y} > \underline{x}$, then it is again clear that player 1 has better information than player 2, since \underline{x} is closer to the true value of zero than \underline{y} is. An informational asymmetry where one player has better information than another, and where the better informed player moves first, can lead to strategically informative signalling. We propose such a model below.

SIGNALLING IN EXTENSIVE FORM GAMES

The extensive form of a game is the appropriate model to choose for any encounter in which the sequence of moves is important. Selten (1983) has introduced the extensive form for biological games in general, and contests of finite duration in particular. In this section, we model signalling as an extensive form game.

The most general form of signalling game can be thought of as consisting of three stages. First, there is a random assignment of roles to players. If there are two possible roles to players, A and B, probabilities are assigned to each of the role configurations (A,A), (A,B), (B,A), and (B,B). The first element refers to the role of player 1. Next, there is a sequence of signals, one by each player. Here we adopt the convention that the player labeled 1 signals first. Selten

(1983, section 4) shows that no generality is lost by this convention. The signals are observed by both players, and then player 2 signals. Random assignment of roles, signal by player 1, and signal by player 2, constitute the signalling stages of the game. If there are two possible signals, left (L) and right (R), one has the tree structure depicted in Figure 1. The endpoints of the tree structure, are labeled (L,L), (L,R), (R,L), and (R,R) indicating signals made by (player 1, player 2).

After the signalling game, one can imagine various continuations of the game based on the role situation, signals emitted and the information available to the players about their roles. For instance, in the context of animal contests, the continuation may be Hawk vs. Dove or War of Attrition (Maynard Smith, 1982). If information is symmetric and complete, and if both players make the same signal and are of the same role, then the ensuing continuation will be symmetric. If even one aspect of the contest is asymmetric, so is the entire contest.

The point of intersection of two or more lines in a game tree is a vertex. An information set, or set of vertices, represents the information a player has about the situation. Figure 1 depicts one information set for player 1 and two information sets for player 2, depending on the behaviour of player 1. A player has perfect information if every one of his information sets contains a single vertex. In such a case, he knows exactly where he is in the game tree.

We impose the following restrictions on signalling:
player 1 is fully informed about the role situation ($P^1 = P^*$),
and player 2 knows his role is different from player 1's. We
further assume that only the first player signals. The

intuition behind this restriction is based on an information asymmetry. Player 1, having complete information, gains nothing from a signal by player 2, and so the outcome of the encounter does not change by allowing 2 to signal. However, an informed player has to act on his information to take advantage of it. Indeed, we exhibit an ESS in the next section at which player 1 in role A always goes left, whereas player 1 in role B sometimes goes right. Such signalling behaviour conveys information about player 1 to player 2.

The signalling game embodying these assumptions is portrayed in Figure 2. Since $\underline{P}^* = \underline{P}^1$ in every case, player 1 is fully informed. \underline{P}^* can take only two values because player 2 differs from player 1. In the event that $\underline{P}^* = (0, 0, 1, 0)$ then $\underline{P}^2 = (0, \underline{x}, 1-\underline{x}, 0)$. Player 2 knows he is different from player 1, but only knows that player 1 is in role A with probability \underline{x} and role B with probability $(1 - \underline{x})$. In the event that $\underline{P}^* = (0, 1, 0, 0)$, then \underline{P}^2 is the same as before. Player 2's information is unresponsive to the actual situation until he can update the role probabilities for Player 1. We can think of the probability \underline{x} as parameterizing the information to be gained in an encounter by player 2. Applying the Shannon measure of information \underline{H} ,

$$\underline{H} = \underline{x} \log(1/\underline{x}) + (1-\underline{x})\log(1/(1-\underline{x})) \quad (2)$$

we see that when \underline{x} takes on its extreme values of 0 or 1, the \underline{H} is zero. In such cases, player 2, already having complete information, can gain no more. At all other values of \underline{x} , \underline{H} is positive. \underline{H} reaches its maximum at $\underline{x} = 1/2$; here, player 2 has the most information to gain through the encounter. We posit this extreme form of information asymmetry, $\underline{H} = 0$ for player 1 and $\underline{H} > 0$ for player 2, in order to see most clearly the

phenomena of assessment and bluffing, which are the concerns of our study.

ESS OF A SIGNALLING GAME

In this section we give a specific interpretation to the roles A and B and supply a continuation of the signalling game, based on Hawk vs. Dove. We then solve for the ESS using the extensive form. We find two ESS behavioural regimes depending on the values of the parameters in the payoff functions. At one of these regimes, the behaviour of the informed player conveys information to the other player about the roles; at the other, behaviours conveys no such information.

Let role A represents high RHP and role B low RHP. Player 1 is known by both players to be the resident on a territory of value V. Both players know that player 2 is an intruder on this territory. In a contest, the player with the higher RHP wins. The cost to a loser of a contest is C. An intruder also has the option of leaving the territory before a contest at no cost. Player 1 moves first, signalling either left (strong) or right (weak). A rough translation of these signals might be "I am strong, don't waste time" and "I am weak, I won't hurt you". These signals are costly and there are a variety of ways to modelling them. We choose the following: A player incurs the signalling cost s only if he misrepresents his role. The results will differ if, for example, signalling costs are role specific. The worth of the territory and the cost of losing a contest are both much

larger than the cost of signalling, $V \gg s$, $C \gg s$. Player 2 moves second, going either left (attack) or right (retreat) in the tree diagram (see figure 3).

Signalling strong or attacking has serious consequences for both the resident and the intruder. A strong signal commits the resident to a serious fight. The intruder can either attack or end the interaction by retreating. There are four possible behavioural sequences, three of which lead to a definite outcome: (strong,attack)—serious fight; the (strong,retreat) and (weak,retreat)—intruder flees. One behaviour sequence (weak,attack) is indefinite: the resident is still free to fight or retreat but the intruder is committed to fighting.

Each player has two information sets (figures 3 and 4). The resident, with the best information, knows whether he or the intruder has greater RHP. His information sets reflect each of these two possibilities. The intruder only knows the probability that he has the lower RHP, x . However, since the informed player moves first, it is conceivable that his signal might improve the intruder's estimate of the real state of affairs. Suppose for instance that the resident always signals strong when he has higher RHP and weak when he has lower RHP. Then the intruder knows, based on this signal, which contestant has the higher RHP. If he observes the resident signal strong, he should retreat, since he is sure to lose the contest and suffer cost C . On the other hand, if he observes the resident signal weak, he should attack, since he is sure to win the contest and gain fitness V . Such signalling behaviour is completely informative, since the signal tells the intruder everything there is to know about the role situation.

Our first result is that completely informative signalling is not evolutionarily stable, and can be invaded by bluffers. There are two kinds of informative signals. In the first of these, the resident signals strong if he has high RHP and weak if low RHP. The intruder, now possessing complete information, attacks in response to signal weak and retreats in response to signal strong. A mutant resident who always signals strong (high or low RHP) can invade. Any intruder will think this mutant has greater RHP, and therefore retreat. Since signalling cost is small relative to the value of the territory, such a resident always receives at least the payoff $\underline{V} - \underline{s} > 0$. The comparable payoff for a resident with lower RHP is 0; hence such a mutant can successfully invade the population. Formally, there is a second type of informative signal, high RHP signals weak and low RHP signals strong. This population can be invaded by a mutant with high RHP which signals strong. Such a mutant gets payoff $\underline{V} > \underline{V} - \underline{s}$.

In general, two kinds of deception or misinformation are possible. The nonaggressive signal weak given by a high RHP resident (role A) is misinformative, since such a player has every incentive to fight for his territory if attacked. Conversely, the aggressive signal strong given by a low RHP resident (role B) is misinformative, since such a player is sure to lose his territory if attacked. We shall term these two kinds of behaviour trap passing and bluffing, respectively. We draw these terms from poker, which has an analogous strategic nature. Just as in poker, where a bluff commits a player to a showdown if called, a bluffing resident is committed to a serious fight if attacked. Again, the cost

to signalling is only incurred if a player uses a signal inconsistent with his RHP. Thus, a bluff is successful when the intruder retreats, just as in poker when the other players fold.

An ESS in an extensive form game specifies a behaviour at each information set on the part of each player. To this end, we introduce the following notation:

b_1 = probability that player 1 in role A signals strong

b_2 = probability that player 1 in role B signals strong

b_3 = probability that player 2 attacks, given that
player 1 has signalled strong

b_4 = probability that player 2 attacks, given that
player 1 has signalled weak.

The probability of signalling weak is $(1-b_1)$ or $(1-b_2)$, depending on role. Let b be a general vector of behaviour strategies: $b = (b_1, b_2, b_3, b_4)$. Then, b is an ESS if a population playing b is uninvadable by a mutant.

We have already seen that the fully informative behaviour strategy $b = (1,0,0,1)$ is not an ESS. We proceed to show what the ESS is for this game. The ESS concept we use is that of Limit ESS (see Selten 1983, section 7, for the technical definition). This is the ESS concept which applies to games in extensive form, when players have multiple information sets, not all of which may be reached by equilibrium play of the games. We present the ESS result and then indicate how it was obtained.

There are two distinct ESS behaviour regimes (see Figure 4 and Table 1), depending on the value of the territory relative to the cost of losing a fight (V/C), and the probability of encountering a high RHP (x).

Regime I. This is the behaviour regime where V/C is low:

$$V/C < x/(1-x) \quad (3)$$

In this part of the parameter space, $b = (1,1,0,0)$ is the ESS. The resident always signals strong, and the intruder always retreats. To see why this is an equilibrium, note first of all that the signal is completely uninformative. Since every resident signals strong, this cannot convey any information to an intruder about the resident's RHP. Thus, an intruder faces the choice between attacking and expecting the payoff

$$x(-c) + (1-x)(V) \quad (4)$$

or retreating and assuring himself of the payoff zero. Given (3), the payoff (4) is always negative; hence, the intruder does best to retreat. On the other hand, residents are receiving the highest possible payoffs in this game, $V-s$ if low RHP and V if high RHP. Low RHP residents are constantly bluffing and getting away with it, the reason being that V/C is too low for intruders who are less well informed to risk a fight.

Regime II. This is the behaviour regime where V/C is high:

$$V/C > x/(1-x) \quad (5)$$

In this part of the parameter space, $b = (1,p,q,1)$ is the ESS, where p and q are defined by

$$p = (C/V)(x/(1-x)) \quad (6)$$

and

$$q = (V-s)/(C+V). \quad (7)$$

Residents with high RHP continue to signal strong, since signalling strong costs less than signalling weak and they win a contest in any case. Low RHP residents however signal strong only with probability p given by (6). Such signalling behaviour does convey information to the intruders. The signal weak

informs the intruder that he has the higher RHP, so that the
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intruder always attacks when the signal weak is given. When the intruder observes the signal strong, he now attacks with probability g , given by (7).

The argument for these mixed strategy behaviours is as follows. Even the signal strong is informative and updates player 2's information. The conditional probability that strong was signalled by a high RHP resident is no longer \bar{x} but

$$\bar{x}/(\bar{x} + (1-\bar{x})p). \quad (8)$$

Conversely, the conditional probability that strong was signalled by a low RHP resident is

$$(1-\bar{x})p/(\bar{x} + (1-\bar{x})p). \quad (9)$$

The expected payoff of attacking in the face of the signal strong (using (7) and (8)) is equal to

$$(-C)(x)/(x + (1-x)p) + (V)(1-x)p/(x + (1-x)p). \quad (10)$$

As before, the expected payoff of retreating is 0. At a mixed strategy equilibrium, these two payoffs (equation 10 and 0) must be equal; (6) then follows from (10). As far as the resident with low RHP is concerned, the expected payoff from signalling strong is

$$S(-C-\bar{s}) + (1-s)(V-\bar{s}), \quad (11)$$

since he is attacked and loses with probability g .

Alternatively, the low RHP resident can signal weak and guarantee himself the payoff 0. Equating (11) with zero, one has (7).

These results are summarized in Table 1. A high RHP resident gets the value of the territory V in either regime. A low RHP resident gets the value of the territory less signalling cost ($V-\bar{s}$) in the all-bluffing regime, but only expects 0 payoff in the

partial-bluffing regime. Finally, intruders get the payoff 0 in either regime.

DISCUSSION

The asymmetric extensive form game model we have presented has an ESS in which signalling and bluffing are evolutionarily stable behaviours. Specifically, under the assumptions of the model, signalling evolves when information is not complete. Bluffing becomes more prevalent as the value of the contested resource increases in relation to the cost of losing a fight for the resource, if the degree of uncertainty in the system is held constant.

To appraise the applicability of these results, we highlight the assumptions of the model with relation to the fighting behaviour of fiddler crabs, *Uca pugilator* and *U. pugnax* (Hyatt & Salmon 1978 and 1979). In *U. pugilator*, males defend burrows with displays and fights. While residents win the majority of contests, their advantage is not absolute. When the intruders win, they are larger than the resident and these contests usually involve more forceful acts. Hyatt and Salmon classified the behaviours into forceful and ritualized acts. They identified four stages in the fiddler crab contests. In our model we collapse their four stages into two. In the first stage, the signal (strong or weak) is ritualized, while in the second stage the behaviour is forceful (attack or retreat). A two-stage game is the logical minimum for modelling information transfer.

The role asymmetry includes resident/intruder and high

RHP/low RHP. For the information asymmetry, we assume that the resident (player 1) has more information than the intruder. In ~~U. pucillator~~ the intruder approaches and acts first by pushing on the resident with his claw (Hyatt and Salmon 1978), a contact that allows the resident to assess RHP of the intruder. The contest we have modeled begins after the resident has had the opportunity to assess the intruder.

The most likely cost of losing a fight in U. pugilator is an increase in the risk of predation. If a predator is attracted to the contestants, a resident can escape to his burrow, while the intruder is left exposed. When contests advance to forceful acts, males rarely show signs of physical injury. It is reasonable to assume that the cost of a signal inconsistent with RHP is much less than the cost of losing a fight, $C \gg s$, since these signals are to some extent ritualized displays. The burrows are necessary for a male to mate, justifying the assumption that $V \gg s$.

In assigning the cost of signalling, we have assumed that giving misinformation is in some way more expensive than giving correct information. It has been suggested that "(a)ll signals are products of coevolution between manipulation and sales-resistance (Krebs & Dawkins 1984)." Since signals are probably complex, in that the receiver uses more than one criterion to assess the opponent, we have assumed that the misinformer has to overcome any information he may inadvertently send about his actual RHP by exaggerating the signal. Krebs and Dawkins (1984) also discuss the repetitive nature of animal displays in terms of manipulation, propaganda, persuasion or advertising. In this sense, a small resident may need to put more energy into a signal

to persuade a large intruder to retreat.

We predict that the occurrence of bluffing is dependent on the value of the resource in relation to the cost of losing a fight for the resource, V/C and the information asymmetry as parameterized by x (see Figure 5). In particular, holding C and x constant for low V , all low RHP individuals bluff (Regime I). If V increases sufficiently, behaviour shifts to bluffing as part of a mixed ESS (Regime II). In *U. pugilator* burrows are more valuable than in the closely related species *U. pugnax*, because they are not as available. If the cost of losing a fight and the extent of information asymmetry is roughly the same across these species, fewer residents should hold onto territories irrespective of size (bluffing) in *U. pugilator* (Regime II) as compared to *U. pugnax* (Regime I). Moreover, contests in *U. pugilator* are more likely to end in an actual fight (in which case a bluffer would be caught) as compared to *U. pugnax*, in which players are more likely to withdraw. While there is no evidence that intruders select smaller residents to fight in *U. pugnax*, there is a tendency in this direction in *U. pugilator*, which suggests that the *U. pugilator* intruders are more effective at assessing RHP.

This model raises several interesting points in light of the conventional view of signalling we outlined in the introduction. First, determining the reliability of displays presents a measurement problem. While Caryl's (1979) re-analysis of the agonistic behaviour of birds showed that correlations between ritualized displays and subsequent behaviour were low, he also found that attack signals were less reliable than escape signals. This is just what one would expect if some of the attack signals

were bluffs. If bluffs are sometimes called, the bluffer loses after signalling attack. Bluffing may be much more common than presently believed, since bluffs that are caught will not correlate with subsequent behaviour or the outcome of encounters.

Second, our results have implications for the type of information that is conveyed. The distinction between choice of behaviours and performance of behaviours assumes that performance is honest or ". . . the reliability of the information being signalled is guaranteed (Enquist 1985)". Our model allows for incorrect signals about RHP. Signalling "I have a greater RHP" automatically says "I intend to fight" because the high RHP is sure to win. In this sense, a signal of RHP is a signal of intent. The distinction between a signal of intent and a signal of type may be difficult to draw.

The observation that informative signals should only contain information about RHP and not intent is based on the concept that RHP signals are costly to bluff. Empirical studies have shown that signals correlating with factors that influence RHP are common (e.g. croaking toads, Davies and Halliday 1978; roaring red deer, Clutton-Brock and Albon 1979). In both of these examples, the cost of signalling is high, and therefore bluffing would be expensive. There are also examples, however, of signals for which the cost to bluffing would be low and yet the signals still convey information. For example Rohwer (1975, 1977) and Ketterson (1979) address the question of status signaling by plumage variability (low cost) and the apparent lack of convergence on signalling "dominant". Maynard Smith (1982) has reasoned that if bluffing does not have a high cost, bluffing

invades and soon it pays for opponents to ignore the signal. The use of extensive form and the behavioural adjustment it allows, leads to a very different result. Even with a small cost to bluffing, a population can remain in the partial-bluffing regime. Incompleteness and asymmetry of information, with the associated informative signalling, are responsible.

Information asymmetries about roles should occur in systems where repeated encounters with the same individual are rare or where roles are highly dependent on previous outcomes. In systems where this is not the case, multiple threat displays may evolve via the mechanism pointed out by Andersson (1980). Walton and Nolan (1986) discuss the effects of imperfect and asymmetric information on the territorial behaviour of male prairie warblers (Dendroica discolor). In most of the cases they observed, the previous owner of a territory won. However the role of intruder and resident was confounded by seasonal nature of the territories. If at the beginning of a season the previous resident and the intruder arrive at the territory simultaneously, there is the possibility of misperceptions about relative roles. In the case when the intruder won, his behaviour suggests he misperceived his role in relation to the previous resident.

In this paper, we have addressed the question of animal signalling - a behaviour adapted to influence the behaviour of other animals - with the theory of extensive form games. Such games allow us to model situations of incomplete information, in which various possible information transfers are inherent. In particular, we have focused on signalling behaviour in territorial contests and its implication for aggressive behaviour. In our model, bluffing is an inevitable outcome of

natural selection. We have framed this specific model to be as simple as possible without sacrificing strategic interest. It is an open question to what extent the conclusions of a model this simple generalize. Several extensions of our model are possible. First, the model allows only signalling by residents. One could allow signalling by both residents and intruders in a two-sided incomplete information framework. One could also allow for more flexibility in responding to signalling behaviour, for instance, by having War of Attrition continuations as well as Hawk vs. Dove. Finally, one could allow for more asymmetries than simply resident/intruder and high RHP/low RHP. However, our main result is robust to such extensions. When the the ratio of V/C is small enough, there will always be selection pressure against signals that correctly reveal an animal's RHP. Such generalization offer attractive prospects for future research.

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Table 1. ESS for the two behavior regimes.

	<u>regime II</u>	<u>regime I</u>
b_1	1	1
b_2	$(C/V)(x/(1-x))$	1
b_3	$(V-s)/(C+V)$	0
b_4	1	0
Payoff $_{1,A}(L)$	V	V
Payoff $_{1,B}(L)$	0	V-s
Payoff $_2$	0	0

Figure 1. Move structure and information sets, 3-move signalling. Information is incomplete.

Figure 2. 2-move signalling game, Player 1 fully informed.

Figure 3. Signalling game in extensive form with payoffs. 1 is the resident and signals strong or weak. 2 is the intruder and attacks or retreats.

Figure 4. ESS behaviour regimes.







