Available online at www.sciencedirect.com
SCIENCE DIRECT®
Journal of Theoretical Biology 241 (2006) 639–648
Journal of Theoretical Biology
www.elsevier.com/locate/yjtbi

Resource holding potential, subjective resource value, and game theoretical models of aggressiveness signalling

Peter L. Hurd*

Department of Psychology, University of Alberta, Edmonton, AB, Canada T6G 2E9

Received 5 June 2005; received in revised form 3 November 2005; accepted 3 January 2006
Available online 9 February 2006

Abstract

Empirical evidence suggests that aggressiveness (willingness to enter into, or escalate an aggressive interaction) may be more important than the ability to win fights in some species. Both empirical and theoretical traditions treat aggressiveness as a distinct property from the ability (RHP) or motivation (subjective resource value) to win a fight. I examine how these three traits are clearly distinct when modelled using a simple strategic model of escalation. I then examine game theoretical models of agonistic communication and demonstrate that models in which aggressiveness is signalled require: (1) a trait, aggressiveness, which is neither a correlate, nor consequence of RHP or motivation, (2) a handicap which negates any benefit to be gained through the use of a particular signal, and (3) the absence of any other asymmetry which could be used to assign roles to players. I conclude that it is unlikely that these assumptions are ever met, and that empirical examples of ''aggressiveness'' are far more likely to represent long-term differences in subjective resource value.

Keywords: Aggressiveness; Communication; Threat displays

1. Introduction

Why are some individuals more aggressive than others? This question asks about variation in aggressive behaviour, but is more specific than the question ''why is there variation in aggressive behaviour?''. Strategic models of aggressive behaviour are predicated upon asymmetries in one of three types of traits: (1) resource holding potential (RHP), (2) relative resource value (V) and (3) aggressiveness. These three traits are distinct, both intuitively and as modelled by game theory. RHP is the ability to win an all-out contest (Parker, 1974; Maynard Smith, 1982; Bradbury and Vehrencamp, 1998), subjective resource value (sometimes called motivation'', e.g. Enquist, 1985; Barlow et al., 1986) refers to variation between individuals in the value of winning the contested resource (e.g. differences in hunger level when competing for food) (Maynard Smith, 1982), and aggressiveness is an individual's tendency to escalate a contest independent of RHP and relative resource value effects (Barlow et al., 1986; Maynard Smith and Harper, 1988). All three of these factors affect the choice of whether and when to escalate. Animals with higher RHP may escalate more as they have less to fear in a physical fight. Animals for whom winning is more important, who have higher subjective resource values, ought also to escalate more. Aggressiveness, called ''daring'' by Barlow et al., differs from subjective resource value in that it is an inherent property of the individual, a persistent personality trait, rather than a variable motivational state (Barlow et al., 1986).

The trait that determines contest outcome for any given species undoubtedly depends upon the precise circumstance of the contest. For instance, among males of various species of cichlids fighting for dominance or territory, fight outcome is predicted by asymmetries in body weight—which are RHP factors (Barlow et al., 1986; Enquist and Jakobsson, 1986; Enquist et al., 1990)—gonad size—which is thought to be a motivation factor (Neat et al., 1998)— or aggressiveness (Barlow et al., 1986). Barlow et al. (1986) have demonstrated that experimental manipulation of a single parameter, resource value, can change which trait, RHP or aggressiveness, will be most important in determining contest outcome. Keeley and Grant (1993)

*Tel.: +780 492 3578; fax: +780 492 1768.
E-mail address: phurd@ualberta.ca.

0022-5193/$ - see front matter
doi:10.1016/j.jtbi.2006.01.001

have demonstrated an effect of resource value manipulations upon aggressive behaviour. Of the three traits, aggressiveness has received the least attention from behavioural ecologists, but may have more importance to an individual's fitness than the other two traits. For example, willingness to enter into an aggressive interaction may be more important in securing a territory in *Anolis* lizards than is ability to win fights (Stamps and Krishnan, 1997, 1998).

These three traits are also clearly distinct when modelled formally. Classic Hawk–Dove models treat decisions to escalate between individuals of identical RHP and subjective resource value (Maynard Smith, 1982), while other models (e.g. Maynard Smith and Harper, 1988) demonstrate the evolutionary maintenance of variation in aggressiveness. Variant Hawk–Dove models (e.g. Hammerstein, 1981) treat contests between individuals with differing RHP, as does the sequential assessment game (Enquist and Leimar, 1983; Leimar and Enquist, 1984). The classic Hawk–Dove game includes an explicit subjective resource value term which affects decisions to escalate (Maynard Smith, 1982). The sequential assessment game also models variation in subjective resource value (Enquist and Leimar, 1987). In addition to these models investigating variation in the decisions to escalate as a function of these three traits, each trait is also modelled distinctly when investigating signalling of trait variation. Models of agonistic display assume displays signal one of RHP (e.g. Enquist, 1985; Adams and Mesterton-Gibbons, 1995; Hurd, 1997), subjective resource value (e.g. Enquist, 1985; Enquist et al., 1998) or aggressiveness (e.g. Kim, 1995). I know of no well-formed model of agonistic communication which models a trait other than these three, or models more than one trait at a time.

In this paper I shall examine game theoretical models of aggressiveness and relate their structure (Hurd and Enquist, 2005) to other game theoretic models of agonistic communication. I show that models of aggressiveness are distinctly different, and that these differences require several restrictive assumptions be met. I suggest that these assumptions are very rarely met and cast doubt upon the ability of models of aggressiveness to explain empirical patterns of agonistic display use.

1.1. A simple model of behavioural choice

Game theoretical modelling is a subset of optimality modelling in that it aims to provide an optimum choice of behaviour given that the costs and benefits of possible behaviours vary as a function of other individuals' choice of behaviour. Models of aggressive behaviour most often take the form of a choice between levels of escalation and lead to one of two types of outcome: winning and losing. The essential difference between aggressiveness on the one hand, and RHP or resource value based decisions to escalate on the other, can be demonstrated by a simple economic model of behavioural choice, introduced in the next section.

Fig. 1 (based on a model from Enquist et al., 1985) depicts three options available to a single individual in an aggressive interaction. These options may be seen as either strategies chosen at the outset, or behaviours chosen at some point during a contest. Whether the options are strategies or behaviours, the consequences, costs and benefits to the alternatives are measured from the point at which the decision is being made until the end of the consequences of the acts, which may be the end of the interaction or longer. The horizontal axis represents variation in the value of winning, the vertical axis represents expected payoff to the individual. Each behavioural option is shown with a line. The expected payoff to a given behavioural option i is

$$W = p_i V - C_i, \tag{1}$$

where p_i is the probability that the choice i leads to a victory, and C_i is the cost of using option i. The probability of winning through the use of behaviour i is shown by the slope of that options' line.

In the example presented in Fig. 1, strategy 2 is the more escalated strategy. It has a higher probability of leading to success, but has a higher expected cost of implementation, so it is worth using only when the value of the contested

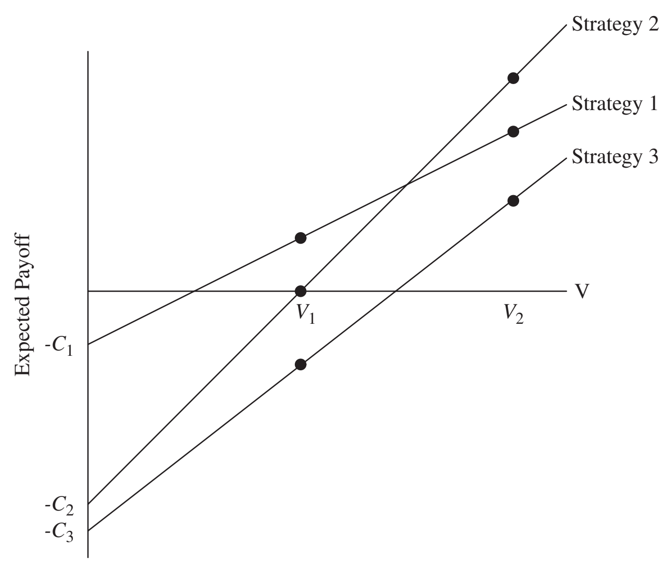

Fig. 1. Expected payoffs ($W = p_i V - C_i$) for three alternative strategies as a function of their costs and probability of winning, over a range of relative resource values. Costs and benefits are shown in the vertical dimension, and the value of winning in the horizontal. At $V = 0$ there is no possible benefit to competing and so the intercept of each strategy, C_i, is the inherent cost of using that strategy. Slopes indicate the probability of winning, p_i, using that strategy. The strategy which yields the highest expected payoff for a given resource value is the optimal strategy. The appropriate option to choose changes over different ranges of values of winning. At V_1 option 1 leads to the highest expected payoff, at V_2 option 2 is preferable. Option 3 is never preferable, and should never be used. Likewise, if a single strategy were better than other strategies over the entire range of V, it should be the only behaviour ever used.

resource is high. At lower resource values strategy 1 is preferable, at some point the resource is worth so little that it is not worth contesting at all. At no point is strategy 3 optimal, and so it ought never to been seen in a natural encounter.

The optimality model shown in Fig. 1 explains how variation in the perceived value of winning may lead an individual to choose one behaviour or strategy over another. I will now use a modified version of this model (Fig. 2) to examine variation between individuals in aggressive behaviour.

Fig. 2 depicts two different individuals, A and B, that differ in their ability to use the alternatives from Fig. 1. Individual A pays less when using strategy 2 than does individual B, and also has a higher probability of winning when using strategy 1 than does individual B. Player A has more RHP, and either pays less for a given behaviour, or has a higher probability of winning with the same behaviour. Such individual variation in the costs of differing behaviours, or in the probability of winning a fight once a decision has been made to escalate, may account for individual variation in behaviour. Player A switches from the less escalated behaviour 1 to the more escalated behaviour 2 at V_1 while player B switches to the more escalated behaviour at V_2. It can be shown that the option switch point will be at higher values of V for individuals with lower RHP whether RHP acts via strategy cost, or probability of winning.

1.2. Aggressiveness

This simple model makes a clear distinction between variation in RHP and subjective resource value. My working definition of aggressiveness is variation in the propensity to escalate independent of the effects of RHP and resource value, and is inspired by Barlow et al. (1986) when they write:

> Motivational and physical components are assumed to be separable. [...] The motivation depends upon V, the value of the resource, and the perceived prowess and motivation of the opponent. [...] but there is an additional component. It is the readiness of the individual to risk an encounter, to dare to escalate, measured when the contest is otherwise symmetrical. It differs from V in that daring appears to be an inherent property of the individual rather than a variable motivational state that is tuned to the value of the resource (Barlow et al., 1986).

While factors such as winner/loser effects (Mesterton-Gibbons, 1999) and dominance effects (Dugatkin and Early, 2004) also influence decisions to escalate, I see these as acting primarily through "the perceived prowess and motivation of the opponent". I therefore consider aggressiveness to be a separate trait, and these other factors to influence either perceived RHP, or more likely, V. In either case model which addressed winner/loser or dominance effects directly would require repeated plays, and is beyond the scope of the present work.

I shall next examine how variation in aggressiveness is depicted in the simple model presented in the last section. An optimality model has little variation to work with. The choice between a more and less escalated behaviour is also a choice between higher and lower expected payoffs, except at single points along the resource value continuum. The point at which the two alternatives yield the same payoff is V_1 for player A, and V_2 for player B (Fig. 2). Only at these points are players indifferent to the consequences of behaviour 1 in comparison to behaviour 2. Only at exactly this level of subjective resource value can either strategy be played and still be optimal. Allowing for some errors in perception of resource value, these points may be thought of as intervals. The essential point, however, is that variation in the choice of alternative behaviours reflecting aggressiveness cannot be between options with higher and lower expected payoffs. Aggressiveness can only be expressed, in this simple optimality model, when the choice is between options with equal expected payoffs. Individuals with equal RHP and equal assessed resource valuations can differ in their choice only when they are essentially payoff-indifferent between those options.

The model depicted in Figs. 1 and 2 is an optimality model. It describes properties that alternative strategies must have in order for variation in aggressive behaviour to exist over ranges of subjective resource value (Fig. 1) and RHP (Fig. 2). The model does not function well as the basis for investigating variation in aggressiveness, but the Hawk–Dove game (Maynard Smith and Parker, 1976; Maynard Smith, 1982) does. The Hawk–Dove game models two individuals—of identical RHP and subjective

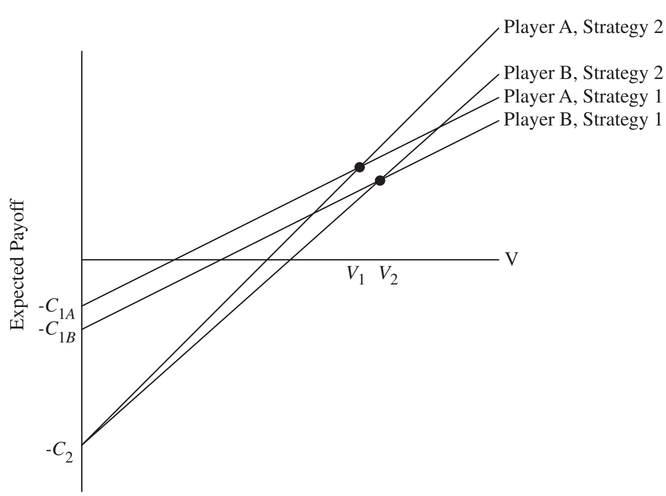

Fig. 2. Expected payoffs for two individuals with different RHPs, axes as in Fig. 1. Individual A pays less when using strategy 2 than does individual B, $C_{1A} < C_{1B}$. Individual A also has a higher probability of winning when using strategy 1 than does individual B. Player A switches from option 1 to the more escalated option 2 at V_1, whereas player 2 switches to the more escalated strategy at V_2. It can be shown that whether the strategies differ in C or p, that the V_{crit} switch point from less to more escalated strategies always increases with a decrease in RHP.

resource value—who make a strategic decision to either escalate (play Hawk) or not (play Dove). Traditionally, the payoffs in this game are phrased using a resource of value V, and a cost of escalated fighting C. It is also traditional to assume that $V<C$, that is to say that the cost of an escalated fight is high enough to dissuade escalation in some cases (Maynard Smith and Parker, 1976). If this were not the case, and $V>C$, then all individuals escalate all the time; there will be no behavioural variation therefore no communication will evolve. Therefore we assume $V<C$. Even given this assumption, many different variations exist in how payoffs are formulated for the Hawk–Dove game (see e.g. Maynard Smith and Parker, 1976; Hammerstein, 1981; Cushing, 1995; Kim, 1995). All of these variants share the essential quality that it pays most to play Hawk when the opponent plays Dove, and Dove when the opponent plays Hawk (Appendix A presents the generic discoordination game, which encompasses all Hawk–Dove variants).

Formal techniques allow us to identify a point at which the switch from Hawk to Dove is optimal (Appendix B). If the probability that the opponent will play Hawk is less than some critical value p, then play Hawk. If the probability that the opponent will play Hawk is more than p, then play Dove. If the probability that the opponent will play hawk is exactly p then any strategy pays equally well. These results follow intuitively from the biological premise, that it pays to escalate if, and only if, the opponent is not going to escalate.

What is slightly less intuitive is that the optimal probability of escalating is either all or none, given any belief that the opponent is more or less likely (than p) to escalate. As is well known (Maynard Smith and Parker, 1976; Selten, 1980; Hammerstein, 1981; Maynard Smith, 1982), this discoordination dynamic leads to two Nash equilibria, one of which will be an ESS; which one depends upon whether or not there is an uncorrelated asymmetry (demonstrated in Appendix C).

1. When no uncorrelated asymmetry exists, the ESS is a Nash equilibrium strategy that mixes the two behaviours (Hawk with probability p and Dove with probability $1-p$).
2. When an uncorrelated asymmetry exists, the ESS is a pure strategy Nash equilibrium in which one player chooses Hawk and the other chooses Dove.

For virtually all Hawk–Dove games, and most discoordination games, the expected payoff in the second, uncorrelated asymmetry, case is higher than in the first, in which there is no uncorrelated asymmetry (Appendix D). Players would rather, that an uncorrelated asymmetry existed. That is, they would rather flip a coin to determine roles than play the mixing Nash. In the next section, I examine a model which uses signals between the players to perform the role of a coin toss.

1.3. Signalling aggressiveness

The aggressiveness signalling game (Kim, 1995) is a Hawk–Dove game preceded by a signalling phase (shown in the extensive form in Fig. 3). The essence of this model is that in the absence of an uncorrelated asymmetry players create one using signals. Players choose one of two signals, a less escalated signal, m_0, and a more escalated signal, m_1. If the signals do not match (subgames "b" and "c", Fig. 3), then an uncorrelated asymmetry exists; the player who chose m_1 plays Hawk, and the player who chose m_0 plays Dove. When the players choose the same signal (subgames "a" and "d", Fig. 3), there is no uncorrelated asymmetry and the players both play the mixing ESS in the endgame.

The subgames at nodes "a" through "d" may be reduced to their ESS outcomes, to produce a 2×2 matrix game (Appendix E) in which the only move is to choose between signals m_0 and m_1. The payoffs for this game are the expected payoffs at the nodes "a" through "d". There is a definite advantage to using the more escalated signal m_1 in

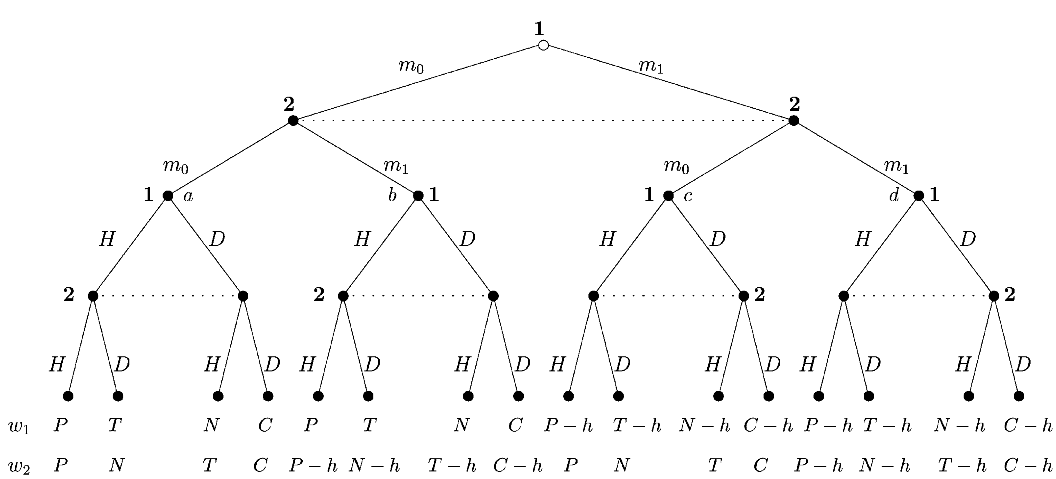

Fig. 3. The aggressiveness signalling game in the extensive form, with generic discoordination game payoffs and a handicap of cost h on the use of signal m_1. Four subgames (labelled a through d) follow after a simultaneous signalling phase.

this game because it causes the opponent to play Dove at the uncorrelated asymmetry node. The inequality (11, in Appendix E) leads to an invariant pure signalling strategy, always play m_1, followed by a mixed strategy in the Hawk–Dove game. Kim's (1995) model adds a handicap cost to signal m_1 to maintain variation in signal. This handicap nullifies the benefit derived by inducing opponents to play Dove, lowering the expected payoffs for m_1 until it is equal to that of m_0. With the more effective signal handicapped, the reduced matrix game becomes a discoordination game. If the opponent plays m_1 then m_0 pays more than m_1, but if the opponent plays m_0 then m_1 pays more than m_0.

2. Violating assumptions

The aggressiveness signalling game is highly robust to variations in the formulation of Hawk–Dove payoffs. The generic discoordination game demonstrates that the results hold true for any underlying model of escalation, as long as it pays one player to escalate only if the other does not. There are two critical assumptions underpinning the model which I shall now investigate:

1. Signal space is limited to two signals.
2. No (uncorrelated or not) asymmetry prior to the signal.

2.1. Limited signal space

The aggressiveness signalling game may be thought of as a rock paper scissors game in which the only moves allowed are "rock" and "scissors". Rock beats scissors, and so no variation in signals will exist unless a cost is imposed upon playing rock which eliminates the net "rock" benefit (as in Kim, 1995).

This need for a handicap can be eliminated in the aggressiveness signalling game by increasing the signal space to include more than two signals. When a discoordination game is preceded by a signalling phase in which three (or more) signals are available—and a rock-paper-scissors type circular dominance interpretation of signals is used by the players—then the equivalent truncated signalling game matrix becomes that shown in Table 1.

The payoff rankings match the classic rock-paper-scissors (Maynard Smith, 1982, pp. 19–20) and the ESS is to mix all three moves with equal probability. This produces a solution in which each individual player chooses randomly among the signals available. The player which chose the dominant signal then plays Hawk, and the other player Dove. If both players chose the same signal, then both will play the mixing ESS in the final Hawk–Dove game. This requires no handicapping cost to "dominant" or "escalated" signals since no signal is dominant or escalated by nature, and all have equal expected payoff.

Table 1
Payoffs for the three-signal aggressiveness game, when the subgames have been solved. The assumed uncorrelated asymmetry convention is play Hawk if: played m_2 and the opponent played m_1, or if played m_1 and the opponent played m_0, or played m_0 and the opponent played m_2. Play Dove: if the signals do not match and the previous rule does not specify playing Hawk. If the opponent chose the same signal then play Hawk with the probability specified by the mixing ESS

Discoordination game			
Player 1	Player 2		
	m_2	m_1	m_0
m_2	$W_{mixing}\backslash W_{mixing}$	$T\backslash N$	$N\backslash T$
m_1	$N\backslash T$	$W_{mixing}\backslash W_{mixing}$	$T\backslash N$
m_0	$T\backslash N$	$N\backslash T$	$W_{mixing}\backslash W_{mixing}$

2.2. No asymmetry prior to signal

The aggressiveness signalling game also requires a total absence of asymmetries, either correlated or uncorrelated, prior to play. The presence of correlated (i.e. payoff relevant asymmetries: variation in RHP or subjective resource value) would produce decisions to escalate based on these traits, and would mask any signalling of evolutionarily stable aggressiveness. Any uncorrelated asymmetry would be used as a discoordination cue for the subgames. There would be no use for a discoordination signal chosen by the players since these only produce discoordination outcomes in some plays of the game, while use of the uncorrelated asymmetry can be used to discoordinate in every play of the game. For this reason, any asymmetry in time of arrival, plumage brightness, initial perch height, positions with respect to the sun, etc. ought to be used as a cue. The adoption of any of these cues will make signalling of aggressiveness, as modelled by this very general game, moot and no communication will evolve.

One case, discussed below, in which the requirement that no uncorrelated asymmetry exists is not so far-fetched is when the signal is chosen prior to the contest.

3. Discussion

Empiricists have identified three distinct traits, RHP, subjective resource value and aggressiveness, which influence escalation decisions in agonistic interactions in cichlids (e.g. Jakobsson et al., 1979; Barlow et al., 1986; Koops and Grant, 1993; Neat et al., 1998) and anolis lizards (e.g. Tokarz, 1985; McMann, 1993; Summers and Greenberg, 1994; Zucker and Murray, 1996; Stamps and Krishnan, 1997, 1998). A simple model of behaviour choice shows that these three traits are easily distinguished theoretically as well as empirically (Figs. 1, 2). Game theoretical models exist that demonstrate the evolutionary stability of threat display communicating information about each of these traits.

Two of these traits, RHP and subjective resource value, affect the expected costs and benefits of fights. The third trait, aggressiveness does not affect payoff. In fact, I have demonstrated, that the choice between threat displays or fighting behaviours that reflect variation in aggressiveness must be between options that lead to equal expected payoffs.

Contrast this with the conventional signalling games in which some players are stronger than others (Enquist, 1985; Hurd, 1997; Hurd and Enquist, 1998) and it is better to be stronger, or some are more desperate (Enquist, 1985; Enquist et al., 1998) and it is better to win when you are desperate. The options in aggressiveness signalling cannot be interpreted as risk averse (the less aggressive signal) and risk prone (the more aggressive signal). If there is any variation between players in preference for risk sensitive strategies, then these are correlated asymmetries, and players will use pure contingent strategies based on this variation. This will change the "meaning" (Smith, 1977) of the signal, from aggressiveness to either cost sensitivity (RHP) or benefit sensitivity (resource value). This means that there cannot be an underlying state in any aggressiveness signalling game. Players in aggressiveness models are not signalling their ability or need, what they are signalling is a non-binding probabilistic "promise" of future action. Such non-committing signals have traditionally posed problems for game theoreticians (see discussion in Adams, 2001).

An analogy may highlight the weakness inherent to models of threats based on aggressiveness. Imagine a bicycle race in which contestants may intimidate rivals into yielding to some degree. Some riders may be better cyclists, or may stand to win larger prizes and may advertise this fact, as in RHP or resource value signalling. But in the case of aggressiveness signalling, a rider who is no better than any other, and does not stand to gain more in the end, intentionally starts some distance behind the starting line and advertises this fact by wearing a jersey bearing bold obscenities. That handicapped rider expects his self-imposed status as a desperado to cause riders to yield to him so that his chances of winning are improved. This improvement is such that his chances are increased exactly to the point that they were before, so that there is no net benefit.

A second problem with aggressiveness signalling is the assumption that no uncorrelated asymmetries exist other than the signal. The classic example of a discoordination game is the game of "Chicken" in which players charge at each other and the first to yield loses. Both players suffer the greatest cost if neither player yields. Any arbitrary cue that serves to give one player an excuse to yield will be used at the ESS. It seems very unlikely that a biological system in which payoff relevant asymmetries do not exist would not have some other cue with which to discoordinate.

These theoretical weaknesses immediately raise the question, if aggressiveness signalling is so improbable how do we explain apparent examples cases in the empirical literature? Models of aggressiveness signalling are usually framed as "badges of status" (Johnstone and Norris, 1993; Kim, 1995). These badges are relatively long lived. This relates to another questionable assumption common to both conventional signalling models and aggressiveness signalling models, that signals are made by both players simultaneously. If badges are so long lived that the badge chosen exists before the contestants meet, then they are effectively simultaneous. Polymorphic throat badges in the lizards *Sceloporus undulatus* and *Urosaurus ornatus* (Rand, 1990; Thompson and Moore, 1991a,b) meet this assumption, the badge type is fixed for life prior to reaching sexual maturity. Are these badges likely candidates for aggressiveness signals or do these badges reflect long-term variation in the resource values? The latter explanation makes sense in the case of the badge associated with the non-territorial floater lizard morphs. The value of winning an aggressive interaction seems likely to differ between polygynous, monogamous and non-territorial males. That the three life-history types are maintained in a rock-paper-scissors type dynamic (Sinervo and Lively, 1996) is superficially similar to the rock-paper-scissors outcome for a multiple signal aggressiveness signalling system. Where these systems differ is that the badges are not associated with a circular relationship of outcomes in agonistic encounters (Hover, 1985; Thompson and Moore, 1991b).

There is no simple empirical test to discriminate between a stable aggressiveness trait on the one hand, and a long-term difference in the subjective value of winning aggressive interactions on the other. The conditions necessary for aggressiveness to be signalled are sufficiently far-fetched that it seems parsimonious to believe that persistent individual variation in the propensity to escalate has more to do with the perceived value of winning than the product of a Hawk–Dove type model.

In conclusion, there are sound empirical and theoretical reasons to believe that there are three types of traits which determine contest outcome. Models of agonistic display based on one of these traits, aggressiveness, depend upon assumptions which are not likely to be met in the real world. For instance, such signals are not evolutionarily stable in the presence of uncorrelated asymmetries. If such signals do exist, then they must either be very few within a repertoire and handicapped, or they may be more numerous, and display a circular dominance of outcomes. While theoretical treatments make a clear distinction between aggressiveness and variation in perceived resource value, these two traits may be empirically indistinguishable. If variation in "aggressiveness" actually reflects long-term variation in subjective resource value, then models based on aggressiveness will be totally misleading. Ideally, models of agonistic communication will incorporate more than one trait to demonstrate that results due to variation in one are robust to variation in the other.

Acknowledgements

This work was partially funded by an NSERC Canada post-doctoral fellowship to the author (# 204862-1998) and an operating grant to Mike Ryan. Don Dearborn, Andy Iwaniuk, Steve Phelps, Gil Rosenthal, Mike Ryan and Chris Sturdy provided helpful comments on the manuscript. Thanks to Sandra Vehrencamp, Eldridge Adams, five anonymous reviewers and, The Coffee House Café in Salem, Oregon, and KRW.

Appendix A. Hawk–Dove and discoordination games

The Hawk–Dove game serves as a basis for much of the work reviewed here, but exists in many payoff variants. In order to demonstrate that the results of this paper are not artifacts particular to any single Hawk–Dove payoff formulation, I will make use of a generic discoordination game. This game has the essential properties common to Hawk–Dove-like games.

The traditional payoffs for the Hawk–Dove game are provided in Table A1.

The essential property of the Hawk–Dove payoffs is that $(V-C)/2<0$, and $V>V/2$. This means that the greatest benefit comes from discoordinating, i.e. choosing the behaviour that the opponent did not choose. This payoff pattern is shown in its simplest form in Table A2. Any 2×2 game in which the payoffs rank as $P<N$ and $C<T$ (Table A2) is a discoordination game, and will have all the properties of the Hawk–Dove game. An additional assumption can be made, without loss of generality, that $T>N$ (the "meanings" of "Hawk" and "Dove" moves are simply reversed if $N>T$).

All Hawk–Dove games modelling variation in escalation behaviour assume

$$T>C\geqslant N>P. \quad (2)$$

Table A1
Payoffs (to Player 1\Player 2) for the standard Hawk–Dove game

Hawk–Dove game		
Player 1	Player 2	
	H	D
H	$(V-C)/2\backslash(V-C)/2$	$V\backslash 0$
D	$0\backslash V$	$V/2\backslash V/2$

Table A2
Payoffs for the generic dis-coordination game, payoffs are temptation, coordination, neutral and punishment

Generic discoordination game		
Player 1	Player 2	
	H	D
H	$P\backslash P$	$T\backslash N$
D	$N\backslash T$	$C\backslash C$

Appendix B. The critical switch point for discoordination games

The critical value p, the probability of the opponent playing Hawk at which playing Hawk and Dove yield equal payoffs, is shown by Maynard Smith (1982, p. 16) to be

$$pP+(1-p)T=pN+(1-p)C,$$

$$p=\frac{T-C}{T-C+N-P}. \quad (3)$$

For the classic Hawk–Dove game this probability is V/C (Maynard Smith and Parker, 1976).

Appendix C. Solutions to the Hawk–Dove and generic discoordination games

This section provides a brief review of the effect of uncorrelated asymmetries (Maynard Smith and Parker, 1976) on discoordination (and by extension all Hawk–Dove-like) games.

C.1. Discoordination game dynamics

The reaction correspondence (Fig. C1) plots each player's optimal probability of playing hawk against the probability that their opponent plays hawk. If no uncorrelated asymmetry exists, then players are restricted to playing strategies that fall along the diagonal line marked "Line of Symmetric Strategies". They must play hawk and dove with the same probabilities when they are player 1 as when they are player 2 simply because they do not know which player they are. In this case, the mixing Nash equilibrium which falls on this line is the ESS.

If the players have a role asymmetry, if they know which of them is player 1 and which is player 2, then the mixing Nash equilibrium is not stable. The Nash equilibrium on the diagonal is not stable if the players can choose strategies which fall off the line of symmetric strategies. In this case the ESS is either of the two pure conditional strategies. The instability of the Nash equilibrium on the line of symmetric strategies is not a function of the relative size of the mixed equilibrium payoff to the other payoffs.

C.2. Generality

Maynard Smith and Harper (2004) refer to the Hawk–Dove game as a coordination game. While there is a sense in which this is correct, it is the strong

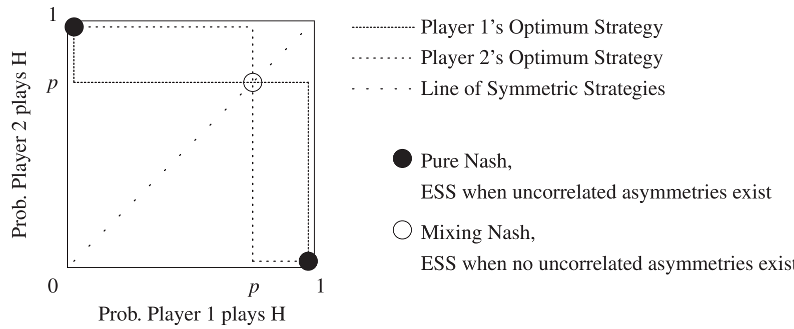

Fig. C1. Reaction correspondences for the players in a Hawk–Dove game. This graphs plots the optimum probability of playing Hawk for both players for all levels of probability that the other player is going to play Hawk. Points at which the correspondences intersect are Nash equilibria, there are three: one in which Player 1 always plays H and Player 2 always plays D; a second is the same as the first, but the roles are reversed; and the third Nash point is a mixing ESS if, and only if, the players are unable to determine which one of them is Players 1 and 2.

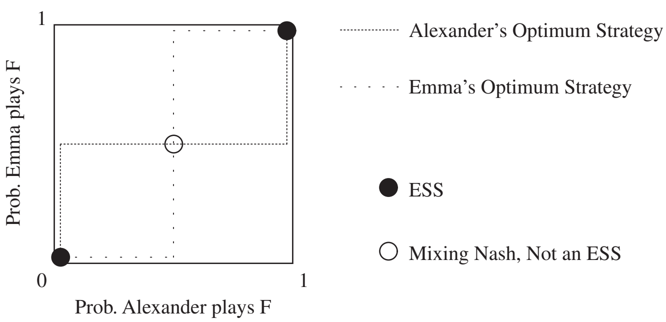

Fig. C2. Reaction correspondences for the players in a Coordination game. This graphs plots the optimum probability of playing for both players for all levels of probability that the other player is going to play fight. As in Fig. C1, the points at which the correspondences intersect are Nash equilibria, there are three: two of which are ESSes, one in which they both go to see the fight, one in which they both go to the opera. A third mixing Nash equilibrium, in which they each choose randomly, is not an ESS.

Table C1
Payoffs for the coordination game. Alexander would prefer they both go see a fight, and Emma prefers they both go see an opera. Both prefer each other's top choice as long as they both attend the same event. Any 2 × 2 game in which the payoffs are greater when the matching strategies are played will have reaction correspondence graphed in Fig. C2. Conflict exists when the preferences in these diagonal cells are reversed between the players. Note that there must be an uncorrelated asymmetry for there to be conflict, there cannot be payoff asymmetry without role asymmetry. The players must know what their preferences are if they are to differ

Coordination game		
Alexander	Emma	
	Fight	Opera
Fight	1\2	0\0
Opera	0\0	2\1

discoordination nature of the Hawk–Dove game which makes Kim's (1995) aggressiveness game work. A true coordination game always has an uncorrelated asymmetry when the players have conflicting interests. Coordination games have reaction correspondences of the form graphed in Fig. C2. These result from games such as the Battle of the Sexes (Luce and Raiffa, 1957), (see payoffs in Table C1).

Note that players in a discoordination game may have a preferred outcome. In the Hawk–Dove game they would prefer to play Hawk against an opponent who plays Dove. None-the-less, given an opportunity to use a coin toss to determine who will play Hawk, and who Dove, both players will abide by the results of the toss. "To cast lots puts an end to disputes and decides between powerful contenders" (Proverbs 18:18). This is the essence of the uncorrelated asymmetry ESS for all discoordination games. Players would prefer chance decide the outcome than decide between themselves.

Appendix D. Expected payoffs at the equilibria

D.1. Classic Hawk–Dove game

The payoff a player receives at the mixing Nash equilibrium is the same whether playing hawk or dove. This payoff is

$$\begin{aligned} W_{mixing} &= p\left(\frac{V-C}{2}\right) + (1-p)V = (1-p)\frac{V}{2} \\ &= \frac{V}{C}\left(\frac{V-C}{2}\right) + \left(1-\frac{V}{C}\right)V = \left(1-\frac{V}{C}\right)\frac{V}{2} \\ &= \frac{V}{2}\left(1-\frac{V}{C}\right). \end{aligned} \tag{4}$$

The payoffs at the pure contingent ESS are V for the hawk player and 0 for the dove player. If an arbitrary external cue is used to create the uncorrelated asymmetry, then the players are equally likely to adopt the hawk playing role and the expected payoff is

$$W_{pure\ cond} = \frac{1}{2}V + \frac{1}{2}0 = \frac{V}{2}. \tag{5}$$

The expected payoff when playing a mixing ESS (4) is less than the expected payoff to the role asymmetric pure contingent ESS (5) (assuming that the player is equally likely to take either role). The implication is that players would rather decide which of them will play hawk and which dove by coin toss than play the mixing ESS.

D.2. Hawk–Dove variants

Three Hawk–Dove payoff variants of note alter the classic payoffs. Hammerstein (1981) subtracts a cost T from the Dove vs. Dove payoff. Kim (1995) goes further and assumes that the Dove vs. Dove payoff is the expected payoff to a War of Attrition (Bishop and Cannings, 1978; Bishop et al., 1978) which is zero, and also equal to the Dove vs. Hawk payoff. Cushing (1995) assumes that a Dove playing vs. a Hawk suffers some fraction, β, of the cost of a fight C.

Payoffs for the mixed Nash in these cases are always lower than for the pure conditional strategy for Hammerstein's and Kim's payoffs. In the case of Cushing's payoffs the mixed Nash pays less if $\beta < \frac{1}{2}$, and more if $\beta > \frac{1}{2}$. We can therefore conclude that most common Hawk–Dove game variants have higher payoffs for the pure contingent outcome than the mixing outcome.

D.3. Generic discoordination game

For the generic discoordination game the mixed ESS payoff is

$$W_{mixing} = pP + (1-p)T = pN + (1-p)C \tag{6}$$

it follows from (6) that,

$$T > C \geqslant W_{mixing} \geqslant N > P. \tag{7}$$

For the pure uncorrelated asymmetry ESS, payoffs are T and N, to the Hawk and Dove player, respectively,

$$W_{pure\ cond} = \tfrac{1}{2}T + \tfrac{1}{2}N. \tag{8}$$

The mixing Nash payoff (6) is greater than the pure contingent, uncorrelated asymmetry, payoff (8) for some payoffs meeting the condition $T > C \geqslant N \geqslant P$. This amounts to about 22% of payoffs where T, C, N and P are random numbers uniformly distributed between 0 and 1 and meet condition (2). Thus, while not all generic discoordination games have higher payoffs for the pure contingent outcome than the mixing outcome, most do.

In either the variant Hawk–Dove or generic discoordination games, the ESS is the bourgeois, pure contingent strategy whenever an uncorrelated asymmetry exists. This appendix merely demonstrates that the payoff for this outcome is higher for this outcome for the classic Hawk–Dove game, and most Hawk–Dove payoff variants and most generic discoordination games.

Table E1
Payoffs for the aggressiveness signalling game, when the ESS strategies are played in the subgames

Reduced aggressiveness signalling game		
Player 1	Player 2	
	m_1	m_0
m_1	$W_{mixing} - h \backslash W_{mixing} - h$	$T - h \backslash N$
m_0	$N \backslash T - h$	$W_{mixing} \backslash W_{mixing}$

Appendix E. 2 × 2 Aggressiveness signalling game

By substituting the expected payoffs at the subgames a through d in Fig. 3 the aggressiveness signalling game becomes the 2×2 game shown in Table E1. The expected payoff to the mixing Nash outcome (see Appendix D) is W_{mixing}, the other cells use the generic discoordination payoffs (Appendix A). The players moves in this reduced game are the simultaneous signal choices (either the escalated m_1 or the non-escalated m_0). The payoff matrix also includes a handicap cost, h, for using the signal m_1.

Let q be the probability the opponent uses m_1. The expected payoffs for m_0 and m_1 are:

$$W_{m_1} = q(W_{mixing}) + (1-q)T - h, \tag{9}$$

$$W_{m_0} = qN + (1-q)(W_{mixing}). \tag{10}$$

When the handicap, h, is equal to zero the payoffs to the m_1 move is always higher than to the m_0 move.

$$q(W_{mixing}) + (1-q)T - h > qN + (1-q)(W_{mixing})$$
$$q(W_{mixing} - N) + (1-q)(T - W_{mixing}) > h. \tag{11}$$

Given that $W_{mixing} > N$ and $T - W_{mixing}$ (7), (11) must be true whenever $h = 0$. In order for m_0 and m_1 to be equal h must have a positive value (Kim, 1995).

References

Adams, E., 2001. Threat displays in animal communication: handicaps, reputation, and commitment. In: Nesse, R. (Ed.), Evolution and the Capacity for Commitment. Russell Sage Foundation, New York, pp. 99–119.

Adams, E.S., Mesterton-Gibbons, M., 1995. The cost of threat displays and the stability of deceptive communication. J. Theor. Biol. 175, 405–421.

Barlow, G.W., Rogers, W., Fraley, N., 1986. Do Midas cichlids win through prowess or daring? It depends. Behav. Ecol. Sociobiol. 19, 1–8.

Bishop, D.T., Cannings, C., 1978. A generalized war of attrition. J. Theor. Biol. 70, 85–124.

Bishop, D.T., Cannings, C., Maynard Smith, J., 1978. The war of attrition with random rewards. J. Theor. Biol. 74, 377–389.

Bradbury, J.W., Vehrencamp, S.L., 1998. Principles of animal communication. Sinauer, Sunderland, MA.

Cushing, B.S., 1995. When a hawk can damage a dove—an extension of game theory. J. Theor. Biol. 175, 173–176.

Dugatkin, L.A., Early, R.L., 2004. Individual recognition, dominance hierarchies and winner and loser effects. Proc. Roy. Soc. London B 271, 1537–1540.

Enquist, M., 1985. Communication during aggressive interactions with particular reference to variation in choice of behaviour. Anim. Behav. 33, 1152–1161.

Enquist, M., Jakobsson, S., 1986. Decision making and assessment in the fighting behaviour of *Nannacara anomala* (Cichlidae, Pisces). Ethology 72, 143–153.

Enquist, M., Leimar, O., 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. J. Theor. Biol. 102, 387–410.

Enquist, M., Leimar, O., 1987. Evolution of fighting behaviour: the effect of variation in resource value. J. Theor. Biol. 127, 187–205.

Enquist, M., Plane, E., Roed, J., 1985. Aggressive communication in fulmars (*Fulmarus glacialis*). Anim. Behav. 33, 1007–1020.

Enquist, M., Leimar, O., Ljungberg, T., Mallner, Y., Segerdahl, N., 1990. A test of the sequential assessment game: fighting in the cichlid fish *Nannacara anomala*. Anim. Behav. 40, 1–14.

Enquist, M., Ghirlanda, S., Hurd, P.L., 1998. Discrete conventional signalling of continuously varying resource value. Anim. Behav. 56, 749–753.

Hammerstein, P., 1981. The role of asymmetries in animal contests. Anim. Behav. 29, 193–205.

Hover, E.L., 1985. Differences in aggressive behavior between two throat color morphs in a lizard, *Urosaurus ornatus*. Copeia 1985, 933–940.

Hurd, P.L., 1997. Is signalling of fighting ability costlier for weaker individuals? J. Theor. Biol. 184, 83–88.

Hurd, P.L., Enquist, M., 1998. Conventional signalling in aggressive interactions: the importance of temporal structure. J. Theor. Biol. 192, 197–211.

Hurd, P.L., Enquist, M., 2005. A strategic taxonomy of biological communication. Anim. Behav. 70, 1155–1170.

Jakobsson, S., Radesäter, T., Järvi, T., 1979. On the fighting behaviour of *Nannacara anomala* (Pisces, Cichlidae) males. Z. Tierpsychol. 25, 257–314.

Johnstone, R.A., Norris, K., 1993. Badges of status and the cost of aggression. Behav. Ecol. Sociobiol. 32, 127–134.

Keeley, E.R., Grant, J.W.A., 1993. Visual information, resource value, and sequential assessment in convict cichlid (*Cichlasoma nigrofasciatum*) contests. Behav. Ecol. 4, 345–349.

Kim, Y.-G., 1995. Status signalling games in animal contests. J. Theor. Biol. 176, 221–231.

Koops, M.A., Grant, J.W.A., 1993. Weight asymmetry and sequential assessment in convict cichlid contests. Can. J. Zool. 71, 475–479.

Leimar, O., Enquist, M., 1984. The effects of asymmetries in owner–intruder interactions. J. Theor. Biol. 111, 475–491.

Luce, R.D., Raiffa, H., 1957. Games and Decisions: Introduction and Critical Survey. Wiley, New York.

Maynard Smith, J., 1982. Evolution and the Theory of Games. Cambridge University Press, Cambridge.

Maynard Smith, J., Harper, D.G.C., 1988. The evolution of aggression: can selection generate variability? Philos. Trans. Roy Soc. London B 319, 557–570.

Maynard Smith, J., Harper, D.G.C., 2004. Animal Signals. Oxford University Press, Oxford.

Maynard Smith, J., Parker, G.A., 1976. The logic of asymmetric contests. Anim. Behav. 24, 159–175.

McMann, S., 1993. Contextual signalling and the structure of dyadic encounters in *Anolis carolinensis*. Anim. Behav. 46, 657–668.

Mesterton-Gibbons, M., 1999. On the evolution of pure winner and loser effects: a game-theoretic model. Bull. Math. Biol. 61, 1151–1186.

Neat, F.C., Huntingford, F.A., Beveridge, M.M.C., 1998. Fighting and assessment in male cichlid fish: the effects of asymmetries in gonadal state and body size. Anim. Behav. 55, 883–891.

Parker, G.A., 1974. Assessment strategy and the evolution of animal conflicts. J. Theor. Biol. 47, 223–243.

Rand, M.S., 1990. Polymorphic sexual coloration in the lizard *Sceloporus undulatus erythrocheilus*. Am. Midl. Nat. 125, 352–359.

Selten, R., 1980. A note on evolutionarily stable strategies in asymmetric animal contests. J. Theor. Biol. 84, 93–101.

Sinervo, B., Lively, C.M., 1996. The rock-paper-scissors game and the evolution of alternative male strategies. Nature 380, 240–243.

Smith, W.J., 1977. The Behavior of Communicating: an Ethological Approach. Harvard University Press, Cambridge, MA.

Stamps, J.A., Krishnan, V.V., 1997. Functions of fights in territory establishment. Am. Nat. 150, 393–405.

Stamps, J.A., Krishnan, V.V., 1998. Territory acquisition in lizards. IV. Obtaining high status and exclusive home ranges. Anim. Behav. 55, 461–472.

Summers, C.H., Greenberg, N., 1994. Somatic correlates of adrenergic activity during aggression in the lizard, *Anolis carolinensis*. Horm. Behav. 28, 29–40.

Thompson, C.W., Moore, M.C., 1991a. Synoptic occurrence of multiple dewlap color morphs in male tree lizards, *Urosaurus ornatus*. Copeia 1991, 493–503.

Thompson, C.W., Moore, M.C., 1991b. Throat colour reliably signals status in male tree lizards, *Urosaurus ornatus*. Anim. Behav. 42, 745–753.

Tokarz, R.R., 1985. Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). Anim. Behav. 33, 746–753.

Zucker, N., Murray, L., 1996. Determinants of dominance in the tree lizard *Urosaurus ornatus*: the relative importance of mass, previous experience and coloration. Ethology 102, 812–825.