



Difficulties remain in distinguishing between mutual and self-assessment in animal contests

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Different theoretical models of contest behaviour are based on different assumptions about what information is used by the opponents. An approach adopted in many empirical studies has been to test predictions about relationships between 'resource-holding potential' (RHP) and contest duration, to determine whether fighting animals assess information about the opponent's RHP or whether they base their decisions only on what they know about their own RHP. Here we show that these two alternatives cannot be distinguished by analysis of RHP measures and contest duration alone and highlight the need to analyse further parameters of contests such as temporal changes in the intensity of agonistic behaviour.

Contests, where individuals compete aggressively and directly against one another, can be considered ubiquitous across animal taxa. Agonistic behaviours that are used during contests are often the result of sexual selection but can also occur over essential resources other than mates such as food, territory or shelter. Since they rarely involve injuries so severe that one of the opponents is compelled to stop fighting, they are settled in most cases by a decision on the part of one opponent, the loser, to 'give up' or

withdraw from the contest. Like any decision this will be based on information, ultimately concerning the costs and benefits of persisting. The benefits will depend on the value of the contested resource, and it is clear that there will often be differences in the perceived resource value (RV) between opponents. The costs may accrue from various sources including time or energy devoted to the contest and therefore unavailable for other activities and injuries that could compromise longevity and the efficiency of carrying out future activities. While the willingness to pay these costs will be influenced by resource value, the ability to pay will be equivalent to fighting ability, 'resource-holding potential' or 'resource-holding power' (both abbreviated to 'RHP').

In the absence of differences in perceived RV, the contest should be settled according to the difference in RHP (Humphries et al. 2006), such that the individual with lower RHP will choose to withdraw first. A key question in contest behaviour that has taxed both theorists and empiricists has been how this decision is made by the loser. The wide range of models of animal contests are informed by one of two assumptions about the type of information concerning RHP that should be available during a fight. First, fighting animals may only have information about their own RHP. The giving-up decision is triggered when the accumulated costs of persisting cross an individual maximum cost threshold. This could be based on time, energy, injuries or a combination of these but should ultimately be envisaged in terms of arbitrary and interchangeable fitness units. The loser will simply be the individual

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whose threshold is reached first. In a straightforward war of attrition without assessment scenario (WOA-WA; [Maynard Smith & Parker 1976](#)), for example, individuals vary in the amount of time they can allocate to a contest, and in its energetic version (E-WOA; [Payne & Pagel 1996](#)) in the amount of energy. This energetic version raises the interesting possibility that individuals will vary not only in the position of their thresholds but also in the rate at which they will accrue costs up to the threshold. Indeed, under a third type of model, where giving up is based on individual thresholds, the cumulative assessment model (CAM; [Payne 1998](#)), each opponent has the possibility of encouraging its rival's progression towards its giving-up threshold by causing greater energy expenditure or inflicting additional costs such as injuries. In these examples of threshold-based models the loser gives up purely on the basis of what it 'knows' about itself, without reference to any information concerning the opponent. This type of giving-up decision has been variously described as 'own RHP persistence', 'own size persistence' (since size is often an important correlate of RHP) and 'self-assessment' ([Taylor & Elwood 2003](#)).

The use of game-theoretical approaches to model contest behaviour emphasizes the importance of frequency dependence in determining the benefits of a particular strategy (e.g. [Maynard Smith & Price 1973](#)). During a fight, two or more individuals interact directly so that the actions of one opponent will clearly influence the benefits of the actions performed by its rival. It is implicit in this type of reasoning that simply persisting up to an individual maximum cost threshold could be extremely wasteful, in terms of costs allocated to the contest. For the weaker individual that would eventually lose anyway it would be better to give up before the maximum threshold was reached. But to make such a decision, information about the opponent's RHP would be needed. For this reason it has been suggested that fighting animals might gather information about their opponent's RHP, and indeed perform agonistic behaviours that provide accurate information on RHP to the opponent. Models such as the asymmetric war of attrition ([Hammerstein & Parker 1982](#)) and the sequential assessment model (SAM; [Enquist & Leimar 1983](#)) therefore assume that the decision to give up is based on 'RHP difference', 'relative RHP' or 'mutual assessment'.

Models such as the A-WOA, SAM, WOA-WA, E-WOA and CAM propose fundamentally different views about the functions of agonistic behaviour (i.e. how it induces the loser to make the giving-up decision) and at their core are split into two groups by these different assumptions about assessment rules. Distinguishing between mutual and self-assessment is thus an important part of understanding agonistic behaviour from a functional perspective. Individuals of low RHP are those that reach their giving-up threshold quickly (either because it is set at a low level, they accrue costs rapidly or a combination of these factors). This means that if the giving-up decision is based on self-assessment only, contest duration should increase as a function of increasing absolute RHP of the weaker opponent. If contests are settled on the basis of mutual assessment, however, it should be easier for the weaker opponent to know it is weaker when the RHP asymmetry is large. Thus contest duration should show a negative relationship between increasing RHP difference and contest duration. This relationship had been used in many studies (reviewed in [Taylor & Elwood 2003](#)) as a marker for the presence of mutual assessment but there is a problem with this approach. RHP difference may show a negative relationship with loser absolute RHP. [Taylor & Elwood \(2003\)](#) used simulation models to show that if this relationship is strong enough, the apparent negative relationship between RHP difference and contest duration could be an artefact of a stronger positive relationship between loser absolute RHP and contest duration ([Taylor & Elwood 2003](#)). In this case it is much more likely that the decision is made through self-assessment than mutual assessment.

Thus, analysis of the relationship between RHP difference and contest duration alone does not demonstrate the presence of mutual assessment.

[Taylor & Elwood \(2003\)](#) therefore suggested that to show that mutual assessment is used it is necessary to examine the relationships between both loser and winner RHP and contest duration. Since the difference in RHP will be easier for the eventual loser to establish when the asymmetry is high, contests should still increase in duration with increasing loser RHP; as losers increase in fighting ability it will be progressively more difficult for them to ascertain that they are weaker than the opponent because the RHP asymmetry will be smaller. By the same logic, there should also be a negative relationship between winner absolute RHP and contest duration; as winners decrease in fighting ability it will also be progressively more difficult for the eventual loser to ascertain that they are the weaker opponent because the RHP disparity will be smaller. Thus, it has been suggested that a positive relationship between loser RHP and contest duration and a negative relationship between winner RHP and contest duration indicate the presence of mutual assessment. See [Gammell & Hardy \(2003\)](#) for graphical representations of these points. Such correlations have recently been found in studies of fighting across a range of species from diverse taxa including shore crabs, *Carcinus maenas* ([Small-egange et al. 2007](#)), house crickets, *Acheta domesticus* ([Briffa 2008](#)), jumping spiders, *Phidippus clarus* ([Elias et al. 2008](#)) and killifish, *Kryptolebias marmoratus* ([Hsu et al. 2008](#)), but owing to factors such as the presence of energetic thresholds (crickets) and ethological details of contest dynamics (shore crabs, crickets, jumping spiders and killifish) it seems unlikely that these contests are settled purely on the basis of mutual assessment.

It therefore appears that considerable difficulties remain in distinguishing between evidence for different modes of assessment in contests. Indeed, it is possible for these relationships to occur even in the absence of mutual assessment. Essentially, the relationships described above occur because the opponents are influenced directly by each other's activities during the agonistic encounter. In the case of mutual assessment discussed above this involves an exchange of information, such that by performing agonistic behaviours each opponent directly influences the information state of its rival. The decision to give up thus depends on the RHP of both opponents, and this is clearly different from wars of attrition where the loser gives up solely on the basis of its own RHP. However, there are other ways in which opponents could influence each other's giving-up decisions without (in theory at least) the exchange of any information. If the opponents can directly influence each other's rate of cost accrual (for example by inflicting injuries) they could increase the rate at which the loser reaches its individual maximum cost threshold. Under this scenario, contest duration should still increase with the absolute RHP of the loser; as losers increase in RHP their cost threshold should increase and the rate at which they approach it should decrease, in both cases prolonging the time before the giving-up decision is made. Furthermore, contest duration could also decrease with increasing RHP in the winner; as winners increase in RHP so will their ability to inflict costs on the opponent, leading to the losers reaching their giving-up threshold more quickly as winner RHP increases. See [Fig. 1](#) for a graphical illustration of this. In terms of relationships between winner and loser absolute RHP and contest duration, this is the same result as would be obtained if the contest was settled by mutual assessment, but here there is no assumption of an exchange of information about RHP.

Contests of this form are described by the CAM ([Payne 1998](#)). Note that while it seems logical that an individual incurring costs as a direct result of the actions of the opponent might benefit from using the severity of these costs to assess its opponent's RHP, this model makes no such assumption that information may be inferred

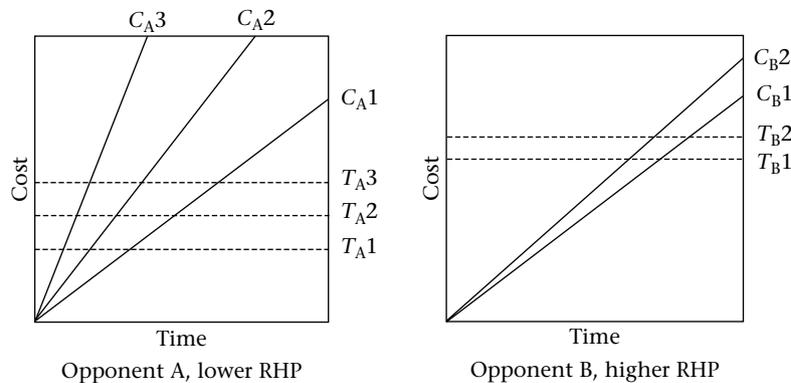


Figure 1. Relationships between contest duration and costs in the absence of mutual assessment. Consider two opponents 'A' and 'B', where A is the individual of lower RHP. A is the weaker individual because its maximum cost threshold T_{A1} , which, once crossed, triggers the giving-up decision, is lower than that of individual B, T_{B1} . For simplicity we have assumed that the initial rates of cost accrual, C_{A1} and C_{B1} , are identical between the two opponents, but note that variation in this could also cause differences in RHP. This means that, if giving up is based solely on the costs that accrue to each individual as a result of performing agonistic behaviour (self-assessment), individual A should give up before individual B. Contest duration will increase as a function of opponent A's RHP. Weak individuals with thresholds T_{A2} and T_{A3} would still lose against opponent B (as their thresholds are still lower) but would persist for longer than if the weaker opponent's thresholds was at T_{A1} . Thus contest duration would show a positive relationship with increasing loser RHP. In this scenario the loser makes its giving-up decision without reference to the RHP of B, but even in the absence of any information exchange the opponents may still influence each other's decisions. Opponent B, for example, might directly inflict costs on opponent A. This would effectively increase the rate of cost accrual for opponent A from C_{A1} without interference to C_{A2} or C_{A3} when B directly inflicts costs on A (for simplicity we assume that the rate of interference by B is constant throughout the contest and that the cost of receiving an action from opponent B is the same throughout the contest). A weak individual receiving costs at rate C_{A3} or C_{A2} , would give up more quickly than a weak individual receiving costs at C_{A1} . But here the difference is a function of variation in the ability of stronger opponents to inflict costs on weaker opponents. Therefore, contest duration would show a negative correlation with the RHP of opponent B. Note that another way for opponent B's RHP to vary is in its maximum cost threshold, but in the absence of mutual assessment this would not influence the negative relationship between contest duration and opponent B's RHP, unless B's threshold co-varied with B's ability to inflict costs on A. In the absence of such a link and in the absence of mutual assessment, fights involving high-RHP opponents with thresholds at T_{B1} and T_{B2} would be of equal duration, even though the RHP of $T_{B2} > T_{B1}$. Clearly this is a simplified situation, where the baseline rate of cost accumulation are the same between the opponents. RHP is determined simply by the maximum cost threshold and the ability to inflict costs on the opponent. Note that the effect of the ability of B to inflict costs on A could be countered by the possibility of A inflicting costs on B (C_{B2}). Although these are likely to be less severe (owing to the lower RHP of A), this scheme does not take into account the various ways in which the two components of RHP, maximum cost threshold levels and ability to inflict costs, may or may not be coupled; rather, we assume that an individual with a high cost threshold is also able to inflict costs on its opponent at a high rate. Nevertheless, this graphical representation shows how, under self-assessment as envisaged in the CAM, relationships between winner and loser absolute RHP and contest duration could yield similar results to contests settled by mutual assessment. This is because in both cases, irrespective of whether any information is exchanged, contests are settled on the basis of RHP difference rather than loser absolute RHP.

in this way. Indeed, although we might expect selection to favour mutual assessment, which appears to make so much sense from the perspective of minimizing costs, factors such as constraints on cognitive abilities may preclude its evolution in certain taxa. As in the E-WOA, giving up in the CAM is simply triggered when the accumulated costs of persisting in the contest cross a maximum cost threshold. The only difference is that in the E-WOA these costs accrue only as a result of performing agonistic behaviours whereas under the CAM the costs inflicted by the opponent are added to these baseline costs of performing agonistic behaviours. Thus, although the opponents directly influence each other's costs, they do not influence each other's information state in terms of providing extraneous information about opponent RHP. Although such contests may yield the same pair of relationships between the absolute RHP of winners and losers and contest duration as seen under mutual assessment, the decision is nevertheless made on the basis of what the loser knows about itself. The presence of these relationships should therefore not be assumed necessarily to indicate the presence of mutual assessment. More accurately, they indicate that the contest is settled on the basis of RHP difference rather than loser RHP alone but, as described above, this is possible both in the presence of mutual assessment and, during CAM-type contests, in the absence of mutual assessment.

How then to distinguish between mutual and self-assessment? Perhaps one solution is to return to the theoretical models that initially proposed and subsequently developed these themes. Commonly tested models (such as the SAM, E-WOA and CAM) have a range of assumptions and predictions, concerning not only contest duration but also contest outcomes and dynamics. For example, although the CAM and SAM make different assumptions about assessment rules, they are both based on the assumption that contest duration is determined by RHP difference and, as we have seen, both types of contest could yield similar relationships

between absolute measures of RHP and contest duration. However, they make different predictions about fight structure. The SAM predicts only escalation between phases and constant intensity within a phase, whereas the CAM allows escalation within phases and, in phases that do not involve injuries, the possibility of de-escalation. Furthermore, the SAM predicts that opponents should match each other's performances while the CAM does not. Conversely, looking only at fight structure alone may also yield limited information. The E-WOA and CAM make similar predictions about fight structure (both under certain circumstances allowing within-phase escalation and de-escalation) but they are based on different assumptions about the nature of assessment rules. As described above, this means that they should make different predictions about relationships between RHP and contest duration, and these models also make different predictions about matching between opponents. Thus, to distinguish between mutual and self-assessment it is necessary both to establish whether contest duration is based on RHP difference or loser absolute RHP and to investigate the ethological details of contest behaviour. See Table 1 for a summary of key distinguishing markers for different assessment models.

Empirical studies on a range of systems illustrate the types of ethological detail that can be readily obtained and complement analyses of relationships between contest duration and RHP. In hermit crabs, *Pagurus bernhardus*, one opponent, the 'attacker', performs bouts of 'shell rapping' by striking its gastropod shell against that of a 'defender' (see Elwood & Briffa 2001; Briffa & Mowles 2008). The bout structure of this activity has been extensively analysed (Briffa et al. 1998, 2003; Briffa & Elwood 2000) revealing that the vigour of shell rapping can both escalate and de-escalate as the contest progresses. The pattern varies between outcomes. Since there are two different roles in these encounters there is no matching between opponents and this, in combination

Table 1
Summary of differences in predictions about contest duration and dynamics between three key models of animal contests

Model	SAM	E-WOA	CAM
Assumptions			
Decision rule based on	Information about opponent	Costs resulting from own actions	Costs resulting from own actions and inflicted by opponent
Information about opponents RHP available?	Yes 'mutual assessment'	No, 'self-assessment'	No, 'self-assessment'
Contest duration driven by	RHP asymmetry	RHP of loser	RHP asymmetry
Predictions about relationships between contest duration and			
RHP asymmetry	Negative	Negative	Negative
RHP of loser	Positive	Positive	Positive
RHP of winner	Negative	Positive	Negative
Predictions about ethological details of contests			
Matching between opponent's?	No	Yes	No
Contest structure	Escalates between phases but not within phases	Constant, escalates or de-escalates within phases	Constant, escalates or de-escalates within phases

Although the CAM is a 'self-assessment' model, it can yield the same relationships between contest duration and relative and absolute RHP as 'mutual assessment' models such as the SAM (see Fig. 1).

with escalation and de-escalation, indicates that a CAM-type model may describe these contests reasonably well. On the other hand, analysis of the energetic status of the opponents (Briffa & Elwood 2001, 2002, 2005), indicates that they may use different decision rules, a possibility that has yet to be modelled. In house crickets, contests are divided into a series of distinct phases of increasing intensity in terms of energy expenditure (Hack 1997a) and losers appear to pay higher energetic costs than winners (Briffa 2008). Furthermore, careful analysis of the agonistic behaviour reveals the presence of escalation and de-escalation in the choice of agonistic tactics used (Hack 1997b). Since duration shows negative relationships with measures of loser RHP and positive relationships with measures of winner RHP (Briffa 2008) these analyses taken together again indicate the presence of a cumulative assessment rule. Contest dynamics can also be investigated during field observations of large animals such as fallow deer, *Dama dama*. Jennings et al. (2005) found that the rate of head-on jump-clashing declined as fights progress, a pattern compatible with self-but not mutual-assessment-based models.

These examples show how ethological details of fight structure and intensity can be readily quantified. It appears that attending to such features, along with other details of agonistic behaviour such as the distance between the opponents (Számádó 2008), in addition to analysing contest duration, is necessary to distinguish between different candidate assessment rules used during contests. In a sense, the real issue concerns the functions of agonistic behaviour, and mutual and self-assessment are, strictly speaking, simply assumptions of different types of model that propose different functions for the behaviours used in aggressive encounters. Nevertheless, the question is still of profound interest to researchers in animal contest behaviour, probably because it

represents a fundamental distinction between what different species can actually do during fights. As noted above, such differences may emanate from factors such as variation in cognitive ability or sensory acuity and thus may vary across the wide range of taxa in which contest behaviour occurs.

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