**Assessments of fighting ability need not be cognitively complex**

*Keywords:* aggression, Lloyd Morgan’s canon, mutual assessment, pure self-assessment, resource-holding potential, sequential assessment model

The rules animals use to decide whether to fight for a resource are a major focus of study in animal behaviour, attracting great theoretical and empirical interest (Briffa & Sneddon 2010). In a series of influential papers published in *Animal Behaviour*, Elwood and colleagues (Taylor & Elwood 2003; Arnott & Elwood 2009; Briffa & Elwood 2009; Elwood & Arnott 2012) have identified ways to distinguish cases in which an individual bases its decision to fight solely on its own strength or fighting ability—termed pure self-assessment—from cases in which an individual also takes into account the fighting ability of its opponent—termed mutual assessment. They also consider cumulative assessment, in which costs inflicted by the opponent influence the decision to continue fighting (Payne 1998). This important body of work urges behavioural biologists to reconsider the decision rules animals use in agonistic contests.

In a recent essay, Elwood & Arnott (2012) argue that assessment of an opponent’s fighting ability is cognitively demanding and therefore probably beyond the capacity of all but the most cognitively advanced species. In reaching this conclusion they invoke Lloyd Morgan’s canon, which states that psychologically simple mechanisms should be preferred in explanations of animal behaviour (Morgan 1894). While we wholeheartedly endorse this canon, we have serious misgivings about how Elwood & Arnott apply it. In the present article we address four issues with this recent interpretation of animal contests. First, we discuss mathematical models of contest behaviour and highlight a misreading of Enquist & Leimar’s (1983) Sequential Assessment Model. Second, we challenge the assumption that assessing an opponent’s fighting ability requires higher cognitive faculties. In many types of contest, very simple mechanisms allow sensitivity to an opponent’s fighting ability, and in fact some forms of combat may make it extremely difficult for individuals to separate the influence of their own fighting ability from their opponent’s. Third, we point out an important limitation of the correlational approach commonly used to distinguish between different forms of assessment, and argue that this is valid only in situations where the precise pattern of assortment between rivals is known. We propose that experimentally staged contests between individuals with the same fighting ability are a more powerful tool for studying contest decisions. Finally, we suggest that a categorical distinction between self-assessment and mutual assessment has outlived its usefulness. To stimulate debate, we present an alternative framework for understanding the assessment strategies used in agonistic contests, based on a two-dimensional continuum in the form of assessment. Our framework builds on an earlier suggestion that the degree of opponent assessment may be continuously variable (Prenter et al. 2006; Arnott & Elwood 2009) and extends this to consider continuous variation in self-assessment as well. The extent to which an individual’s contest decisions depend on its own and its opponent’s fighting abilities is likely to be constrained by the type of contest, but may also change dynamically during the course of an interaction.

Throughout this discussion we use the term ‘assessment’ in a broad sense. We make no assumption that this involves an explicit mental representation of fighting ability, which is something unknowable for any non-human species. By ‘assessing’ fighting ability, all we imply is that an animal’s contest decisions are affected in some way by that fighting ability. In many cases this may happen through a purely physiological, non-cognitive response. While this definition may seem odd to some readers, it is entirely consistent with the way that forms of assessment are inferred from contest data in non-human animals, relating proxies of fighting ability to contest duration (e.g. Taylor & Elwood 2003). Our main goal in this article is to show that complex cognitive mechanisms need not be invoked when animals are observed to base their decisions on their own or their opponent’s fighting ability. Simple mechanisms can account for such patterns and, contrary to what Elwood & Arnott suggest, these mechanisms are fully compatible with Enquist & Leimar’s (1983) Sequential Assessment Model.

**MISINTERPRETING MODELS OF CONTEST BEHAVIOUR**

In their article, Elwood & Arnott discuss four different mathematical models—the Hawk–Dove game (Maynard Smith & Price 1973), the Sequential Assessment Model (SAM; Enquist & Leimar 1983), the Energetic War of Attrition (E-WOA; Payne & Pagel 1996) and the Cumulative Assessment Model (CAM; Payne 1998)—and examine the extent to which they fit empirical data drawn from animal contests. We feel that the inclusion of the Hawk–Dove game in this analysis is unhelpful and potentially misleading, because its aims and scope are distinct from those of the other three models. The Hawk–Dove game is a highly conceptual model, designed to gain insight and expose the logic of animal conflict, rather than capturing all the biological details of a real contest. It was used by Maynard Smith & Price (1973) to explain restrained contest behaviour entirely in terms of individual-level selection, to counter the group-selectionist argument that the injury of many individuals ‘would militate against the survival of the species’ (Huxley 1966) and offer an alternative to the kin-selectionist argument that highly aggressive animals would risk injuring their close relatives (Hamilton 1971). Thus, the Hawk–Dove game is a tool for understanding the evolution and frequency-dependence of ‘limited war’ strategies (*sensu* Maynard Smith & Price 1973). It makes predictions about whether individuals should engage in a fight, but has nothing to say about assessment of fighting abilities or contest duration. In contrast, the other models (the SAM, E-WOA and CAM) discussed by Elwood & Arnott all model dynamic contest decisions, whereby the animal’s decision (whether or not to continue fighting) is continually revised during the course of the contest. The Hawk–Dove model should not be seen as an alternative to these three.

When discussing the SAM, Elwood and Arnott make a serious error. The critical point of contention is their claim that the SAM assumes a more cognitively demanding form of assessment than the other models: ‘First, it presumes that contestants know their own abilities, second that they gather information about the opponent and third that they compare the two’ (p. 1096). This three-step assessment process, which Elwood and Arnott term ‘mutual assessment’, is a misrepresentation of the SAM. Instead, the contestants in Enquist & Leimar’s (1983) original model base their decisions on error-prone estimates of their *relative* fighting ability—specifically the ratio of the costs they incur in each step of the fight. Mathematically, this is represented in the model as ln(*cB*/*cA*), where *cA* and *cB* are the costs incurred by the focal individual and its opponent, respectively (see equation (1) in Enquist & Leimar 1983). This convenient formula should not be taken as a description of the actual psychological or physiological mechanisms through which the animal implements its fighting decisions. Most obviously, it does not imply that the animal is cognitively capable of performing logarithmic calculations; but nor does it imply that the animal forms separate mental representations of *cA* and *cB*. The implication is simply that the animal’s decisions are influenced by its estimate of how much stronger or weaker it is than its opponent. No calculation or explicit comparison of the two strengths is required, because it is assumed that the information is directly transmitted as a relative measure. As we explain below this seems biologically reasonable for many types of contests, such as wrestling and other forms of combat based on trials of strength. Elwood & Arnott’s claim that the SAM implies advanced cognition thus hinges on an incorrect and overly complex interpretation of the model.

**HOW COGNITIVELY DEMANDING ARE ASSESSMENTS OF FIGHTING ABILITY?**

We agree with Elwood & Arnott that a three-step process of mutual assessment, involving the independent assessment of two fighting abilities followed by an explicit, cognitive comparison between the two, is unlikely for most animals. But individuals could gather information about their opponent more simply by directly assessing their relative fighting ability, as modelled by Enquist & Leimar (1983) in the SAM. This doesn’t require complex cognitive mechanisms; all the animal needs to do is to continue fighting until it is statistically likely that its opponent is stronger, and then withdraw. At the neuronal level, very simple processes could implement such a decision. In fact, Elwood & Arnott acknowledge the possibility of simple mechanisms in their ‘motivational’ model of contest behaviour, which relies on the neuronal integration of different sensory inputs rather than ‘a more complex system to compare two values’ (p. 1098).

In some types of contests, particularly those involving physical contact, relative assessments seem not only possible, but inevitable. Consider two stags in a wrestling contest, antlers locked. By paying attention to whether it is gaining or losing ground, each stag has a direct (albeit error-prone) estimate of whether it is stronger or weaker than its opponent. It may also be able to assess the degree of mismatch between them, if it is sensitive to the speed at which it is gaining or losing ground. But can a stag extract from this information two separate estimates of its own fighting ability and its opponent’s fighting ability? This might not be straightforward at all. A similar argument applies in cases where an individual is willing to incur a threshold level of costs inflicted by its opponent, as in the CAM (Payne 1998); again, the decision to withdraw depends on relative fighting ability, rather than separate assessments of each combatant. Even for two humans having a punch-up, it seems unlikely that they would independently estimate their own fighting ability and their opponent’s fighting ability—a simpler decision rule would be to admit defeat as a function of how quickly and comprehensively they are getting beaten up (i.e. the rate at which they are accumulating damage), which depends on their relative fighting ability. Applying Lloyd Morgan’s canon, some form of relative assessment (without implying an explicit cognitive representation of this) seems the more parsimonious explanation.

Prior to physical contact there are no such direct measures of relative fighting ability, but contestants might still be sensitive to their relative fighting ability through mutual displays. For example, before locking antlers, red deer (*Cervus elaphus*) stags often roar at each other, revealing information about their fighting ability from their roaring rate (Clutton-Brock & Albon 1979) and formant frequencies (Reby & McComb 2003). The contest may then progress to a ritualised ‘parallel walk’ phase, which perhaps facilitates visual assessment at close quarters (Clutton-Brock & Albon 1979). In a range of vertebrate and invertebrate taxa, mutual displays allow rivals either to size each other up directly (Enquist et al. 1990; Panhuis & Wilkinson 1999; Elias et al. 2008; Egge et al. 2011) or assess signals that correlate with size (Reby & McComb 2003; Logue et al. 2011).

Elwood and Arnott accept that such displays may allow assessment of the opponent, but suggest that the contestants are typically insensitive to their own display: ‘it is difficult to imagine how an animal might gather information about its own body length, the length of a caudal sword or the size of its mandibles … the focal animal might have no knowledge of its own display feature and thus cannot use it to vary its persistence in the contest’ (p. 1098). We agree entirely that animals will not, in general, assess their own display traits. Displays have evolved because of the effect they have on the behaviour of the receiver, often by communicating the sender’s ability or quality (Maynard Smith & Harper 2003). But Elwood & Arnott view this as problematic for the SAM, because, they argue, the ability of an individual to compare its own display with that of its opponent ‘is central to the SAM’ (p. 1098). Here we disagree: the SAM makes no such assumption. The form of assessment in Enquist & Leimar’s (1983) model does require that an individual’s contest decisions are influenced by both its own fighting ability and that of its opponent. But whereas animals possess an evolved response to their opponent’s display, they should be sensitive to their own attributes without having to observe their own display. Elwood & Arnott hint at this in their essay but appear to view relative assessment, as modelled in the SAM, as more complex.

We see at least two possible sources of information available to an animal about its own fighting ability. First, there might be direct neuroendocrine correlates of body condition that influence aggressive tendencies (Moore & Jessop 2003), without any cognitive assessment of physical attributes. This is likely to be adaptive in situations where the population distribution of fighting abilities is relatively stable. Second, depending on their level of experience, animals will often have a reliable indication of their ability to win fights from the outcomes of past contests. Indeed, the ability of animals to learn about their own strength from previous victories and defeats is one of the main evolutionary explanations for winner and loser effects (Whitehouse 1997; Mesterton-Gibbons 1999; Fawcett & Johnstone 2010) and is consistent with evidence from experiments manipulating prior experience (e.g. Hsu et al. 2009). This does not imply any great degree of cognitive sophistication: all that is required is that fight outcomes precipitate physiological changes which in turn affect future aggressive tendencies (e.g. Oyegbile & Marler 2005). Through repeated experiences, such a process may allow individuals in uncertain competitive environments to arrive at a level of aggression appropriate to their relative fighting ability (Hsu et al. 2006; Kasumovic et al. 2010). As with other aspects of quality assessment in contests (Mowles & Ord 2012), analogous processes may operate in mate choice, whereby individuals modulate their choosiness or courtship effort in response to the interest they receive from the opposite sex (Fawcett & Bleay 2009; Royle & Pike 2010).

Elwood & Arnott also claim that ‘Comparative decision making, as required for mutual assessment, involves complex cognitive processing’ (p. 1097). But decades of psychological research have taught us that animals’ judgements tend to be relative, involving comparison with other available options or situations experienced in the past (Flaherty 1996; Bateson & Healy 2005; McNamara et al. in press). In a wide range of contexts, animals are routinely expected to compare the magnitude of different things. For example, mate-choice decisions are made by comparing the magnitude of male displays or ornaments, not only in cognitively advanced species but also in small-brained animals such as *Drosophila* (Carson 2002) or stalk-eyed flies (*Teleopsis dalmanni*; Egge et al. 2011). Similarly, foraging organisms often face choices between different patches of resources, and even slime moulds (*Physarum polycephalum*) are able to make sensible choices to this effect, preferring better-quality patches of food over lower-quality ones and factoring risk into their decisions (Dussutour et al. 2010). As a final example, hermit crabs (Paguroidea) are able to compare the quality of different gastropod shell shelters before deciding which to occupy (Elwood & Neil 1992). Such evidence is inconsistent with the suggestion that comparative decision-making is too cognitively complex for most animals.

**DISTINGUISHING BETWEEN FORMS OF ASSESSMENT**

We have argued above that complex cognitive abilities are not required for an animal to base its contest decisions on either its own or its opponent’s fighting ability. Thus we do not believe that Lloyd Morgan’s canon should lead us to favour self-assessment over relative assessment as modelled in the SAM, in which the opponent’s fighting ability is also taken into account. But which form of assessment individuals actually use is, of course, an empirical question. If individuals assess their relative fighting ability then contests should last longer when the rivals are closely matched in size and other correlates of fighting ability (Enquist & Leimar 1983). For this reason, a negative relationship between contest duration and size difference has been suggested as a diagnostic feature of combined assessment, in which contest decisions are influenced by the fighting ability of both contestants. However, Taylor & Elwood (2003) used simulation data to show that a negative relationship between contest duration and size difference is also consistent with pure self-assessment, assuming that contestants meet at random. This is because the maximum possible size difference is constrained by the loser’s size, but under pure self-assessment the loser’s size also determines the contest duration. Because of this complication, Taylor & Elwood recommended relating contest duration to the winner’s size and to the loser’s size independently, instead of to the size difference between them.

Taylor & Elwood’s (2003) correlational approach has been widely adopted in studies of contest behaviour (reviewed in Arnott & Elwood 2009) and is endorsed by Elwood & Arnott. We agree that the method can be useful, but its applicability to empirical data on contests is more restricted than many researchers seem to realise. The correlations predicted by Taylor & Elwood depend on the pattern of assortment, which in their simulations was random. Using these specific predictions to infer assessment strategies is therefore valid for experiments in which rivals are paired randomly (e.g. Prenter et al. 2006), but not for experiments using non-random assortment (e.g. Stuart-Fox 2006) or observational studies of fights occurring naturally in the field (e.g. Jennings et al. 2004). In natural populations it seems plausible that animals will avoid confrontations with very large rivals, or at least with rivals they perceive to be much larger than themselves. For example, in the fiddler crab *Uca mjoebergi*, intruder males pick fights with residents whose claw size is similar to their own (Morrell et al. 2005). Size-assortative fighting invalidates the assumption of random assortment and will change the predicted correlations between contest duration and measures of fighting ability.

We demonstrate this in Fig. 1, using a modification of Taylor & Elwood’s simulation approach. When individuals refuse to fight conspecifics much larger than themselves, the resulting correlations (lower panels) are different from those expected under random assortment (upper panels) and in some cases, depending on the degree of assortment (cf. Morrell et al. 2005), may show no significant relationship. In Fig. 1 this is illustrated for a form of combined assessment in which contest duration depends directly on the absolute size difference between the combatants, but the same principle applies when an individual’s persistence is based solely on its own fighting ability (self-assessment) or its opponent’s fighting ability (opponent assessment). In all cases, the precise pattern of assortment in fights must be known for the system being studied if these correlations are to be interpreted correctly. Simply applying Taylor & Elwood’s predicted correlations ‘off the shelf’, without first checking that opponents assort at random or imposing this experimentally, is flawed.

An alternative approach, proposed by Enquist & Leimar (1983) and also discussed by Elwood & Arnott (see also Taylor & Elwood 2003; Arnott & Elwood 2009), is to stage contests experimentally between size-matched opponents. This yields unambiguous and contrasting predictions for self-assessment, opponent assessment and combined (e.g. relative) assessment. With increasing size of the contestants, self-assessment predicts increasing contest duration, opponent assessment predicts decreasing contest duration and combined assessment predicts no change in contest duration (Table 1). By imposing a known pattern of assortment this simple experimental method avoids the statistical problems mentioned above, making it a powerful way to distinguish between forms of assessment. We therefore believe that size-matched contests should be the preferred method to investigate causal effects of the size of one or both rivals on contest decisions. In systems where experimentally staged contests are not feasible, Taylor & Elwood’s (2003) correlational approach may be used as an alternative, but only if the pattern of assortment is known and is used in statistical simulations to generate corresponding predictions.

**CONTINUOUS VARIATION IN ASSESSMENT STRATEGIES**

Elwood & Arnott focus on two main categories of assessment, self-assessment and mutual assessment, with a brief consideration of opponent-only assessment. This coarse categorisation of assessment strategies is entrenched in the literature on animal contests (for a review see Briffa & Sneddon 2010). Taking an alternative view, Prenter et al. (2006) proposed that individuals possess varying degrees of information about the fighting ability of their opponent, leading to a continuum of strategies between pure self-assessment and mutual assessment (see also Elias et al. 2008; Arnott & Elwood 2009). We like this idea, but the range of possible assessment strategies is in fact much richer: as well as variation in the extent to which individuals base contest decisions on their opponent’s fighting ability, there may also be variation in the influence of their own fighting ability, leading to a two-dimensional continuum of possible assessment strategies. To illustrate this, in Fig. 2 we represent the strategy space along two orthogonal axes.

According to our scheme, self-assessment covers cases where contest decisions are based (to a variable degree) on an individual’s own fighting ability, but its opponent’s fighting ability has no effect. The opposite situation is opponent assessment, where an individual’s own fighting ability has no effect but its opponent’s fighting ability does (again, to variable degree). In cases of no assessment, contest decisions are not influenced by the fighting ability of either contestant. This third possibility is rarely considered in studies of contest behaviour, but it is expected to occur if the resource is either (i) of such great value that it is worth fighting for even when faced with much stronger opponent, or (ii) of so little value that it is not worth fighting for even when faced with a much weaker opponent. For example, high resource value may explain why female–female aggression in Texas cichlids (*Herichthys cyanoguttatum*; Draud et al. 2004) and jumping spiders (*Phidippus clarus*; Elias et al. 2010) is insensitive to differences in fighting ability, consistent with a ‘desperado’ effect (Grafen 1987).

Moving away from the extremes of self-assessment, opponent assessment and no assessment, we have a zone of combined assessment, in which an individual’s contest decisions are influenced by both its own fighting ability and its opponent’s fighting ability. We deliberately avoid the term ‘mutual assessment’ here to avoid confusion with Elwood & Arnott’s three-step assessment process. Within this zone there may be wide variation across species and contest types in which of the two has the stronger influence, the individual’s own fighting ability or its opponent’s fighting ability. The extent to which an individual bases its contest decisions on these factors may be a flexible decision or it may be constrained by the type of contest. For example, as we argued above, trials of strength may make it difficult to extract separate estimates of own fighting ability and opponent’s fighting ability from a combined estimate of the two. In other situations, prior to physical contact individuals may have much more information about their own capacity to persist than their opponent’s, particularly if contest outcome is strongly influenced by exhaustion from recent fights. On the other hand, in contests largely decided by visual or vocal displays, information about the opponent may be readily available even from a considerable distance. Rather than being strongly limited by cognitive capacity, we suspect that in most cases the form of assessment will be determined primarily by the sensory ecology of the species in question, the type of contest and the associated costs, benefits and constraints of gathering information.

Whether an individual’s contest decisions are influenced by its own and/or its opponent’s fighting ability is a separate issue from how information about those abilities is stored and processed cognitively (if at all). In our scheme, combined assessment thus encompasses the SAM (relative assessment), the CAM and Elwood & Arnott’s three-step process of mutual assessment. Most authors, including Elwood & Arnott, subsume the CAM under self-assessment, but in our view this model implements a form of combined assessment since contest decisions are influenced by the fighting ability of both contestants. Under the CAM an individual’s tolerance threshold (point of giving up) is dependent on its own fighting ability, but how quickly that threshold is reached is affected by the opponent’s fighting ability (Payne 1998). In this sense, individuals that rapidly reach their threshold and withdraw early in a conflict can be said to have perceived their opponent’s superior fighting ability.

Distinguishing between the different forms of combined assessment is potentially tricky; we cannot rely on the diagnostics shown in Table 1, because the CAM and the SAM (both involving combined assessment) may result in the same outcome. Elwood & Arnott argue that in the CAM ‘we would expect to see a positive relationship between absolute size of the pair and duration’ (p. 1097), contrasting this with the predicted lack of relationship in the SAM. But under the CAM, larger individuals both inflict greater damage and can also withstand greater damage, so these may cancel one another out. Thus, in size-matched contests involving animals that adhere to the CAM, one might also expect a lack of relationship between size and contest duration. Instead, to distinguish between the CAM and the SAM it may be necessary to examine contest dynamics, particularly patterns of escalation as the contest progresses (Enquist et al. 1990; Payne 1998; Briffa & Sneddon 2010). The SAM predicts that contests will be structured as an escalating sequence of discrete behavioural phases, with the intensity of fighting increasing between phases through the appearance of new behavioural elements but staying relatively constant within each phase (Enquist et al. 1990). The CAM, in contrast, predicts that fighting may either escalate, de-escalate or remain stable within phases except when it is physically dangerous, in which case it is always expected to escalate (Payne 1998; see also Briffa & Sneddon 2010). Examining escalation patterns is therefore a potentially useful technique for discriminating between competing models. However, researchers should bear in mind that predictions will be less clear-cut if animals use different assessment strategies in different phases of a contest (see below).

**DYNAMIC ASSESSMENT STRATEGIES**

There is a tacit assumption in many studies of contest behaviour that the assessment strategy is static, with the competing rivals constrained to use one particular form of assessment. This ignores the possibility that animals may switch dynamically between different forms of assessment during the course of a contest (Arnott & Elwood 2009; Briffa & Sneddon 2010). For example, when contestants escalate through different phases of contest behaviour, as in the red deer mentioned earlier (roaring—parallel walk—antler wrestling), they may also transition from one form of assessment to another. Elias et al. (2008) conclude that individual male jumping spiders (*P. clarus*) utilise both combined assessment and self-assessment during their fight sequences. In mangrove killifish (*Kryptolebias marmoratus*; Hsu et al. 2008), early stages of fights appear to involve combined assessment whereas the later stages, which include mouth wrestling, may be based on self-assessment. Researchers have often fallen into the trap of assuming that animals are constrained to follow a particular model of assessment, when in fact they may move dynamically through the continuous assessment space shown in Fig. 2 as time, resource value and/or information permits.

Likewise, the assessment strategy an animal uses is not necessarily fixed throughout its life. This has been shown in the context of mate choice (Coleman et al. 2004) but not, to our knowledge, in aggressive interactions. We can imagine that a young red deer stag without any previous experience of fighting has a poor estimate of its own fighting ability, but is reasonably well informed about the fighting ability of other males from listening to their roars or observing visual cues of strength. At this stage, its contest decisions might best fit a pattern of opponent assessment. As it matures and gains experience in fights, it acquires valuable information about its own fighting ability to complement the information gleaned about its rivals, leading to combined assessment. Later, as it grows old and its eyesight and hearing deteriorates, assessment of rivals may become less accurate and its contest decisions increasingly determined by its own fighting ability. It would be interesting to investigate whether assessment strategies do indeed vary with age in this way.

One final complication is that the two contestants sometimes have asymmetrical roles and therefore fight in different ways (Arnott & Elwood 2009; Briffa & Sneddon 2010). A good example is the shell-fighting behaviour exhibited by the hermit crab *Pagurus bernhardus*, in which an ‘attacking’ crab attempts to take the gastropod shell owned by a ‘defending’ individual. The attacking crab performs an agonistic signal termed ‘shell-rapping’ (Briffa et al. 1998) by rapidly and repeatedly hitting its shell against that of the defender, whilst the defender remains withdrawn inside its own shell for most of the encounter. The shell-rapping signal of attackers appears to advertise their stamina (Mowles et al. 2010) and their decision to withdraw seems to be based on the E-WOA, giving up when energetic costs cross a threshold (Briffa & Elwood 2001). In contrast, the defender’s decision of when to relinquish its shell may have elements in common with both the CAM and the SAM, as they must withstand blows inflicted by the raps of the attacker’s shell (Mowles et al. 2011).

**SUMMARY**

To conclude, we support the use of Lloyd Morgan’s canon in analysing contest behaviour, but we disagree with the inferences that Elwood & Arnott have drawn from it. There is little basis for assuming that self-assessment is cognitively simpler than the assessment of an opponent; this depends on the type of contest. Very simple mechanisms may enable individuals to base their contest decisions on both their own fighting ability and their opponent’s fighting ability, as modelled by Enquist & Leimar (1983) in the SAM. In trials of strength such as pushing or wrestling contests, relative assessment seems inevitable. Prior to physical contact, individuals may be sensitive to cues of their opponent’s fighting ability transmitted through evolved displays, and to their own fighting ability from past experiences and/or neuroendocrine correlates of strength.

For distinguishing between different forms of assessment, experimentally staged contests between size-matched opponents remain the most powerful approach. Investigating statistical correlations between contest duration and proxies of fighting ability can also be useful, but requires that the precise pattern of assortment in fights is known and is used to generate valid predictions. However, it seems to us that the notion of a strict dichotomy between self-assessment and mutual assessment, in which assessment strategies are constrained by cognitive complexity, has outlived its usefulness. A more promising way forwards would be to consider continuous variation in the extent to which individuals base contest decisions on their own and/or their opponent’s fighting ability. Categorising animal contests neatly into one of the standard assessment models is not always possible because assessment strategies may change dynamically with the contestant’s role, age and the phase of the contest.

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**Figure 1.** Predicted associations between contest duration and three size measurements (size of smaller rival [a,d], larger rival [b,e] and their absolute difference [c,f]) for 250 simulated fights between rivals either selected at random (upper panels, a–c) or assorted by size (lower panels, d–f). Following Taylor & Elwood (2003), individual sizes were drawn from a normal distribution with a mean ± SD of 30 ± 6 mm. Here we illustrate a form of combined assessment in which contest duration depends directly on the size difference between rivals, according to the relationship *duration* (s)= 30 − *absolute size difference* (mm), plus or minus some normally distributed noise (0 ± 5 s). In the size-assorted case (d–f), we assume that rivals will only start to fight if their size difference is less than 9 mm (i.e. 1.5 standard deviations).

**Figure 2.** The continuum of possible forms of assessment used by animals in agonistic contests. In theory, contest decisions can be based to a variable extent on an individual’s own fighting ability, and also to a variable extent on its opponent’s fighting ability. Self-assessment (SELF) refers to cases where only its own fighting ability has an influence; opponent assessment (OPPONENT) refers to cases where only the opponent’s fighting ability has an influence; no assessment (NONE) refers to cases where neither contestant’s fighting ability has an influence; and combined assessment (COMBINED) refers to cases where both have an influence. In all cases, darker shades of grey indicate a stronger influence.