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The role of skill in animal contests: A neglected component of fighting ability

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Short title: Skill in fighting animals

This is a manuscript version of an article published in *Proceedings of the Royal Society: Biological Sciences* **284** (1863): 20171596. The version of record can be found at https://dx.doi.org/10.1098%2Frspb.2017.1596

ABSTRACT

What attributes make some individuals more likely to win a fight than others? A range of morphological and physiological traits have been studied intensely but far less focus has been placed on the actual agonistic behaviours used. Current studies of agonistic behaviour focus on contest duration and the vigour of fighting. It also seems obvious that individuals that fight more skilfully should have a greater chance of winning a fight. Here, we discuss the meaning of skill in animal fights. Since the activities of each opponent can be disrupted by the behaviour of their rival, we differentiate between ability, technique and skill itself. In addition to efficient, accurate and sometimes precise movement, skilful fighting also requires rapid decision making, so that appropriate tactics and strategies are selected. We consider how these different components of skill could be acquired, through genes, experiences of play-fighting and of real fights. Skilful fighting can enhance resource holding potential (RHP) by allowing for sustained vigour, by inflicting greater costs on opponents and by minimising the chance of damage. Therefore, we argue that skill is a neglected but important component of RHP that could be readily studied to provide new insights into the evolution of agonistic behaviour.

KEY WORDS: Contest, Fight, Skill, Vigour, RHP, agonistic behaviour

INTRODUCTION

Competing skilfully enhances the ability to win in a variety of situations including courtship in animals [1] and sports in humans [2]. Here we discuss the role of skill in contests, a central feature in the lives of most animals where the potential importance of skill has attracted relatively little attention. Although a few traits that might contribute to fighting ability (e.g. body size, weapon size) have been heavily studied, these traits are often relatively fixed and thus do not directly account for the interactive nature of fighting. Furthermore, the importance of these traits will vary across species and thus it is still not clear whether there could be general traits that differentiate winners from losers across diverse species of fighting animals [3]. Here we argue that how skilfully an individual fights is driven by both intrinsic and extrinsic factors associated with fighting. Skill could therefore provide a more accurate measure of fighting ability that offers a better explanation for fight outcomes across a diverse range of animal taxa.

What makes a good fighter?

For animals, unequal access to food, shelter, territories and even social status and mates can constrain survival and reproductive rates [4]. Thus, individuals are likely to come into severe conflict, particularly with conspecifics that require exactly the same resources. When these conflicts are concentrated upon the ownership of a single indivisible resource unit the result is a discrete interaction called a contest [4]. In addition to a resource, contests are characterised by a set of opponents (usually two individuals), the use of agonistic behaviour and an outcome that produces winners and losers. The word *contest* is often used synonymously with *fight*, whereas some authors prefer to reserve the latter term only for the most intense examples of contests where sustained physical contact occurs and there is the possibility of injury. In less intense contests, outcomes might be decided by the use of signals or by trials of strength, as in pushing or wrestling matches. In this review we use *fight* to describe all of these levels of contest behaviour because they all involve the use of *agonistic behaviour*. This is defined as aggressive or defensive behaviour used when attempting to directly exclude other individuals from access to a resource that is usually indivisible [5] (although see [6] for an example where resource units can be shared if opponents are evenly matched).

Fights are usually characterised by asymmetries in fighting ability between the opponents. Fighting ability, often termed Resource Holding Potential (or Resource Holding Power, RHP [7]), represents the phenotypic variation that differentiates winners from losers. If both opponents value the resource equally, the individual with greater RHP should prevail [8]. Therefore, enhanced RHP should offer a selective advantage and it is not surprising that a central question in the study of contests should thus be centred on understanding which traits contribute to RHP: In other words, what makes a good fighter? The importance of this question goes beyond the initial identification of RHP traits. Once these are known they can be used along with data on contest duration [9,10] and escalation patterns [10,11] to test the hypothesis that losers reach their decision to give up either by comparing their RHP to that of the opponent [12] or simply when their own individual threshold of costs is crossed [13,14]. Studies of fighting typically focus either on differences in physical or physiological RHP traits [15] or on uncorrelated asymmetries between opponents that are determined by the specific context of the fight, such as resource value [16] or the effect of prior ownership of the resource [17]. It seems obvious that larger individuals should be likely to defeat smaller ones [18,19] but differences in size can be further broken down into differences in weapon size [20,21] and strength [3,22]. Strength is an example of a performance capacity and overall stamina has also been revealed as an important performance capacity that can increase the chances of victory [23]. Stamina in turn is dependent on energy reserves, aerobic capacity [24] and metabolic rate [25]. Thus, morphological and physiological traits seem fundamentally important to the outcome of animal fights.

The nature of fighting

Are brute force and high stamina always enough to secure victory? A consideration of the characteristics of fighting across a broad range of examples suggests that the answer is often no. In some cases where dangerous agonistic behaviour is used to kill or maim, powerful weapons, strength and overall bulk are of obvious importance. For example, in northern elephant seals, males use their teeth to maul their opponent's head and neck [26], and massive size might predispose animals to dangerous fights if weapons grow faster than defences [27] . However, injurious fighting is not restricted to massive animals. During the duels of Asian rhinoceros beetles, *Trypoxylus dichotomus*, males try to pinion their opponent on their head horn, which enables them to puncture the opponent's elytra using the sharp spikes of the thoracic horn [28]. Although it is not surprising that fighting can lead to injury, basic game theory [29] shows that this need not be the case and in many examples we see the frequent use of relatively dove-like tactics. In large and powerful mammals such as red deer, *Cervus elephas*, and fallow deer, *Dama dama*, most fights are settled without injurious fighting even though injuries can occur in the most escalated contests [30]. Diametrically opposed to injurious fights are contests that are settled purely on the basis of agonistic displays without any physical contact at all. Various species of butterfly, for instance, use aerial displays to compete for favoured territories where males use flashes of sunlight reflected off their wing scales to ward off competitors (see [31] for a short review).

Each of the above examples, regardless of whether opponents must be physically overpowered or only given a display, involves the use of challenging agonistic behaviours that are specific to fighting and distinct from routine activity patterns. In examples where physical contact is involved, the level of challenge is raised even further, because neither opponent passively allows its rival to perform agonistic behaviour without interference. Courtship is another context where animals have to perform challenging and unusual behaviours and parallels between courtship and agonistic behaviour have recently been discussed [11,32]. During courtship, individuals that perform their displays well tend to be more successful than those that perform poorly [1]. This ability to perform a challenging behaviour well has been described in the context of sexual selection as *skill* [1]. Similarly, we should expect that individuals that can perform agonistic behaviour skilfully should have a greater chance of victory than those that perform poorly [33]. In the following sections, we discuss what 'performing well' during a fight might mean, and what might underpin variation in the capacity to do this. Crucially, a distinction can be drawn between skilful and vigorous behaviour [1] and in the following sections we show that this distinction can be applied to agonistic behaviour as well as to courtship. We will then consider the components of skilful fighting and show that, because opponents might interfere with one another's agonistic behaviour, it is necessary (in the context of fighting) to further distinguish between *skill, technique* and *ability*.

VIGOROUS FIGHTING

When studies of fighting move beyond the measurement of physical traits and outcomes to include analysis of agonistic behaviour itself, the focus tends to be on vigour [18]. Vigour is defined as the intensity and rate of performance of an agonistic behaviour [34] and can be most readily quantified for tactics that are performed repeatedly. In hermit crabs, for example, attackers try to take the gastropod shell of a defender. While defenders remain withdrawn into their shells, attackers perform bouts of shell rapping by repeatedly striking their shell against the defender's shell in a series of bouts. The intensity of shell rapping can vary through the amount of power supplied to each rap [35] and the rate of shell rapping also varies in several ways. These include the number of raps in each bout, the intervals between raps within a bout and the duration of pauses between bouts [36,37]. Attacking hermit crabs are more likely to win the shell fight, evicting the defender from its shell, when they rap vigorously using powerful raps at a high rate [35]. In addition, these aspects of vigour vary during the fight, with successful attackers escalating in vigour as the fight progresses while unsuccessful attackers de-escalate. Understanding escalation patterns during fights such as those between hermit crabs is key to determining how losers make the decision to give up. 'Escalation' during a fight is actually used in two different senses. First, as described above, it can refer to the pattern of change in the vigour of a single behaviour as the fight progresses. Escalating winners and de-escalating losers suggests that the agonistic behaviour is demanding to perform and that losers become constrained by fatigue, a result supported by studies of the energetic costs of fighting [15]. However, escalation could also refer to changes in agonistic tactics as the fight progresses, usually from less costly to more costly activities. This type of escalation is predicted by the sequential assessment game [12], where giving up decisions are assumed to be made by each opponent through comparing its own RHP to that of its rival. As we discuss below both types of escalation are relevant to the question of skill.

While it is possible to show that on average winners fight more vigorously, and are more likely to escalate than losers, there is a difficulty in establishing a given individual's actual capacity for vigorous fighting. This is because an individual's vigour will vary from fight to fight, as a consequence of variation in resource value and the RHP (and agonistic behaviour) of different opponents. Thus, individual performance capacities have to be quantified independently of fighting by measuring traits such as locomotor endurance [23] or the closing force of appendages [22]. Studies applying these approaches indicate that agonistic behaviour is energetically challenging and that the ability to fight vigorously is strongly correlated with endurance capacity.

SKILFUL FIGHTING

While vigour and the chance of winning can vary with a host of physiological parameters that drive endurance [15], endurance and hence sustained vigour might also be influenced by how efficiently the required motor patterns are executed. Efficient movement is one component of skill, which in the context of sexual selection Byers et al. [1] distinguish from vigour as follows: If *vigour* represents the rate and intensity of a challenging behaviour, *skill* represents how well the challenging behaviour is performed. In the context of fighting (and perhaps courtship as well), how well a behaviour is performed encompasses its efficiency, accuracy, precision and appropriateness to the situation. While *efficiency* refers to the minimum amount of movement (and hence energy expenditure) required to perform a behaviour effectively, *accuracy* refers to the degree of congruence between the motor patterns required (i.e. the patterns that will influence the behaviour of recipients) and what is actually performed. As well as signals that are attuned to the psychology of receivers (sensu [38]), accuracy could encompass the delivery of strikes if the opponent must be struck on a specific body part (e.g. on the telson in fighting mantis shrimp [39]). In addition to accuracy, *precision* may also be important if victory depends on the consistency of agonistic behaviour within a fight, for example repeatedly striking the same area of the opponent within narrow parameters of variation. *Appropriateness* refers to the choice of agonistic tactics used in cases where there is a range of possible choices and where the optimum tactic can vary between and within fights, typically showing a pattern of escalation towards more costly tactics as the fight progresses [12]. This is analogous to the concept of 'game intelligence' in human sports [2]. Inefficient agonistic behaviour would lead to reduced endurance while inaccurate or inappropriate agonistic behaviour will produce ineffectual fighting. Thus, although vigour and skill may be functionally linked (for example if sustained vigour is dependent on efficient movement [34]) it is nevertheless possible to distinguish between the two, if vigour describes temporal parameters of agonistic behaviour (rates) and skill refers to the spatial parameters [1] of efficiency, accuracy, precision and appropriateness (Table 1).

Skill is underpinned by ability and technique

As with observations of vigour, if we can detect differences in motor patterns between winners and losers, we could infer that variation in skill contributes to fighting success. But for a given individual the level of skill employed might vary from fight to fight due to interference from opponents. This constraint on our ability to measure an individual's skill highlights a distinction between the potential to fight well and what is actually achieved in a particular fight.

In sports training an analogous distinction is drawn between the potential to perform movements well and the level of realised skill that is actually displayed in a real competition. *Technique* is defined as the capacity to perform specific movement patterns whereas skill is defined as the capacity to use these movements effectively during a competition. In association football for example, dribbling the ball past static obstacles would require a particular set of techniques. But using these techniques to dribble the ball past a real player, without being dispossessed, would be an example of skill. Here, the correct ball-dribbling techniques must be rapidly chosen and adjusted to counter the tackles of the defending player. Similarly, in combat sports such as judo, the movement patterns required to throw the opponent can be practised in training on a partner who will not resist. But again using the same techniques against a real opponent, who will resist being thrown, would be an example of skill.

Thus in interactions between animals that do not involve direct contact and mutual interference (such as courtship displays and some agonistic displays), technique and skill may be identical.. But the amount of automatic correspondence between technique and skill is likely to diminish as physical contact and opportunities for interference increase. Technique in turn can be acquired through a combination of ability and experience. Here we use the term *ability* to represent innate capacities for (a) good technique in terms of forming motor patterns efficiently and accurately, and (b) for choosing the most appropriate technique to use at different stages of fights. Typically (in sports science) innate capacities are thought of as being determined by genes but there is also the possibility that developmental experiences will alter the expression of those genes. Thus we distinguish between two types of experiences that could influence the techniques used in fights. First, there are general developmental experiences that can interact with genes to drive variation in basic ability. Second, any instances where the specific motor patterns involved in fighting are practised could offer the opportunity to convert ability into technique, and to improve technique. In the following section we discuss potential sources of variation in ability, technique and skill (Table 2).

VARIATION IN ABILITY, TECHNIQUE AND SKILL

Variation in ability

In sexually selected displays the ability to perform coordinated movement patterns has been linked to investment in musculoskeletal, nervous and sensory systems [1]. The general principle that coordinated movement should be underpinned by the architecture of nervous and sensory systems, and by how these interface with motor systems, is well established. In vertebrates, for example, the cerebellum is responsible for the overall integration of sensory inputs with stored information about the capabilities of individual body parts, and damage to this brain area severely reduces motor coordination [40]. More specifically, in birds the quality of song will depend on the ability to coordinate muscles used in ventilation and phonation; specific nerves, areas of the forebrain and feedback-loops responsible for this coordination have been elucidated [41]. However, direct links between variation in the structure of musculoskeletal, nervous and sensory systems and variation in sexual displays are relatively rare and, although likely to be present, such links with agonistic behaviour have yet to be established.

Variation in the musculoskeletal, nervous and sensory systems that should drive variation in ability can be separated into genetic and environmental components. The genes controlling neurogenesis are highly conserved across animals [42] and development of key structures such as the cerebellum in vertebrates is increasingly well understood [43]. In contrast, there are few examples where a direct link between genes and specific behaviours have been demonstrated (see [44] for a review). In a more general sense, the links between genotype and behaviour, including examples of variation in abilities that underpin technique, can be demonstrated using quantitative genetics. In the field cricket, *Gryllus integer,* males emit a stridulated call to attract females. The proportion of calls with long bout durations, which are preferred by females, is highly repeatable across males. Call duration is also heritable, indicating that much of this variation in calling ability between males is under genetic control [45]. As well as being influenced by genes the structures that underpin variation in ability will also be subject to developmental plasticity. Compensatory growth, for example, allows individuals that are subjected to a poor diet early in life to achieve large body size, via a prolonged growth phase, if diet improves later on during development. However, developmental plasticity can come at a cost, for example in the swordtail, *Xiphophorus hellerii*, prolonged growth results in reduced swimming speed and fighting ability [46]. Thus, variation in ability is likely to be driven by interactions between genes and environment.

Variation in technique – the roles of development and experience

Ability may provide the foundation for skilful fighting but it is unlikely to be enough on its own. Rather it must be converted into technique, meaning that individuals with similar potential (based on ability) could still demonstrate different proficiencies in technique. As noted above, participants in human combat sports may acquire technique by practising in the absence of an opponent or against an opponent who offers reduced resistance. In many animals these controlled scenarios are unlikely, making it difficult to observe technique independently of skill. For some animals, however, there are situations that can offer the opportunity for practice fighting, for example, during play.

There are a number of explanations for play behaviour in animals (reviewed in [47]), but two hypotheses seem particularly pertinent to the acquisition of fighting technique. First, the *motor training hypothesis* (MTH) posits that play promotes the adaptive development of neuromuscular systems and (in vertebrates) the cerebellar synapses that allow for specific motor patterns [48]. Here, play is expected to be concentrated during sensitive periods of development. This type of play might also optimise the development of standard RHP traits, such as strength and stamina, but if it promotes changes in synaptic connections it could also allow for the development of technique. A second explanation for the function of play is the *training for the unexpected hypothesis* (TUH) [47]. This includes situations where an animal simply has to recover from losing its footing through to situations where an individual's options are directly impacted by the unpredictable actions of others. For instance, Spinka et al. [47] describe situations such as being "knocked over", "pinned down" or "shaken vigorously", all of which might occur during a fight.

A prediction of MTH is that play should be focussed on activities similar to those used in real situations. In contrast, TUH predicts that animals at play should seek more unusual activities that can even appear to be somewhat contrived so as to offer unlikely scenarios. Such play could lead to generalised improvement in performance across a range of contexts, and thus play activities need not mirror real fights closely. Young mammals frequently indulge in play-fighting but these interactions do not necessarily involve agonistic tactics or the targeting of body parts that feature in real fights [49]. Rather, examples across a range of mammals show a diversity of levels of realism in play-fighting. In black bears, *Ursus americanus*, play-fights are very similar to real fights, but in muroid rodent species aggressive behaviours are targeted towards different areas of the opponent's body in comparison with real fights [49]. On balance it seems that play-fighting does provide some practise of tactics that are at least similar to those used in real fights. On the other hand, although fights are often ritualised it is unlikely that an individual will be able to predict what its rival will do next, because fighting animals should conceal their future intentions [5].

Indeed, it is not certain that most animals can even perform the (perhaps deceptively) simple task of assessing their opponent's RHP during escalated fighting [10]. Therefore, the ability to cope with unexpected contingencies, in terms of agonistic behaviour of the opponent (and updated assessments of RV; see below), could also enhance the ability to fight skilfully. Thus, both routes may allow animals to build techniques that are useful during fights. Overall, differences in technique might arise from variation in the quantity and quality of play, which can be influenced by a range of intrinsic factors, including consistent variation in aggressiveness, and extrinsic environmental factors [50].

Variation in skill

While individuals with similar abilities could achieve different levels of technique (depending on their experiences), it also follows that technique need not necessarily translate directly into skill. Again experience seems key, and real fights, in addition to play-fights, also represent experiences that could influence future combat (e.g. see [17, 51]). In jungle fowl, for example, females that have prior experience of fighting, regardless of winning or losing, are more likely to achieve dominance when transplanted to a new group [52]. Real fights should not only allow animals to practise technique but also to practise the application of these techniques. Individuals are likely to differ in their experience of fighting for a number of reasons. First, availability of resources will drive the motivation to fight, the likelihood of engaging in a fight being inversely proportional to the availability of resources and proportional to the value of the contested resource unit [16]. Second, individuals might vary in aggressiveness and highly aggressive individuals should experience more fights than those with lower levels of aggression [53].

As well as the opportunity to practise the application of technique, real fights are characterised by outcomes (winning or losing) that could influence skill in a more direct way. First, winners will obtain enhanced access to resources such as food. While energetic constraints on vigour are well established, initial evidence from animal contests [34] and combat sports [54] indicate that the efficiency and accuracy of agonistic behaviour can also decline with fatigue. Thus, winners that gain more food might be better placed to sustain skilful fighting in future combat due to an enhanced energy balance. Second, in injurious fights losers are more likely to sustain injuries than winners. If these injuries affect the musculoskeletal, nervous and sensory systems that determine innate ability, this will ultimately reduce the capacity for fighting skilfully. Finally, in addition to efficient and accurate motor patterns, skilful fighting requires appropriate tactics to be chosen. Intra-specific variation in information gathering, assessment and decision making is well documented [55] and such variation in cognitive ability could also lead to differences in skill during fights, particularly with respect to the selection of appropriate tactics.

HOW COULD SKILL PROMOTE SUCCESSFUL FIGHTING?

Thus, skilful (efficient, accurate, precise and appropriate) fighting is dependent on three capacities (ability, technique and realised skill itself) and these are likely to vary between individuals (Figure 1). But given that RHP is already known to be influenced by several other traits [3] how important is skill likely to be in influencing the outcome of fights? As noted above, at present there are very few studies of fighting skill in animals [34,56] and only one of these [34] looks at the effect of motor patterns on outcomes. Nevertheless, when other

RHP traits are similar between opponents, differences in skill could determine the outcome and below we highlight scenarios where skill could make the difference.

Skill reveals underlying qualities

During courtship, receivers of dynamic and repetitive signals (usually females) might be interested in the level of skill displayed *per se*, since skilful behaviour may indicate the underlying quality of the performer. Indeed, studies of sexual displays in birds [57,58] and humans [59] indicate that the receivers of such signals are sensitive to this type of variation. Signals that reveal underlying quality might also be pertinent during a fight between males if the fight is observed by females that use information on skill to subsequently choose a mate [56]. Similarly, if skilful agonistic behaviour correlates with persistence capacity or strength, then skill could reveal information about RHP during contests settled through mutual assessment [12]. On the other hand, contests can also involve costs that accrue to individuals through the repeated performance of energetically challenging behaviour [13], as well as costs that opponents inflict directly on one another through injuries [14]. Therefore, the level of skill used in a fight could be important not only because skill *per se* is directly assessed by a potential mate or a rival but also because skill level will influence the costs accrued through performing agonistic behaviour and the costs that can be inflicted on the opponent.

Efficiency and endurance

Vigorous fighting involves the repetition of challenging behaviours, so performing these motor patterns efficiently seems imperative. In the example of shell fighting in hermit crabs, Briffa & Fortescue [34] quantified the motor patterns involved in individual raps by measuring the distance through which the attacker's shell was displaced. As well as rapping more vigorously than attackers that failed to evict the defender, successful attackers displaced their shells through shorter distances and there was a negative correlation between displacement distance and vigour. Over-displacement of the shell might have reduced the capacity for vigorous rapping, possibly by wasting energy. Interestingly, sustaining low displacement distance presented a stronger challenge to certain attackers. Those that evicted the defender showed a gradual reduction in displacement as the fight progressed whereas those that failed to evict the defender showed increasing displacement over the fight. Although analyses of motor patterns during animal fights have rarely been undertaken, similar approaches have been used to study human combat sports. Ashker [54] analysed the proportion of punches on target over three-round boxing matches and found that although winners fought with greater accuracy overall, for both winners and losers the proportion of on target punches declined from round to round. These examples indicate that the ability to fight skilfully (in terms of accuracy), as well as vigorously, is constrained by fatigue.

Accuracy and damage

Some fights involve inflicting direct blows on the opponent, which have the potential to cause injury. Recipients of attempted blows would benefit from making rapid decisions on appropriate defensive moves, such as evasion or blocking, that are executed accurately so as to match the anticipated site of impact. For individuals attempting to strike the opponent the accuracy of agonistic behaviour will determine their effectiveness, for instance by targeting the most vulnerable part of the body. Furthermore, as inflicting damage has recently been shown to sometimes result in injury to the attacker as well as the recipient [60], the ability to effectively target attacks for maximum impact may reduce the costs incurred by the attacker. Particularly in the Pancrustacea, self-inflicted damage costs could be avoided by the accurate targeting of strikes on weakly armored, rather than strongly armored, regions of the opponent’s body (see [27]). Individuals that are better able to land targeted blows may also be able to secure a victory through a single attack, whereas other less skillful fighters may have to strike several times before causing the opponent to retreat. By deploying multiple attacks, individuals not only increase the likelihood of sustaining substantial self-inflicted damage, but also give their opponent the time and chance to strike back and thus may incur even higher damage costs. Therefore skillful individuals could be able to win injurious fights faster, by inflicting single blows with maximal impact and minimum cost.

Appropriate choice of tactics

Different tactics may be employed during different phases of fights [12] but even within a given phase a range of tactics may be available and, notwithstanding energetics constraints, different levels of vigour may be chosen. Selecting the best course of action from among the options available will require decision-making based on the integration of several sources of information. In hermit crabs, fighting with high vigour involves powerful as well as rapid shell rapping. When attackers are prevented from delivering powerful raps (through experimentally dampening their shells with silicone) they increase the proportion of an alternative tactic, shell rocking [61]. This indicates that attackers change their technique based on an assessment of the effectiveness of their own agonistic behaviour.

Skill and strategic decisions

Thus far we have considered how skill may promote victory (i.e. act as an RHP trait) for individuals committed to winning the contest in order to obtain a valuable resource. Under certain circumstances, however, persisting in a contest through to victory may not be the appropriate strategy, since fighting is costly and RV may not necessarily outbalance the costs needed to secure victory. Animals that decide to enter into fights should place a high value on the resource but the perceived balance between RV and costs could change as the fight progresses. First, perceived RV could be updated during the fight, for instance in situations where an intruder only comes into close contact with the resource once the fight is under way as in hermit crabs fighting over shells [62] or guppies fighting over shelters [63]. The ability to make such assessments can vary with experience [62, 63]. Second, for contests that involve mutual assessment, the perceived costs of victory could be updated as more information is revealed about the opponent. In such cases, where it becomes apparent that the resource is not worth fighting for relative to the anticipated costs of victory, persisting in the fight should not be the optimal strategy. Thus, as well as making appropriate tactical decisions, about which agonistic behaviours to use, making appropriate strategic decisions to 'cut ones losses' is also an ability that could increase with experience of real fights [62, 63].

CONCLUSIONS AND FUTURE DIRECTIONS

A popular approach to the study of animal fighting is to focus on morphological RHP traits and performance capacities, coupled with analysis of contest duration and outcome. This closely follows an established framework [9,10] for determining whether contests are settled through mutual-or self-assessment. However, we have previously argued [10,11] that there is much to gain from quantifying actual agonistic behaviours within fights, specifically by investigating vigour. Here we suggest that in addition to vigour we should also attempt to analyse skill. Like vigour, initial evidence shows that skill can drive outcomes and varies as fights progress [34,54] and the pattern of change in skill within fights can differentiate winners from losers [34].A wide range of approaches could be taken to the study of skill in animal contests and it is likely that the relevance of any one approach will vary greatly between study species due to the diversity of fighting behaviour among animals [4]. For example, complex and diverse song is known to correlate with success in male birds but without knowledge of this aspect of their natural history variable song patterns could be misinterpreted as lacking in precision. With this caution in mind, potential approaches to the study of fighting skill include the following: Kinematic studies could characterise agonistic behaviour in 3 dimensions [64] such that the spatial components of skill can be quantified. One might then quantify between-fight variance in the aiming of blows or strikes to estimate accuracy and within-fight variance to estimate precision. Two approaches could be taken to disentangle skill from technique. First, measuring overall motor performance capacities in a context other than fighting could be useful if it is reasonable to assume that these will correlate with technique. Second, one might observe individuals across multiple fights, to account for the influence of opponents [64]. Longitudinal studies could also be used to track (or manipulate) play fighting and real fighting during ontogeny, especially in long lived species, to test the idea that experience [hsu] allows the conversion of ability to technique. Finally, studies of skill should ideally incorporate more traditional RHP measures (e.g. body size) so that the relative contribution of skill can be assessed. An interesting question relates to the possibility of alternative fighting phenotypes; might skill be more important for some (e.g. smaller) individuals whilst other (e.g. larger) individuals can rely more on strength and stamina?

Although some initial evidence is available, the contribution of skill to fight outcomes and decision making during fights remains a largely open question. If fighting animals have evolved to compete skilfully as well as vigorously then we should see variation in the efficiency, accuracy, precision and appropriateness of agonistic behaviour between fight outcomes (winners versus losers) and between individuals with different levels of experience of fighting and different life history trajectories. .

AUTHOR CONTRIBUTIONS

MB conceived of this review and it was written jointly by MB and SML.

FUNDING

SML is supported by funding from the BBSRC. We are grateful to Bob Elwood and two other reviewers for their constructive comments.

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Table 1: Components of skilful agonistic behaviour

Component	**Definition**	**Example**
Efficiency	Performing agonistic behaviours with the minimum amount of movement required for that behaviour to be effective	An attacking hermit crab avoiding excessive displacement of its shell during shell rapping
Accuracy	Performing agonistic behaviour that matches a template needed to elicit capitulation in the rival	A boxer connecting their punches with an opponent; a mantis shrimp striking an opponent's telson
Precision	Performing repeated instances of agonistic behaviour with low variance	Consistently performing a given displacement distance or consistently targeting the same body part of an opponent
Appropriateness	Choosing the optimal tactic from the range of possible tactics available	A male fallow deer choosing to vocalise rather than initiate jump-clashes during the opening phase of a fight; a hermit crab switching from rapping to rocking if rapping is ineffective

Table 2: Sources of variation in ability, technique and skill

Trait	Definition	Driven by	Sources of variation
Ability	Potential to perform efficient and accurate motor patterns needed for agonistic behaviour	Musculoskeletal, nervous and sensory systems	Genes and environment including during development
Technique	Capacity to perform agonistic behaviour in the absence of significant interference or resistance from a rival	Ability (co-ordinated movement) Practice	Experience of play fighting, experience of real fighting (including winning and losing)
Skill	Capacity to fight efficiently, accurately, precisely and appropriately against a real opponent	Technique Ability (cognition) Practice Agonistic behaviour of the opponent	Experience of real fighting (including winning and losing), opponent's RHP including skill

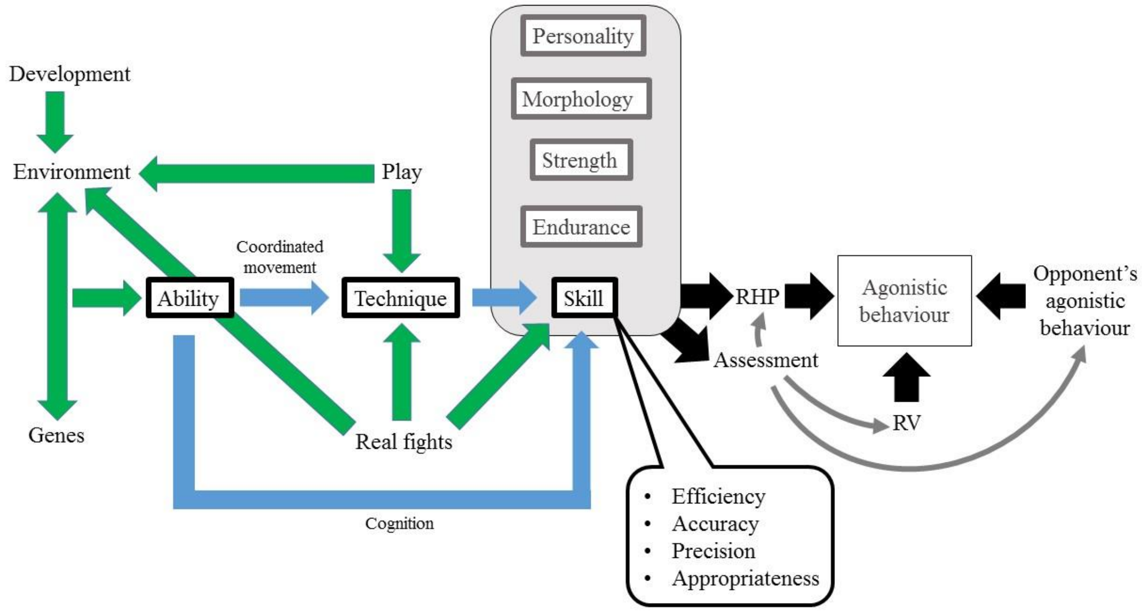

Figure 1: Schematic representation of relationships between ability, skill and technique, applied to animal contests. In sports opponents try to thwart one another's attempts to win and in sports training it is therefore necessary to distinguish between innate ability, technique in the absence of significant opposition and skill, where techniques are used against real opponents. Fighting is also characterised by opponents that interfere with one another and similar distinctions must be made when considering the role of skill in animal fights. The blue arrows show how fighting skill is underpinned first by ability and then by technique. Green arrows represent hypotheses for the causes of variation in ability, technique and skill. The components of skill are listed in the clear callout box. On the right hand side of the figure skill is grouped with other traits that contribute to resource holding potential (RHP), which along with resource value (RV) and the agonistic behaviour of the opponent, will determine a fighting individual's agonistic behaviour. In addition to influencing the ability to win fights (RHP) skill could also influence the ability to make strategic decisions about whether to initiate or persist in a fight, as more experienced individuals might be better at gathering and utilising (assessing) information on RV, their own RHP and in some cases the opponent's

RHP. Note also that all of these RHP traits may interact with one another (e.g. skill might influence endurance) and drive some of the hypothesised causes of variation in skill (e.g. aggressiveness might influence the number of play fights or real fights experienced, see [50]). While other RHP traits have been investigated at length they do not explain all of the observed variation in contest outcomes [3]. In contrast, the role of skill has been neglected and its contribution to RHP remains an open question.